

Chapter 7

Significant Theories, Principles, and Approaches that Emerged Within Landscape Ecology During the Previous Thirty Years

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Introduction

What is landscape ecology?

As with the science of ecology, several individuals are frequently mentioned during recorded antecedents as pioneers to this emerging field of science or paradigm. For example, German zoologist, Ernst Haeckel (1869), coined the term “ecology.” In his first edition, *On the Origin of Species*, Charles Darwin outlined the theory of natural selection (which Haeckel termed “the struggle for existence”) that remains a mainspring of ecology (Darwin 1859). The writings of Hippocrates, Aristotle, and other philosophers of ancient time also clearly contain references to ecological topics.

Sauer (1925) defined landscape as a unit concept in geography, while describing the areal features and morphology of the landscape. For example, Harper et al. (1993) investigated how the geometry of landscape patches influences small mammal (*Microtus pennsylvanicus*) home-range size and shape. He also noted distinction between natural and cultural landscape.

Tansley (1935) was the first to define the term “ecosystem” as an intrinsically self-coherent entity of a living community and environmental factors. Troll (1939) was the first to define the term “landscape ecology” as the harmonic interplay of climate, soil, and vegetation, including the equally important interconnectedness of animal life, parasites, and soil fauna. Turner (2005) noted that landscape ecology offers a spatially explicit perspective focusing on the relationships between ecological pattern and process that can be applied across a range of scales. Most defini-

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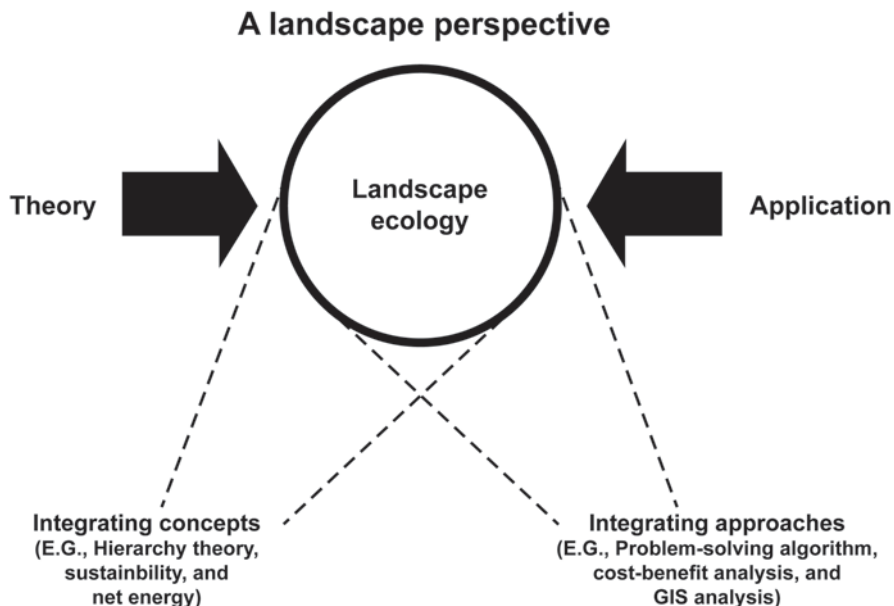


Fig. 7.1 Landscape ecology as an integrative paradigm wedding ecological theory with practical application

tions of landscape ecology share the explicit focus on the importance of spatial heterogeneity on ecological processes—processes that transcend across all levels of organization.

Originators of landscape ecology include German biogeographer, Carl Troll (1939), who coined the term, “landscape ecology,” and Karl Friedrich Schreiber (1990), who described the early history of landscape ecology in Europe—a field of study that developed in close association with land-use planning. Originating from this rich European tradition, landscape ecology in North America, especially in the United States, is now a well-established field of study, nationally and internationally. The concepts of landscape ecology (patch dynamics, metapopulation theory, and hierarchical theory), its tools (Geographical Information Systems (GIS), remote sensing, spatial modeling), and transdisciplinary approaches (problem-solving algorithms, cost-benefit analyses, and scaling) are now widely used in most ecological and related disciplines, such as forestry, wildlife biology, conservation, and resource management (Barrett 1985; Fortin and Agrawal 2005; Turner 2005). Landscape ecology also provides an excellent venue to integrate basic and applied science (Barrett and Bohlen 1991). Landscape ecology is an integrative paradigm that weds ecological theory with practical application (Fig. 7.1).

In this chapter, we focus on significant theories, principles, concepts, and approaches that emerged within landscape ecology during the previous 30 years. Emphasis will be placed on the United States Regional Association of the International Association for Landscape Ecology (USIALE) where appropriate.

Description and Importance of Landscape Components or Elements

It is now widely accepted that the three basic elements of landscape ecology are patches, corridors, and the landscape matrix. Forman and Godron (1986) described how patches differ fundamentally in origin and dynamics, also noting that patch size, shape, and spatial configuration are important. They organized four types of corridors in landscapes: line corridors, strip corridors, stream corridors, and network corridors. Later, Odum and Barrett (2005) defined five types of corridors: remnant (e.g., corridors connecting virgin patches of timbered forest); disturbance (e.g., power line cutting through a forest habitat); planted (e.g., trees established during the Shelter Belt project in the 1930s); resource (e.g., stream meandering through a watershed); and regenerated (e.g., fencerow in secondary succession). Earlier, Pickett and Thompson (1978) discussed patch dynamics in context with the design of natural reserves. They build on the Island Biogeography Theory (MacArthur and Wilson 1967) describing how population confined in small areas such as “islands” is more prone to extinction due to internal dynamics of the small area; that is, small areas increase the probability of extinction principally due to reduced population size (Simberloff 1974).

Wiens (1976), building on the concept of resource availability (low and high), expressed how spatially defined social organization is a function of the expense to defend these resources, ranging from territoriality and home range to refuge and herds or flocks of organisms. In essence, he was one of the first landscape ecologists to describe population responses to patchy environments.

Several investigators, early on, described the relationship of landscape corridors or connectivity to population survival and patterns of movement. For example, Wegner and Merriam (1979) monitored movements of birds and small mammals in farmland habitat, showing how fencerows, which connect woods within the surrounding agricultural mosaic, concentrate the activity of avian and small mammal species into the habitat corridor, thus relieving the isolating effect of the farmland surrounding the wooded forest habitat. Later, Pulliam (1988) described how high-quality patches serve as a reservoir of reproductive surpluses from “source habitats” to maintain populations in “sink habitats,” where local reproductive success fails to keep pace with local mortality. Also, Lefkovitch and Fahrig (1985) described how populations of *Peromyscus leucopus* in isolated patches have lower survival probabilities than those populations that are connected to other forest patches.

Much research also has been focused on how the “edge” of landscape patches and edge habitats influence plant and animal interactions, such as predation, nesting and foraging behavior, and changes in abiotic factors. Leopold (1933) in his classic book, *Game Management*, perhaps, was the first to bring attention to the concept of “edge effect” or “edge species.” Pratt and Barrett (2012) described how two species of small mammals, the golden mouse (*Ochrotomys nuttalli*) and white-footed mouse (*P. leucopus*), are considered edge species because both species are most abundant in forest-edge habitats. Pratt and Barrett (2012) also scaled the

edge concept to the regional biome level, describing how a latitudinal mean annual temperature isotherm, within the eastern deciduous forest biome, defines a switch in reproductive strategies for northern versus southern populations of *O. nuttalli* and *P. leucopus*. Corridor presence and width also play a major role regarding the use and movement of interior versus edge species (Lapolla and Barrett 1993; Haddad and Baum 1999; Haddad et al. 2003).

The Importance of Understanding Temporal and Spatial Scales

Landscape carries with it an intrinsic spatial implication. Accordingly, in the initial development of landscape ecology, a great deal of effort was devoted in attempts to define landscapes and their extent in time and space. There were large implications in exactly how the time and space domains of a landscape were determined, and which phenomena would best incorporate the pattern and dynamics of a landscape. As a prelude to discussing some of these issues, a brief history of temporal scale in ecological systems seems appropriate.

Time and Space Scales and the Ecosystem Concept

In an issue of *Ecology* to Henry Chandler Cowles, Tansley (1935) defined a concept that he called the “ecosystem” as a contrasting alternative to the views of Phillips (1934, 1935a, b) and Clements (1916) on ecological succession as the supra-organismic development of a community. There is little doubt as to what Tansley meant with the word, ecosystem. The term “ecosystem” was first printed in a sentence that also was its definition,

...the more fundamental conception is, as it seems to me, the whole system (in the sense of physics), including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment of the biome—the habitat factors in the widest sense. Though the organisms may claim our primary interest, when we are trying to think fundamentally we cannot separate them from their special environment, with which they form one physical system.

It is these systems so formed which, from the point of view of the ecologist, are the basic units of nature on the face of the earth [Earth]. Our natural human prejudices force us to consider the organisms (in the sense of the biologist) as the most important parts of these systems, but certainly the inorganic “factors” are also parts—there could be no systems without them, and there is constant interchange of the most various kinds within each system, not only between the organisms but between the organic and the inorganic. These ecosystems, as we may call them, are of the most various kinds and sizes. They form one category of the multitudinous physical systems from the universe as a whole down to the atom. (Tansley 1935, p. 299)

Tansley emphasized that ecosystems “were of the most various kinds and sizes” and essentially defined an ecosystem as what a systems scientist would term “system

of definition”—an arbitrary system defined by the specific considerations for a particular application. Ecosystem as defined by Tansley often conforms well to more mathematical, interactive systems concepts in other sciences. His systems-oriented definition requires the consideration of time and space scales found in other sciences, particularly physical-based sciences.

So how might scale and systems-of-definition come together in the modern ecosystem concept? Figure 7.2 displays the Delcourt et al. (1983) conceptualization of the time and space scales of external inputs (disturbances), the internal ecological processes that are excited by these inputs, and the resultant patterns (e.g., associations, formations) for forest ecosystems. For purposes of example, we have designated two of a possible myriad of forest ecosystems. One indicated by the blue circles in Fig. 7.2 defines a forest ecosystem that is driven by climate variations operating on processes of forest succession to produce changes in subtypes of forests; the other (red circles) denotes a second forest ecosystem responding to glacial cycles and plate tectonics, which operate on evolution and diversity change to produce the global pattern of vegetational formations (e.g., rainforests, deciduous forests, dry forests). Each of these could be called a “forest ecosystem.” Each considers inputs, processes, and patterns that are not in the domain of the other. Both are forest ecosystems in the Tansley construct. With the Tansley ecosystem, the questions of which disturbances are most important in an ecosystem depend on the time and space domains over which the scales are defined.

Discussions on the Time and Space Domains of Landscapes

If the time and space scales are a prerequisite to knowing how to formulate the concept of an ecosystem, then this is no less true in the case of landscape. For mosaics of different ecological systems on landscapes, even if these patches are noninteractive but of different ages of the same sort of ecosystem, it is fairly easy to demonstrate that the dynamics of the individual patches can be very different from the dynamics of the landscape summation of the patches. This simplest case of landscape dynamics is a classic concept in forest ecology.

Dynamics of Forest Landscapes with Noninteractive Patches

Understanding the noninteractive dynamics of mosaic systems has deep roots in the ecological literature. Watt (1947) developed a classic paper that is the wellspring for subsequent ideas and extensions of the basic concept that the structure of a mature forest (at the scale of several hectares) is a heterogeneous mixture of patches in different phases or stages of gap-phase replacement. The mature forest should have patches with all stages of gap-phase dynamics and the proportions of each should reflect the proportional duration of the different gap replacement stages.

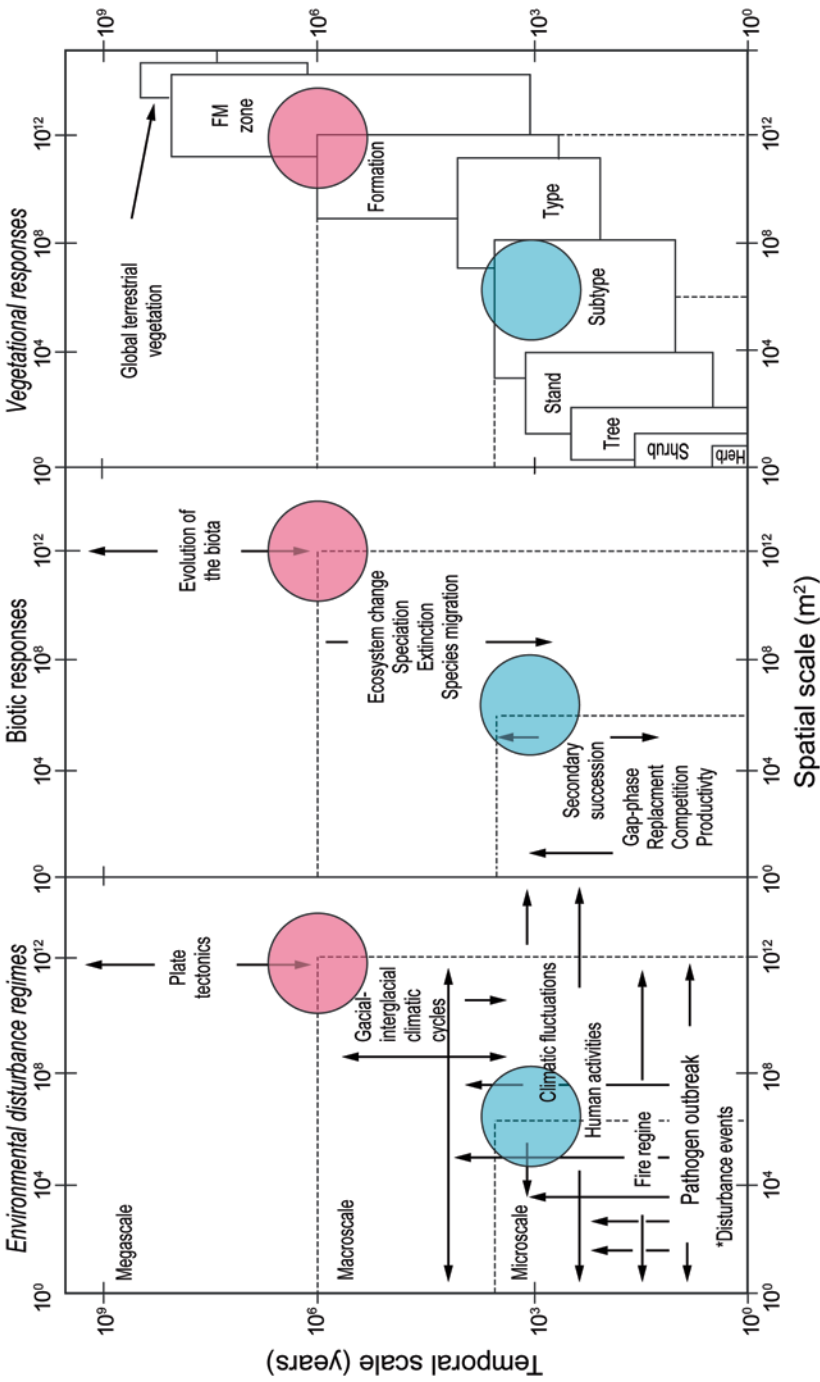


Fig. 7.2 Environmental disturbance regimes, biotic responses, and vegetational patterns viewed in the context of time and space domains in which the scale for each process or pattern reflects the sampling intervals required to observe it. The timescale for the vegetational patterns is the time interval required to record their dynamics. The vegetational units are mapped as a nested series. *Blue circles* denote an ecosystem involving climate variations operating on forest succession to produce changes in subtypes of forests; *red circles* mark a second ecosystem involving glacial cycles and plate tectonics operating on evolution and ecosystems change to produce the global pattern of vegetational formations (rainforests, tundra, deserts). (After Delcourt et al. 1983)

This has significant implications for the apparent dynamics of forests when viewed at different spatial resolutions. The biomass dynamics for a single canopy-sized piece of a forest (Fig. 7.3a) is quasi-cyclical or in the form of a saw-toothed curve (Shugart 1998). The spaces between the “teeth” in the saw-toothed, small-scale biomass curve are determined by how long a particular tree lives, and for how much time growing is required for a new tree to dominate a canopy gap. After a clear-cutting or forest fire, for example, the summation of several of these biomass curves can be summed to predict the biomass change for a forest landscape. The result is the expected change from deforested land being restored to a forest condition in an effort to increase the regional storage of organic carbon.

This landscape scale biomass dynamic is a simple statistical consequence of summing the dynamics of the parts of the mosaic. If there has been a synchronizing event, such as a clear-cutting, one would expect the mosaic biomass curve to rise as all of the parts are simultaneously covered with growing trees (I in Fig. 7.3b). Eventually, some patches produce trees of sufficient size to dominate the local area; and there is a point in the forest development when the local drops in biomass are balanced by the continued growth of large trees at other locations leveling out the mosaic biomass curve (II in Fig. 7.3b). If the trees over the area have relatively similar longevities, there is also a subsequent period when several (perhaps the majority) of the pieces that comprise the forest mosaic all have deaths of the canopy dominant trees (III in Fig. 7.3b). Over time, the local biomass dynamics becomes desynchronized and the biomass curve varies about an equilibrium biomass value (IV in Fig. 7.3b).

The occurrence of such patterns has been documented for several different mature forest systems. For example, patches of shade-intolerant trees present within mature undisturbed forest are but one observation consistent with the mosaic dynamics of mature forests. The scales of the mosaics in many natural forests are somewhat larger than one would expect from gap filling of a single tree gap, indicating an importance of phenomena that cause multiple tree replacements. Also, the relatively long records (*circa* 40 years in most cases) that are available for forests indicate a tendency for the forest composition to fluctuate with species showing periods of relatively weak recruitment of individuals to replace large trees and strong recruitment in other periods (Jones 1945; Rackham 1992). The carbon storage dynamic (Fig. 7.3) implies that carbon taken up by reforestation and growth of trees may be partially released back into the atmosphere in the future.

When disturbances are sufficiently small or frequent, they are incorporated into the environment of the ecosystem; when sufficiently large and infrequent, they are catastrophic (Fig. 7.4a). There is an intermediate scale of extent and occurrence at which disturbance enforces a mosaic pattern to the ecological landscape. In this case, the landscape pattern is a mosaic of patches, each patch with an internal homogeneity of recent disturbance history different from the surrounding patches.

The mosaic landscape is a statistical assemblage of patches. As in any sampled system, when the number of such patches is small, the variability is relatively large with related increased unpredictability (Fig. 7.4a). If the number of patches making up a landscape is large, the landscape dynamics will become more predictable. Large-scale environmental change, human land-use changes, and natural or

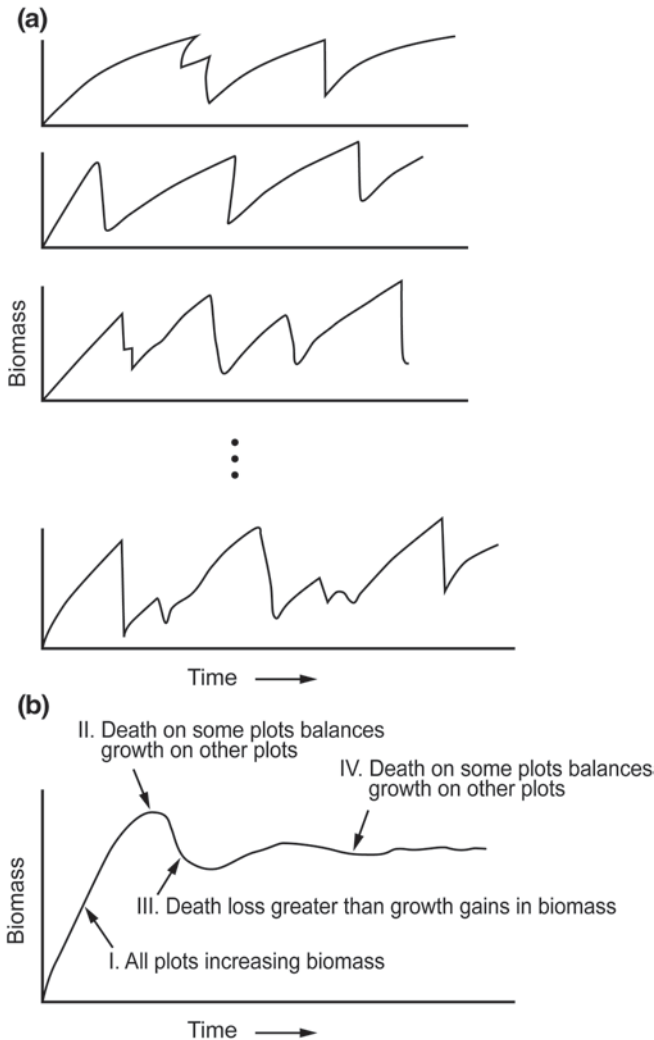


Fig. 7.3 Biomass dynamics for an idealized landscape. The response is from a relatively large, homogeneous area composed of small patches with gap-phase biomass dynamics. **(a)** Individual dynamics of the patches that are summed to produce the landscape biomass dynamics. **(b)** Sections of the landscape biomass dynamics curve are: (I) increasing landscape biomass curve rising as all of the patches are simultaneously covered with growing trees; (II) local drops in biomass are balanced by the continued growth of large trees at other locations (landscape biomass curve levels out); (III) if the trees have relatively similar longevities, there is a period when several (perhaps the majority) of the patches that comprise the forest mosaic all contain deaths of the canopy-dominant trees; and (IV) local biomass dynamics become desynchronized and the landscape biomass curve varies about an equilibrium biomass value

human-induced changes in the climate can alter the spatial and temporal domain of disturbances, and thus change the degree to which we predict landscape behavior. Climate change and human land-use changes tend to increase the size and synchronization of disturbances and make landscape dynamics less predictable.

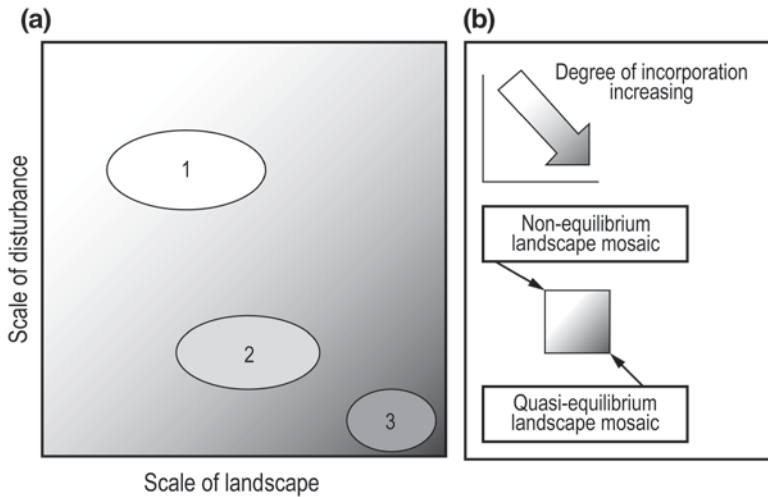


Fig. 7.4 Landscape and disturbance scales. (a) The relationship between the size range of disturbances and of the landscapes on which they operate can be used to categorize landscape dynamic behavior. 1 indicates a disturbance regime whose spatial scale extent is so large that it could be termed a catastrophe; 2 indicates a disturbance regime whose spatial scale is smaller and is a disturbance in the usual sense of the word; and 3 indicates a disturbance regime whose spatial scale is so small with respect to the landscape that it would normally be considered an internal landscape process. (b) Quasi-equilibrium landscapes are much larger than the disturbances that drive them and the average behavior of these landscapes is relatively more predictable. When the disturbance scale is relatively large with respect to a given landscape system, the resultant landscape is effectively a nonequilibrium system and is predictable only when the disturbance history is known. The relatively smaller a disturbance, the greater is the degree of incorporation into the functioning of the landscape

The characterization of a forested landscape as a dynamic mosaic of changing patches was well expressed by Bormann and Likens (1979) in what they call the “shifting mosaic steady-state concept of ecosystem dynamics,” which is derived from Watt (1947). Exemplified in the paragraphs above, this is an old concept in ecology (Aubréville 1932, 1938; Watt 1947; Whittaker and Levin 1977). In a landscape composed of many patches, the proportion of patches in a given successional state should be relatively constant, and the resulting landscape should contain a mixture of patches of different successional ages of a quasi-equilibrium landscape (Shugart 1998; Fig. 7.4b). In small landscapes (or landscapes composed of relatively few patches), the stabilizing aspect of averaging large numbers is lost. The dynamics of the landscape and the proportion of patches in differing states making up the landscape also become increasingly subject to chance variation. If a landscape is small, it takes on many of the attributes of the dynamically changing mosaic patches that make it an effectively nonequilibrium landscape (Shugart 1998).

In Fig. 7.5, landscape area is plotted along the vertical axis; typical disturbance area for each landscape type is plotted along the horizontal axis. The 1/50 ratio of disturbance area to landscape area is shown as a line. The 1/50 ratio was derived (Shugart and West 1981) from using individual-based tree models (Shugart 1998) to determine the needed number of samples of simulated plots to be averaged for a statistically reliable estimate of landscape biomass. Approximately 50 plots, taken

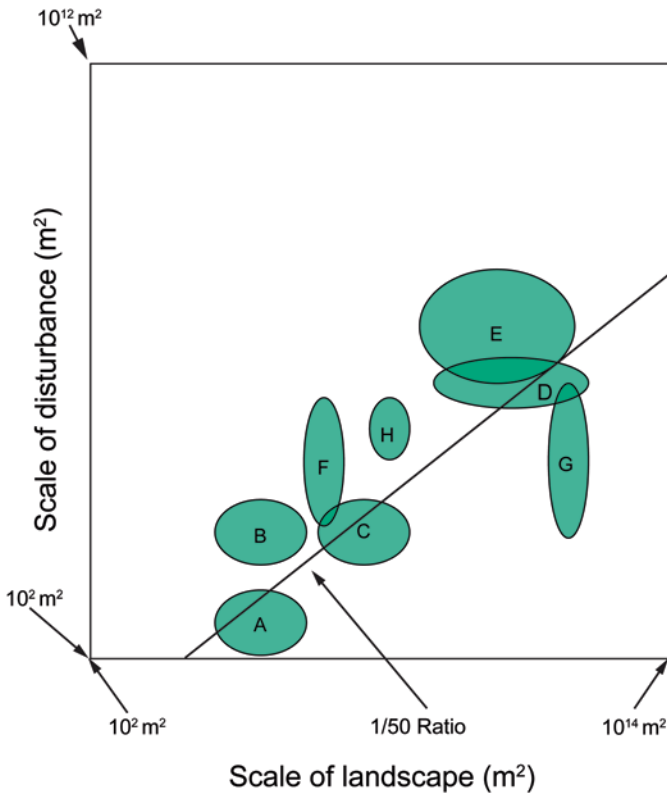


Fig. 7.5 Examples of quasi-equilibrium and effectively nonequilibrium landscapes. **A** Tree fall size versus size of watershed of first-order streams in the Appalachian region of the United States. **B** Wildfire size versus size of watershed of first-order streams in the Appalachian region of the United States. **C** Wildfire size versus size of national parks in the Appalachian region of the United States. **D** Wildfire size versus spatial extent of the species ranges for commercial Australian *Eucalyptus* species. **E** Size of hurricanes versus spatial area of islands in Caribbean. **F** Size of wildfires in Siberia versus size of a forest stand. **G** Size of wildfires in Siberia versus land area of Siberia. **H** Size of floods versus size of floodplain forests

on average, tend to produce a fairly predictable landscape level biomass response, and are used as an arbitrary delineation between quasi-equilibrium and effectively nonequilibrium landscapes. Please note that the comments that follow would hold if this ratio were 1/10 or 1/200.

For example, in Australia, the amount of land burned each year by fires approaches the size of the actual species ranges of a large number of the commercial tree species (Fig. 7.5D). Entire species populations do not have stable age distributions over the entire continent. Some overrepresented tree ages are of individuals regenerated in a particular fire and not subsequently destroyed by later fires. *Eucalyptus delegatensis* tree populations in Australia were disturbed in a tremendous set of forest fires in 1939 that burned over the species' range. For this reason, there are fewer trees than expected that are older than 60 years. A large number of trees regenerated following the 1939 fire; this cohort is overrepresented continental-

ly. There were other fires that also created big mortality events followed by big birth events since 1939 (notably in 1984). Thus, for *E. delegatensis* throughout southeast Australia, most of the trees are only of a few age classes. This situation has important consequences. One of these is that several species of animals that require old *E. delegatensis* trees, as habitat, are now considered endangered species. Many of the Australian forests dominated by *Eucalyptus* species are effectively nonequilibrium landscapes with respect to their biomass dynamics.

If the fall of the tree is the disturbance of interest (gap-scale disturbances), then watersheds of first-order streams in the Appalachian mountains (Fig. 7.5A) would be quasi-equilibrium landscapes. However, if Appalachian wildfires are the focal disturbance (Fig. 7.5B), these same watersheds are relatively too small, and the dynamics of their biomass would be unpredictable without knowing the fire history (as for an effectively nonequilibrium landscape). Indeed, only in the largest parks within the Appalachian region of the United States (Fig. 7.5C) are landscapes large enough to average away the effects on biomass dynamics of the disturbance from typical-sized forest fires. Similarly, forest fires in Russia are large enough to make Siberian forest stands effectively nonequilibrium landscapes (Fig. 7.5F), but Siberia as a whole may be large enough to average away these variations to qualify as a quasi-equilibrium landscape (Fig. 7.5G).

In some cases, the entire biota may inhabit effectively nonequilibrium landscapes. Continental-scale examples have been discussed concerning *Eucalyptus* forest biomass dynamics under the Australian fire disturbance regime (Fig. 7.5D) and Siberian forests (Fig. 7.5F). As further example, the size of hurricanes, which disturb forests of the West Indies, is large when compared with the size of the islands in the Caribbean (Fig. 7.5E). The Caribbean islands are small with respect to the spatial scale of a major climatologic feature that disturbs them, and for this reason, might effectively function as nonequilibrium landscapes. A similar example would be the spatial extent of floodplain forests and floods in large rivers (Fig. 7.5H).

Time and Space as a Fundamental Issue Initially Concerning Landscape Ecology

The discussion of landscape scale developed among ecologists and others who already had ideas of important factors, including external drivers, processes, and patterns that conformed to their particular idea of a landscape. The word landscape itself appears to be appropriated from art history. Landscape as an English word derives from the Dutch word *landschap* from Dutch landscape painting or *landsschappen* (Zonneveld 1990). Certainly, the origins of the fine arts in landscape lend credulity to issues of beauty in landscape as scenery, a topic that is often found in the early issues of *Landscape Ecology*. This is an early interpretation of landscape, traditionally found within landscape architecture, that includes, although has moved beyond, simply the aestheticism of land surfaces (Cramer et al. 1984; Barrett and Barrett 2008; Barrett et al. 2009).

If to some a landscape is what you pay for when you go to a restaurant with a view, others saw landscapes as having heterogeneous patterns as an intrinsic

feature. Combinations of geological, ecological, or hydrological spatial data sets produce spatial patterns of landscapes. These combinations create patches of landscape with different rates of responses and ecological functions. In many systems, these patches and their arrangement repeat in a way that implies a unity of processes. When one flies down the eastern coast of New South Wales, there are rock headlands covered with shrubby, protean heathlands that yield to crescent beaches with dune vegetation, then to *Eucalyptus* forests behind the dunes. Such landscape ecosystems form dynamic repeating patterns and interact to reform these patterns after major disturbances.

Along with different points of view as to what a landscape actually was, there were also other important developments that influenced the appropriate scale to consider in landscape ecology. Ecologists have had a long tradition of studying relatively pristine systems with the idea that in remote areas with mature systems, the complications of the human impact on these systems could be controlled quasi-experimentally. At about the time of the emergence of landscape ecology, the realization that human influence was everywhere on the planet was producing a refocusing of study sites to locations that somehow incorporated human impacts. The importance of including humankind meant the scale of human systems somehow should be included (Naveh and Lieberman 1984). An increasing capability of satellite remote sensing focused attention upon landscape scales that matched the spatial resolution and orbital revisit intervals of the satellites (Frohn 1988). The increasing capability and application of spatial statistics mitigated for particular sampling regimes (Dale and Fortin 2002). The advent and innovation of modern GIS represented a growing technological capacity to manipulate, display, and interact with complex spatial data (Haines-Young et al. 1993).

Thus, when the United States National Science Foundation (NSF) sponsored workshop met at Allerton Park, Illinois, during April 1983, to formulate a basis for landscape ecology, the discussions defining a landscape were extended and vigorous. In retrospect, these discussions carried a significant subtext of important process, the issue of whether humans could be considered in landscape or not, remote sensing and spatial resolution application, sampling structures, and spatial statistics. The importance of these issues has been elucidated more sharply as landscape ecology has progressed as a discipline.

Emergence of a Hierarchical Perspective for Understanding Landscape Ecology

Particular phenomena emerge as being more or less important at different scales in time and space. Hence, understanding space and time scales in ecological systems is a necessary preamble to understanding how ecosystems will respond to large-scale environmental change (O'Neill 1988). The experience in building interdisciplinary research teams indicates that an attention to space and time scales may not guarantee success—but to not do so seems to enhance the likelihood of failure (Shugart and Urban 1988). This attention to scale is highlighted in the development of the Hierarchy Theory in ecology (Allen and Starr 1982; O'Neill et al. 1986; O'Neill 1988).

For landscape ecology, the Hierarchy Theory represented a substantial reinforcement of the ecosystem concept as originally formulated by Tansley (1935). Schneider (2001) reviewed the use of the word “scale” in the ecological literature. He found the frequency of “spatial scale” in *Ecology* and *Ecological Monographs* increased approximately 18 percent per year from 1972 to 1991 starting with papers by Marten (1972) and Wiens (1973). Time and space diagrams first appeared in Steele (1978). These diagrams essentially delineate time and space scales at which different factors control the dynamics of ecosystems. The Hierarchy Theory has sometimes been summarized as, “scale matters” (Wiens 1999) in the context of landscape ecology. It is clear that scale and its formalization as Hierarchy Theory are components of the philosophical underpinnings of landscape ecology.

Scaling-Up Landscape Models for Smaller Scale Empirical Investigations

If 25 years ago, landscape ecology synthesized themes of remote sensing, spatial statistics, and awareness of scale in ecology, it also sprung from an era in which ecological models were becoming a part of the fabric of ecology. Starting in the 1960s and continuing to the present, several different scientific disciplines (astronomy, ecology, physics) independently began to apply computers to the tasks of “book-keeping” the changes and interactions of individual entities. Early versions of these models in ecology, developed by population ecologists interested in including animal behavior in population models, led to a diverse array of applications for fish, insects, and birds (Holling 1961, 1964; Rohlf and Davenport 1969). Exemplary of these applications was the use of Individual-Based Models (IBMs) to represent forests by simulating the trees.

A second and more recent development has been the implementation of complex models that transcend several scales to combine plant geography, physiology, and demography to interact with the current suite of General Circulation Models (GCMs) of the planet’s climate, and Dynamic Global Vegetation Models (DGVMs). The need in the development of DGVMs was for models that could represent the canopy processes that linked the ground surface into the commodities simulated by the climate models. The importance of the terrestrial surface in the decades to century storage and release of carbon also implied a representation of the carbon budget of vegetation.

Individual Based Models (IBM) of Forest Dynamics, Particularly Gap Models

IBMs are models examining vegetation dynamics at a spatial scale corresponding to the area occupied by a small number of mature individuals, approximately the size of a plot or quadrant used for vegetation sampling. Among the earliest IBMs in

ecology were IBMs of forest succession based on the growth of the individual trees. These models were developed by quantitatively oriented foresters and were focused toward practical issues in production forestry (Shugart et al. 1992).

There are several, rather different, modeling approaches that produce IBMs. Indeed, many of the models developed for element cycling and carbon metabolism in ecosystems (notably the developments during the International Biological Program (IBP) of the 1960s and 1970s) were developed to duplicate experimental or observational results from a relatively small tract of land. The principal feature of IBMs was their emphasis on the dynamics of ecosystems at relatively small spatial scales. The initial reasons for this emphasis lay with a need to model at the spatial scale at which data are collected and with the necessity to assume a degree of spatial homogeneity in the model formulation. Recently, recognition of the importance of treating phenomena that do not “scale-up” easily to larger spatial scales has reinforced an interest in individual-based modeling.

Computer models that simulate the dynamics of a forest by following the fates of each individual tree in a forest stand were developed initially in the mid-1960s. The earliest model was developed by Newnham (1964) and followed by similar developments at several schools of forestry. The models predicted change in a small patch of forest using a digital computer to dynamically change a map of the sizes and positions of each tree in a forest. These early individual tree-based simulators took what was known from yield tables and other data sets and developed a more flexible, quantitative methodology for prediction. Some of the earliest attempts to apply such models were very successful and produced results of surprising detail.

An important subcategory of individual organism-based IBMs that has been widely used in ecology (as opposed to traditional forestry applications) is the term “gap” models (Shugart and West 1980). The first such model was the JABOWA model (Botkin et al. 1972) developed for forests in New England. Over the past 20 years, gap models have been developed for a wide variety of forest ecosystems, from boreal to tropical, and the general approach has been extended to nonforested ecosystems such as grasslands, shrub lands, and savannas.

Dynamic Global Vegetation Models

The factors involved in the development of DGVMs originated in the interests of global climate modelers, who realized that surprisingly there were significant feedbacks between the atmosphere and terrestrial surface. They had by this time begun to wrestle with the most significant atmosphere/earth surface feedbacks; ocean currents transport a significant amount of heat. The freezing of seas is one of the largest changes in the surface albedo. Seawater absorbs much of the solar radiation that strikes it; ice reflects much of the same radiation. These factors lead climate modelers to consider the atmosphere/ocean interactions as a high priority, but the surface changes in vegetation increasingly were seen as significant with the development of climate models. This trend continues today. One of the natural model elements

in the synthesis to develop DGVMs was the canopy process model. These also are called Soil Vegetation Atmosphere Transfer (SVAT) models in the current global climate formulations (Bonan 2008). The aim in developing DGVMs was to maximize the use of mechanistic models (Whitmore 1982). The primary example of such models is that of photosynthesis, which drives the carbon cycle. The Farquhar et al. (1980) formulation, a biochemical model of photosynthesis designed to simulate the net photosynthetic effects of changes in CO_2 or light, has been tested in a range of situations and proven most effective in DGVMs.

Another aspect of many early DGVMs was a fusion of physiological models with biogeographical algorithms to understand the changes in physical structure (leaf areas, heights, amount of biomass) that go with changes in vegetation types, as well as differences in the ecosystem functioning of these vegetations. Early precursors to the modern DGVMs comprised a model developed by Woodward (1987) that was “rule based” with broad functional types of plants categorized, but their low temperature limits to survival and growth were based on the ranges of required growing season lengths, warmth, and the degree of their water requirements were met through precipitation. An early fusion of hydrology and plant canopy function was the Forest BGC model (Running and Coughlan 1988; Running and Nemani 1988; Running et al. 1989; Running and Gower 1991). Forest BGC (hydrology and plant canopy function) has been melded to an individual tree-based forest model providing a capability to dynamically simulate the change in forest structure over time (Friend et al. 1993).

In 1997, an asynchronously coupled GCM and DGVM were found to produce relatively small and positive feedbacks on climate (Betts et al. 1997). Asynchronous coupling indicates that one model is run for a period of time, then its results are fed into the second model, which is also run based on these inputs, and then the second models’ results are fed into the first model, and so on. Just a few years later, a fully coupled GCM called “TRIFFID” (Cox et al. 2000) produced quite alarming results—under a future-warming scenario, the terrestrial biosphere turned from a sink of anthropogenic CO_2 at 2050 to a source by 2100. The source strength was so strong that atmospheric CO_2 concentrations were 250 parts per million (ppm) greater by 2100, with an associated 1.5°C extra warming above the 4°C case that occurred when the vegetation and atmosphere were not coupled. This effect has been speculated about in the past as the runaway greenhouse effect in which change begets more change. More recently, 11 coupled GCMs (Friedlingstein et al. 2006) were compared to investigate differences in future simulations of the global carbon cycle. The differences in land uptake of carbon considerably differ from large uptakes to large releases up to the end of the century. It is interesting to note that the TRIFFID DGVM, coupled within the Hadley Centre GCM that was used in the initial coupled simulation (Cox et al. 2000), had the largest changes in vegetation activity over the twenty-first century.

In the case of both gap models or IBMs and the DGVMs, there is a direct attempt to scale processes up to the global levels by a synthesis of processes normally considered in landscape ecology. How successful was this leap of several quanta in scale remains a challenge for landscape ecology theory and theory testing.

Landscape Boundaries and Connectivity

A landscape boundary may be *physical*, such as the edge of a watershed, *political*, such as the jurisdiction of a natural reserve (Schonewald-Cox 1988), *ecological*, such as an isolated forest patch in an agricultural landscape matrix, or *functional*, such as home-range size of a small mammal. Several publications have focused on landscape boundaries during the past 30 years (Lefkovitch and Fahrig 1985; Opdam et al. 1985; Wiens et al. 1985; Holland et al. 1991). Barrett (1985) described the importance of defining boundaries (i.e., a defined universe) when using a problem-solving approach to resource management. Boundaries define watersheds, home-range size, and experimental landscape patches. Defining the experimental universe is essential for estimating such parameters as biotic diversity, species abundance, and resource availability.

Fahrig and Merriam (1985) were among the first to investigate connectivity in the study of population survivorship. They viewed connectivity as a model that measures the difference in survivorship of populations in patches that are interconnected at the landscape scale. Forman and Godron (1986) defined “connectivity” as a measure of how spatially continuous a corridor or matrix exists. The greater the number of connections between landscape patches, the greater the connectivity of the patch in the landscape. Forman and Godron (1986) pointed out that landscape corridors also may function as physical or biotic barriers.

Landscape connectivity plays a major role in local–regional plant species diversity (Damschen and Brudvig 2012), seed predation (Orrock and Damschen 2005), survivorship of small mammal species (Fahrig and Merriam 1985), and metapopulation source–sink dynamics (Pulliam 1988). Haddad et al. (2003), for example, investigated ten different species, including butterflies, small mammals, and bird-dispersed plants, resulting in higher movement between connected than between unconnected landscape patches; their findings show that movements of disparate taxa with different life histories and functional roles are directed by corridors.

Thus, landscape ecologists have gained increased understanding regarding the structure and function of spatial heterogeneity, and how the application of landscape ecology will broaden our scope in natural resource management (Turner 2005). We will next discuss how the field of landscape ecology has emerged as a new paradigm (i.e., a new “level of ecological organization” or “level of integration”).

Viewing Landscape as a Level-of-Organization Concept

The evolution of the level-of-organization concept has a long and rich history (Sears 1949; Wright 1959; Rowe 1961) during which the concept has been challenged as well (Guttman 1976). MacMahon et al. (1978) advanced the concept, focusing on an organism-centered approach. Earlier ecology textbooks omitted the landscape as an emerging and valid level of organization. Interestingly, as alluded to earlier in this volume, most recent editions of ecology textbooks now include a chapter devoted to landscape ecology (Cain et al. 2008; Molles 2008; Ricklefs 2008; Smith and Smith

2012), and some textbooks specifically identify the landscape as a level-of-organization (Odum and Barrett 2005) or level-of-integration (Krebs 2008) concept. Barrett et al. (1997) described how 7 major processes (behavior, development, diversity, energetics, evolution, integration, and regulation) transcend 11 ecological levels of organization, ranging from the ecosphere to the cell, including the landscape level. Barrett et al. (2009) introduced aesthetics as an eighth transcending process through these selected 11 ecological levels of organization. An understanding of aesthetics as economy (energetic efficiency) of survivorship allows the integration of nonmarket (i.e., ecosystem services) and market (i.e., monetary currency) values (Fig. 7.6).

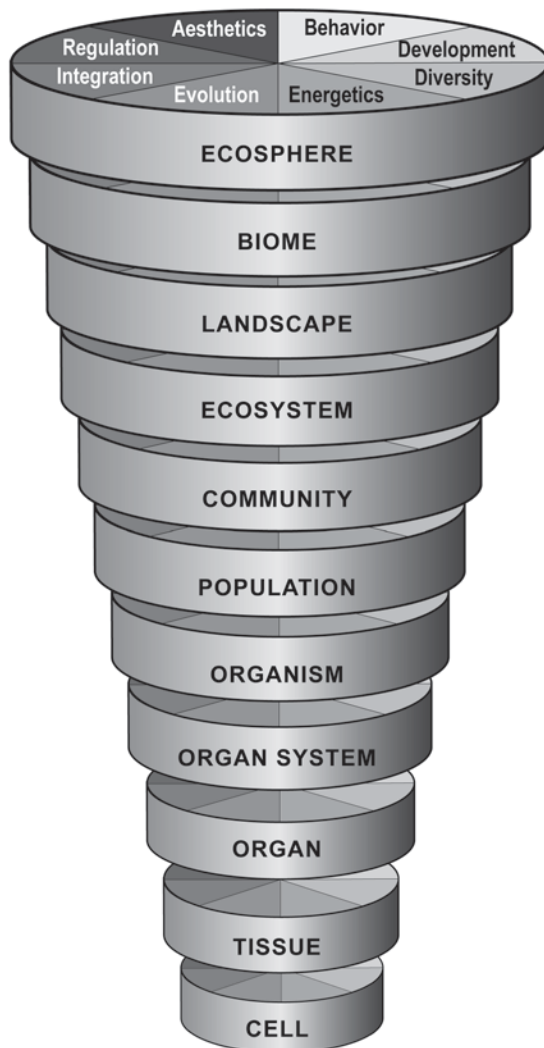


Fig. 7.6 Eight major processes through 11 selected ecological levels of organization. (After Odum and Barrett 2005; Barrett et al. 2009)

Thus, during the past half century, landscape ecology has become a cornerstone of ecological research, learning, and resource management. Although landscape ecology is typically referred to as a subdiscipline of ecology (Cain et al. 2008), much like decades ago when ecology was considered a subdiscipline of biology (Barrett 2001), we now recognize landscape ecology as an emerging paradigm or standalone interdisciplinary field of study. Perhaps landscape ecology is best defined as the study of the relationship between spatial pattern and ecological process over a range of scales (Wu and Hobbs 2006), or perhaps as a pertinent example of a transdisciplinary, integrative science for future generations of problem solvers and resource managers (Barrett 1985, 2001).

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