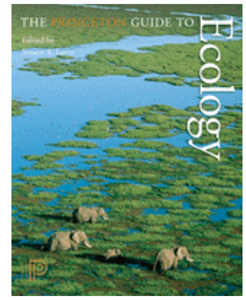
In: Simon Levin (ed.) 2009. ***Princeton Guide to Ecology***, Princeton University Press, pp.438-444.



Ecological Dynamics in Fragmented Landscapes

Jianguo Wu
Arizona State University, Tempe, AZ 85287, USA

ABSTRACT

Landscapes will likely become increasingly fragmented for biological organisms and ecological processes as the human population and its demands for resources continue to escalate. Landscape fragmentation results in habitat loss and alterations in the composition and spatial arrangement of landscape elements, consequently affecting population and ecosystem processes. Thus, to protect biodiversity and ecosystem functioning and to understand how nature works in the changing world, we must understand how organisms, populations, communities, and ecosystems interact with spatially heterogeneous landscapes in which they reside -- that is, ecological dynamics in fragmented landscapes. This paper discusses the effects of landscape fragmentation on population and ecosystem processes as well as major approaches to studying these effects.

Glossary

- Landscape connectivity: The ability of a landscape to facilitate the flows of organisms, energy, or material across the patch mosaic. Landscape connectivity is a function of both the structural connectedness of the landscape and the movement characteristics of the species or process under consideration.
- Landscape ecology: The science and art of studying and influencing the relationship between spatial pattern and ecological processes on multiple scales. Land use and land cover change and its ecological consequences are a key research topic in landscape ecology.
- Landscape fragmentation: The breaking-up of vegetation or other land cover types into smaller patches by anthropogenic activities, or the human introduction of barriers that impede flows of organisms, energy, and material across a landscape. Habitat fragmentation is a similar term to landscape fragmentation, but has a more explicit focus on changes in habitat of organisms.
- Landscape pattern: The composition (diversity and relative abundance) and configuration (shape and spatial arrangement) of landscape elements, consisting of both patchiness and gradients.
- Metapopulation: The total population system that is composed of multiple local populations geographically separated but functionally connected through dispersal.
- Patch dynamics: A perspective that ecological systems are mosaics of patches exhibiting non-equilibrium transient dynamics and together determining the system-level structure and function.

Spatial Heterogeneity and Landscape Fragmentation

To study ecological dynamics in fragmented landscapes, it is necessary to characterize the spatial pattern of landscapes and understand the causes and mechanisms of the pattern. As described in Chapter 2, landscapes are spatially heterogeneous geographic areas in which patches and gradients of different kinds, size and shape are interwoven. This spatial heterogeneity is ubiquitous in both terrestrial and aquatic systems on all scales in space and time. Several types of factors are responsible for the creation of landscape heterogeneity. First, the physical template of landscapes is usually heterogeneous in terms of geomorphologic features and distribution of energy and abiotic resources. Second, disturbances, be they natural (e.g., fires, droughts, floods, and windstorms) or anthropogenic (e.g., human-induced fires, urbanization, deforestation, and highway constructions), are frequently the primary cause for landscape heterogeneity. Third, biological processes (e.g., herbivory, species competition, deceases, and allelopathy) and fine-scale variability in topography and soil resources can also contribute to landscape heterogeneity. In general, abiotic conditions (e.g., climate, topography, and geomorphology) provide the context in which biological and anthropogenic processes often interact to generate landscape pattern. For example, the spatial pattern of temperature and precipitation determine the broad-scale distribution of biomes, within which the characteristics of ecosystem types are influenced by topographical features and meso-scale climatic variations. The structure and function of local ecosystems, however, are often affected significantly by biological processes.

Spatial heterogeneity gives rise to landscape pattern, of which patches -- relatively homogeneous areas that differ from their surroundings -- are the fundamental units. Patches can be characterized by their size, shape, content, duration, structural complexity, and boundary characteristics. Landscape pattern is usually considered to have two components: composition (the diversity and relative abundance of different kinds of patches) and configuration (the shape and spatial arrangement of patches). (See Chapter 2 for more detail on this). Spatial heterogeneity is an important source for the biological diversity, ecosystem services and scenic wonders of the natural world. In other words, the world is naturally and wonderfully patchy. However, landscape fragmentation -- the process of breaking up contiguous landscapes or their elements by human activities -- has profoundly transformed the spatial pattern of most if not all natural landscapes around the world, and has become one of the greatest threats to biodiversity and ecosystem functioning. As landscapes are fragmented, extant vegetation is removed and new land-cover types are created. This process simultaneously results in both decrease in the total amount of habitat (habitat loss) and increase in the degree of isolation for remnant habitat patches (habitat fragmentation per se or habitat isolation). Also, during landscape fragmentation the number of patches usually increases whereas the average size of patches tends to decrease.

Quantifying landscape pattern is necessary for comparing and contrasting patterns between different landscapes, monitoring and projecting changes of a given landscape, and understanding how ecological processes are affected by, and affect, landscape pattern. Many quantitative methods have been developed to quantify landscape pattern in the field of landscape ecology. Two general types of methods can be used to quantify landscape pattern: landscape metrics and spatial statistics. Landscape metrics (Li and Wu 2007) usually are synoptic indices designed to describe the typological, geometric, and distributional characteristics of landscapes at the levels of individual patches, patch type (or class), and the entire landscape. The underlying causes for landscape heterogeneity are spatial dependence and spatial autocorrelation (things that are closer are more similar), which are the fundamental assumptions for spatial statistical methods. As opposed to traditional statistics, spatial statistics quantifies how variables of interest are distributed and related to each other in space (Fortin and Dale 2005). There have been numerous studies that use both approaches to characterize landscape patterns and relate them to population and ecosystem processes.

Population and Species Dynamics in Fragmented Landscapes

Most of the studies on ecological dynamics in fragmented landscapes have focused on the effects of landscape fragmentation on populations and species. This section discusses major findings of the effects of landscape fragmentation on population processes and species persistence and examines several main theories and approaches in this research area.

Effects of landscape fragmentation on population dynamics and species persistence

In reality landscape fragmentation simultaneously leads to habitat loss and habitat isolation. These changes can certainly affect the demographic and genetic processes of populations. A great number of theoretical and empirical studies have been carried out to understand how habitat fragmentation affects population dynamics and species persistence in the past several decades. This section provides an overview of the major findings up to date.

Findings of the effects of landscape fragmentation on population dynamics and species persistence have been, more often than not, incongruent because of several reasons. First, the term "landscape (or habitat) fragmentation" is often used to denote both habitat loss and habitat-habitat isolation (i.e., habitat fragmentation per se), and consequently the effects of the two factors are confounded in the results of such studies. Second, various measures that reflect different aspects of landscape pattern at different scales have been used to quantify habitat fragmentation. Some measures focus on habitat loss, others are indicative of changes in habitat configuration, and still others are mixtures of both. Also, habitat fragmentation is measured either at the scale of individuals patches (as in most metapopulation models) or the scale of the entire landscape (as in most landscape ecological studies). Third, different theories and models have different assumptions about what is important in fragmented landscapes in terms of population dynamics and species persistence, and these differences in assumptions often translate into discrepancies in results. Nevertheless, studies in recent decades have produced several important findings.

The relative effects of habitat loss and habitat isolation have been one of the central topics. Increasing empirical evidence indicates that habitat loss usually has much stronger effects on population dynamics and species persistence than habitat isolation. In general, the effects of habitat isolation tend to be stronger when the total amount of habitat in the landscape is small and when the species under consideration have limited dispersal abilities. The effects of habitat loss are consistently negative whereas those of habitat isolation can be either negative or positive depending on the idiosyncrasies of the landscape pattern (e.g., the spatial configuration of habitat patches) and the species under consideration (e.g., abilities for local competition and regional dispersal). The negative effects of habitat loss are easier to understand because the removal of habitat usually results in reduction in the number of species, the abundance of populations, and the carrying capacity of the landscape.

The effects of fragmentation per se, however, are more complex because the outcome depends on how the species responds to the specific features of the fragmented habitat and altered interactions with other species in the landscape. The negative effects of habitat isolation may be caused by the disruption of dispersals, increased local extinction rates in small patches, and detrimental edge effects. The positive effects of habitat isolation may be attributable to relaxed interspecific competition, reduced predation, and disrupted spreading of disturbances. However, it is important to note that the effects of spatial patchiness occurring naturally are different from the effects of habitat fragmentation by human activities. In the latter situation, species usually do not have enough time to adapt to the newly changed environment, and thus positive fragmentation effects are less likely, especially, for non-edge species.

The size of habitat patches has significant effects on population dynamics and species persistence simply because large patches tend to have larger populations (thus with lower extinction probabilities) and more species (due to both pure area effect and higher habitat diversity). In general, patch size has strong positive effects on interior species that require sufficiently large and relatively stable habitat. As patch size increases, the relative area of edge habitat decreases, resulting in negative effects of patch size on edge species. For generalist species that do not distinguish between edge and interior habitat, the effects of patch size usually are insignificant. The effects of patch size on population dynamics and species persistence may also vary with species that have different behavioral characteristics. For example, some studies have suggested that more mobile or dispersive species would be less strongly affected by landscape fragmentation. However, recent studies show that the opposite may be true when more mobile species suffer severe dispersal mortality in the landscape matrix (Fahrig 2003, 2007). Other patch characteristics such as shape, orientation, and boundary conditions can also affect population processes. Their effects seem less significant than those of patch size, and usually are even harder to generalize across different species and habitat types.

Landscape connectivity, which is conversely related to habitat isolation, plays a crucial role in maintaining population abundance and species persistence by affecting the movement of organisms and propagules, dispersal mortality, and gene flows. Studies from landscape ecology based on percolation theory have suggested that, as habitat area decreases to some critical value, landscape connectivity drops abruptly, indicating a possible extinction threshold for species with limited dispersal ability or high dispersal mortality (With 2004). This finding corroborates the hypothesis that the effects of habitat isolation on population and species dynamics tend to be more important with decreasing habitat amount in the landscape. Thus, landscape connectivity exhibits threshold behavior and is species- or process-specific. Corridors, as a means of increasing habitat connectivity, can promote species persistence (by enhancing recolonization) and genetic integrity (by preventing genetic drift and bottleneck effects). However, corridors may also increase the spread of diseases and other disturbance agents across the landscape.

Theories and approaches

Theory of island biogeography. The theory of island biogeography (MacArthur and Wilson 1967) has had pervasive influences on the development of theoretical and empirical approaches to the study of ecological dynamics in fragmented landscapes. The theory asserts that the number of species on an island is determined primarily by two processes: immigration and extinction. Immigration rate decreases with distance from the continental pool of species because of variable dispersal abilities of species (distance effect), whereas extinction rate decreases with island area because of larger populations often found on larger islands (area effect). When immigration and extinction rates are equal, species diversity of the island has reached a dynamic equilibrium state. Thus, the theory relates the dynamics of species diversity directly to the size and isolation of islands. It has inspired much of the research concerning ecological dynamics in patchy environments and, in the many terrestrial applications, "islands" include individual plants, vegetation fragments, reserves or parks, and local ecosystems of all kinds.

However, both the validity of the equilibrium theory itself and its applications in terrestrial landscapes are unwarranted although its heuristic value is still widely recognized. The theory is a typical example of the classic equilibrium paradigm which has a number of problems when it is carefully scrutinized against reality. Given that landscapes are ever-changing, most of which are being increasingly fragmented, the equilibrium assumption behind the theory is hard to justify. Also, it does not consider several factors that are important to ecological dynamics in patchy environments, including habitat heterogeneity, disturbances, edge effects, multiple sources of colonizing species, and complex influences on the patch of concern from the surrounding landscape matrix.

Metapopulation theory. The concept of metapopulation, a population of subpopulations that go extinct locally and recolonize regionally, resembles the theory of island biogeography in that both consider extinction and colonization as the two key processes. However, the former is concerned with population dynamics and species persistence while the latter focuses primarily on species diversity and turnover. Also, sources for species colonization in most metapopulations are neighboring habitat patches that themselves are subject to local extinctions.

The classic (or Levins) metapopulation models are commonly known as "patch-occupancy" models in which the proportion of habitat patches occupied by a species is modeled as a function of local extinction and inter-patch colonization (Fahrig 2007). These models assume that there are an infinite number of identical habitat patches in the landscape, and that within-patch population dynamics and the landscape matrix are not important to metapopulation dynamics. The classic metapopulation models are not really spatial models. More spatially sophisticated metapopulation modeling approaches have been developed in the past several decades. For example, many population models based on diffusion-reaction equations, which consider both local population processes and patch attributes (e.g., size, relative distance to other patches), are relevant to the study of metapopulation dynamics. However, these are quasi-spatial models which can not explicitly consider the locations and geospatial relations of habitat patches and the heterogeneity of the landscape matrix. The prevailing metapopulation modeling approach now is the so-called spatially realistic metapopulation models that incorporate the effects of habitat patch size and isolation on extinction and colonization rates into the classic metapopulation models. While these models are spatially realistic, like the classic models they are concerned only with two states of habitat patches: presence and absence of a species under study, not with population processes within habitat patches. Also, the heterogeneity of the landscape matrix is usually ignored in spatially realistic metapopulation models.

Metapopulation theory has been increasingly used in conservation biology in the past three decades, replacing the prominent role of island biogeography theory. However, its use for the practice of biodiversity conservation is limited by its species-specific focus and inadequate consideration of the heterogeneity of landscape matrix and socioeconomic processes. In reality, populations neither live in habitat patches that can always be neatly delineated nor reside in a homogeneous landscape matrix. Rather, they are situated in heterogeneous and dynamically complex landscapes that are shaped by a myriad of physical, biological, and socioeconomic processes. Thus, the metapopulation approach is useful, but certainly not adequate for achieving the overall goal of conserving all levels of biodiversity.

Population viability analysis. The question of how many individuals of a species are enough to ensure the long-term persistence of the species is important both theoretically and practically. The concept of "minimum viable populations" (MVP), the smallest size of a population that can persist for a sufficiently long time with a high probability in face of demographic, environmental, and genetic stochasticities as well as natural disasters, attracted much research attention in the 1980s and the early 1990s. The MVP concept implies that there exists a threshold population size for species persistence. The process of estimating MVP or the extinction risk of species of interest has been known as "population viability analysis" (PVA) (Reed et al. 2002), and a number of conceptual procedures and computer software packages for PVA have been developed in the past few decades. Most PVA models consider multiple populations of a species in a fragmented landscape, and the general structure of PVA models is similar to that of metapopulation models. However, some recent PVA models have incorporated the effects of landscape heterogeneity on dispersal and colonization processes.

Because MVP connects the size of a population directly with its probability of extinction, its utility to species conservation is seemingly obvious. The use of MVP and PVA in conservation practices is limited by its focus on single specie, demands for detailed information on the species under study, and the reductionist nature of the methodology. For many species, deriving a reliable value of MVP may not be possible simply because of data scarcity and uncertainties, and in other situations such a species-specific approach may not work simply because it is too time-consuming or costly. In addition, it is hard to imagine the MVP or extinction risk of a given species will remain constant when the landscape in which it resides keeps changing due largely to socioeconomic drivers. Nevertheless, PVA remains a useful tool for assessing the effectiveness of alternative conservation or management plans for protecting rare and endangered species.

Landscape approach to population and species dynamics. With the rapid development of landscape ecology, a more comprehensive approach has emerged to understand population dynamics and species persistence in fragmented landscapes. In contrast with metapopulations, "landscape populations" emphasize not only the dynamics of, and interactions between, local populations, but also the effects of the heterogeneity of the landscape matrix. Landscape population models are truly spatially explicit, meaning that the size, shape, and spatial arrangement of all habitat and non-habitat elements are represented. In metapopulation models, habitat fragmentation is usually represented in terms of patch-scale features (e.g., various measures based on the nearest neighboring patches), which is unable to capture the landscape-scale characteristics of fragmentation. In landscape population models, fragmentation is measured at the scale of the entire landscape, and thus its effects on population processes are assessed more adequately. Also, the landscape population approach allows for explicit examination of how idiosyncratic features of habitat patches and the landscape matrix affect the dispersal of organisms or propagules. In addition, this spatially explicit approach facilitates mechanistic understanding of source-sink dynamics in which large or high quality patches serve as sources of immigrants to small or poor-quality patches whose population growth rates are negative (sinks).

The theory of island biogeography, metapopulation theory, and most PVA models all focus on the "islands" in a homogeneous matrix, be they oceanic or habitat islands. In contrast with this island perspective, the landscape population approach explicitly considers all landscape elements and their spatial configuration in relation to population dynamics across a heterogeneous geographic area. While landscape population models are more realistic in representation, they are structurally more complex and mathematically less tractable. They are usually implemented as computer simulation models, often linked with GIS (geographic information systems) which enable the storage, manipulation, and analysis of spatial data. In general, the metapopulation approach tends to be less detailed but more general, and thus more valuable for theoretical investigations, whereas the landscape population approach is better suited to meet the practical expectations in biodiversity conservation and ecosystem management. Thus, the major type of population models used in PVA has changed from island models to metapopulation models, and now is moving towards landscape population models.

Ecosystem Dynamics in Fragmented Landscapes

Landscape fragmentation not only affects population processes and biodiversity but also ecosystem processes such as energy flows and material cycling. These effects are caused by changes in both abiotic and biotic conditions induced by landscape fragmentation. Compared to the effects of habitat fragmentation on population and species dynamics, ecosystem effects have so far received much less attention. This section discusses the current understanding and research approaches in this area.

Effects of landscape fragmentation on ecosystem dynamics

Ecosystem ecology, the study of energy flow and material cycling within an ecosystem composed of the biotic community and its physical environment, traditionally has adopted a systems perspective, which emphasizes stocks, fluxes, and interactions among components without explicit consideration of spatial heterogeneity within the system and effects of the landscape context. With the rapid development of landscape ecology since the 1980s, more and more ecosystem studies have adopted a landscape approach that explicitly deals with within-system spatial heterogeneity and between-system exchanges of energy and matter.

An increasing number of recent studies have shown that landscape fragmentation can influence ecosystem dynamics in several ways. First, the loss and creation of patches directly change the spatial distribution of pools and fluxes of energy and materials in the landscape (e.g., biomass, ecosystem productivity, nutrient cycling, decomposition, evapotranspiration). Second, the altered configuration of landscape elements, particularly introduced edges and boundaries, may not only affect the flows of organisms but also the patterns of lateral movements of materials and energy within and among ecosystems (e.g., hydrological pathways and erosion-deposition patterns). Third, landscape fragmentation can affect ecosystem processes through microclimatic modifications due to altered surface energy balance (e.g., changes in albedo, radiation fluxes, soil temperature, soil moisture, wind profile and pattern) especially near the boundaries of remnant patches (edge effects). Fourth, all the effects of landscape fragmentation on population dynamics and species persistence have bearings on ecosystem processes because both plants and animals play an important role in ecosystem processes.

Landscape approach to ecosystem dynamics

A landscape approach to ecosystem dynamics is characterized by the explicit consideration of the effects of spatial heterogeneity, lateral flows, and scale on the pools and fluxes of energy and matter within an ecosystem and across a fragmented landscape (Turner and Cardille 2007). This new approach to ecosystem studies highlights the fact that ecosystems are neither homogeneous internally nor closed externally. Such a perspective seems in sharp contrast with the traditional equilibrium view that ecosystems are self-regulatory, self-repairing, and homeostatic, and is particularly appropriate when fragmented landscapes are considered. Guided by this spatial approach, several key research questions have emerged: How do the pools of energy and matter and the rates of biogeochemical processes vary in space? What factors control the spatial variability of these pools and processes? How do land use change and its legacy affect ecosystem processes? How do patch edges, boundary characteristics, within-system spatial heterogeneity, and the landscape matrix influence ecosystem dynamics and stability? How do ecosystem processes change with scale and how can they be related across scales (i.e., scaling)? How do the responses of populations and ecosystem processes to landscape fragmentation interact? How do the composition and configuration of fragmented landscapes affect the sustainability of landscapes in terms of their capacity to provide long-term ecosystem services?

A landscape approach to ecosystem dynamics promotes the use of remote sensing and GIS in dealing with spatial heterogeneity and scaling in addition to more traditional methods of measuring pools and fluxes commonly used in ecosystem ecology. It also integrates the pattern-based horizontal methods of landscape ecology with the process-based vertical methods of ecosystem ecology, and promotes the coupling between the organism-centered population perspective and the flux-centered ecosystem perspective.

Hierarchical Patch Dynamics

Understanding ecological dynamics in fragmented landscapes requires a paradigm shift away from the traditional notion of "balance of nature", which implies that ecosystems maintain a permanence of structure and function with a harmonious order if left alone. The idea of the balance of nature has profoundly influenced both the theory and practice of ecology for the past several decades. The imprints of the balance of nature are obvious in the supraorganismic concept of plant communities, the biocybernetic concept of ecosystems, and a number of similar concepts such as equilibrium, steady-state, stability, and homeostasis. Such ideas have penetrated pervasively into the guiding principles and practice of biodiversity conservation and environmental protection. However, the equilibrium paradigm is of limited use in understanding real landscapes that are heterogeneous in both space and time. Thus, since the 1980s main-stream ecological perspectives have shifted their focus from equilibrium, homogeneity, determinism, and single-scale phenomena to nonequilibrium, heterogeneity, stochasticity, and multi-scale linkages of ecological systems. The theories and approaches discussed in previous sections are examples.

This new ecological perspective has been known as "patch dynamics", and more recently "hierarchical patch dynamics" (HPD) as the result of the integration between hierarchy theory and patch dynamics (Wu and Loucks 1995, Wu and David 2002). While the specific meaning of a patch varies across scales and biological systems, patch dynamics has been increasingly used as a unifying concept in both marine and terrestrial systems. The major tenets of HPDP include: (1) ecological systems are spatially nested patch hierarchies, in which larger patches are made of smaller patches, (2) the dynamics of an ecological system can be studied as the composite dynamics of individual patches and their interactions at adjacent hierarchical levels, (3) pattern and process are scale dependent, and interactive when operating in the same domain of scale in space and time, (4) nonequilibrium and stochastic processes are not only common, but also essential for the structure and functioning of ecological systems, and (5) ecological stability frequently takes the form of metastability that is achieved through structural and functional redundancy and incorporation in space and time (Wu and Loucks 1995).

These tenets can be illustrated by the structure and dynamics of metapopulations: metapopulations are hierarchies of patch populations; metapopulation dynamics result from the local population dynamics and between-patch interactions; metapopulation processes take place on patch and landscape scales, and interact with the spatial pattern of habitat patches; local populations are subject to frequent extinctions, exhibiting nonequilibrium dynamics; and metapopulations tend to be more stable than local populations as a result of recolonization and asynchronous dynamics of individual patches across the landscape. Ecosystem processes such as primary productivity and nutrient cycling can also be perceived in similar ways. Because patches represent basic spatial units in which both population and ecosystem processes occur, the hierarchical patch dynamics paradigm provides a unifying framework for integrating population and ecosystem perspectives in fragmented landscapes.

References and Further Reading

DeFries, R., G. Asner, and R. Houghton, editors. 2004. Ecosystems and Land Use Change. American Geophysical Union, Washington, DC.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology and Systematics 34:487-515.

Fahrig, L. 2007. Landscape heterogeneity and metapopulation dynamics. Pages 78-91 in J. Wu and R. Hobbs, editors. Key Topics in Landscape Ecology. Cambridge University Press, Cambridge, UK.

Fortin, M.-J. and M. R. T. Dale. 2005. Spatial Analysis: A Guide for Ecologists. Cambridge University Press.

Hanski, I. and O. E. Gaggiotti, editors. 2004. Ecology, Genetics, and Evolution of Metapopulations. Elsevier Academic Press, Amsterdam.

Levin, S. A., T. M. Powell, and J. H. Steele. 1993. Patch Dynamics. Springer-Verlag, Berlin.

Li, H. and J. Wu. 2007. Landscape pattern analysis: Key issues and challenges. Pages 39-61 *in* J. Wu and R. Hobbs, editors. Key Topics in Landscape Ecology. Cambridge University Press, Cambridge, UK.

Lovett, G. M., C. G. Jones, M. G. Turner, and K. C. Weathers, editors. 2005. Ecosystem Function in Heterogeneous Landscapes. Springer, New York.

MacArthur, R. H. and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

Reed, J. M., L. S. Mills, J. B. Dunning, E. S. Menges, K. S. McKelvey, R. Frye, S. R. Beissinger, M.-C. Anstett, and P. Miller. 2002. Emerging issues in population viability analysis. Conservation Biology **16:**7-19.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5:18-32.

Turner, M. G. and J. A. Cardille. 2007. Spatial heterogeneity and ecosystem processes. Pages 62-77 *in* J. Wu and R. Hobbs, editors. Key Topics in Landscape Ecology. Cambridge University Press, Cambridge, UK.

With, K. 2004. Metapopulation dynamics: Perspectives from landscape ecology. Pages 23-44 in Hanski, I. and O. E. Gaggiotti, editors. 2004. Ecology, Genetics, and Evolution of Metapopulations. Elsevier Academic Press, Amsterdam.

Wu, J. and J. L. David. 2002. A spatially explicit hierarchical approach to modeling complex ecological systems: Theory and applications. Ecological Modelling **153**:7-26.

Wu, J. and O. L. Loucks. 1995. From balance-of-nature to hierarchical patch dynamics: A paradigm shift in ecology. Quarterly Review of Biology **70**:439-466.