

Chapter 4

Landscape Ecology: Past, Present, and Future

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4.1 Historical Origins of Landscape Ecology

In the preceding chapters we discussed the central role that spatial and temporal variability play in ecological systems, the importance of addressing these explicitly within ecological analyses and the resulting need to carefully consider spatial and temporal scale and scaling. Landscape ecology is the science of linking patterns and processes across scale in both space and time. Thus landscape ecology is, in a real sense, the foundational science for addressing the central issues of sensitive dependence of ecological process on spatial and temporal variability. This chapter reviews the historical origins and evolution of landscape ecology, discusses its current scope and limitations, and then anticipates the following chapter by looking forward to identify how the field could best expand to address the central challenges of ecological prediction in spatially complex, temporally disequilibrium, multi-scale ecological systems.

Landscape ecology has emerged as an integrative, eclectic discipline, focusing explicitly on spatial structure and dynamics of landscape systems (Turner 1987). Traditionally, ecological science has largely been limited to the study of relationships between the structure and function of entities assumed for simplicity to be spatially homogeneous and temporally stable (Pickett and Cadenasso 1995). Landscape ecology, in contrast, views spatial heterogeneity as a prime causal factor in ecological interactions. Pickett and Cadenasso (1995) state that the primary insight to emerge from landscape ecology is the realization that spatial heterogeneity at various

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scales exerts important influences on many ecological interactions. They define the goal of landscape ecology as “showing how processes at various scales interact to shape ecological phenomena and exposing regularities that have wide explanatory potential.” Godron and Forman (1981) identify primary areas of enquiry in landscape ecology as the study of the distribution patterns of landscape elements, flows of material, biological or energetic units between the elements and the dynamics of landscape morphology, while Naveh and Lieberman (1994) define landscape ecology more broadly as the scientific basis for landscape study, planning and conservation.

The development of landscape ecology has been cosmopolitan and eclectic, borrowing perspectives from a host of biological and geographical sub-disciplines and also being the heir to separate traditions originating in Europe, Russia and the United States (Forman and Godron 1986; Naveh and Lieberman 1994). The roots of landscape ecology may be said to begin in the middle nineteenth century with the introduction of “landscape” as a scientific term by the explorer-geographer Alexander Von Humboldt (Naveh and Lieberman 1993). Humboldt viewed landscapes as exhibiting coherence in spatial distribution and interconnectedness of phenomena, and was a pioneer in the study of spatial relationships between biological and physical phenomena (Dickinson 1970). Von Humboldt’s work laid the foundations for much of modern geography and led directly to advances in the study of landscape characteristics.

Extending Von Humboldt’s work, S. Passarge proposed “landscape science” as a new subfield of geography in 1919 (Troll 1971). Passarge’s framework for landscape science was adopted and expanded by a series of Russian geographers. C.S. Berg described a landscape as a “community of a higher order, consisting of communities of organisms...together with the complex of inorganic phenomena” (Troll 1971).

In 1935 A.G. Tansley first proposed the scientific concept of the ecosystem (Tansley 1935). This prompted the German geographer Carl Troll to advance the term “landscape ecology” in 1939 (Troll 1971). Troll described landscape ecology as “the study of the main complex causal relationships between the life communities and their environment in a given section of the landscape.” Troll’s original goal was to show ecological distributions within landscapes. Importantly, the initial focus of the Russian and German efforts in landscape science and landscape ecology focused on continuous patterns of environmental variability and continuous population processes, in a way presaging the gradient concepts of American community ecology later proposed by Gleason (1926) and Whittaker (1967). However, landscape ecology shortly thereafter departed from this gradient framework, and instead evolved into an effort to divide landscapes into small components and ascertain the logic through which they were grouped and interacted as a landscape mosaic (Troll 1971).

Following World War II, landscape ecology emerged as quasi-independent disciplines in the Soviet Union and several central European nations (Naveh and Lieberman 1994). In Germany, E. Neef, J. Schmithusen, and G. Haase made the first major contributions to quantification of landscape structure (Forman and Godron 1986). In the 1960s The Institute of Care and Nature Protection at the Technical

University of Hanover made important contributions to methods for using landscape ecology as a tool for landscape management and planning (Naveh and Lieberman 1993).

At about the same time, in the Netherlands C. Van Leeuwen provided original insights into the linkage of temporal variation and spatial heterogeneity in landscapes (Forman and Godron 1986). Zonneveld (1972) stressed the importance of studying landscapes as holistic amalgamations of separate components. He viewed the structure of the abiotic environment as central to landscape ecology, and held that the field was more naturally considered a subunit of geography and not ecology. Important theoretical contributions to the conceptualization of landscapes as mosaics of discrete elements were also made by workers in Australia and Switzerland (Naveh and Lieberman 1993).

While in Europe landscape ecology was developing powerful techniques for the description and analysis of the physical structure of landscape mosaics, American scientists were following a different route. Late in the nineteenth century American ecologists began to focus for the first time on the rigorous study of communities of living organisms (Krebs 1994). This trend was given direction by S.F. Forbes' classic paper, "The Lake as a Microcosm" (Forbes 1887). Forbes proposed the idea of an ecological community as an organic complex of mutually interdependent entities, and focused on how a "balance of nature" was maintained by competition between species for limited resources. Forbes' community approach was very insightful, but assumed that communities functioned as homogeneous units isolated from surrounding ecological systems.

At the beginning of the twentieth century American ecologists were beginning to make connections between landscape structure and community function, yet the development of truly landscape level science was still far behind that of European investigators (Troll 1971). In 1925 the American geographer C.O. Sauer wrote "The Morphology of Landscape" which provided, for the first time in the United States, a critique of European Landscape science (Sauer 1965). He sought to give new vigor to American geography by introducing the patch mosaic landscape perspective as a central focus of geography (Forman and Godron 1986).

Work on plant succession by H.C. Cowles (1899) and F. Clements (1916) provided some of the first truly landscape level investigations of ecological phenomena in America. In particular, Cowles' "physiographic ecology" emphasized constant interactions between plant communities and underlying geological formations, and viewed flora in a landscape as an ever-changing panorama (Real and Brown 1991). However it wasn't until Egler's work on plant ecology in the 1940s that a holistic view of plant associations and their interactions with human influences came to prominence in America (Egler 1942).

What is commonly thought of as modern landscape ecology may be considered to have begun in the United States with the work of a number of ecologists in the 1950s and 1960s (Forman and Godron 1986). Dansereau (1957) developed a system of classification of landscape elements based on tropic levels of energy transfer, and argued that the landscape unit was the highest level in the hierarchy of ecological structure. Christian (1958) advanced a model of discretely defined land units forming

a spatial mosaic. Dickinson (1970) developed an approach termed “regional ecology” which focused on qualitative description of spatial associations among phenomena over the earth’s surface. Isard (1975) further added to the theoretical base of regional science, emphasizing social problems with regional and spatial characteristics. The emergence of transportation theory also added new insights to landscape ecology (Forman and Godron 1987). Taaffe and Gauthier’s “Geography of Transportation” (1973) and Lowe and Moryada’s “Geography of Movement” (1975) were path breaking in the study of network structure and connectivity, which would become one of the central interests of landscape ecology in the coming two decades. Also, their work set the foundations for the quantitative study of flow of ecological entities, such as nutrients, organisms and energy across landscape networks (Forman and Godron 1986).

The modern view of landscape structure as being composed of a mosaic of patches in a matrix was first formally put forth by Forman (1981) and Forman and Godron (1981). Modern landscape ecology is based on the patch mosaic paradigm, in which landscapes are conceptualized and analyzed as mosaics of discrete patches (Forman 1995; Turner et al. 2001). Sometimes the “patch mosaic” model is referred to as the “patch-corridor-matrix” model after Forman and Godron (1986) and Forman (1995) in order to recognize the different major landscape elements that can be present in a patch mosaic. Any reading of the published landscape ecology literature shows near uniformity in the adoption of this approach. Consequently, our current state of knowledge regarding landscape pattern-process relationships is based almost entirely on a categorical representation of spatial heterogeneity. The patch mosaic model has led to major advances in our understanding of landscape pattern-process relationships (Turner 2005) and has been applied to landscapes across the globe. Its strength lies in its conceptual simplicity and appeal to human intuition. In addition, it is consistent with well-developed and widely understood quantitative techniques designed for discrete data (e.g., analysis of variance). Furthermore, there is ample evidence that it applies very well in landscapes dominated by severe natural or anthropogenic disturbances (e.g. fire dominated landscapes and built landscapes).

Modern landscape ecology is characterized by several variant conceptions of the patch mosaic paradigm of landscape structure and change (Wiens 1994, With and King 1999). These perspectives largely differ in how the focal habitat is perceived and represented relative to other landscape elements, and whether the landscape structure is viewed as relatively static (i.e., unchanging) or dynamic (i.e., constantly changing). Although there are many variations, two paradigms have emerged that provide alternative frameworks for conceptualizing the habitat loss and fragmentation process.

4.1.1 Static Island Biogeographic Model

The first paradigm we call the “static island biogeographic model.” In this model, habitat fragments are viewed as analogues of oceanic islands in an inhospitable sea or ecologically neutral matrix. Under this perspective, discrete habitat patches are

seen as embedded in a uniform matrix of non-habitat. Connectivity is assessed by the size and proximity of habitat patches and whether they are physically connected via habitat corridors. The key attributes of the model are its representation of the landscape as a binary system of habitat and inhospitable matrix, and that, once lost, habitat remains matrix in perpetuity. In extreme cases, the process of habitat loss and fragmentation continues until the target habitat is eliminated entirely from the landscape. This scenario is perhaps best exemplified by urban sprawl and agricultural development, where remnant habitat fragments are maintained in an otherwise relatively static matrix or are eventually eliminated entirely from the landscape.

The static island biogeography paradigm has been the dominant perspective since the inception of the fragmentation concept. The major advantage of the island model is its simplicity. Given a focal habitat, it is quite simple to represent the structure of the landscape in terms of habitat patches contrasted sharply against a uniform matrix. Moreover, by considering the matrix as ecologically neutral, it invites ecologists to focus on those habitat patch attributes, such as size and isolation, that have the strongest effect on species persistence at the patch level. The major disadvantage of the strict island model is that it assumes a uniform and neutral matrix, which in most real-world cases is a drastic over-simplification of how organisms interact with landscape patterns. Not all matrix is created equal. Moreover, the strict island model usually assumes a static landscape structure, at least with respect to the matrix. Once habitat is lost, it remains matrix. This, too, is not realistic in many landscapes, especially those driven by natural disturbances and/or forest management activities.

The landscape transformation process as conceptualized under the idealized static island biogeographic model can be divided into several broad stages or phases that are demarcated by significant changes in the pattern or function of the landscape (Forman 1995). In reality, these phases are not strictly separate from each other since they may take place simultaneously; however, a dominant phase can often be identified.

1. *Perforation* – Often, the first stage of habitat loss and fragmentation involves the perforation of natural habitat through direct loss, usually resulting from conversion to other land uses (e.g., agricultural clearing, housing development, timber harvesting). Perforation creates holes in otherwise contiguous habitat. Here, there is both a direct loss of habitat and a change in the spatial distribution of remaining habitat. The degree of impact on habitat configuration will depend on the pattern of perforation (see below). However, at this stage, the habitat is still physically well connected.
2. *Dissection* – The second stage of habitat loss and fragmentation involves the dissection of natural habitat. In most cases, a perforated pattern will become a dissected pattern at certain threshold levels of habitat loss. Dissection may precede or occur in conjunction with perforation. A common route to habitat dissection is through the construction of roads or other transportation corridors that span the landscape. In most cases, there is relatively little reduction in habitat area caused by dissection. However, the resulting linear landscape elements can be a significant source of disruption to the natural community because

they can provide avenues for the intrusion of edge predators, invasive species, exotics, diseases and pathogens that adversely affect the organisms of interest. In addition, these linear elements can affect landscape connectivity by altering movement patterns of organisms. Perhaps most importantly, some dissecting agents such as roads provide human access to the natural habitats and establish a network by which future habitat loss and alteration will occur. Of course, as in all cases, the effects of dissection will depend on the habitat and the organism(s) of interest.

3. *Subdivision* – The third stage of habitat loss and fragmentation involves the subdivision of habitat into disjunct patches. Forman (1995) referred to this phase as “fragmentation”, but like Jaeger (2000), who referred to this phase as “dissipation”, we prefer to use the term fragmentation to refer to the entire sequence rather than a single phase. During this phase, the landscape undergoes an important phase transition from a landscape characterized by physically connected habitat to a landscape in which the habitat is broken up into disjunct fragments. At this point, the areal extent of habitat may still be quite large and may not yet be significantly limiting landscape function for the organism(s) of interest. However, at this point, the habitat is physically disconnected and may disrupt movement patterns of the target organism(s) and cause the subdivision of populations into separate units. The consequences of this population subdivision will be discussed later. Note, this phase may be confused or confounded with the “dissection” phase. The dissection phase, as idealized, typically occurs as a result of road-building in which the habitat is subdivided or dissected by linear features that do not result in significant reduction in habitat area. In contrast, the subdivision phase is typically characterized by concurrent habitat loss and results when the remaining habitat becomes subdivided into disjunct patches embedded within a matrix of “non-habitat.”
4. *Shrinkage and Attrition* – The final stage of habitat loss and fragmentation involves the shrinkage and, in some cases, complete disappearance of the focal habitat. Here, the landscape is in a critical state with respect to the viability of the target habitat. As habitat patches are reduced in size and become more isolated from each other, the function of the landscape is seriously jeopardized for organisms associated with the target habitat. Under the island-biogeographic model, the remaining habitat fragments represent true islands in an inhospitable sea. Of course, the hostility of the matrix will depend on the organisms and how their life-history and vagility characteristics interact with landscape patterns, as discussed below.

This four-stage conceptualization of the landscape transformation represents an idealized and oversimplified view of habitat loss and fragmentation processes under the static island biogeographic model; no real landscape follows this trajectory exactly. Nevertheless, it depicts the general sequence of events characteristic of habitats undergoing reduction and fragmentation caused by urban and/or agricultural development. Although this simple conceptual model provides a useful framework, it is important to understand that there are many alternative scenarios or patterns of habitat loss and fragmentation associated with the above landscape transformation. Forman (1995) refers to such variations as “mosaic sequences.”

5. *Random Model* – Habitat is lost progressively in a random pattern. Although not representative of any real-world pattern of habitat loss and fragmentation, it provides a useful null model against which to compare other scenarios.
6. *Contagious Model* – Habitat is lost in a contagious (i.e., aggregated) pattern. In this case, the fragmentation of habitat is controlled by the degree of contagion in the residual habitat. Thus, under a maximum contagion scenario, the residual habitat would be aggregated into a single patch, and the habitat would not be fragmented per se.
7. *Dispersed Model* – Habitat is lost in a dispersed (i.e., disaggregated) pattern. Under a maximum dispersion scenario, habitat would be perforated by dispersed ‘openings’ and would eventually be broken into discrete fragments.
8. *Edge Model* – Habitat is lost progressively in a wave-like manner, beginning on one edge of the landscape and moving progressively across the landscape. In this scenario, there is no fragmentation of habitat per se, since the original habitat is not subdivided into disjunct patches, but simply reduced in size steadily over time. This process is typical of urban expansion outward from a city or some large-scale forestry operations.
9. *Corridor Model* – Habitat is first bisected by corridor development (e.g., roads) and then lost progressively outward from the corridors. In this scenario, the habitat is both reduced and fragmented. This process is typical of rural and suburban residential development in many areas.
10. *Nuclear Model* – Habitat is lost progressively from nuclei that may be dispersed in a random, uniform, or clumped pattern. Perforations in the habitat grow steadily in size in radial fashion until eventually the habitat is subdivided (i.e., becomes disconnected). The rate and pattern of fragmentation per se will depend on the dispersion of nuclei. This process is typical of rural development and timber harvesting.

These models represent alternative patterns by which habitat may be lost from a landscape, and although idealized and oversimplified, they illustrate the wide range of possible patterns of habitat loss. More importantly, they illustrate the quantitative differences in habitat loss and fragmentation that can result under various scenarios (Forman 1995: page 425). For example, given the same trajectory of habitat loss, the edge model maintains the largest patches of habitat in the landscape without causing fragmentation. Conversely, the dispersed model results in the quick elimination of large patches from the landscape and, at some point, causes the fragmentation of the habitat that remains.

4.1.2 Dynamic Landscape Mosaic Model

The second major conceptual paradigm is the dynamic landscape mosaic model. In this paradigm, landscapes are viewed as spatially complex, heterogeneous assemblages of cover types, which can’t be simplified into a dichotomy of habitat

and matrix (Wiens et al. 1993; With and King 1999). Rather, the landscape is viewed from the perspective of a particular ecological process or organism. Habitat patches are bounded by other patches that may be more or less similar (as opposed to highly contrasting and often hostile habitats, as in the case of the island model) and the mosaic of patches itself changes through time in response to disturbance and succession processes. Connectivity is assessed by the extent to which movement is facilitated or impeded through different land cover types across the landscape. Land cover types may differ in their “viscosity” or resistance to movement, facilitating movement through certain elements of the landscape and impeding it in others. This perspective represents a more holistic view of landscapes, in that connectivity is an emergent property of landscapes resulting from the interaction of organisms with landscape structure.

The dynamic landscape mosaic paradigm has only recently emerged as a viable alternative to the static island biogeographic model. The major advantage of the landscape mosaic model is its more realistic representation of how organisms perceive and interact with landscape patterns. Few organisms exhibit a binary (all or none) response to habitat types, but rather use habitats proportionate to the fitness they confer. Moreover, movement among suitable habitat patches usually is a function of the character of the intervening habitats. Two suitable habitat patches separated by a large river may be effectively isolated from each other for certain organisms, regardless of the distance between them. In addition, the landscape mosaic model accounts for the dynamics in landscape structure due to the constant interplay between disturbance and succession processes. This is especially important in forested landscapes where natural disturbances and timber harvesting are the major drivers of landscape change. The major disadvantage of the landscape mosaic model is that it requires detailed understanding of how organisms interact with landscape structure; in particular, how the landscape mosaic composition and configuration affect movement patterns. Unfortunately, it is exceedingly difficult in practice to collect the needed quantitative information, rendering this model less practical. However, even in the absence of detailed information about how target organisms interact with entire landscape mosaics, it is often beneficial to characterize the landscape more realistically than as a simple binary map of habitat and matrix.

4.2 Spatial Components of the Patch-Mosaic Landscape Model

Whatever landscape paradigm one ascribes to, it is essential to understand what a given change in a landscape means physically. This requires explicit attention to the spatial components of landscape structure. There are conceptually many different spatial attributes which characterize a landscape mosaic pattern. Thus, a multivariate perspective is required and it is unreasonable to expect a single metric, or even a few metrics, to be sufficient.

Habitat loss and landscape fragmentation involve changes in both landscape composition and configuration (McGarigal and Marks 1995; Cushman and McGarigal 2002). *Landscape composition* refers to the presence and amount of each habitat type within the landscape, but not the placement or location of habitat patches within the landscape mosaic. *Landscape configuration* refers to the spatial character and arrangement, position, orientation, and shape complexity of patches in the landscape. We recognize five major components of landscape composition and configuration affected by habitat loss and fragmentation, even though the distinctions among these components can be somewhat blurry at times.

1. *Habitat Extent* – As noted previously, habitat loss and fragmentation are almost always confounded in real-world landscapes. Therefore, it is essential that habitat extent be considered in conjunction with any assessment of habitat fragmentation. Indeed, as described later, it is difficult, and in some cases impossible, to interpret many fragmentation metrics without accounting for habitat extent. Habitat extent represents the total areal coverage of the target habitat in the landscape and is a simple measure of landscape composition.
2. *Habitat Subdivision* – Habitat fragmentation fundamentally involves the subdivision of contiguous habitat into disjunct patches, which affects the overall spatial distribution or configuration of habitat within the landscape. Subdivision explicitly refers to the degree to which the habitat has been broken up into separate patches (i.e., fragments), *not* the size, shape, relative location, or spatial arrangement of those patches. Because these latter attributes are usually affected by subdivision, it is difficult to isolate subdivision as an independent component.
3. *Patch Geometry* – Habitat fragmentation alters the geometry, or spatial character, of habitat patches. Specifically, as patches are subdivided via habitat loss (Figs. 3 and 4), they become smaller, contain proportionately less core area (i.e., patch area after removing the area within some specified edge-influence distance), typically extend over less area, and often have modified shapes, although the nature of the change may vary depending on the anthropogenic agent (e.g., Krummel et al. 1987).
4. *Habitat Isolation* – Habitat fragmentation increases habitat insularity, or isolation. That is, as habitat is lost and fragmented, residual habitat patches become more isolated from each other in space and time. Isolation deals explicitly with the spatial and temporal *context* of habitat patches, rather than the spatial character of the patches themselves. Unfortunately, isolation is a slippery concept because there are many ways to consider context. In the temporal domain, isolation can be considered as the time since the habitat was physically subdivided, but this is fraught with practical difficulties. For example, rarely do we have accurate historical data from which to determine when each patch was isolated. Moreover, given that fragmentation is an ongoing process, it can be difficult to objectively determine at what point the habitat becomes subdivided, since this is largely a function of scale. In the spatial domain, isolation can be considered in several ways, depending on how one measures the spatial context of a patch. The simplest measures of isolation are based on Euclidean distance between nearest

neighbors (McGarigal and Marks 1995) or the cumulative area of neighboring habitat patches (weighted by nearest neighbor distance) within some ecological neighborhood (Gustafson and Parker 1992). These measures adopt an island biogeographic perspective, as they treat the landscape as a binary mosaic consisting of habitat patches and uniform matrix. Thus, the context of a patch is defined by the proximity and area of neighboring habitat patches; the role of the matrix is ignored. However, these measures can be modified to take into account other habitat types in the so-called matrix and their affects on the insularity of the focal habitat. For example, simple Euclidean distance can be modified to account for functional differences among organisms. The functional distance between patches clearly depends on how each organism scales and interacts with landscape patterns (With and King 1999); in other words, the same gap between patches may not be perceived as a relevant disconnection for some organisms, but may be an impassable barrier for others. Similarly, the matrix can be treated as a mosaic of patch types which contribute differentially to the isolation of the focal habitat. For example, isolation can be measured by the degree of contrast (i.e., the magnitude of differences in one or more attributes between adjacent patch types) between the focal habitat and neighboring patches.

5. *Connectedness* – Habitat loss and fragmentation affect the connectedness of habitat across the landscape. Connectedness integrates all of the above components and involves both a structural component (i.e., the amount and spatial distribution of habitat on the landscape; also referred to as “continuity”) and a functional component (i.e., the interaction of ecological flows with landscape pattern; also referred to as “connectivity”). Structural connectedness refers to the physical continuity of habitat across the landscape. Contiguous habitat is physically connected, but once subdivided, it becomes physically disconnected. Structural connectedness is affected by habitat extent and subdivision, but also by the spatial extensiveness of the habitat patches (Keitt et al. 1997). Specifically, as habitat patches become smaller and more compact, they extend over less space and thus provide for less physical continuity of habitat across the landscape. Structural connectedness as considered here adopts an island biogeographic perspective.

What constitutes “functional connectedness” between patches clearly depends on the organism of interest; patches that are connected for bird dispersal might not be connected for salamanders. As habitat is lost and subdivided, at what point does the landscape become functionally “disconnected?” As With and King (1999) notes, “what ultimately influences the connectivity of the landscape from the organism’s perspective is the scale and pattern of movement (i.e., scale at which the organism perceives the landscape) relative to the scale and pattern of patchiness (i.e., structure of the landscape);...i.e., a species’ gap-crossing or dispersal ability relative to the gap-size distribution on the landscape” (Dale et al. 1994; With and Crist 1995; Pearson et al. 1996; With et al. 1997). Hence, functional connections might be based on: (1) strict adjacency (touching) or some threshold distance, e.g., a maximum dispersal distance); (2) some decreasing function of distance that reflects the

probability of connection at a given distance; or (3) a resistance-weighted distance function, e.g., where the distance between two patches is computed as the least cost distance on a resistance surface, where each intervening location between habitat patches is assigned a resistance value based on its permeability to movement by the focal organism. Then various indices of overall connectedness can be derived based on the pairwise connections between patches.

4.3 Looking Forward – The Gradient Concept of Landscape Structure

In the past 20 years the patch mosaic paradigm of landscape ecology has been expanded through integration with spatial population theory (e.g. MacArthur and Wilson 1963; Terborgh 1976; Kareiva and Wennergren 1995), and emerging technologies such as remote sensing (Hobbs and Mooney 1990, and GIS (Haslett 1990; Haines-Young 1993). The revolutionary new computational capabilities of modern computers, coupled with the flexible raster analysis capabilities of GIS, and inexpensive, broadly available remotely sensed imagery provided new inspiration for the evolving field of landscape ecology. It is a dramatic case of the theory of landscape ecology lagging well behind the state-of-the-art in computation, spatial analysis and available spatial data. The landscape mosaic framework is well suited to systems which are dominated by clearly defined, internally homogeneous units, with the advantage of simplicity of representing and analyzing them. However, there are many situations when the patch mosaic model fails or is at best sub-optimal. The patch mosaic model does not accurately represent continuous spatial heterogeneity (McGarigal and Cushman 2005). Once categorized, patches subsume all internal heterogeneity, which may result in the loss of important ecological information. When applying the patch mosaic model in practice, it is prudent to ask whether the magnitude of information loss is acceptable. Most fundamentally, there appears to be a major disjunction between modern ecological theory in the fields of community and population ecology and the patch-mosaic conception of landscape structure. In the first chapter we discussed science as a historical process which is based on underlying conceptual caricatures of natural systems. Given the base assumptions of these underlying models, each field then proceeds to develop theory, collect data, propose relationships. However, rarely are these underlying conceptual models themselves the focus of scrutiny. This results in what we called a “boring-in” whereby these underlying paradigms become entrenched as quasi-dogmatic beliefs. We believe that the patch-mosaic model in landscape ecology is a classic example of this. In the previous two chapters we argued that spatial and temporal variation in ecological systems fundamentally alter pattern-process relationships in a highly scale-dependent way, and that reliable inferences are frequently only obtained by linking mechanisms with responses directly at operative scales and integrating these over space and time. Given this framework, in the following

sections of this chapter, we evaluate the traditional patch-mosaic model of landscape structure relative to community ecology theory and propose an alternative framework for landscape ecology.

The modern scientific study of ecological communities is often traced to Clements (1907, 1916), who posited that the composition of species within a community is a deterministic product of regional climate and time since disturbance. Species composition within a community was thought to be highly predictable as deterministic as functions of regional climate and seral condition. However, the Clementsian view of communities as analogous to super-organisms was fundamentally challenged by Gleason (1917, 1926), who argued that identification of categorical vegetation types was inconsistent with the large amounts of heterogeneity in plant communities, arguing that areas of vegetation are actually similar to one another only by degrees and not in kind. He questioned delineating patch-mosaic maps of community types and opposed grouping of species in nameable associations. As an alternative, Gleason offered the individualistic concept of the plant association in which “the phenomena of vegetation depend completely upon the phenomena of the individual” species (Gleason 1917).

This individualistic concept of vegetation ecology is the foundation of modern community ecology. The fusion of individualistic community ecology (Gleason 1926; Curtis and McIntosh 1951; Whittaker 1967) with the Hutchinsonian niche concept (Hutchinson 1957) enabled a broad integration of ecological theory, spanning all the way from Darwinian evolution, to the niche characteristics of individual species, to the composition, structure and dynamics of ecological communities. Each species is seen responding to local environmental and biotic conditions. The biotic community in this context is conceived as a collection of species that are occurring together at a particular place and a particular time due to overlapping tolerances of environmental conditions and vagaries of history, rather than an integrated and deterministic mixture. Research in this paradigm focuses on extending the individual concept to quantitative analysis of species distribution along environmental gradients and the effort to quantify the fundamental niche of each species in terms of the range of resources and conditions needed for that species to survive. The natural level of focus of such analyses is the species, not community type, assemblage or patch type; the natural focal scale for such analyses is the location or pixel, rather than the stand or patch (McGarigal and Cushman 2005; Cushman et al. 2007).

4.3.1 Clementsian Landscape Ecology

Landscape ecology has been variously described as the study of the structure, function and management of large heterogeneous land areas (Forman 1995) or, more generally, the study of spatial pattern and process (Turner 1989, 2005). Likewise, landscapes are typically described in terms of patches, corridors, and matrix (Forman 1995). These definitions explicitly frame the scope of landscape

ecology within a categorical patch-mosaic paradigm, and any reading of the published landscape ecology literature shows near uniformity in the adoption of this approach. In the patch-mosaic paradigm, each patch is implicitly treated like an individual of the super organism of each “patch type”, and it is assumed that by measuring the area and configuration of patch types we can represent the most important attributes of the landscape, including the distribution and abundance of plant and animal species.

However, if biological communities are multivariate gradients of species composition, with each species responding individually to particular combinations of limiting factors, is a categorical patch-based representation appropriate? Put another way, isn't representing biological communities as categorical patches in a mosaic a de facto ratification of a Clementsian model of community composition at the landscape level? Most ecological attributes are inherently continuous in their spatial variation (at least at some scales; Wiens 1989), even in human-dominated landscapes. Consider soil properties such as depth, texture and chemistry, and terrain properties such as elevation, slope and aspect. These physical environmental properties typically vary continuously over space despite discontinuities in above-ground land cover that might exist due to natural or anthropogenic disturbances. Even above-ground land cover defined on the basis of vegetation more often than not varies continuously along underlying environmental gradients, except where humans have substantially modified it (Austin and Smith 1989; Austin 1999).

These observations have led several authors to propose alternatives to the patch mosaic model of landscape structure for situations where spatial heterogeneity is continuous rather than discrete. McIntyre and Barret (1992) introduced the “variegation” model as an alternative to the “island biogeographic” model, in which habitat is viewed as a continuous gradient instead of discrete patches within a homogeneous matrix. Later, Manning et al. (2004) defined the “continua-umwelt” model as a refinement of the variegation model in which habitat gradients are species-specific and governed by ecological processes in a spatially continuous and potentially complex way. Fischer and Lindenmayer (2006) offered an additional refinement of the continua-umwelt model by suggesting that the landscape be defined on the basis of four specific habitat gradients (food, shelter, space and climate) that are closely related to ecological processes that affect the distribution of animals. Importantly, these alternative conceptual models are all habitat-centric; that is, they propose a gradient model of “habitat”; they do not provide a general purpose model of landscape structure.

McGarigal and Cushman (2005) introduced a general conceptual model of landscape structure based on continuous rather than discrete spatial heterogeneity; they referred to this as the “landscape gradient” model. In this model, the underlying heterogeneity is viewed as a three-dimensional surface and can represent any ecological attribute(s) of interest. The most common example of a landscape gradient model is a digital elevation surface, but there are many other possibilities. Of course McGarigal and Cushman (2005) were not the first to recognize the need to characterize three-dimensional surfaces for ecological purposes. Geomorphologists, for example, have long sought ways to characterize land surfaces for the purpose

of understanding the relationships between landforms and geomorphological processes (e.g., Strahler 1952; Schumm 1956; and Melton 1957), and biologists as early as 1983 have sought ways to assess topographic roughness for the purpose of characterizing fish and wildlife habitat (e.g., Beasom 1983; Sanson et al. 1995). To this end, many methods have been developed to quantify surface complexity (e.g., Pike 2000; Wilson and Gallant 2000; Jenness 2004). However, until recently these methods have focused almost exclusively on characterizing topographic surfaces at the scale of the individual pixel or cell (e.g., Moore et al. 1991; Jenness 2005), or as the basis for mitigating the source of error associated with the planimetric projection of slopes in the calculation of patch metrics (e.g., Dorner et al. 2002; Hoechstetter et al. 2008). Only recently has attention been given to the application of surface metrics for the purpose of quantifying surface heterogeneity at the scale of entire landscapes (McGarigal and Cushman 2005; Hoechstetter et al. 2008; McGarigal et al. in press).

Largely unknown to landscape ecologists, researchers involved microscopy and molecular physics have made large advances in the area of three-dimensional surface analysis, creating the field of surface metrology (Stout et al. 1994, Barbato et al. 1995; Villarrubia 1997; Ramasawmy et al. 2000). Over the past two decades structural and molecular physicists have been developing surface metrics which we believe will be highly applicable to landscape gradients (e.g., Gadelmawla et al. 2002). Until recently, however, there have been no landscape ecological applications of these surface metrics. Recently, McGarigal et al. (in press) described the use of surface metrics for quantifying landscape patterns. Specifically, they (1) clarify the relationship between the patch mosaic and gradient models of landscape structure and the metrics used to characterize landscapes under each model; (2) describe a variety of surface metrics with the potential for quantifying the structure of landscape gradients; (3) evaluate the behavior of a large suite of surface; and (4) discuss the challenges to the application of surface pattern metrics in landscape ecological investigations.

4.4 Conclusion

The analysis of landscape pattern to infer process is the underlying tenant in the field of landscape ecology (Forman and Godron 1986; Forman 1995; Turner et al. 2001). One's ability to effectively explain ecological processes therefore depends on correctly representing ecological patterns. Landscape ecology traditionally adopts a patch mosaic model of ecological patterns, implicitly assuming discretely bounded and categorically defined patches are sufficient to explain pattern-process relationships (McGarigal and Cushman 2005). However, most ecological attributes are inherently continuous and classification of species composition into vegetation communities and discrete patches provides an overly simplistic view of the landscape and limits our ability to explore the continuous nature of plant distributions (Cushman et al. in press, McGarigal et al. in press; Evans and Cushman in press).

The fusion of individualistic community ecology with the Hutchinsonian niche concept enabled a broad integration of ecological theory, spanning all the way from the niche characteristics of individual species, to the composition, structure and dynamics of ecological communities. Landscape ecology has been variously described as the study of the structure, function and management of large heterogeneous land areas. Any reading of the published landscape ecology literature shows near uniformity in the adoption of a categorical patch-mosaic paradigm. However, if biological communities are multivariate gradients of species composition, with each species responding individually to particular combinations of limiting factors, is a categorical patch-based representation appropriate?

If one adopts a niche-based (Hutchinson 1957), individualistic concept (Gleason 1926; Whittaker 1967) of biotic communities then it would be more appropriate to represent ecological patterns as continuous measures rather than the traditional abstraction into categorical community types represented in a mosaic of discrete patches (McGarigal and Cushman 2005; Cushman et al. 2007, Cushman et al. in press). Although the problem of categorizations of the landscape failing to represent continuous ecological patterns has been identified (McIntyre and Barret 1992; Manning et al. 2004; McGarigal and Cushman 2005; Cushman et al. 2007), few approaches have been proposed to predict gradients in a modeling environment (McGarigal et al. in press; Evans and Cushman in press). The next chapter presents a detailed evaluation of this gradient concept of landscape structure and how it ties into the concepts related to spatial and temporal complexity and scaling presented in the previous three chapters. Specifically, we discuss how a range of ecological questions, including mapping vegetation composition and structure, modeling wildlife habitat relationships, predicting habitat connectivity and measuring the genetic structure of populations all may best be addressed using flexible, multivariate, multi-scale gradient approaches. By moving from a landscape ecological paradigm based on categorical patches to one based on quantitative species and environmental responses across continuous space it may be possible to both produce much more effective predictions of species distributions and ecological processes and remove much of the disjunction between landscape ecology and mainstream community ecology theory.

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