# Ecological Processes That Affect Populations in Complex Landscapes

John B. Dunning; Brent J. Danielson; H. Ronald Pulliam

# Ecological processes that affect populations in complex landscapes

John B. Dunning, Brent J. Danielson, and H. Ronald Pulliam, Inst. of Ecology and Dept of Zoology, Univ. of Georgia, Athens, GA 30602, USA (present address of BJD: Dept of Animal Ecology, Iowa State Univ., Ames, IA 50011-3221, USA)

**Summary.** We describe a general framework for understanding the ecological processes that operate at landscape scales. The composition of habitat types in a landscape and the physiognomic or spatial arrangement of those habitats are the two essential features that are required to describe any landscape. As such, these two features affect four basic ecological processes that can influence population dynamics or community structure. The first two of these processes, landscape complementation and landscape supplementation, occur when individuals move between patches in the landscape to make use of nonsubstitutable and substitutable resources, respectively. The third process, source-sink dynamics, describes the consequences of having different individuals in the same population occupy habitat patches of different qualities. The fourth process, the neighborhood effect, describes how landscape effects can be amplified when the critical resources are in the landscape immediately surrounding a given patch. Definition of these landscape features and general processes will allow a better synthesis of how landscape variation affects populations and communities.

Traditionally, many ecologists have assumed that the most important ecological processes affecting populations and communities operate at local spatial scales. Animal species richness and abundance, for example, are often considered to be functions of variation in local resource availability, vegetation structure, and the size of the habitat patch (MacArthur and MacArthur 1961, Willson 1974, Cody 1985). Habitat variation exists at a variety of scales, however; and ecologists have become increasingly aware of the importance of examining ecological processes at the spatial and temporal scales relevant to both the organisms and the processes under study (Turner 1989, Wiens 1989a). This often means that scales larger than those traditionally used in most field studies must be considered (Wiens 1989a).

One spatial scale that has been the focus of recent investigation is that of the landscape. We use the term landscape to refer to the mosaic of habitat patches in which a particular patch (i.e., a "focal patch") is embed-

ded. Landscape size would differ for different types of organisms; however, landscapes generally occupy some spatial scale intermediate between an organism's normal home range and its regional distribution. By emphasizing these intermediate spatial scales, the study of landscape-level patterns and processes may form a bridge between the local microscale studies that have been common in population and community ecology, and macroscale (regional or global) investigations (Delcourt and Delcourt 1988).

Landscapes and their effects have been studied in several ways. First, landscape ecologists have described features of landscapes that are useful in quantifying and comparing landscape patterns (Turner 1989, Turner and Gardner 1991). Secondly, a growing number of empirical papers have shown some of these landscape features to be important in the population dynamics of a particular species, or in determining the structure of particular communities (see review by Kareiva 1990). Finally, theoretical papers in landscape ecology have considered some general approaches that one may take in examining scale-related phenomena using concepts such as hierarchy theory (Allen and Star 1982, O'Neill et al. 1986) and ecological neighborhoods (Addicott et al. 1987). Each of these approaches provides important steps toward the integration of landscape-level phenomena into mainstream ecological research (Forman and Godron 1986).

Although empirical studies have shown landscape effects to be important in specific cases, there has been little synthesis to date of the kinds of ecological processes identifiable at the landscape scale that may have important effects on the growth and persistence of populations. A classification of general landscape processes would help guide community and population ecologists in examining landscape effects, just as Turner's (1989) review of landscape patterns helped organize research on the physical properties of landscapes. In this paper

we offer a preliminary list of ecological processes that operate at the landscape scale, with examples of studies that have demonstrated effects of these processes on specific populations or communities.

## Some preliminary definitions

Landscapes are distinguished by particular spatial relationships between component parts, a patterning that Turner (1989) calls landscape structure. Turner (1989) has described how landscape structure can be quantified through a number of measures, such as fractal dimension, relative patchiness, patch contagion, etc. The various measures of landscape structure can be grouped into two general categories, those measuring landscape physiognomy and those measuring landscape composition, both of which are useful in the describing how landscapes affect population-level processes.

*Landscape physiognomy* refers to features associated with the physical layout of elements within the landscape. These features, such as patch isolation or patch contagion (Turner 1989), are measures of the placement of patch types relative to other patch types, the boundaries of the landscape, or other features of interest. Landscape models that deal with physiognomic effects are constructed so that the physical placement of each patch is explicitly incorporated into the model and the effect of changing the locational properties of the landscape can be studied. In his review of landscape theory, Kareiva (1990) groups these models together in an general class of models that he calls "stepping stone models."

A second aspect of landscape structure is the relative amounts of each habitat type contained within the landscape. We refer to this component as *landscape composition,* and include in this category those landscape metrics that measure the presence, absence, or relative proportions of landscape components. Examples of landscape composition metrics include landscape dominance, relative richness, and landscape diversity (Turner 1989). Landscape composition models are constructed so that the amounts of each patch type within the landscape are specified, but the placement of the patches are not. With these models, one can investigate the influence of changing the relative proportions of habitat types in the landscape. Models of this type have been labeled "island models" by Kareiva (1990).

Both physiognomic and compositional variables can be measured on the same landscape at the same scale. The difference between landscape physiognomy and composition can be understood by considering an analogous dichotomy proposed in studies of avian community ecology (e.g., Rice et al. 1984, Rotenberry 1985). Habitat structure in these studies is composed of two elements, habitat physiognomy (the purely physical structure of the habitat as provided by vegetation, etc.), and

habitat floristics (the types of plant species present). Indices such as foliage height diversity are used to measure habitat physiognomy, while relative densities or abundances of plant species are used to quantify floristics. Habitat physiognomy and floristics, as used by terrestrial community ecologists, provide direct parallels to the concepts of landscape physiognomy and landscape composition in measuring the structure of the environment at different spatial scales.

A particular landscape element can affect populations through either landscape physiognomy or composition, or both. For example, the presence of corridors linking habitat patches in a landscape can greatly increase dispersal between patches, which in turn may increase the persistence of species that otherwise could not cross patches of unsuitable habitat. Consider a landscape in which the corridors are distinguishable from the habitat patches, such as a landscape where shrubby fencerows act as corridors between isolated woodlots, for species that breed only in the woodlots (e.g., Fahrig and Merriam 1985). If the presence of the corridors in the landscape increases dispersal regardless of where the corridors are located or which woodlots are connected, then the corridors may increase the population persistence of the species through a landscape composition effect.

If, however, the corridor effect is seen only when specific woodlots are connected, then the increased persistence is a physiognomic effect. An example of this latter effect would be a landscape consisting of a large central woodlot surrounded by a variety of smaller patches, each of which may not contain enough resources to maintain the local subpopulation in all years. Corridors that link the central patch with the smaller peripheral patches may have a stronger effect on the metapopulation's overall probability of extinction than would the same number of corridors running between the peripheral patches. In this example, the value of the corridors does not depend simply on their presence in the landscape, but also on the size and quality of habitat patches being linked, that is, the precise location of the corridors within the landscape.

## A general classification of landscape processes

In this section we describe four types of ecological processes (sensu Wiens 1989b) that operate at the landscape scale, and give examples from the literature that illustrate the processes.

*Landscape complementation.* Consider a landscape composed of different types of patches, each containing different resources, and a single species that requires at least two different resources at some point in the species' life cycle. The organism must travel between patches, since the critical resources are found in patches of different types. The resources are non-substitutable
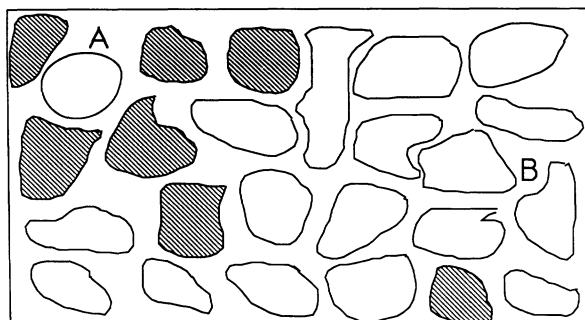
Fig. 1. Landscape complementation. A species requires non-substitutable resources found in two habitats (shaded and open). Regions of the landscape where both habitats are relatively close (area A) will support more individuals than regions where one habitat is relatively rare (area B).

(sensu Tilman 1982); that is, both resources are required by the organism, but for different reasons. Examples of non-substitutable resources might include foraging patches, winter roost sites, and breeding sites.

Landscape complementation occurs when both patch types occur in close proximity within a landscape and thus support a larger population than do landscapes in which these habitats are far apart (Fig. 1). The larger populations might result from a variety of specific causes. For instance, individuals could collect both resources more efficiently when patches are close, or they might reduce the time exposed to predators while traveling between patches. The important point is that the presence of resources in one patch is complemented by the close proximity of the resources in a second patch, so that larger populations can be supported in the area of proximity. The term landscape complementation is analogous to Tilman's (1982) resource complementation which refers to an individual's resource use on a finer spatial scale.

Landscape complementation was demonstrated in Petit's (1989) study of the winter distribution of woodland birds. Patches of one habitat type are used for foraging by these birds, while patches of a second type contain roosts providing cover from winter storms. The only usable foraging patches are those close to the patches with roost sites. Thus, the distribution of the birds in the foraging patches is determined by the relative isolation of the two habitat types, which is an aspect of landscape physiognomy.

Landscape complementation was also shown by McIvor and Odum (1988), who studied the distribution of fish within regions of a salt marsh. The fish feed at high tide in the marsh and retreat to tidal streams at low tide. Some of the tidal streams become pools at low tide and, therefore, provide a predator-free refuge during non-feeding periods. The largest fish populations are found in those areas of the marsh that are opposite streams with refuge pools at low tide.

Landscape complementation can also affect popula-

tion persistence. Weiss et al. (1988) studied the topographic determinants of habitat quality for checkerspot butterflies (Euphydryas editha). Hillsides that are cooler than average yield better growth for prediapause larvae, while warmer slopes are high-quality habitat for post-diapause larvae and pupae. Local areas of high topographic relief, where cool and warm slopes are close together, allow limited dispersal of larvae between slopes. Butterfly populations persist best in the regions of the landscape that have the proper topographic relief features in close proximity.

Landscape supplementation. Organisms can also respond to the distribution of patches with substitutable resources. In the process of landscape supplementation, the population in a focal patch may be increased if that patch is located in a portion of the landscape that contains additional available resources. The organisms could supplement their resource intake by using resources in nearby patches of the same habitat (Fig. 2), or by using a substitutable resource in nearby patches of a different type. Through this mechanism, a population may be maintained in a patch that is too small to sustain the population solely on the resources found within the patch itself. Like landscape complementation, landscape supplementation is analogous to the smaller-scale process of resource supplementation (Tilman 1982).

Whitcomb et al. (1977) described an example of landscape supplementation in their survey of bird populations in several small woodlots in a fragmented landscape. They found several species in these woodlots that are normally restricted to much larger patches of habitat, such as barred owls (Strix varia) and pileated woodpeckers (Dryocopus pileatus). These species were resident in the small woodlots because they were able to forage in other nearby patches of woodland habitat, increasing the effective size of the isolated woodlots.

Landscape supplementation is also illustrated by the movements of bluegill (Lepomis macrochirus) between habitat patches within small ponds. Werner et al.



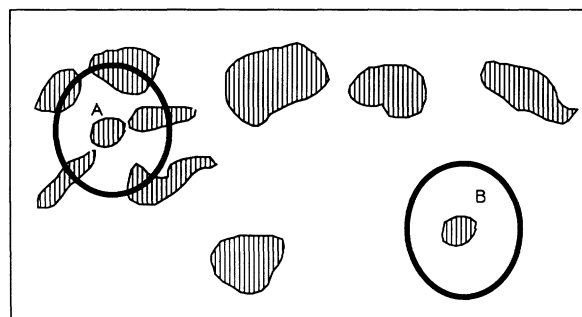Fig. 2. Landscape supplementation. A species requires resources found in the shaded habitat patches. Patches A and B are too small to support populations on their own. However, patch A may support a population if individuals can supplement their resource levels by moving to patches providing the same or similar resources, as long as these patches are within an accessible portion of the local landscape (dark oval).
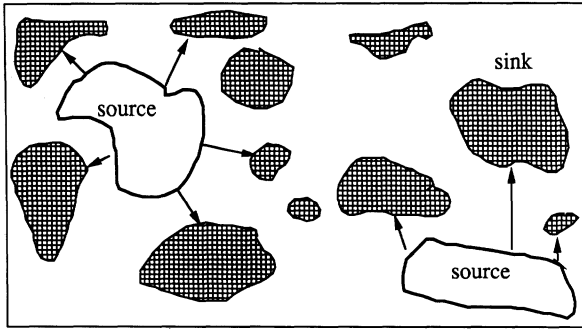
Fig. 3. Sources and sinks. Species occupies two habitat types: a rich patch type (sources: open patches) capable of producing excess individuals, and a poor patch type (sinks: shaded patches) which do not produce enough individuals to maintain local population. Populations in sink patches are dependent on dispersers (arrows) from nearby sources.

(1983a) showed that bluegill maximize their foraging rates by feeding primarily in the open water column. In the presence of predatory bass (*Micropterus salmoides*), however; the smallest, most vulnerable size-class of bluegill shifts to feeding in pond vegetation (Werner et al. 1983b). In this alternative habitat, the bluegills are safe from predation, but their feeding rates are lowered. Thus, because the two habitat types both provide food resources of different quality (substitutable resources), the fish can move between patches in response to the distribution of predators in the system.

Different habitat types can also serve as substitutable resources for individuals dispersing to new breeding locations. In the red-winged blackbird (*Agelaius phoeniceus*), dispersing males prefer to settle in wetlands and hayfields (Clark and Weatherhead 1987). At high population densities, however, not all individuals can find open territories in these high-quality habitats, and some males must settle in croplands and human-occupied areas. The presence of these low-quality habitats increases the total population size supported locally even though these alternative habitats have very low productivities for the species (see also Pulliam and Danielson 1991).

*Source/sink relationships.* A third type of landscape process occurs when relatively productive patches serve as sources of emigrants, which disperse to less productive patches called sinks (Lidicker 1975, Van Horne 1983, Roughgarden and Iwasa 1986, Pulliam 1988). Subpopulations in the patches of sink habitat would go extinct without this immigration (Fig. 3), and under the proper conditions, large sink populations can be maintained by dispersers from a relatively small amount of source habitat (Pulliam 1988). The mechanism for maintenance of sink populations through immigration is the same as the rescue effect, proposed by Brown and Kodric-Brown (1977) for island populations.

Pulliam and Danielson (1991) demonstrated in a series of simulation models that population size in a source/sink landscape can be affected by a landscape's composition. They varied the amount of sink habitat present in a landscape, while holding the amount of source habitat constant. Total population size increases when a small amount of sink habitat is added to the landscape, because excess offspring from the predominant source patches could settle in nearby sink patches and produce a few offspring. As the amount of sink habitat in the simulated landscape increases, however, available source patches are not always discovered by dispersing individuals. The process is similar to searching for a few needles in successively larger haystacks. The more hay (sink patches) to search through, the fewer needles (source patches) are found. When sink habitat is abundant and dispersers are limited in their searching ability, enough source patches may not be found to maintain the same population size as would have occurred in landscapes with lesser amounts of sink habitat. Species with limited dispersal abilities may not exist at all in landscapes where source habitat is severely diluted in a sea of sink habitat.

The change in population size resulting from increases in sink habitat is a landscape composition effect, since it is the relative ratios of source to sink habitat, and not the exact placement of the habitat patches, that affects the organism's ability to find source patches. Source/sink models have been used to investigate some landscape physiognomic effects, however. For example, a model of the population dynamics of a nonmigratory sparrow shows that the proportion of patches occupied increases when there is source habitat within the immediate surrounding landscape (Pulliam et al. 1992).

Few empirical studies have described natural populations that have source and sink habitats. This is at least partially due to the difficulty of measuring dispersal and reproductive success in several habitat types. Source habitats, where local production is great enough that some individuals must regularly emigrate, are commonly reported (e.g., Tamarin et al. 1984). Fewer studies have demonstrated that these dispersers can maintain populations in a sink habitat. Meyer and Bell (unpubl. data) have shown that copepod (*Metis* sp.) populations in shallow seagrass meadows are probably maintained by dispersal of individuals from populations in deeper water. The shallow water populations regularly go extinct in late summer and, therefore, may be sinks.

Perhaps the best example of a source/sink population has been provided by Kadmon and Shmida (1990). They examined populations of a desert grass, *Stipa capensis*, that grew in two adjacent habitats. Grass populations in the relatively rich wadi habitat produce enough seed to account for population changes between years. The smaller populations found in the surrounding slope habitat do not reproduce at a rate great enough to account for observed population sizes in the slope habitat. Seed production in the slope habitat is apparently augmented by dispersal of seeds from nearby wadi hab-
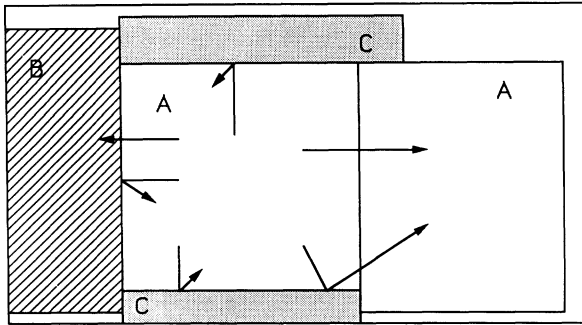
172

Fig. 4. Neighborhood effects. Boundary effects are one type of neighborhood effect. Dispersers (arrows) from central patch of habitat type A move into neighboring patches if boundaries are permeable (Habitat A) or semipermeable (Habitat B). Dispersers are unable to colonize Habitat C, with an impermeable boundary.

itat patches. Thus, population size in sink habitat may depend on the distance between the sink habitat and the closest source (Pulliam 1988), a landscape physiognomic feature.

*Neighborhood effects.* A species' abundance in a particular focal patch may be more strongly affected by characteristics of contiguous patches than by those of more distant parts of the landscape. This is because the resources in these adjacent patches are usually more accessible than resources in more distant patches. An example of this type of influence was shown in the study cited above in which patch occupancy in a source/sink landscape was dependent on the occupancy of the surrounding patches (Pulliam et al. 1992). Buechner (1989) used the term "small-scale landscape effects" to describe these local influences; however, we prefer the term "neighborhood effects," since the neighborhood concept can apply to any spatial scale (Addicott et. al. 1987). Neighborhood effects are explicitly physiognomic, because they are dependent on the placement of patches within the landscape.

An organism's ability to use the resources in adjacent patches depends on the nature of the boundary between the patches (Fig. 4) and, to some degree, the shape and size of the focal patch itself. In some landscapes, the boundaries between patches can have distinctive enough characteristics to be considered a separate edge habitat (Reese and Ratti 1988).

Bach (1988a, b) demonstrated the importance of boundary conditions for insect herbivores dispersing between clusters of squash plants. When tomato plants are planted as a distinct edge around the squash clusters, movements of herbivores between patches are inhibited. Populations within some patches increase because insects attempting to disperse from those patches are repelled by the tomato boundary and are reflected back into their original patch. Thus, the nature of the edge affects the population's dynamics within the patches.

While Bach studied how emigration from patches can be affected by the habitat type of neighboring patches, Hardt and Forman (1989) examined how the shape of a boundary between two different patches affected emigration. Invasion of trees and shrubs from woodland patches into grassland patches was greater where the border of the woodlands was concave (i.e., where grassy patches projected into the woods) compared to areas where the woodland border was straight or convex. Hardt and Forman hypothesize that this effect is probably an indirect effect of the spatial use of the boundary area by large grazing herbivores, which are more likely to move into parts of the grassland that are surrounded by woodland edge on three sides.

## Indirect landscape effects

Any of the above processes could indirectly affect an organism by directly impacting the organism's competitors, predators, or mutualists. Some predators, for example, are strongly associated with particular landscape features; thus, increases in these features may decrease prey populations (Hansson 1989). Avian nest predators and brood parasites are associated with strip corridors and edges between fields and woodlands. Increased fragmentation in a woodland landscape can make edges and corridors more common, resulting in decreased nesting success for some bird species in the remaining woodland patches (Wilcove 1985, Small and Hunter 1988). Thus, fragmentation indirectly decreases forest bird populations by increasing the area of the forest within a critical distance of forest edge, and thereby increasing the influence of edge-associated nest predators.

A second example of an indirectly-mediated effect of landscape composition is Holt's (1977) description of apparent competition in hares. Arctic hares (*Lepus arcticus*) in Newfoundland were originally found in both tundra and woodland habitats. When snowshoe hares (*Lepus americanus*) were introduced into the woodlands, arctic hare populations declined until they were restricted to tundra habitats, a change that could be interpreted as direct competition between the hares. However, the difference in habitat use by the arctic hares is actually a result of lynx predation on both species. When high populations of snowshoe hares are present in the woodland habitat, a larger population of lynx can be supported, and arctic hare populations are depressed by increased predation. In landscapes without the snowshoe hares, fewer lynx can exist, and arctic hares are more abundant. Thus, the population dynamics of arctic hares show a landscape pattern that is the result of landscape supplementation for the hare's predator (Bergerud 1967, Holt 1977).

## Effects on community structure

If landscape-level processes affect the persistence of populations, then these processes also have an effect on local community structure. Regions of the landscape where one or more populations cannot maintain themselves will have lower local species richness compared to portions of the landscape where these populations persist. Alternatively, landscape diversity may be increased if different species respond positively to the habitat dispersions found in different portions of the landscape. We present two types of studies here as examples of how the effects of the processes described above can be measured at the community level.

Whitcomb et al. (1977) described how bird populations in a focal patch may be dependent on the presence of supplemental resources in the landscape. If such resources are lacking, then local species richness should decline in isolated patches. Blake (1983) and Askins and Philback (1987) document this type of effect in isolated populations of forest-breeding birds. Population declines and local extinctions were associated with decreases in wooded habitat within the local landscape.

Landscapes composed of source and sink habitats can also have effects on local community structure. Since source and sink habitats are species-specific, few studies have considered impacts on more than one population. By considering the effect of such landscapes on species interactions (e.g., Kareiva 1987), one may be able to bridge between the population and community levels. Danielson (1991) modified the Pulliam and Danielson (1991) single-species model described previously by adding a second competing species, whose source habitat was the first species' sink habitat. When the second species occupies its preferred habitat, the first species may benefit by being able to locate its source patches more easily. This assumes that dispersers of the first species waste less time sampling sink habitat patches, because some of these patches are occupied by its competitor. With fewer sink patches to sample, the first species becomes more efficient at finding its source patches. In this special case, the presence of a competitor in an unfavorable landscape effectively "improves" the landscape, resulting in an increase in the first species' total population size. Thus, the response (either positive or negative) of a species to the introduction of a competing species may depend on the composition of the landscape under consideration.

## Conclusions

A landscape perspective is required to understand how species are distributed across complex mosaics of habitat patches. We believe that the general importance of landscape variation can best be assessed when studies of large-scale patterns and processes are interpreted within an ordered framework. This framework would consist of the structural (compositional and physiognomic) features of the landscape (Turner 1989), the habitat-specific responses of the organisms (Kareiva 1990), and the ecological processes described in this paper that link the landscape variation to the population dynamics of the organism.

Generalizing the potential types of processes that can occur in landscapes should assist in predicting how populations and communities will vary over large areas. One of the important points that a consideration of landscape processes yields is that the sum of the parts of a landscape will likely not add up to the observed whole. An understanding of the interrelatedness of the parts is required to predict the changes in population dynamic or community structure resulting from a change in landscape structure. In an age when human modifications of natural landscapes are increasingly cited as agents of population extinction, understanding the role of landscape processes is of critical importance.

One of the primary requirements of a good experimental design is the independent manipulation of each experimental variable. Changing landscape composition by manipulating the amount of a particular type of habitat may incidentally also change the landscape's physiognomy unless the experiment is designed with care. We hope that by discriminating between landscape physiognomy and composition, future studies will be better able to assess the relative importance of different landscape features.

## References

Addicott, J. F., Aho, J. M., Antolin, M. F., Richardson, J. S. and Soluk, D. A. 1987. Ecological neighborhoods: scaling environmental patterns. – Oikos 49: 340–346.

Allen, T. F. H. and Star, T. B. 1982. Hierarchy. – Univ. of Chicago Press, Chicago, IL.

Askins, R. A. and Philbrick, M. J. 1987. Effect of changes in regional forest abundance on the decline and recovery of a forest bird community. – Wilson Bull. 99: 7–21.

Bach, C. E. 1988a. Effects of host plant patch size on herbivore density: patterns. – Ecology 69: 1090–1102.

– 1988b. Effects of host plant patch size on herbivore density: underlying mechanisms. – Ecology 69: 1103–1117.

Bergerud, A. T. 1967. The distribution and abundance of Arctic Hares in Newfoundland. – Can. Field-Nat. 81: 242–248.

Blake, J. G. 1983. Trophic structure of bird communities in forest patches in east-central Illinois. – Wilson Bull. 95: 416–430.

Brown, J. H. and Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. – Ecology 58: 445–449.

Buechner, M. 1989. Are small-scale landscape features important factors for field studies of small mammal dispersal sinks? – Landscape Ecol. 2: 191–199.

Clark, R. G. and Weatherhead, P. J. 1987. Influence of population size on habitat use by territorial male Red-winged Blackbirds in agricultural landscapes. – Auk 104: 311–315.

Cody, M. L. 1985. Habitat selection in birds. – Academic Press, Orlando, FL.

Danielson, B. J. 1991. Communities in a landscape: the influence of habitat heterogeneity on the interactions between species. – Am. Nat. 138: 1105–1120.

Delcourt, H. R. and Delcourt, P. A. 1988. Quaternary landscape ecology: relevant scales in space and time. – Landscape Ecol. 2: 23–44.

Fahrig, L. and Merriam, G. 1985. Habitat connectivity and population survival. – Ecology 66: 1762–1768.

Forman, R. T. T. and Godron, M. 1986. Landscape ecology. – J. Wiley, New York.

Hansson, L. 1989. Predation in heterogeneous landscapes: how to evaluate total impact. – Oikos 54: 117–119.

Hardt, R. A. and Forman, R. T. T. 1989. Boundary form effects on woody colonization of reclaimed surface mines. – Ecology 70: 1252–1260.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. – Theor. Popul. Biol. 12: 197–299.

Kadmon, R. and Schmida, A. 1990. Spatiotemporal demographic processes in plant populations: an approach and a case study. – Am. Nat. 135: 382–397.

Kareiva, P. 1987. Habitat fragmentation and the stability of predator-prey interactions. – Nature 326: 388–390.

– 1990. Population dynamics in spatially complex environments: theory and data. – Phil. Trans. R. Soc. Lond. B 330: 175–190.

Lidicker, W. Z., Jr. 1975. The role of dispersal in the demography of small mammals. – In: Golley, F. B., Petrusewicz, K. and Ryszkowski, L. (eds), Small mammals: their productivity and population dynamics. Cambridge Univ. Press, NY, pp. 103–128.

MacArthur, R. H. and MacArthur, J. W. 1961. On bird species diversity. – Ecology 42: 594–598.

McIvor, C. C. and Odum, W. E. 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. – Ecology 69: 1341–1351.

O'Neill, R. V., DeAngelis, D. L., Wade, J. B. and Allen, T. F. H. 1986. A hierarchy concept of ecosystems. Monogr. Pop. Biol. 32. – Princeton Univ. Press, Princeton, NJ.

Petit, D. R. 1989. Weather-dependent use of habitat patches by wintering woodland birds. – J. Field Ornithol. 60: 241–247.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. – Am. Nat. 132: 652–661.

– and Danielson, B. J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. – Am. Nat. 137: S50-S66.

– , Dunning, J. B. Jr. and Liu, J. 1992. Population dynamics in a complex landscape: a case study. – Ecological Applications, in press.

Reese, K. P. and Ratti, J. T. 1988. Edge effect: a concept under scrutiny. – Trans. N. Am. Wildl. Nat. Res. Conf. 53: 127–136.

Rice, J., Anderson, B. W. and Ohmart, R. D. 1984. Comparison of the importance of different habitat attributes to avian community organization. – J. Wildl. Manage. 48: 895–911.

Rotenberry, J. T. 1985. The role of habitat in avian community composition: physiognomy or floristics? – Oecologia 67: 213–217.

Roughgarden, J. and Iwasa, Y. 1986. Dynamics of a metapopulation with space-limited subpopulations. – Theor. Popul. Biol. 29: 235–261.

Small, M. F. and Hunter, M. L. 1988. Forest fragmentation and avian nest predation in forested landscapes. – Oecologia 76: 62–64.

Tamarin, R. H., Reich, L. M. and Moyer, C. A. 1984. Meadow vole cycles within fences. – Can. J. Zool. 62: 1796–1804.

Tilman, D. 1982. Resource competition and community structure. – Monogr. Pop. Biol. 17. Princeton Univ. Press, Princeton, NJ.

Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. – Annu. Rev. Ecol. Syst. 20: 171–197.

– and Gardner, R. H. 1991. Quantitative methods in landscape ecology: the analysis and interpretation of landscape heterogeneity. – Springer, New York.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. – J. Wildl. Manage. 47: 893–901.

Weiss, S. B., Murphy, D. D. and White, R. R. 1988. Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. – Ecology 69: 1486–1496.

Werner, E. E., Mittelbach, G. G., Hall, D. J. and Gilliam, J. F. 1983a. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. – Ecology 64: 1525–1539.

– , Gilliam, J. F., Hall, D. J. and Mittelbach, G. G. 1983b. An experimental test of the effects of predation risk on habitat use in fish. – Ecology 64: 1540–1548.

Whitcomb, B. L., Whitcomb, R. F. and Bystrak, D. 1977. Island biogeography and "habitat islands" of eastern forest. III. Long-term turnover and effects of selective logging on the avifauna of forest fragments. – Am. Birds 31: 17–23.

Wiens, J. A. 1989a. Spatial scaling in ecology. – Functional Ecol. 3: 385–397.

– 1989b. The ecology of bird communities. – Cambridge University Press, Cambridge, MA.

Wilcove, D. 1985. Nest predation in forest tracts and the decline of migratory songbirds. – Ecology 66: 1211–1214.

Willson, M. F. 1974. Avian community organization and habitat structure. – Ecology 55: 1017–1029.