

Metapopulation Dynamics and Landscape Ecology

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I. INTRODUCTION

The fusion of metapopulation studies and landscape ecology should make for an exciting scientific synthesis (Hanski and Gilpin, 1991)

The synthesis of metapopulation studies and landscape ecology anticipated by Hanski and Gilpin has barely yet begun. There are at least two reasons for this (Wiens, 1995a). First, as many of the chapters in this volume illustrate, metapopulation theory continues to be tied to a view of spatial patterning of environments in which patches are embedded in a featureless background matrix. Second, landscape ecology seems still to be in the process of defining what it is about and describing complex spatial patterns, but it has not developed much theory to deal with spatial patterning. By focusing on some shared areas of interest, perhaps the synthesis of these disciplines can be accelerated.

In this chapter, I consider the relationship between the emerging (but yet immature) discipline of landscape ecology and the emerged (but perhaps adolescent) discipline of metapopulation dynamics. I will argue that considerations of metapopulation structure may often be incomplete unless they are framed in the context of the underlying landscape mosaic.

II. APPROACHES TO PATCHINESS

Ecologists have always known that nature is patchy and heterogeneous, even if much of their theory has not treated it so. Habitats in areas used by humans occur as sharply defined blocks or fragments, and the patchwork nature of the landscape mosaic is especially evident in such environments. Even in more natural settings, however, habitats are heterogeneous at virtually any scale of resolution. Although patch boundaries in such situations may sometimes be indistinct gradients rather than sharp discontinuities (Wiens, 1992b), the spatially variable character of environments still remains. In this chapter I will follow the convention that has become widespread in ecology of considering such variation under the rubric of “patchiness,” even though “patches” are not always evident in nature.

Dealing with such spatial heterogeneity has been a major challenge in both empirical and theoretical ecology. Faced with the daunting complexity of spatial patterns in the real world, field ecologists historically tended to focus on patterns and dynamics of ecological systems within relatively homogeneous habitat types (e.g., watersheds, woodlots) or aggregated spatial variation into dimensionless indices of heterogeneity or dispersion. More recently, it has become fashionable to map spatial patterns at broad scales using geographic information systems and spatial statistics, but the link between such technologies and ecologically important questions is not always apparent.

Spatial variance also strains the capacities of analytical models and theory if it is viewed explicitly (i.e., by location) rather than averaged as “noise.” As a consequence, many theoreticians concerned with heterogeneity have contented themselves with simple models in which spatial patterning is collapsed into patches and an ecologically neutral “matrix” (Kareiva, 1990b; Wiens, 1995a). Such patch–matrix theory is usually spatially implicit (Hanski, 1994c), in that the locations of patches in the matrix are not specified (Wiens, 1996a). The interesting dynamics occur in the patches, which are usually considered to be internally homogeneous; the matrix is viewed as inhibiting interactions among patches (e.g., migration, colonization, gene flow, prey discovery by predators).

Traditional metapopulation theory is an elaboration on this patch–matrix theme. Levins’ metapopulation model (1970; Hanski, this volume) considered the habitat of a population to be subdivided into an infinite number of similar patches occupying undefined locations in a background matrix. As metapopulation modeling has progressed, however, details about patch sizes, patch clumping, individual movement capacities, local patch dynamics, and explicit patch locations have been incorporated (Hanski, 1994a,c; see Hanski, this volume; Gyllenberg *et al.*, this volume).

Most patch theory deals with the dynamics of populations occupying a patchy environment (Wiens, 1976; Levin, 1976; Kareiva, 1990b; Shorrocks and Swingland, 1990). Another approach to heterogeneity has focused on the dynamics of the patches themselves. Although the spatial pattern of some patches, such as the islands considered in island biogeography theory, may be relatively static in ec-

ological time, the patch structure of most environments is not. Patches are destroyed and generated by disturbances at multiple scales. They undergo change through successional development. These “patch dynamics” (Pickett and White, 1985) produce changes in the spatial patterns and relationships of patches in a matrix. Attempts to model these dynamics have generally followed analytical approaches (patch demography; Levin and Paine, 1974; Hastings, 1991) or have simulated the spatial and temporal dynamics of patchy environments (e.g., Fahrig, 1990). Most of this work has followed the patch–matrix conceptualization of spatial patterns.

The recent emergence of landscape ecology as a discipline (Risser *et al.*, 1984; Forman and Godron, 1986; Merriam, 1988; Turner, 1989; Wiens, 1992a; Wiens *et al.*, 1993; Hobbs, 1995) offers the prospect for going beyond a simple patch–matrix approach to adopt a more realistic, spatially textured view of heterogeneity. In landscape ecology, the “matrix” is itself spatially structured, and spatial relationships play an active role in determining the dynamics within the “patches” of interest. Patches are viewed as components in a landscape mosaic, and what happens within and among the patches in a landscape may be contingent on the composition and dynamics of other elements of the landscape mosaic (Wiens *et al.*, 1993; Andrén, 1994; Wiens, 1995a, 1996a).

III. WHAT IS LANDSCAPE ECOLOGY?

One of the first tasks of an emerging discipline is to define its topic and itself. “Landscape” has been defined as “a heterogeneous land area composed of a cluster of interacting ecosystems” (Forman and Godron, 1986), “a mosaic of heterogeneous land forms, vegetation types, and land uses” (Urban *et al.*, 1987), or “a spatially heterogeneous area” (Turner, 1989). Accordingly, “landscape ecology” is “a study of the structure, function, and change in a heterogeneous land area composed of interacting ecosystems” (Forman and Godron, 1986) or “the investigation of ecosystem structure and function at the landscape scale” (Pojar *et al.*, 1994). It emphasizes “broad spatial scales and the ecological effects of the spatial patterning of ecosystems” (Turner, 1989) and “offers a way to consider environmental heterogeneity or patchiness in spatially explicit terms” (Wiens *et al.*, 1993).

If these definitions are a bit nebulous, it may reflect the multifarious historical development of landscape ecology and continuing uncertainty or disagreement over what it is really about. Landscape ecology began in northern Europe during the 1960s as a merging of holistic ecology with human geography, with infusions from land-use planning, landscape architecture, sociology, and other disciplines (Turner, 1989; Wiens *et al.*, 1993) (Fig. 1, top). From the outset, the emphasis was practical and applied: the focus was on the interaction of humans with their environment at a broad (landscape) spatial scale. In the early 1980s, the discipline colonized North America (and other continents, most notably Australia). The

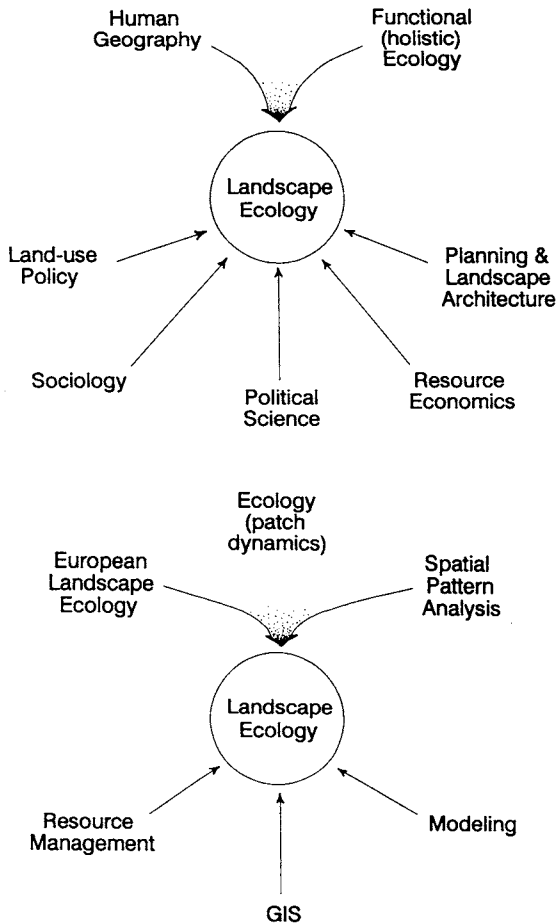


FIGURE 1 Contributors to the historical development of landscape ecology in Europe (top) and North America (bottom).

beachheads in North America were small and initially somewhat isolated. Perhaps through founder effects or mutations, the development of landscape ecology there followed a somewhat different trajectory (Fig. 1, bottom). The linkage with traditional ecology was much stronger than in Europe, and as a consequence the questions asked and approaches used differed considerably. There was a more self-conscious emphasis on concepts (Wiens, 1995a), a greater reliance on quantitative procedures (Turner and Gardner, 1991), and an application of the landscape perspective to a broad range of basic as well as applied problems.

These pathways of historical development have led to three rather different views of the primary focus of landscape ecology. Continuing in the European

tradition, one view portrays landscape ecology as “a new holistic, problem-solving approach to resource management” (Barrett and Bohlen, 1991). It is a synthetic, holistic, human ecology. The second view, which has become most prevalent among ecologists, treats “landscape” as a level of organization (e.g., O'Neill *et al.*, 1986; Gosz, 1993) or as a scale of investigation (i.e., tens to thousands of ha; Forman and Godron, 1986; Hansen *et al.*, 1993; Hobbs, 1994; Pojar *et al.*, 1994). In the latter case, the questions are often no different from those that ecologists have always asked; they are just asked at a much broader scale. The third view more explicitly emphasizes the structure and dynamics of landscape mosaics and their effects on ecological phenomena (Turner, 1989; Wiens *et al.*, 1993; Wiens, 1995a). Rather than restricting the focus to broad scales, the scale of investigation is dictated by the organisms studied and the questions asked (Wiens, 1989a; Haila, 1991; Pearson *et al.*, 1996). In this view, landscape ecology is more than just spatially explicit ecology, because the patterns and interactions of entire mosaics are the focus of investigations.

This diversity of views suggests that landscape ecology is “a science in search of itself” (Hobbs, 1994). In addition to being a young discipline, it is also intellectually immature, in that it lacks conceptual unity (cf. Loehle, 1987; Hagen, 1989). It has no well-defined theoretical framework (Turner, 1989; Wiens, 1995a) and tends to be more qualitative than quantitative (Wiens, 1992a). Despite all of this, several prevailing themes of landscape ecology have emerged:

- Elements in a landscape mosaic (patches) vary in quality in both space and time. In a landscape, patch quality is a continuous rather than a categorical (i.e., suitable vs unsuitable, or patch–matrix) variable. Patch quality can be viewed as a spatially dependent cost–benefit function (Wiens *et al.*, 1993; Wiens, 1996a).

- Patch edges or boundaries may play critical roles in controlling or filtering flows of organisms, nutrients, or materials over space (Wiens *et al.*, 1985; Holland *et al.*, 1991; Hansen and di Castri, 1992). What happens at boundaries may have important effects on both within-patch and between-patch dynamics.

- The degree of connectivity among elements in a landscape mosaic has major consequences on patch interactions and landscape dynamics (Lefkovich and Fahrig, 1985; Taylor *et al.*, 1993). How disturbances propagate over a landscape, for example, may be dictated by landscape connectivity as well as boundary effects (Turner *et al.*, 1989). Connectivity involves much more than corridors.

- Patch context matters. What happens within a patch is contingent on its location, relative to the structure of the surrounding mosaic. A patch of the same habitat may be of quite different quality, depending on the features of adjacent or nearby elements of the landscape (Wiens *et al.*, 1993). Contrary to island biogeography theory (or, implicitly, patch-matrix theory), no patch is an island (cf. Janzen, 1983). It is this contextual dependency that requires landscape ecology to be spatially explicit.

IV. HOW IS LANDSCAPE ECOLOGY RELEVANT TO METAPOPULATION DYNAMICS?

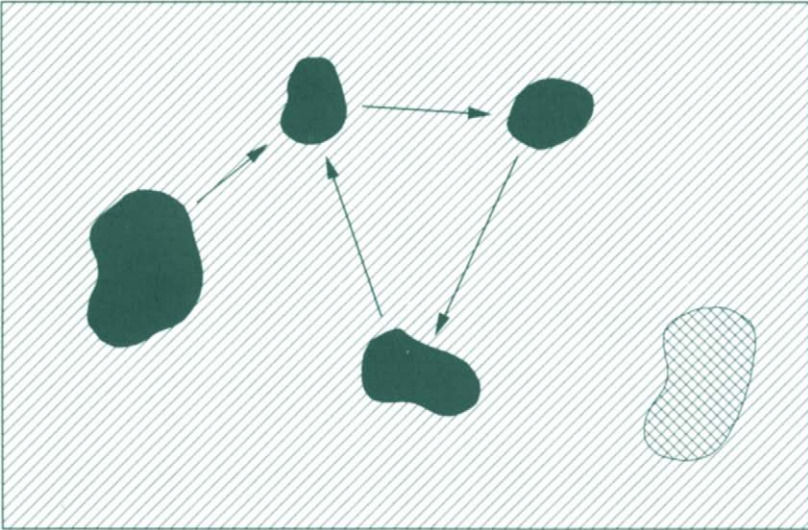
To see how these themes may relate to metapopulation dynamics, we must review briefly the essential features of metapopulation theory (see Hanski and Simberloff, this volume). "Metapopulations" have been defined in various ways, but generally a metapopulation is spatially subdivided into a series of local (patch) populations. The classical view emphasizes a balance between extinctions and recolonizations of local populations that facilitates long-term persistence of the metapopulation (Levins, 1970; Hanski and Thomas, 1994; Hanski, this volume). The dynamics of local populations are density-dependent within patches but asynchronous among patches, and migration (dispersal¹) among patches links them together. Interpatch movement is the key. If migration is large relative to interpatch distances (and other spatially uncorrelated sources of population variability are not important), the dynamics of local populations will be mixed together and they will act as a single large population. On the other hand, if movement among patches is infrequent it may not be adequate to ensure recolonization of habitat patches in which local populations have suffered extinction, dooming the entire metapopulation to global extinction.

The contrast between this classical view of metapopulations and a landscape-based view is perhaps most apparent graphically. In a traditional (theoretical) metapopulation, local populations occur in habitat patches in a featureless matrix (Fig. 2A). Not all patches are occupied at a given time, and local populations wink into and out of existence as extinction and recolonization occur. Patches may vary in size or shape, but the primary determinants of patch-colonization probability are movement rates and interpatch distances. Making a metapopulation model spatially explicit is therefore necessary, but not sufficient, to cast it in a landscape context. In reality, the local populations of a metapopulation occur in habitat patches that are immersed in a complex mosaic of other habitat patches, corridors, boundaries, and the like (Fig. 2B). The most obvious effects of this landscape structure are on individual movement patterns among patches and, consequently, on patch-recolonization probabilities. In a landscape mosaic, interpatch distances are not Euclidean (e.g., Fig. 2A), but are a complex function of boundary permeabilities and relative patch viscosities to moving organisms (e.g., Fig. 2B; Wiens *et al.*, 1993). Other aspects of metapopulation structure, such as the dynamics of the patches themselves (and, consequently, patch-extinction probabilities), may also be influenced by landscape structure.

Because very little empirical work that directly links landscape ecology to

¹ To be consistent with usage elsewhere in this volume, I use "migration" rather than "dispersal" to refer to one-way movements of individuals beyond their home ranges. Although "migration" is customarily used in this sense by geneticists and entomologists, to an ornithologist like myself the term has a specific meaning that is different from "dispersal." In examples dealing with birds, I will therefore use "dispersal" rather than "migration." Stenseth and Lidicker (1992b) discuss these terminological issues.

A



B

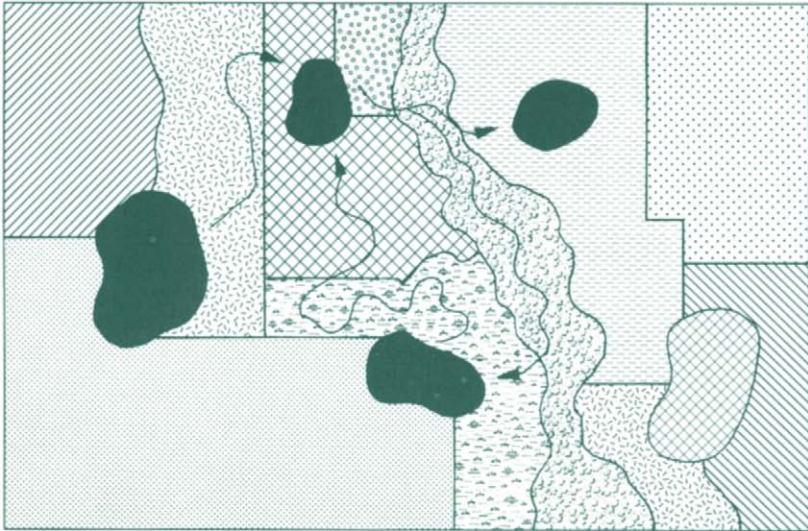


FIGURE 2 (A) Metapopulations in theory. The solid patches are occupied and are linked by intermittent migration, whereas the hatched patch is suitable habitat that is presently unoccupied. The background matrix has no effect on interpatch movements, although the distance between patches and their arrangement may. (B) Metapopulations in reality. The patches are the same, but the “matrix” is a landscape mosaic of various patches and corridors. Movement pathways among suitable patches, and the probability that migrating individuals will reach the patches, are affected by the explicit spatial configuration of the landscape.

metapopulation dynamics has been done, a discussion of how the major themes of landscape ecology—spatial and temporal variations in patch quality, boundary effects, landscape connectivity, and patch context—affect the three components of metapopulation dynamics (local extinction, interpatch movement, and recolonization) must necessarily be somewhat abstract and conceptual. It may be useful, therefore, to preface this discussion with a few examples of the effects of landscape structure in the real world. Additional examples are provided by Angelstam (1992), Fahrig and Freemark (1993), and Hobbs (1995).

A. Some Examples of Landscape Effects

Some of the effects of landscape structure are related to patch characteristics such as patch size or spacing. For example, the size of habitat patches has been related to the persistence of local populations of forest birds (Verboom *et al.*, 1991a; Villard *et al.*, 1992), and the degree of spacing of habitat patches has been shown to affect the likelihood of recolonization of vacant patches by the Glanville fritillary (*Melitaea cinxia*) in Finland (Hanski *et al.*, 1995a). Both patch size and spacing influenced the use by brown kiwis (*Apteryx australis*) of remnant forest fragments in an agricultural matrix in New Zealand (Potter, 1990). Kiwis are flightless, so they must walk between isolated remnants. All fragments less than 80 m from other forest remnants were used by the birds, regardless of their size. Movements of more than a kilometer from the reserve, however, were accomplished by using small fragments as “stepping stones.” In this situation, the spatial interspersal of habitat patches was a critical factor in determining the effects of patch isolation and, consequently, the potential for metapopulation dynamics.

Patch edges and their configuration may also be important. The emigration of Glanville fritillaries from patches of suitable habitat, for example, increases with the proportion of the patch boundary that is bordered by open fields (Kuussaari *et al.*, 1996). Gates and Gysel (1978) found that the abundance of passerine birds increased at the boundary between fields and forests, and they suggested that individuals might be drawn to the edge as nesting habitat because of greater food availability there. Numerous studies (e.g., Angelstam, 1992; Andrén, 1992, 1995), however, have documented that predation rates may be greater at such ecotones, presumably due to predators living in adjacent areas. For some species, edges may function as an “ecological trap” by attracting individuals to areas in which predation losses are great (Gates and Gysel, 1978). Predation risks at habitat edges vary as a function of the surroundings (Wilcove, 1985; Angelstam, 1992; Wiens, 1995b), so the landscape context of patches is also important. Pearson’s (1993) work on habitat occupancy by birds in the Georgia Piedmont also illustrates the effects of landscape context. There, the composition of the surrounding matrix explained as much as 74% of the variance in habitat occupancy by some species but was unimportant for other species. The demographic consequences of such edge- and context-related effects have received very little attention, but they may have important effects on metapopulation dynamics, es-

pecially where populations are subdivided among many small habitat patches and predation risk is significant.

The effects of corridors linking elements in a landscape mosaic have also been documented by field studies (although not to the degree that the widespread adoption of corridors as a management option would lead one to believe; Bennett, 1990, 1991; Hobbs, 1992). In Western Australia, for example, Carnaby's cockatoos (*Calyptorhynchus funereus*) use roadside vegetation as a pathway for foraging movements among woodland patches in their large home ranges (Saunders, 1990). Where woodland patches are not linked or are not visually apparent to the cockatoos, they are not used, even though food may be available there. On the other hand, singing honeyeaters (*Lichenostomus virescens*), which are habitat generalists, readily fly across farmland with little vegetation (Merriam and Saunders, 1993) and apparently make little use of corridors. Osborne (1984) found that hedgerow area was the best predictor of bird species richness in an area of Great Britain, and the presence of red squirrels (*Sciuris vulgaris*) in wooded fragments in The Netherlands was positively related to the amount of hedgerow surrounding the fragments (Verboom and van Apeldoorn, 1990). In Australia, the occupancy of corridors by arboreal marsupials could not be predicted by habitat features within the corridor but required additional information on the composition of the surrounding landscape (Lindenmayer and Nix, 1993).

B. Movement and Migration

Individual movement is the most important unifying element in both metapopulation dynamics and landscape ecology (Saunders *et al.*, 1991; Wiens, 1992b, 1995a; Wiens *et al.*, 1993; Ims, 1995). Moreover, how fast and how far organisms move imposes a scale on the environment: highly vagile animals integrate heterogeneity over broader scales than do sessile individuals and therefore perceive the environment with a coarser filter or "grain" (Wiens, 1985; Fahrig and Paloheimo, 1988; Kotliar and Wiens, 1990; De Roos *et al.*, 1991; With, 1994). At the outset of any field study or modeling exercise, then, the mean and shape of a species' migration function determine the scale(s) at which population responses to environmental patchiness must be investigated.

In the tradition of island biogeography theory, most metapopulation models use interpatch distance and migration rates as the major determinants of patch-colonization probabilities (e.g., Hanski, 1994a). The Fahrig and Paloheimo (1988) simulation studies of the effects of the spatial configuration of patches on population abundances in a metapopulation, for example, indicated that migration distance, rather than migration rates alone (or demographic features such as birth rate), was critically important, especially when interpatch distances were great. In contrast, when Liu *et al.*, (1995) modeled Bachman's sparrow (*Aimophila aestivalis*) population dynamics, they found that demographic parameters were more important than mortality during dispersal (although not necessarily dispersal

rate or distance). These differences may stem from differences in model structure, but they may also reflect basic differences in the life histories of the organisms modeled.

Traditional metapopulation models usually do not consider the details of movement in even an abstract sense. Movement is modeled as transition probabilities among cells in a grid (Liu *et al.*, 1995) or movement rates and distances are simply specified or are drawn from frequency distributions. Whether movement through the matrix between patches is directional (e.g., Fig. 2A) or follows a diffusion, correlated random walk, or some other algorithm (e.g., Okubo, 1980; Turchin, 1989; Johnson *et al.*, 1992a) is not considered, even though the differences among these movement patterns can produce substantial differences in the probability of encountering a patch in the matrix. This is especially true if migration rates are low or if the number of individuals available to migrate is quite limited (as may occur when local populations are small).

Movement patterns such as diffusion or random walks are handy modeling devices that may have some relevance to how real organisms move through a featureless matrix, but they are of limited value (other than as neutral models) in specifying how individuals might respond to a complex landscape mosaic (e.g., Fig. 2B). Conceptually, the movements of individuals through a landscape may be viewed as a consequence of their movements within individual patches and their movements between patches (Fig. 3A; Wiens *et al.*, 1993). Within-patch movement patterns vary among different patch types. The probability that an individual will encounter a patch boundary during a specified time interval is a function of these patch-specific movements and of patch size and shape (perimeter: area ratio). Whether or not an individual will cross a patch boundary upon encountering it is a function both of features of the boundary itself (boundary "permeability"; Stamps *et al.*, 1987; Wiens, 1992b) and of the characteristics of the adjoining patch (patch context). [This is where another behavior, patch or habitat choice, becomes important.] Both costs (e.g., predation risk, physiological stress) and benefits (e.g., shelter, food availability, mating opportunities) may differ among elements in a mosaic, and movement patterns within and between patches may reflect these relative costs and benefits (i.e., patch quality), at least in part (Wiens *et al.*, 1993; Wiens, 1996a). Some simulation models of metapopulation migration in patchy environments (e.g., Pulliam *et al.*, 1992; Adler and Nuernberger, 1994) vary migration costs as a function of distance or incorporate differences in patch quality.

To make such an individual-based conceptualization of mosaic movements relevant to metapopulation dynamics, it must be extended to the scale of population rather than individual patches (Fig. 3B). In simple terms, this is a matter of shifting the scale from that of movements and patches defined by individual home ranges to the broader-scale movements of populations (i.e., migration) and the scale of patchiness represented by interactions within a local population (i.e., nodes in a metapopulation). Exactly how the translation from individual movements to population distribution and interactions should be accomplished is one

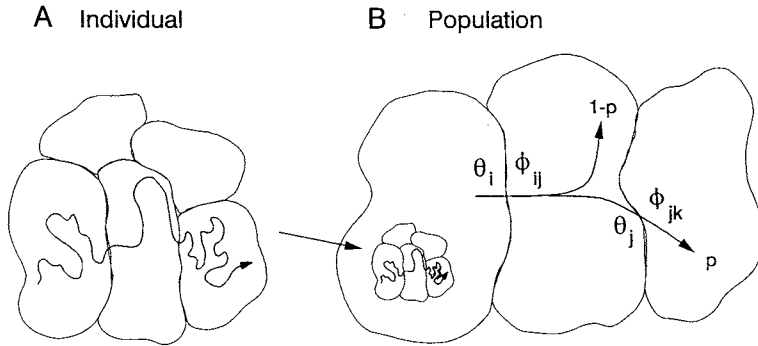


FIGURE 3 (A) Patterns of movement of an individual among elements of a landscape in its home range. The movement pathway consists of within-patch and between-patch components; both may be affected by the characteristics of patches and by their spatial configuration (patch context). (B) Extension of individual movements to the population level. A local population may occupy patch i , within which individuals move according to the local habitat heterogeneity within that patch. These movements (characterized by a function, θ_i) determine the probability that individuals will encounter the boundary between patch i and patch j during a given time interval. The probability that individuals encountering the boundary will cross into patch j , ϕ_{ij} , is a function of the permeability of the boundary and the behavior of the organisms (e.g., patch choice). Within patch j , a proportion of the dispersing individuals ($1-p$) may die or establish residency in the patch. Movements within patch j (θ_j) determine the probability that the boundary between patch j and another element in the landscape (patch k) will be encountered; ϕ_{jk} determines p , the proportion of dispersers from patch i that move into patch k . Values of θ and ϕ are patch-specific (as is patch density, which may have density-dependent effects on movement and migration). Developed from Wiens *et al.* (1993).

of the most vexing problems confronting a metapopulation-landscape synthesis. It is part of the more general problem of translating across scales in ecology (Wiens, 1989a; King, 1991; Rastetter *et al.*, 1992).

My colleagues and I have used systems of small animals (insects) moving through grassland "microlandscapes" as experimental model systems (Ims *et al.*, 1993; Ims, 1995) to investigate how movements are affected by mosaic structure, following the framework of the model of Wiens *et al.* (1993). Initial studies of tenebrionid beetles (*Eleodes* spp.) indicated that individuals moved differently in microlandscapes of a few square meters that differed in internal heterogeneity, as measured by the fractal dimension of the landscape pattern (Wiens and Milne, 1989). Movement alternated between matching the predictions of an ordinary diffusion model and those of anomalous diffusion depending on movement "rules," landscape pattern, and spatial and temporal scales (Johnson *et al.*, 1992a). In particular, diffusion exponents changed significantly at spatial scales corresponding to the size of vegetation patches (a radius of ≈ 42 cm), suggesting that the effects of spatial heterogeneity on beetle movements at finer scales differed fundamentally from those at broader scales. Other work (Crist *et al.*, 1992) demonstrated that variations in vegetation structure within 25 m² areas had significant

effects on beetle movements and that these effects differed among *Eleodes* species. The net displacement of individuals per unit time, for example, was greater in areas dominated by bare ground and by continuous low grass cover than in more heterogeneous areas that contained cacti or shrubs, and larger beetle species exhibited greater displacements in a given habitat type than did smaller beetles. The relative complexity (fractal dimension) of the movement pathways, however, was insensitive to variation among species or habitat types, at least at the 25 m² scale of resolution. On the other hand, broader comparisons among beetles, harvester ants, and grasshoppers in the same landscape mosaics revealed significant differences in fractal dimensions of pathways (Wiens *et al.*, 1995), indicating fundamental differences in the ways these taxa respond to landscape heterogeneity at this scale.

These studies were conducted at relatively fine, "within-patch" scales and recorded how individual animals responded to landscape patterns. To determine how such movements might translate into patterns of population distribution at broader spatial scales, With and Crist (1995) used a cell-based simulation model to project the dispersion patterns of populations of grasshoppers over a broader mosaic. Individuals moved within a cell of a given habitat type according to the empirically observed movement parameters for that habitat. Movement characteristics changed when individuals entered cells of a different habitat type, according to a specified transition probability (this corresponds to the between-patch component, ϕ , of Fig. 3B). The landscape mosaic was dominated (65% coverage) by a single habitat type. Under certain specifications of transition probabilities, a large species, *Xanthippus corallipes*, moved rapidly through this cover type. As a consequence, it had increased patch-residence time (and an aggregated distribution) in the remaining 35% of the landscape. A smaller species, *Psoloessa delicatula*, was much more sedentary and preferred a habitat comprising only 8% of the landscape. Given its low vagility, there was a low likelihood of individuals of this species locating and aggregating within cells of the relatively rare, preferred habitat. The model simulations suggested that the distribution of this species would not diverge from the random distribution used to initiate the simulations. In fact, in the field both species exhibited the general dispersion patterns predicted by the model.

How do these observations and model analyses of patch-specific movements relate to the four components of landscape ecology (patch quality, boundary effects, patch context, and connectivity)? The differences in within-patch movement patterns may indicate differences in patch quality, but the sensitivity of model predictions to the value of transition probabilities between patch types indicates that knowledge of within-patch movement patterns by itself is not adequate to predict broad-scale population distributions. Something else is needed. The most likely factors affecting the translation from individual, within-patch movements to population distribution over a landscape are patch boundary effects and the influences of patch context. If individual beetles react behaviorally to the patch

boundary itself, the likelihood of moving from one patch to another will be altered. If patch context is important, then the particular characteristics of what is beyond a given patch boundary will further modify transition probabilities.

Landscape controls over movement patterns have yet to receive detailed attention in either models or field studies. Moreover, all of these approaches consider the structure of the landscape mosaic to be fixed; patch dynamics in time would add another level of realism (and further computational complications) to the research program.

One aspect of landscape structure that is implicit in the spatial arrangement of mosaic elements and the transition probabilities among them is connectivity. Landscape connectivity refers to the degree to which the landscape facilitates or impedes movement among patches (Taylor *et al.*, 1993). Corridors of similar habitat linked together are thought to enhance connectivity (Bennett, 1990; Hobbs, 1992), but dissimilar habitat patches among which transition probabilities are high may also result in high connectivity. Through the patterns of connectivity that characterize a landscape, movement pathways are directed in spatially non-random manners (Fig. 2B), which can either increase or decrease the likelihood that movement among specific patches in the landscape (e.g., subpopulations in a metapopulation) will occur.

Connectivity is related to the coverage of a given habitat type in the landscape, but the relationship is strongly nonlinear. If a continuous habitat is broken into fragments by habitat conversion, the initial effects are due primarily to the loss of habitat coverage alone. As coverage drops below some threshold value, however, the effects of patch isolation begin to be more important. In landscapes with a low proportion of suitable habitat, further decreases in coverage result in a rapidly increasing distance between habitat patches and even greater isolation effects (Fig. 4). For example, Andr  n (1994) found that habitat loss was a good predictor of fragmentation effects on birds and mammals in landscapes with > 30% coverage of suitable habitats, but in more highly fragmented landscapes the effects of patch isolation and size also became important.

Such threshold effects also emerge in simulation studies based on percolation theory. In simple percolation models, a landscape mosaic is divided into suitable and unsuitable habitat patches (cells) that are distributed over the landscape at random, with a specified coverage or proportion, p , of the suitable patches (Gardner *et al.*, 1987, 1989). Above some critical threshold, p_{crit} , cells of the suitable habitat are likely to form a continuous cluster that spans the landscape. An organism in this "percolating cluster" will be able to move or "percolate" across the landscape; connectivity is high (O'Neill *et al.*, 1988). For a random landscape in which organisms move only to adjacent (but not diagonal) cells, p_{crit} has a value of 0.5928. If the landscape pattern is generated using a nonrandom algorithm (e.g., fractal curdling; Lavorel *et al.*, 1993; With *et al.*, in press), the value of p_{crit} is lower (0.29–0.50). Similar reductions in p_{crit} occur with changes in the movement patterns to allow individuals to move to any adjacent cell or to cross

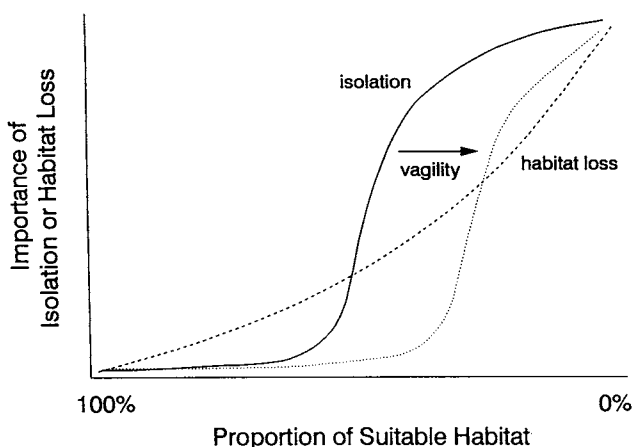


FIGURE 4 A hypothesized relationship between the proportion of suitable habitat in a landscape and the relative importance of habitat loss and patch isolation to individual movement or population dynamics. As the availability of suitable habitat decreases, the importance of habitat loss increases monotonically. The effects of patch isolation (the inverse of landscape connectivity) are relatively slight when coverage of suitable habitat is high, but increase sharply when a connectivity threshold is passed (p_{crit} in percolation theory parlance). Increases in individual vagility will move this threshold to lower coverage values of the suitable habitat.

gaps where suitable cells are not immediately adjacent (Dale *et al.*, 1994; Pearson *et al.*, 1996). Field experiments with *Eleodes* beetles moving through random landscapes (Wiens *et al.*, in press) indicated a threshold change in movement patterns when coverage of grass in a bare-ground matrix increased from 0 to 20%.

Changes in either the spatial pattern of the landscape or the scale over which individual organisms “perceive” landscape patterns (as judged by their movements) can therefore produce high connectivity in a mosaic even when the favored habitat type occupies a relatively small proportion of the landscape. Differences in vagility among organisms (e.g., the grasshoppers studied by With and Crist, 1995) may also affect the location of a percolation threshold (Fig. 4), as Fahrig and Paloheimo (1988) also suggested in a somewhat different context. Details of the spatial arrangement of habitat patches in the mosaic, such as those modeled by Lefkovich and Fahrig (1985) or Adler and Nuernberger (1994), are likely to become important only around or below this threshold.

Most models that link animal movements to landscape structure assume that movement parameters are fixed species traits and that migration can adequately be represented using average values. Individuals do vary in movement characteristics, of course, and the effects of this variation may be profound. For example, Lens and Dhondt (1994) found that crested tit (*Parus cristatus*) young dispersed 1 week later from small, isolated pine stands than did those in large pine forests.

Chicks from second broods were also more likely to disperse into less suitable habitat fragments than were young from first broods. Collectively, these movement characteristics reduced the probability that second-brood young would be integrated into winter flocks, which would affect their overwinter survival probabilities. In another vein, the simulation studies of Goldwasser *et al.* (1994) suggested that variability among individuals could markedly increase the rate of spread of a population, even if only a few individuals in the population migrated rapidly. The prospect that individual movement behavior may be facultatively adjusted to landscape patterns such as the interspersions or isolation of suitable habitat patches (Matthysen *et al.*, 1995; Fahrig and Merriam, 1994) may further complicate attempts to model migration dynamics in heterogeneous landscapes. Nonetheless, it is apparent that the complex interplay between fine-scale movement patterns, broad-scale migration dynamics, and the nonlinear effects of landscape-mosaic structure may have fundamentally important effects on the interpatch movements that lie at the heart of metapopulation dynamics.

C. Local Extinction and Recolonization

In addition to interpatch movement, the extinction of local populations in habitat patches and the subsequent recolonization of those patches are what drive metapopulation dynamics. Local population extinctions are often associated with the stochastic dynamics that characterize small populations. Deterministic local habitat changes, however, can produce patch dynamics in the landscape that also result in the extinction of local populations (Thomas, 1994c). If this is the case, the local patch environment may remain unsuitable for some time after extinction occurs. Under these conditions, the persistence of the metapopulation depends on how well the organisms can track the shifting spatial locations of suitable habitat patches. Because the location of suitable patches may be unpredictable in time as well as in space, how organisms move through the landscape mosaic and the scales on which they perceive environmental patchiness become all the more important.

The pattern of interspersions of suitable habitat patches through a landscape mosaic also influences extinction and colonization probabilities. The degree to which a patch is connected to other suitable areas or is isolated may have little direct effect on extinction, although it may influence the immigration flow and therefore determine the magnitude of the "rescue effect" (Brown and Kodric-Brown, 1977). Colonization, on the other hand, is clearly related to the interplay between individual migration abilities and *both* the distribution (i.e., isolation) and the connectivity of habitats in the landscape. If fragmentation alters the landscape so that the interspersions of habitat patches no longer coincides with the migration patterns of a species, metapopulation dynamics may be disrupted. To some degree, this situation characterizes the Glanville fritillary in Finland (Hanski *et al.*, 1995a).

D. When Is a Landscape Approach Necessary?

In all but a few situations, landscapes, rather than patches in a featureless matrix, are reality. Given this, one might conclude that any attempt to model or understand metapopulation dynamics that does not explicitly include landscape structure would be futile. The essence of theory, however, is simplification of reality. Good theory simplifies in a way that does not violate reality too much, while incorporating its essential features. In this sense, patch–matrix theory represents a significant improvement over theories based on spatial homogeneity (Wiens, 1995a). When can the details of landscape structure reasonably be ignored or simplified?

Green (1994) and Fahrig (Fahrig and Paloheimo, 1988, personal communication) have addressed this question using simulation models. Green considered the effects of habitat connectivity in relation to population and community persistence and concluded that in highly connected landscapes one could treat the entire landscape as a single element (in which case metapopulation theory is no longer very relevant). If the landscape is strongly disconnected, on the other hand, it may be possible to treat each element as a separate unit and ignore all but the most basic descriptors of patch structure (e.g., patch size and separation). Closer to the percolation threshold (Fig. 4), on the other hand, the explicit spatial arrangement of patches in the landscape and the details of individual movements and patch transition probabilities may become much more important. Fahrig's simulation analyses suggested that a landscape approach may not be required when suitable habitat is abundant and widespread, when individual movement distances are large relative to interpatch distances (i.e., the "grain" of the environment is finer than that of the organisms), when movement patterns do not differ greatly among different elements of the landscape (i.e., transition probabilities are roughly equal and high), or when the habitat pattern is ephemeral. In most of these situations, either the environment approaches homogeneity or the organisms treat it as such. If this occurs at a broad, population scale, then it is unlikely that metapopulation dynamics will develop. The kind of interplay between local patch structure, individual movements, and local extinction and recolonization that is the essence of metapopulation dynamics would seem to require a certain form of patchiness, one that is in the vicinity of the connectivity threshold and does not meet the conditions specified in Fahrig's analysis. Under these conditions, attention must be given to the details of landscape structure.

V. METAPOPOPULATIONS, LANDSCAPES, AND CONSERVATION

The relevance of metapopulation dynamics to conservation issues is treated in detail in many other chapters in this volume, so I will not dwell on it here. If

metapopulations are to be viewed in a landscape context, however, some implications for conservation practice cannot be ignored.

The traditional focus of conservation has been on reserves, and much of the debate about reserve design has dealt with the size, shape, and number of reserves. Reserves have usually been viewed as habitat islands (patches) in a background matrix. Metapopulation theory has become important in conservation biology because it fits neatly into this patch–matrix tradition and because the widespread occurrence of habitat fragmentation has subdivided populations (Wiens, 1995b, 1996b), creating spatial patterns that appear to match those of metapopulations. Metapopulation theory also predicts stability solutions, offering the hope of population persistence in the face of local extinctions.

Habitat fragmentation, however, involves much more than changes in the size and isolation of habitat patches. When a landscape is fragmented, habitats are replaced by other habitats, patch boundaries are often sharpened and patch context changed, connectivity patterns are altered, and the cost–benefit contours of the landscape shift. Simple island biogeography theory does not deal with such complexity of spatial patterns, and this is one reason why its value in conservation efforts is quite limited (Simberloff and Abele, 1982, 1984; Soberón, 1992; Haila *et al.*, 1993; and Wiens, 1995b, give other reasons). Island theory, for example, predicts a loss of species with a reduction in island (patch) area—the well-known species–area ($S-A$) relationship. A scatter of points above the $S-A$ curve has been interpreted as evidence of community “supersaturation,” which will inevitably lead to a loss of species (“faunal relaxation”), whereas points lying much below the curve have been explained as results of island disturbance (e.g., volcanic eruptions) or extreme isolation (see Wiens, 1989b). Because terrestrial habitat patches are immersed in a landscape mosaic, it seems more likely that such scatter represents (at least in part) the effects of connectivity, patch context, or edge conditions (Fig. 5). The specific ways in which landscape configuration might affect species–area relationships have not been explored.

These and other considerations have led to challenges to the “reserve mentality” (Brussard *et al.*, 1992), the belief that conservation problems are solved by establishing reserves and ignoring the surroundings. Reserves are necessary, to be sure, but areas outside of reserves may also play important roles (Noss and Harris, 1986; Saunders *et al.*, 1991; Woinarski *et al.*, 1992; Barrett *et al.*, 1994; Hanski and Thomas, 1994; Turner *et al.*, 1995; Wiens, 1995b, 1996b). For habitat generalists or species that move widely, management of landscape mosaics over large areas may be essential. In Australia, for example, the endangered Gouldian finch (*Erythura gouldiae*) has a limited and patchy distribution (Woinarski *et al.*, 1992). Large breeding populations still exist in several areas, and these can be protected by reserves. However, the population leaves these areas in postbreeding movements, with transient groups appearing in widely spaced (and unpredictable) locations over the landscape. Management by a series of static reserves will not work during this phase, when considerable mortality occurs.

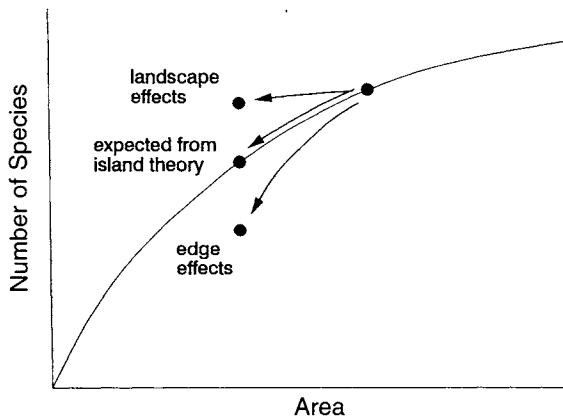


FIGURE 5 The species–area relationship. If the area of a habitat in the landscape is reduced (e.g., by fragmentation), island biogeography theory predicts that a new equilibrium number of species that is appropriate to the new habitat area will be reached. Landscape effects (e.g., connectivity, patch context), however, can reduce the species loss by providing habitat refugia or increasing the likelihood that local habitat patches will be rapidly recolonized. On the other hand, edge effects (e.g., low boundary permeability, increased predation mortality in habitat edges) may reduce species number below that expected from equilibrium island theory. Some of the scatter of points about reported species–area relationships may reflect the effects of such mosaic features.

The solution to such problems may be to shift from reserve management to “mosaic management,” in which reserves are combined with areas that receive varied (and perhaps intense) human use. If one wishes to enhance a metapopulation structure in an area, for example, it may be necessary to manage not only the habitat patches that contain (or could contain) local populations but the landscape features that facilitate or impede interpatch movement as well. Too often, such considerations are cast in terms of corridors of like habitat linking patches together (e.g., the management plan for northern spotted owls (*Strix occidentalis caurina*); J. W. Thomas *et al.*, 1990), rather than evaluating overall landscape connectivity. Proper mosaic management requires that attention be given to *all* of the features of a landscape and how they interact to determine the fate of local populations in habitat patches. I maintain that the key to accomplishing this objective lies in understanding how landscape structure affects movement patterns within and among patches (Wiens, 1996b).

VI. CONCLUSIONS

The main message of this chapter is that landscape structure may often be an important component of metapopulation dynamics. Variations in patch quality in space and time, the form and permeability of patch boundaries, the composition and characteristics of surrounding mosaic elements, and the connectivity among

landscape components may all influence the dynamics of local populations and, especially, the ways in which populations are linked by movements of organisms. The synthesis of landscape ecology with metapopulation dynamics *is* important.

Although I have emphasized the contributions that landscape ecology can make in developing an understanding of metapopulation dynamics, the relationship between these disciplines should not be one-sided. Metapopulation dynamics may also contribute to the development of landscape ecology, in two ways. One is by emphasizing the *dynamics* that occur in a landscape. The spatiotemporal patterns of local extinctions and patch recolonizations create a shifting distribution of populations among patches. Understanding what controls these dynamics addresses issues of spatial relationships and mosaic composition that are at the heart of landscape ecology. Moreover, an emphasis on these dynamics can draw attention away from the map-based descriptions that characterize some approaches to landscape ecology.

The second way in which metapopulation dynamics can contribute to landscape ecology is in the area of theory. In contrast to many other areas of ecology, landscape ecology has developed rather little theory. The lack of theory may stem in part from the diverse historical roots of the discipline (Fig. 1), but it may also reflect the complexity of landscapes and their linkages. The variety of landscape patterns is virtually unlimited, and thus there is no single mosaic pattern (or small set of patterns) about which theory can be generated (Wiens, 1995a). In contrast, patch theory has developed at least in part because "patchiness" can be collapsed into simple patterns of patches and matrix (or so we believe). Further development of landscape ecology as a predictive rather than a descriptive science requires concepts or theories that link landscape patterns to their consequences. As metapopulation theorists continue to add complexity and realism to simple patch-matrix models, they come closer and closer to developing true mosaic models. Quite beyond the value of such models in enhancing our understanding of metapopulation dynamics, they may provide a wedge that landscape ecologists can use to develop models of landscape interactions. A linkage of metapopulation theory with percolation theory might be especially fruitful (see With, *in press*).

Throughout this chapter I have emphasized the importance of understanding movement. Whether or not a spatially subdivided population functions as a metapopulation depends on how individuals move among patches. How individuals migrate is, in turn, affected in a myriad of ways by landscape structure. Understanding these effects on movements is of fundamental importance, yet we know very little about movement in an ecological context (May and Southwood, 1990; Opdam, 1991; Dunning *et al.*, 1995). Existing theory will not provide much help here. Instead, we must focus our attention on well-designed empirical studies of how individual movements are affected by the explicit spatial patterning of environments. Such investigations can provide the information and insights necessary to bring metapopulation dynamics and landscape ecology together.

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