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# Ecosystem Function in Heterogeneous Landscapes



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## 6 Population Ecology in Spatially Heterogeneous Environments

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### Abstract

Historically, population ecologists have equated environmental spatial heterogeneity with habitat spatial structure. Early models represented habitat spatial structure simply as population subdivision into habitat patches. Later models included at first partially and then fully explicit representation of the spatial relationships among habitat patches. More recently, landscape population ecologists have broadened the view of spatial heterogeneity to include the composition and configuration of the whole landscape. A change in landscape composition refers to a change in the cover types in the landscape, the proportions of each, or both. A change in landscape configuration refers to a change in the spatial pattern of cover types, independent of any change in landscape composition. We hypothesize that changes in landscape composition generally have much larger effects on population persistence than changes in landscape configuration. Landscape configuration should have a large effect on population persistence when both (i) configuration has a large effect on among-patch movement of the organism and (ii) among-patch movement has a large effect on population persistence. The first condition should hold for species whose movement direction is constrained, and the second condition should hold either (i) when colonization of empty habitat is important for persistence or (ii) for species that require more than one type of habitat. We discuss extensions of these ideas to the effects of landscape configuration on ecosystem processes.

### Introduction

The potential effects of environmental spatial heterogeneity on population dynamics and interactions have been of concern to population ecologists for decades. In this chapter, we review the ways in which spatial heterogeneity of the environment has been incorporated in models of population dynamics and interactions. We then discuss the current view of spatial heterogeneity

in landscape population ecology, and we review the evidence for effects of *compositional heterogeneity* and *configurational heterogeneity* on population ecology. Finally, we present a hypothesis that predicts the circumstances in which a change in landscape configuration should have a large effect on population ecology, and we discuss possible extensions of the hypothesis to effects of landscape configuration on ecosystem processes.

## History of Environmental Spatial Heterogeneity in Population Ecology

The ways in which population ecologists incorporate environmental heterogeneity into population models have changed markedly over time. In this section, we review the implicit and explicit representation of environmental spatial heterogeneity in models of population dynamics and population interactions. Our review is limited to models in which the underlying environment is spatially heterogeneous in some way. We do not include the many spatially explicit population models in which the underlying environment is assumed to be homogeneous, such as reaction-diffusion models of population spread in a homogeneous environment (e.g., Lewis 1997), cellular automata models of disease spread in a homogeneous environment (e.g., Holmes 1997), or models exploring the generation of population spatial pattern in a homogeneous environment (e.g., Pacala and Levin 1997). Note that this review is not exhaustive; we have selected representative examples for each method of incorporating environmental spatial heterogeneity into models. In each case, we focus on the earliest examples that we know of, even though all the views of spatial heterogeneity persist simultaneously in the current literature.

### Population Subdivision

The first theories of population ecology assumed spatial homogeneity of the environment (e.g., Verhulst 1838; Lotka 1925; Volterra 1926; Nicholson and Bailey 1935). However, with Gause's classic experiments in 1934, population biologists began to understand that population theories based on spatial homogeneity are likely to fail in the real world. Gause showed that a predator-prey relationship was "inherently self-annihilative"; it could persist only when a portion of the prey population was protected by a "privileged sanctuary," or when reintroductions of prey occurred at intervals. This implied that persistence of natural populations depends on environmental patchiness or spatial heterogeneity. Laboratory experiments by Huffaker (1958) and Pimentel (1963) supported this conclusion.

Theoretical examination of the influence of environmental spatial heterogeneity on populations began with models that represented spatial heterogeneity as habitat subdivision, resulting in separation of the population

into a number of subpopulations inhabiting habitat patches (e.g., Levins 1969, 1970; Reddingius and den Boer 1970; Hassell and May 1973; Roff 1974a,b; Vandermeer 1973; Levin 1974; Slatkin 1974; Hastings 1977; den Boer 1981; Shmida and Ellner 1984; Chesson 1985). *Metapopulation* or *patch occupancy* models predicted the proportion of patches that were occupied, based on rates of local extinction and colonization (Figure 6.1). Local population dynamics were not included in these models; the patches were either occupied or not occupied. The rate of colonization of empty patches was assumed to be independent of the spatial location of the patch (i.e., the models were not spatially explicit). In patchy population models, the population was divided into a number of subpopulations within which population dynamics and interactions occurred. Dispersal between subpopulations

### Representation of Spatial Heterogeneity in Population Models

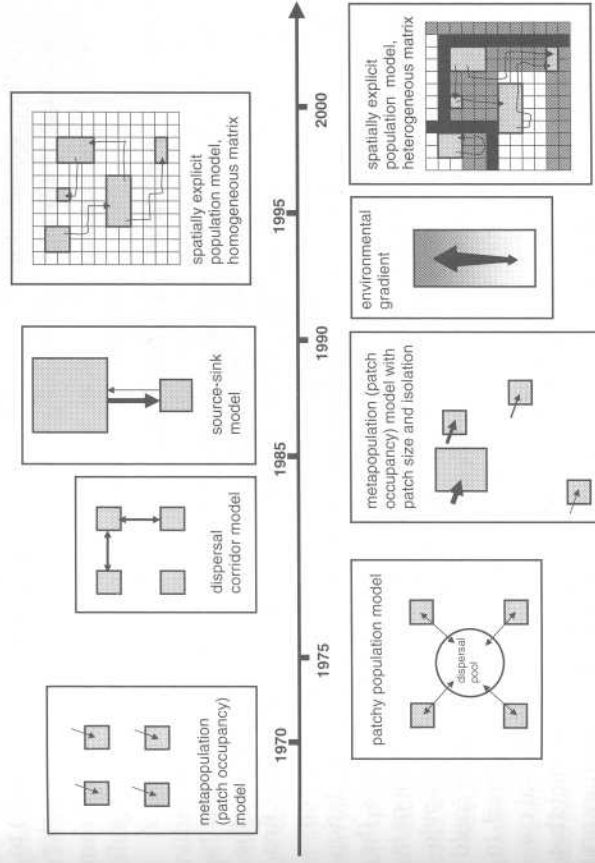


FIGURE 6.1. Representation of the progression of spatial heterogeneity in population models over four decades of ecological research. Time period for each model type represents the period over which it was established. Research using all model types continues to the present. Light gray rectangles represent habitat patches. In the metapopulation, or patch occupancy models, arrows represent colonization of patches; arrows only enter patches, to indicate that these models do not include emigration from patches. In the source-sink model, the patch sizes represent relative patch quality. In the spatially explicit model, the arrows represent movement paths of individuals. In the spatially explicit model with heterogeneous matrix, white, dark gray, and black areas represent matrix cover types; the black cover type represents a movement barrier (e.g., roads).

was "global," meaning that all patches were equally accessible to dispersers. Conceptually, this can be thought of as a *dispersal pool* into which a proportion of each subpopulation entered, and from which the dispersers were then redistributed among the subpopulations; again, these models were not spatially explicit (Figure 6.1).

This early theory suggested that under specific conditions, habitat subdivision could stabilize single-species population dynamics and species interactions. When local disturbances are asynchronous, population subdivision was predicted to stabilize single species dynamics by reducing the probability of simultaneous extinction of the whole population. Environmental patchiness was predicted to enhance the persistence of a predator-prey system if the prey species dispersed more readily than the predator species. Patchiness was also predicted to enhance two-species coexistence if there was a trade-off between dispersal rate and competitive ability. This trade-off, along with asynchronous disturbances that locally removed the superior competitor, would allow the inferior competitor (but superior disperser) to colonize the empty patches first, before being later displaced by the superior competitor.

### *Spatially Explicit Habitat Pattern*

Although the early theory did examine the effect of spatial heterogeneity *per se* (habitat subdivision or patchiness), it was not spatially explicit; the spatial relationships among subpopulations were not modeled. The first approaches to including such spatial relationships in a heterogeneous environment were intermediate between patch occupancy or patchy population models and fully spatially explicit models. In dispersal corridor models, the population was again assumed to be composed of several subpopulations in patches. However, dispersal was only possible between a pair of subpopulations if they were spatially connected (Figure 6.1). Spatial connection could represent patches that were close enough to each other for dispersal to occur or patches that were connected by a dispersal route or dispersal corridor. Lefkovich and Fahrig (1985) used this type of model to predict that population persistence depends on the number of patches and how they are interconnected. The source-sink model (Pulliam 1988) was a version of the dispersal corridor model for a population divided into two linked subpopulations in patches of unequal quality. Dispersal between the subpopulations was asymmetric, with a higher dispersal rate from the high-quality patch to the low-quality patch (Figure 6.1). Source-sink models were conceptually the end-points of one-dimensional models in which habitat quality was represented as a continuous environmental gradient that influences dispersal rate (Thomas and Kunin 1999). Such models predicted that the interaction between organism movement and an environmental gradient can alter predator-prey dynamics (McLaughlin and Roughgarden 1991; Benson et al. 1993; Pascual and Caswell 1997).

Models in which immigration or colonization depended on patch size and isolation (e.g., Fahrig and Paloheimo 1988; Hanski 1991, 1994) also represented an intermediate approach between non-spatially-explicit patchy or metapopulation models and the truly spatially explicit models discussed below. They generally predicted that population persistence increases with increasing patch size and decreasing patch isolation. Particular patches (large, nonisolated ones) were predicted to be important for metapopulation persistence and persistence of systems of interacting species (e.g., Moilanen and Hanski 1995). Hanski (2001) labeled this type of model *spatially realistic*.

Although metapopulation models and patchy population models have continued to be used and developed in population ecology, fully spatially explicit population models, called *grid* or *lattice* models, have been used in population ecology since about the late 1980s (e.g., Nachman 1987; Fahrig 1991; Perry and Gonzalez-Andujar 1993; Dytham 1995; Wilson et al. 1998; Bonsall and Hassell 2000; Schiegg et al. 2002). These models represent the landscape as a spatial grid, in which each grid *cell* is either habitat or nonhabitat. Individuals or portions of the patch or cell populations move through the grid, according to movement parameters that determine movement distance and direction. Shugart (1998) labelled this type of model *interactive*.

A few grid models represent habitat quality as a continuous variable rather than the usual two-state variable (habitat or nonhabitat). For example, Colasanti and Grime (1993) assigned different resource levels to cells on a grid, arranged in a resource gradient. Engen et al. (2002) presented a model in which habitat quality varied continuously over the landscape and spatial heterogeneity was represented as spatial autocorrelation in local carrying capacities. Thomas and Kunin (1999) proposed representing habitat spatial heterogeneity in grid models by assigning a *neighborhood* value to each cell, which is a function of the distances to and qualities of all other cells on the grid.

Several studies have shown that the predictions of spatially explicit population models can be very different from the predictions of analogous non-spatially-explicit models (Adler and Nuernberger 1994; Bascombe and Solé 1994; Durrett and Levin 1994; Swihart et al. 2001; Buttel et al. 2002; Higgins and Cain 2002). For example, Swihart et al. (2001) compared predator-prey interactions in a patchy population model with global dispersal versus a spatially explicit model. They found large differences between the models in the predicted equilibrium levels of the predator and prey populations. The spatially explicit model predicted much higher abundances of the predator, and much lower sensitivity of the predator to habitat removal than did the non-spatially-explicit model. Higgins and Cain (2002) compared two-species competition in a metapopulation model and a spatially explicit model. They found that coexistence in the metapopulation model depended on a trade-off between competitive and dispersal abilities, whereas this trade-off was not necessary for coexistence to occur in the spatially explicit model.

What do spatially explicit population models predict regarding the effect of habitat spatial heterogeneity on population persistence? Spatial heterogeneity is typically highest at intermediate levels of habitat amount. Heterogeneity increases with increasing fragmentation of habitat, where fragmentation is defined as the breaking apart of habitat, independent of habitat loss (Figure 6.2). Spatially explicit population models predict that population persistence increases with increasing amount of habitat on the landscape and decreases with increasing fragmentation of the habitat (Henein et al. 1998; Hill and Caswell 1999; With and King 1999; Fahrig 2001; Flather and Bevers 2002). These models therefore predict that (i) a reduction in habitat from a high to a moderate amount (A/B to C/D in Figure 6.2) should produce a negative effect of increasing heterogeneity on population persistence, (ii) an increase in habitat from a low to a moderate amount (E/F to C/D in Figure 6.2) should produce a positive effect of increasing heterogeneity on population persistence, and (iii) a shift from low to high fragmentation (A/C/E to B/D/F in Figure 6.2) should produce a negative effect of increasing heterogeneity on population persistence.

Empirical studies confirm the predicted positive effect of habitat amount but do not generally confirm the predicted negative effect of habitat fragmentation (breaking apart of habitat; reviewed in Fahrig 2003). We are aware of 13 empirical studies of the effects of habitat fragmentation (independent of habitat amount) on the abundance and/or distribution of individual species (McGarigal and McComb 1995; Collins and Barrett 1997; Wolff et al. 1997; Collinge and Forman 1998; Meyer et al. 1998; Rosenberg et al. 1999; Trzcinski et al. 1999; Drolet et al. 1999; Flather et al. 1999; Villard et al. 1999; Caley et al. 2001; Langlois et al. 2001; Hovel and Lipcius 2001; reviewed in Fahrig 2003). In general, these studies indicate that habitat loss has a much larger effect than habitat fragmentation on population abundance and/or distribution. Of the species that were found to be affected by fragmentation, 9 showed declines and 17 showed increases in abundance or distribution with increasing fragmentation. Note that the observed positive effects of fragmentation cannot simply be explained as responses by "weedy," habitat generalist species. For example, McGarigal and McComb (1995) studied abundances of bird species that nest only in mature forest, in response to forest amount and fragmentation. They found that of the seven species that responded to fragmentation, six responded positively. Therefore, the direction of the relationship between habitat heterogeneity and population persistence is not consistently positive or negative. Possible explanations for both positive and negative effects of fragmentation are reviewed in Fahrig (2003).

For predator-prey or host-parasite interactions, increasing habitat heterogeneity by reducing habitat amount and/or increasing habitat fragmentation can result in outbreaks or persistently higher levels of the prey/host (Kareiva 1987; Roland 1993). It is hypothesized that habitat loss and fragmentation disrupt the ability of the predator or parasite to

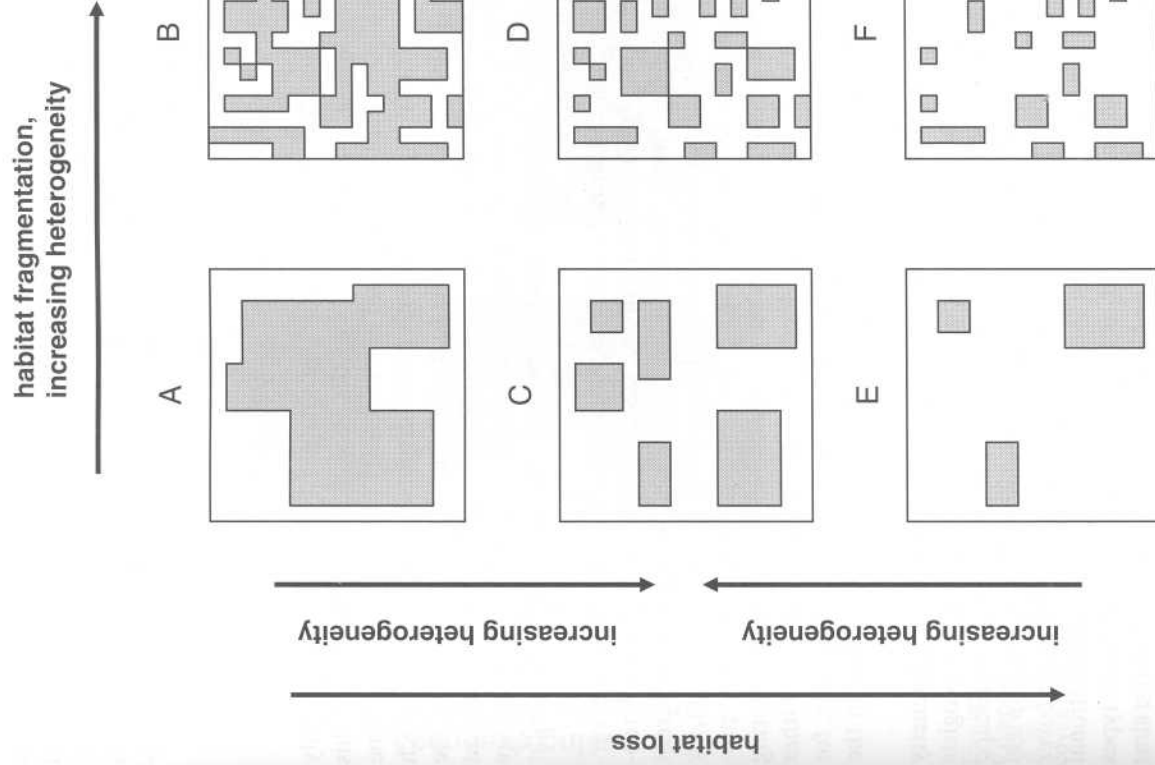


FIGURE 6.2. Effects of habitat fragmentation and habitat loss on habitat heterogeneity. Habitat heterogeneity increases from high to moderate habitat amount (from A to C, or B to D), and from low to moderate habitat amount (from E to C, or F to D), and increases with increasing habitat fragmentation (from A to B, or C to D, or E to F).

find and control the prey/host populations in time to avoid outbreaks. With et al. (2002) demonstrated the plausibility of this mechanism in an experimental study of the effects of habitat loss and fragmentation on patterns of aggregation of an insect predator-prey system. Some researchers have modeled effects of spatial heterogeneity of habitat on

predator-prey interactions using reaction-diffusion equations, where diffusion occurs along an environmental gradient (McLaughlin and Roughgarden 1991; Benson et al. 1993; Pascual and Caswell 1997). These models predict that the environmental gradient interacts with organism movement to determine predator-prey dynamics, which can include outbreaks and chaos.

### Landscape Composition and Configuration

Most of the literature discussed so far deals implicitly or explicitly with only one kind of habitat, the habitat used by the species in question. Within this framework, consideration of spatial heterogeneity has increased over time from homogeneity to patchiness with global dispersal, to variation in patch sizes and connectedness, and finally to explicit spatial representation of the habitat on the landscape (Figures 6.1 and 6.2). The vast majority of current studies of the effect of environmental spatial pattern on population ecology still describe the landscape in terms of habitat and nonhabitat (nonhabitat is also called *matrix*).

In real landscapes, the matrix is not homogeneous but is composed of various cover types (final panel in Figure 6.1). Some of the cover types will represent habitat for the species in question. These may include different habitat cover types representing habitats that vary in quality resulting in, for example, different reproductive rates. Different cover types may also provide different types of resources that are needed at different times during the organism's life history (e.g., feeding habitat, mating habitat). Other cover types represent nonhabitat, which, again, may differ in quality, for example, in the probability of mortality of the organism while it is in the cover type.

What effect does taking account of this additional spatial heterogeneity have on our understanding of population ecology? Landscape ecologists describe landscape structure in terms of two main components: landscape composition and landscape configuration (Dunning et al. 1992; McGarigal and McComb 1995). Landscape composition refers to the different cover types present in the landscape and the proportions of each. Compositional landscape heterogeneity increases as the number of different cover types increases (Figure 6.3, from A to B or C to D), and if they occur in more similar proportions (Figure 6.3, from A to C or B to D). Compositional heterogeneity can be measured using, for example, the Shannon-Wiener diversity index applied to the number and proportions of cover types in the landscape (e.g., Jonsen and Fahrig 1997).

A change in landscape configuration refers to a change in the spatial pattern of cover types independent of any change in landscape composition (Figure 6.4). Configurational landscape heterogeneity increases with increasing interspersal of the different cover types, accompanied by increasing edge density in the landscape (Figure 6.4, from A to B or from C

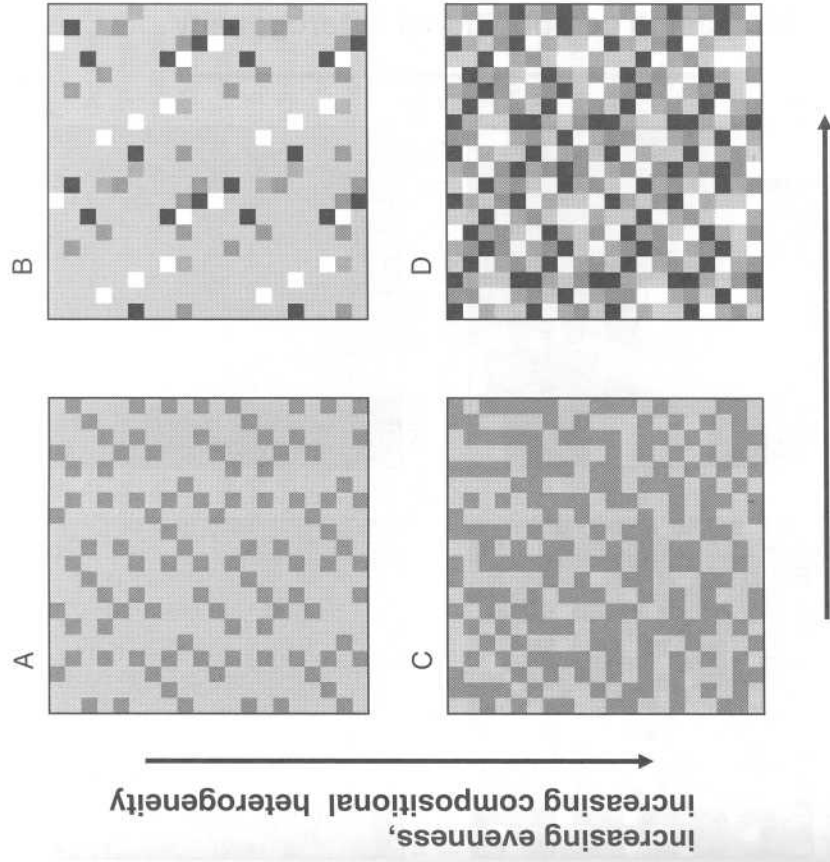


FIGURE 6.3. Illustration of the two components of compositional heterogeneity. Compositional heterogeneity increases with increasing number of cover types (from A to B, or C to D) and with increasing degree of evenness of representation of the cover types (from A to C, or B to D).

to D). Configurational heterogeneity can be measured using, for example, indices of edge density, shape complexity, edge contrast, and landscape subdivision (McGarigal 2002). Note that it is possible for landscape configuration to change without a change in landscape composition (Figure 6.4). Similarly, a change in the cover types while maintaining patch locations represents a change in landscape composition, with no change in landscape configuration. However, landscape composition and configuration are not completely independent; in particular, it is not possible to change the proportions of the different cover types (a change in composition) without changing landscape configuration.

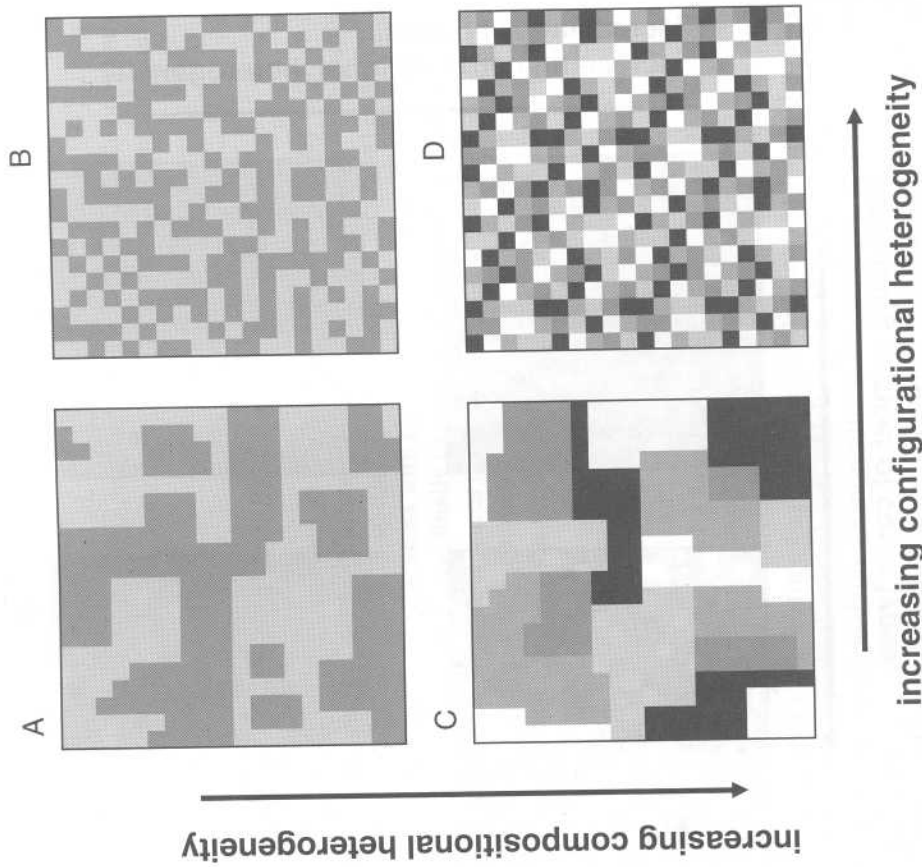


FIGURE 6.4. Illustration of configurational heterogeneity in comparison to compositional heterogeneity. (A) and (B) have the same compositional heterogeneity (50% of each of two cover types), but (B) has higher configurational heterogeneity than (A) because there is more interdigitation of the cover types. Similarly, (C) and (D) have the same compositional heterogeneity (20% of each of five cover types), but (D) has higher configurational heterogeneity than (C).

### Effects of Compositional and Configurational Heterogeneity on Population Ecology

There has to date been very little study of the effects of landscape heterogeneity on population ecology, so the following arguments represent mainly inference and conjecture. If the species relies on one kind of habitat only, then, as discussed above, an increase in compositional heterogeneity can imply a reduction in the amount of preferred habitat, which will cause a

reduction in population persistence probability. For example, in Figure 6.3, landscape D contains less dark gray habitat than does landscape C, and D is more heterogeneous than C. If dark gray represents wetland and the species of interest relies solely on wetland habitat, this increase in heterogeneity will result in a reduction in the persistence probability of the population.

However, if the species relies on more than one kind of habitat, an increase in compositional heterogeneity may permit the species to persist in a landscape in which it otherwise would not. For example, Figure 6.3C contains no white habitat. If the species requires both dark gray and white habitats for persistence, it will not occur in landscape C but may occur in landscape D. This represents a positive effect of compositional heterogeneity on population persistence. The cooccurrence of two or more required habitat types within a landscape was labeled *landscape complementation* by Dunning et al. (1992). The importance of landscape complementation was demonstrated by Pope et al. (2000), who showed that leopard frog populations were more likely to occur in landscapes containing both large numbers of breeding ponds and accessible terrestrial habitat for foraging during the summer. Similarly, Thies and Tschamtko (2002) found that heterogeneous landscapes were more likely to harbor populations of parasites of an agricultural pest species than were homogeneous landscapes, presumably because the heterogeneous landscapes provided habitats containing resources for the parasites in addition to those offered by the habitats containing the pests.

Species that require landscape complementation may also be positively affected by increasing configurational heterogeneity. For the same landscape composition, a more heterogeneous landscape will have more interdigitation of different habitat types (Figure 6.4: from A to B, and from C to D). This should increase landscape complementation (Law and Dickman 1998; Tschamtko et al. 2002).

### Relative Effects of Landscape Composition and Configuration on Population Persistence: A Hypothesis

The only empirical studies of which we are aware that have examined the relative effects of landscape composition and landscape configuration are the studies discussed above (and reviewed in Fahrig 2003) on the effects of habitat fragmentation (a component of landscape configuration) and habitat loss (a component of landscape composition). These studies indicate that effects of fragmentation are generally much weaker than the effects of habitat loss. Does this conclusion hold for landscape composition and configuration in general? Are there situations in which the effect of landscape configuration is expected to be large? In this section, we propose a hypothesis for the conditions under which configuration should have a large effect on population persistence.

Before presenting the hypothesis, we emphasize that landscape spatial structure must be described from the point of view of the particular species of interest. For example, if a species of bird is susceptible to nest predation and nest predators occur preferentially in forest edges, then a configurational change to the forest that results in more forest edge (e.g., forest fragmentation) will have a negative effect on the bird species. However, because forest edges are of lower quality for the species than is the interior of forested areas, forest fragmentation also represents a compositional change to the landscape (i.e., a decrease in amount of high-quality habitat and an increase in amount of low-quality habitat). Therefore, to avoid potential ambiguity between composition and configuration effects, for this species it would be important to map forest edge as a separate cover type of lower quality. Conversely, if a species prefers habitat edges or shows higher growth rates in edges (e.g., Bowers and Dooley 1999), then edges should be mapped as a separate cover type of higher quality. The question can then be asked: Is there an effect of a change in landscape configuration (i.e., fragmentation) over and above the effect of changing landscape composition (i.e., increase in the amount of edge cover type)? As another example, for some species, very small patches of forest are of very low quality (Burke and Nol 2000), and patches smaller than some minimum patch size will not be occupied at all (Huhta et al. 1998). Such small patches should not be mapped as breeding habitat. In all of the discussion below, we are assuming that the landscape maps represent the landscape cover types correctly from the perspective of the particular species of interest.

Landscape composition has large, direct effects on population dynamics and persistence through its direct effects on reproduction and mortality. Landscape configuration, on the other hand, generally affects population dynamics indirectly through its effect on among-patch movement. To see this, imagine a species that does not move at all. Assume we begin with 100 individuals in each of landscapes A and B in Figure 6.4, equally divided between the light gray and dark gray areas (50 individuals in each). The overall reproductive rate and mortality rate will be exactly the same in the two landscapes, even though their configurations are very different. The only way that the difference in landscape configuration can affect population dynamics is if it affects among-patch movement and if among-patch movement affects population dynamics.

The effect of configuration on population persistence could also occur indirectly through its effect on among-patch movement of any mass, energy, or information that can influence the population in question. For example, if landscape configuration affects movement of a predator species, and predation by that species has a large effect on a prey species, this could produce an indirect effect of landscape configuration on the prey population dynamics. In this case, even though configuration is not affecting the movement of the prey, it affects the prey through its effect on the movement of the predator. Similarly, a population of denitrifying bacteria may indirectly be

affected by landscape configuration if landscape configuration affects among-patch movement of nitrate. This leads to the interesting conclusion that landscape configuration could indirectly affect a population through its effect on an ecosystem process. In the section "Application to Ecosystem Processes" below, we present some examples of how landscape configuration might affect ecosystem processes. In the following, we present our hypothesis ignoring these indirect effects; we limit our consideration of movement to the movement of the organism in question.

We hypothesize that the effect of landscape configuration on population persistence is through its effect on (organism) movement, either facilitating or hindering habitat accessibility. Landscape configurations that facilitate habitat accessibility can indirectly increase the number of births and decrease the number of deaths in the population. This can occur through two processes, "landscape complementation" and "landscape supplementation" (Dunning et al. 1992). As discussed above, landscape complementation occurs when all required cover types are accessible to an organism that needs more than one landscape cover type to complete its life history. Landscape supplementation occurs when the organism can move among several resource patches of the same type to obtain sufficient resources for survival and reproduction. In either case, landscape configuration may facilitate or limit the ability of the organism to move about and obtain the resources required to avoid mortality and to reproduce successfully. For example, if roads represent a barrier to movement of the organism, then the particular placement of roads on a landscape may affect the ability of the organism to obtain crucial resources, which will affect the reproduction and/or mortality rate of the population, ultimately affecting its persistence.

Landscape configuration affects among-patch movement within the landscape when movement direction is highly constrained by the landscape. For example, some species are very reluctant to cross certain types of boundaries in the landscape (Tischendorf 2001). If the probability of crossing a boundary into a particular cover type (e.g., road surface) is low, this cover type represents a movement barrier in the landscape. If an organism is very reluctant to cross the boundary of its habitat into matrix, the configuration of habitat can have a large effect on population persistence. In this case, each habitat patch is isolated, so the persistence of the population in the landscape depends on the size of the largest piece of habitat (Figure 6.5). Movement within a stream network represents another example of highly constrained movement; Cumming (2002) showed that the form of the stream network can have a large effect on overall movement rate through the network.

Recent simulation studies suggest that strong effects of boundary type on boundary-crossing rates leads to a large effect of landscape configuration on among-patch movement rate through the landscape. Goodwin and Fahrig (2003) conducted simulations of animal movement on a grid containing habitat and two matrix cover types. They assumed that animal movement



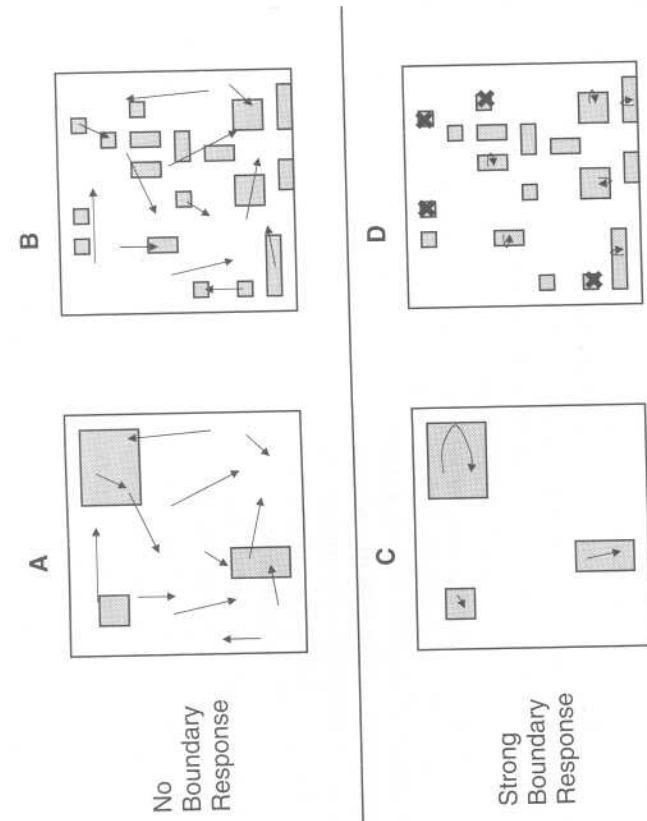


FIGURE 6.5. Comparison of the effect of landscape configuration on a species that does not respond to boundaries (top) versus a species that will not cross the habitat matrix boundary (bottom). Landscape configuration has no effect on persistence of the species with no boundary response (A vs. B). For the species with strong boundary response, population persistence will be higher in the less fragmented configuration (C) than the more fragmented configuration (D).

rates and directionalities differed between the matrix cover types but that the animal showed no boundary responses. In contrast, Bender (2002) conducted simulations of animal movement in which different matrix cover types elicited different boundary-crossing probabilities by the simulated organism. Goodwin and Fahrig found no effect of matrix configuration on among-patch movement rate, whereas Bender found a very large effect of matrix configuration on among-patch movement rate. This suggests that landscape configuration is likely to have a large effect on movement rate for organisms that show strong behavioral responses to boundaries in the landscape.

A second way in which constrained movement can create an effect of landscape configuration on population persistence is when movement has an overall direction within the landscape. For example, if larval fish can only move downstream, the relative position of larval habitats and spawning habitats within the stream system can have a large effect on population persistence. Stream systems with larval habitat downstream relative to spawning habitat are more likely to contain viable populations than stream

systems with larval habitat upstream of spawning habitat, even if they have the same amount of habitat (M. Power, personal communication).

It is important to note here that a large effect of landscape configuration on among-patch movement does not necessarily imply a large effect of landscape configuration on population persistence, relative to the effect of landscape composition, for several reasons. First, landscape composition also affects among-patch movement. Two empirical studies have examined the independent effects of landscape composition (habitat amount) and configuration (habitat fragmentation) on animal movement (Bélisle et al. 2001; With et al. 2002). Both found much larger effects of composition than configuration on movement. Second, population persistence at the landscape scale is ultimately determined by numbers of births and deaths, not movement within the landscape. Movement of an individual from one location to another within the landscape does not by itself affect overall population size. It can only affect population size indirectly if, by entering a new location, the individual changes its chance of reproducing or surviving. Landscape composition affects births and deaths directly, as well as indirectly through its effect on animal movement. Landscape configuration, on the other hand, only affects births and deaths indirectly through its effect on movement. Finally, some theoretical studies predict an interaction effect between composition and configuration, in which configuration affects population persistence only below certain threshold composition values (Fahrig 1998; Flather and Bevers 2002).

If landscape configuration affects population persistence through its effect on among-patch movement, then landscape configuration should have a large effect on population persistence when both (i) configuration has a large effect on among-patch movement and (ii) among-patch movement has a large effect on population persistence.

The hypothesis can be summarized as follows. (1) Landscape composition generally has a much larger effect than landscape configuration on population persistence, because composition directly affects births and deaths, whereas configuration only affects births and deaths indirectly through its effect on movement. (2) Landscape configuration has a large effect on among-patch movement for species whose movement direction is highly constrained. (3) Among-patch movement has a large effect on population persistence (i) when colonization of empty habitat is important for persistence or (ii) for species that require more than one type of habitat (landscape complementation). Note that condition (i) will occur when the probability of local extinction is high (e.g., high seasonal mortality) and following habitat restoration (Huxel and Hastings 1999). (4) Finally, landscape configuration has a large effect on population persistence when conditions under both (2) and (3) hold simultaneously. We emphasize that this is a general hypothesis; it is not limited to any particular sorts of species or landscapes, but it does depend on the assumption that the landscapes are correctly mapped from the point of view of the species of interest (see

above). Interestingly, this hypothesis is not consistent with metapopulation theory, which predicts large effects of landscape configuration on population persistence, even for randomly moving organisms (Hill and Caswell 1999); a possible explanation for this difference is discussed in Fahrig (2002).

Recall here that the effect of landscape configuration on a population can also occur indirectly through its effect on movement of an interacting species or other mass, energy, or information that affects the species of interest. Our hypothesis can therefore be extended to state that landscape configuration can have a large effect on a population when both (i) movement direction of the interacting species, other mass, energy, or information is highly constrained, and (ii) the interacting species, other mass, energy, or information has a large effect on population persistence.

At this point, our hypothesis is supported only through the verbal arguments above; to date it has not been directly tested. Empirical testing will require comparisons across species and across landscapes. For example, we may know from previous studies that small mammal populations undergo frequent local extinctions (Merriam and Wegner 1992), which implies that movement is important for small mammal population persistence. From our hypothesis, we could then predict that the abundance of a small mammal species that shows strong avoidance of roads (i.e., its movement is highly constrained by roads) should be affected by a change in landscape configuration, whereas the abundance of a small mammal species that shows no behavioral response to roads should not be affected by a change in landscape configuration. To test this prediction, we would need first to study small mammal movement responses to roads to identify species that avoid roads and species that do not respond to roads. We would then compare the abundances of these small mammal species across a set of landscapes that vary in configuration (e.g., degree of habitat fragmentation). It will be important to select the landscapes in such a way that we can control for the effects on small mammal abundance of both road density and the amount of small mammal habitat (e.g., forest) in the landscapes. In particular, it is important that neither of these landscape composition variables is correlated with landscape configuration across the set of landscapes chosen for the study. There are clearly several challenges inherent in this type of research; these are discussed in Brennan et al. (2002).

### *Application to Ecosystem Processes*

We suggest that our hypothesis can be extended to the effects of landscape composition and configuration on ecosystem processes. A few examples illustrate parallels among the movement and persistence of organisms on the landscape and the flux and transformation of energy and nutrients that control ecosystem processes. Here, too, the composition of the landscape exerts the most direct influence over the net ecosystem functions of the

entire landscape. Indeed, the trophic state of an ecosystem (i.e., oligotrophic, mesotrophic, or eutrophic) is often defined in terms of the type and biomass density of the primary producers (i.e., composition).

Landscape configuration may influence ecosystem function, depending on the distribution of areas of production and uptake relative to the pattern of movement of nutrients and energy, which may be affected by barriers that impede these fluxes. For example, consider the net processing of nutrients that move through an ecosystem in surface water and groundwater. Clearly, there will be a different effect on nutrient processing of wetlands taking up nutrients mobilized from farm fields, depending on whether the wetlands are located generally upstream or downstream of the farm fields. Where the conformation of the landscape generally acts to retard flow, nutrients are more subject to uptake and transformation by vegetation and microbial processes or to sequestration by sorption and sedimentation (Vollenweider 1975; Seitzinger 2000; Mitsch et al. 2001). Indeed, reengineering the landscape to promote these processes constitutes one of the principal tools used in environmental remediation and restoration (Mitsch et al. 2001; NRC 2002; Toth et al. 2002). Barriers to the movement of organisms can also affect ecosystem function. For example, fencing to exclude direct access by livestock to natural water bodies is an effective strategy for reducing the flux of nutrients into these surface water bodies and consequent effects on water quality and ecosystem processes downstream (NRC 2002; Mitsch et al. 2001). In the ocean, the seasonal development of strong, thermal stratification constrains phytoplankton from moving below the photic zone, and this triggers the increase in primary productivity observed as the spring plankton bloom (Sverdrup 1953). All these examples suggest that landscape configuration has its largest effect on ecosystem processes in situations where movement is constrained and/or directional.

The hypothesis may also apply to the propagation of disturbances across a landscape. For example, it appears that landscape configuration affects the spread of forest fire only when the fire is strongly limited by forest boundaries. In this situation, the total amount of forest burned is lower in landscapes where the forest is fragmented into small patches than in landscapes where the forest occurs in large tracts. Fires that start in small patches are unlikely to spread to the rest of the forest because there is low fuel availability between forest patches (Weir et al. 2000; Ricotta et al. 2001; Pitkänen et al. 2003). However, this boundary response can be reduced or eliminated in high winds, in very dry weather conditions, and in landscapes where there is a small difference in fuel load across the edge (Hargrove et al. 2000; Bessie and Johnson 1995; Moritz 2003). In these conditions, landscape configuration is unlikely to affect fire spread (Ricotta et al. 2001). Thus, landscape configuration only affects fire spread in situations where fire movement is constrained by forest boundaries (Figure 6.5, where the arrows now represent movement of fire rather than movement of organisms).

in both compositional and configurational heterogeneity. Landscape complementation will therefore be a central issue in developing a general understanding of the effects of spatial heterogeneity on population ecology.

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## Temporal Heterogeneity

In this paper, we have discussed the effects of spatial heterogeneity on population ecology. We do not mean to imply that temporal heterogeneity is unimportant. A small number of studies (all theoretical) have examined the combined effects of spatial heterogeneity and temporal heterogeneity on population persistence and population interactions. In general, these studies find that the rate and frequency of change of the landscape is extremely important. Fahrig (1992) and Bhar and Fahrig (1998) predicted that the rate of change of the landscape is much more important than habitat configuration in affecting population persistence. Keymer et al. (2000) predicted that the rate of landscape change has a large effect on the extinction threshold (i.e., the minimum amount of habitat required for population persistence). Finally, Bowers and Harris (1994) and Gourbiere and Gourbiere (2002) predicted that the outcome of interspecific competition depends strongly on the rate of environmental change.

## Conclusions

The incorporation of environmental spatial heterogeneity into population ecology has been a gradual process over a period of several decades. The concept itself has evolved from simple population subdivision, to effects of patch size and isolation, to spatially explicit representations of habitat, to spatially explicit representations of landscapes. At each level of heterogeneity, there are important predicted effects on population ecology. The overall picture is quite complicated, however, because although the way that population ecologists view environmental spatial heterogeneity has changed over time (Figure 6.1), all these views persist simultaneously in the current literature. In addition, the characteristics of the species studied (e.g., movement behavior) influence how the different aspects of spatial heterogeneity affect a population. Successful generalization will depend on cross-study comparisons, which, in turn, will depend on clear delineation of the important aspects of heterogeneity and species attributes. For example, it will be important to differentiate clearly between compositional heterogeneity and configurational heterogeneity, as these two aspects can have different predicted effects (Fahrig 2003).

Nevertheless, some tentative generalizations are possible. First, where increasing compositional heterogeneity reduces the amount of habitat available for a species, this will have a negative effect on population persistence. Second, information on organism movement behavior, in particular the responses of organisms to boundaries, will be important for predicting the likely effect of configurational heterogeneity on population ecology. Third, species that require landscape complementation can benefit from increases

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## 7 Heterogeneous Processes Modeling

CHRISTINA TAC

### Abstract

Heterogeneity of aspects of the hydrology. Observed heterogeneity is a hydrology. Observed from within-canopy spatial variation in precipitation strategies for addressing heterogeneity at scale and type of address heterogeneity of underlying heterogeneity and of heterogeneity in described, and applications modeling are discussed. bilistic approaches, address heterogeneity process heterogeneity based hydrologic modeling hydrologic and ecological

### Introduction

Analysis of heterogeneity to characterize and ultimately of its forms—solid, transported and stored heterogeneity depends both particular hydrologic processes include fluxes (e.g., evaporation, precipitation, runoff, infiltration, etc.)