

# Ecological consequences of habitat fragmentation: implications for landscape architecture and planning

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## Abstract

Habitat loss and isolation associated with land conversion for human activities constitute the most serious threat to the Earth's biological diversity. The study of habitat fragmentation provides an important link between the concepts and principles of landscape ecology and the practice of landscape architecture and planning. Here I review ecological literature to examine current understanding of the ecological consequences of habitat fragmentation, and briefly suggest ways in which the results of these studies may guide decision-making by landscape architects and planners. Two theoretical developments in ecology have informed studies of habitat fragmentation and have provided testable hypotheses for empirical studies: island biogeography theory and metapopulation dynamics. Ecologists have examined the influences of habitat fragment size, shape, degree of isolation, context, and habitat quality or heterogeneity on plant and animal population persistence, community composition, and ecosystem processes.

Disruption of continuous habitat usually results in an increase in the length of the boundary between fragments and their surrounding habitats. Newly created edges experience shifts in microclimatic characteristics, which may significantly alter the native plant and animal communities present. The size of a habitat fragment markedly influences the ecological processes occurring therein, largely due to the changes induced by these habitat edges. In general, species richness declines as fragment area decreases. Vegetated corridors may facilitate the movement of plants and animals among habitat fragments, however, more information is needed regarding the efficacy of corridors in reducing species loss from fragmented habitats. Fragments with highly irregular, convoluted boundaries will likely have greater exchange of nutrients, materials, and organisms with adjacent habitats than will those with less convoluted boundaries. Adjacent habitat types, land management regimes, and intensity of human activities influence boundary permeability and thus flow among habitat fragments. Large fragments are likely to be more heterogeneous than small fragments; they contain a greater variety of soil types, greater topographic variation, and a greater number of habitat types. An integrated view of the spatial characteristics of habitat fragments and their ecological consequences improves our ability to predict the outcomes of, and to design, particular patterns of land conversion.

*Keywords:* Habitat fragmentation; Biological diversity; Environmental planning

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## 1. Introduction

Landscape architecture and planning are disciplines focused on landscape change. Ecological con-

cepts and principles have long been considered in landscape architectural design and planning, from Olmsted's Emerald Necklace in Boston to The Woodlands New Town near Houston, Texas (Lewis, 1969; McHarg, 1969; McHarg and Sutton, 1975; Lyle, 1985; Zube, 1986). Landscape architects and planners have recently begun to incorporate the principles of landscape ecology into design and planning proposals for a variety of landscape interventions aimed at preserving and enhancing biological diversity, minimizing soil erosion and sedimentation, and reducing exotic species invasions (Kreiger, 1991; Thorne et al., 1991; Knaapen et al., 1992; Federowick, 1993; Sauer, 1993; Post, 1994; Rodiek and DelGuidice, 1994; Carr et al., 1994; Yahner et al., 1995).

Recent contributions of landscape ecological studies are particularly relevant to current theory and practice of landscape architecture and planning. The goal of such ecological studies is to understand the implications of particular landscape spatial patterns, such as the size, shape and configuration of habitat remnants, for ecological processes (Forman and Godron, 1986; Turner, 1989; Gardner et al., 1993; Collinge, 1995; Forman, 1995; Hansson et al., 1995). The design professions are concerned with the spatial pattern or composition of particular forms or parts, and landscape architectural design and planning focus on the spatial composition of the landscape. Thus, spatial pattern in the landscape is the common denominator of landscape ecology and landscape architecture and planning. Ecologists are only beginning to appreciate the implications of landscape spatial structure for a variety of ecological processes, and the application of this knowledge to landscape architectural design and planning is still in its infancy. The integration of landscape ecological research with landscape architectural and planning practice provides a rich opportunity for understanding the implications of, and directing, future landscape change.

In the process of land conversion for human use, native ecosystems are transformed from prairie to agricultural field, from old-growth forest to clear-cut, and from coastal scrub to housing development. Land transformation may severely compromise the integrity of ecological systems through loss of native species, invasion of exotic species, pronounced soil

### Habitat Fragmentation

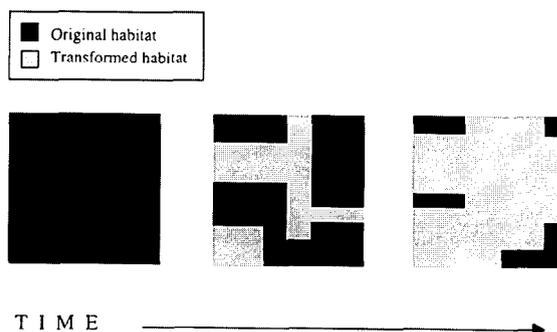


Fig. 1. Diagrammatic representation of the generalized process of habitat fragmentation. Dark areas refer to the original habitat type, light areas to transformed habitat. Over time, the original habitat type is reduced in area, and remnants of the original habitat type are isolated from one another.

erosion, and decreased water quality (Harris, 1984; Forman and Godron, 1986; Wilcove et al., 1986; Hunter, 1990; Bierregaard et al., 1992). The remnants of native vegetation left after such modifications are generally reduced in size and disconnected from adjacent, continuous habitat (Fig. 1). As a result, the populations of plants and animals which occur in these remnants also are subdivided and reduced, which may either exclude certain species immediately or increase their probability of extinction (Wilcox, 1980; Wilcove et al., 1986; McNeely et al., 1990; Saunders et al., 1991). Ecologists, conservationists, and land managers generally refer to these two components of land transformation, habitat loss and isolation, as 'habitat fragmentation'. Habitat fragmentation has been called "the most serious threat to biological diversity and... the primary cause of the present extinction crisis" (Wilcox and Murphy, 1985, p. 884).

In the Earth's history, naturally occurring events such as glaciation, fires, floods, hurricanes, and volcanic eruptions have frequently disrupted continuous expanses of native vegetation, resulting in the isolation and reduction of plant and animal populations. Habitat fragmentation is nothing new, in this sense. However, dramatic increases in global human population growth in this century have been accompanied by the intensification of commercial and residential development, agriculture, and deforestation (Whitney

and Somerlot, 1985; Harris and Scheck, 1991; Miller and Tangley, 1991; Groom and Schumaker, 1993). The proliferation of these human activities has rapidly accelerated the pace of land conversion, resulting in widespread changes in the spatial structure of native habitats.

In its strictest sense, 'fragmentation' is the breaking of a whole into smaller pieces (American Heritage Dictionary, 1979; Zipperer, 1993; Forman, 1995). Habitat 'fragmentation' may therefore not be the most appropriate description of the spatial pattern resulting from many processes of land transformation, i.e. not all land-conversion processes necessarily involve a spatial pattern of fragmentation in this sense. For example, aerial photos of a forested landscape taken 50 years apart which show two large forest patches followed by several small forest patches may represent an increase in habitat loss, a decrease, or no net change in area of forest habitat. Fragmentation may be considered as only one of at least five spatial processes of land transformation (Franklin and Forman, 1987; Hansen et al., 1992; Zipperer, 1993; Collinge, 1995; Forman, 1995), all of which typically involve habitat loss and isolation. Because land conversion patterns differ in their spatial configuration, they may differ significantly in their impact on ecological processes as well (Franklin and Forman, 1987; Hansen et al., 1992; Li et al., 1993; Collinge, 1995; Forman, 1995).

How do spatial patterns of land transformation due to human activities vary? An expanse of native habitat may effectively shrink in size over time due to landscape change at its periphery, but remain as a single tract of habitat. Alternatively, the area of native habitat may be bisected initially, due to the construction of a road, for example, and then continue to shrink as development converts native habitat along the road. The habitat may be divided initially into many pieces, as when agricultural cultivation converts native prairie to crop fields. Those pieces will shrink as land conversion intensifies. Finally, land conversion may begin in the core of an expanse of native habitat and expand outward to the periphery, such that the habitat is perforated. Specifying these particular spatial characteristics of land transformation (Hansen et al., 1992; Zipperer, 1993; Collinge, 1995; Forman, 1995) and identifying the ecological consequences of such patterns, will greatly

increase the precision with which we may understand, predict, and guide future changes to the landscape.

My major emphasis in this paper is to address the question: what are the consequences of habitat fragmentation for ecological processes? Here I refer to habitat fragmentation in the sense that it is generally used in the ecological literature to describe habitat loss and isolation, while recognizing the importance of distinguishing specific spatial patterns of land conversion (Forman, 1995; Forman and Collinge, 1996; Collinge and Forman, in preparation). I focus first on the theoretical underpinnings of ecological research on habitat fragmentation, then review results of ecological studies focused on the influences of fragment size, connectivity, shape, context, and heterogeneity on both abiotic and biotic processes. I examine recent research efforts to understand the ecological implications of particular habitat spatial configurations. Finally, I briefly review three recent landscape architecture and planning proposals and suggest ways in which the results of ecological studies may guide further decision-making in landscape architecture and planning.

Projected rates of continued human population growth will place increasing demands on natural resources and will continue to alter the spatial structure of native habitats. Landscape architects and planners are uniquely positioned to incorporate this knowledge of the ecological consequences of landscape spatial structure into creative landscape design and planning solutions. Proposals which include such information are likely to achieve great environmental benefit.

## 2. Theory

Ecologists have approached the study of habitat fragmentation for the past 25 years largely within the framework of two key theoretical developments in community and population ecology: the theory of island biogeography (MacArthur and Wilson, 1963, 1967) and metapopulation dynamics (Levins, 1969). In the context of habitat fragmentation, the theory of island biogeography has guided study focused primarily on the influences of habitat fragment size and

isolation on species composition (Forman et al., 1976; Pickett, 1979; Newmark, 1986; Blake and Karr, 1987; Bierregaard et al., 1992; Robinson et al., 1992), while the metapopulation dynamics concept has focused attention on connectivity and interchange between spatially distributed populations (Fahrig and Merriam, 1985; Lankester et al., 1991; Hanski et al., 1995).

The equilibrium theory of island biogeography was proposed to explain species composition of animal communities on oceanic islands. In particular, this theory postulated that the size of an oceanic island and its distance from a continental source of colonizing species would determine the number of species present on the island. Islands close to a mainland would likely have higher immigration rates than more distant islands, while large islands would likely have lower extinction rates than small islands. Thus, large islands close to continents were predicted to have a higher number of species than small islands more distant from continents. The authors suggested that while this theory focused on species composition on oceanic islands, the predictions may be consistent for plant and animal communities inhabiting terrestrial 'islands' (MacArthur and Wilson, 1967). This theory provides the conceptual foundation for much research in conservation biology; fragment size and distance from continuous habitat have repeatedly been considered in studies of habitat fragmentation and in recommendations regarding nature reserve design (Diamond, 1975; Diamond and May, 1976; Pickett and Thompson, 1978; Wright and Hubbell, 1983; Lynch, 1987; Soulé et al., 1988; Kruess and Tschardtke, 1994).

Metapopulation theory was originally conceived (Levins, 1969) to describe and predict the population dynamics of species occupying naturally patchy habitats, such as mountaintops (Brown, 1971). A 'metapopulation' is a set of spatially separated groups of conspecific individuals. In this model, local populations of organisms undergo periodic colonization and extinction, while the metapopulation as a whole persists indefinitely. Ecologists have directly applied the understanding of the oscillations of such naturally transient populations to predicting the persistence of species which occur in human-induced habitat fragments (Harrison, 1994; Doak and Mills, 1994; Hanski et al., 1995).

### 3. Spatial and ecological attributes of habitat fragments

Numerous ecological studies have investigated the consequences of habitat fragmentation for plant and animal population persistence, community composition, and ecosystem processes. For example, many studies relate the number of animal or plant species observed in fragments to some designated fragment characteristics, usually area, shape, degree of isolation, context, or some measure of habitat quality or heterogeneity. While each of these attributes plays an individual role in determining ecological function, they may also interact to influence ecological processes. Here I consider each of these fragment characteristics separately, recognizing that there are correlations among them.

#### 3.1. The 'edge' phenomenon

Conversion of continuous habitat into disjunct habitat remnants usually increases the length of the border between fragments and their surrounding habitats. Particularly in forests, because of their dominant vertical structure, removal of vegetation from an area results in dramatic changes in the structural characteristics of the habitat (Murcia, 1995). Isolated forest remnants, which were once embedded in continuous forest, are exposed to the altered physical environment of the adjacent cleared area. The amount of light reaching plants is obviously higher at the edge of a forest fragment than in the forest interior. Consequently, temperature increases and relative humidity decreases at the forest edge. Moreover, wind velocities are higher at the edge than in the interior of the forest (Harris, 1984). The changes in light, moisture, temperature, and wind, most pronounced at the fragment edge, may significantly alter the plant and animal communities which occur there. This 'edge effect' may not only influence the environment at the edge of the fragment, but may permeate the habitat remnant for tens of meters (e.g. Ranney et al., 1981; Harris, 1984; Lovejoy et al., 1986; Chen et al., 1992). Additionally, the extent to which the edge experiences these environmental changes may be significantly influenced by the aspect or orientation of the edge (Wales, 1972; Ranney et al., 1981; Brothers and Spingarn, 1992; Brothers, 1993; Mat-

lack, 1993a; Young and Mitchell, 1993). In the Northern Hemisphere, south-facing edges are generally warmer, drier and wider than north-facing edges; the opposite is true in the southern hemisphere (Young and Mitchell, 1993). Similarly, windward edges of forest patches tend to be warmer, drier and wider than leeward edges (Ranney et al., 1981).

Research in temperate forests of North America has documented several microclimatic changes at forest edges. In deciduous forest patches of southeastern Wisconsin, microenvironmental changes were estimated to extend at least 15 m from the forest edge to the interior (Ranney et al., 1981). Old-growth forest remnants studied in central Indiana exhibited significant increases in light levels and temperature, and a significant decrease in humidity at the forest/field edge (Brothers and Spingarn, 1992). These microclimatic differences ceased to exist beyond 8 m into the forest for these 8–23 ha forest fragments. Similarly, temperature and light decreased within relatively short distances in eastern deciduous forest fragments of Pennsylvania and Delaware (Matlack, 1993a), but humidity and leaf litter moisture continued to change 50 m into the forest interior. In Douglas fir forests of the Pacific Northwest, microclimatic edge effects may extend as far as 240 m into the forest (Chen et al., 1990).

Trees growing along the edge of a forest fragment may be exposed to greater wind velocities than those occurring in forest interior. For example, in the Douglas fir forests of the Pacific Northwest, higher wind velocities were recorded from the forest edge to 60 m into the forest interior (Fritschen, 1971; cited in Harris, 1984; Chen et al., 1992). Increased wind velocities at the forest edge may result in increased incidence of mortality due to treefall, especially for shallow-rooted tropical trees. In an isolated 10-ha forest patch in Brazil, the overwhelming majority of tree mortality along the margins was on the windward margin of the patch (Lovejoy et al., 1984; Bierregaard et al., 1992); annual tree mortality rates were estimated to be 2.6% in isolated patches versus 1.5% for continuous forest.

Associated with the changes in light, temperature, moisture and wind conditions at forest edges are changes in the structure and composition of the existing plant communities. For example, in the deciduous forest patches of southeastern Wisconsin

studied by Ranney et al. (1981), forest edges typically contained more pioneer and xeric plant species than the interior, higher densities of shrubs and herbaceous groundlayer vegetation for several meters into the forest, and higher species richness than the interior. Higher species richness in forest edges may often be due to the invasion of exotic plant species (Brothers and Spingarn, 1992). Edge orientation also influenced species composition: south- and west-facing edges contained more xeric plant species than did north- and east-facing edges (Wales, 1972; Ranney et al., 1981), due to variation in light and moisture conditions. These authors further suggested that the composition of these forest patches may eventually change as a result of increased seed dispersal from the edge to the interior, with shade-intolerant edge species (e.g. hickory, *Carya* sp., and hawthorn, *Crataegus* sp.) replacing shade-tolerant plants of the interior (e.g. sugar maple, *Acer saccharum*, and American beech, *Fagus grandifolia*) (Ranney et al., 1981).

In addition to environmental changes, forest edges in suburban areas experience altered conditions due to human activity. For example, suburban residents may dump grass clippings, Christmas trees, or building rubble in nearby forest remnants, or they may gather firewood, prune limbs, or build treehouses in these habitats (Matlack, 1993b). In a northern Delaware suburban landscape, 95% of these human activities occurred within 82 m of the forest edge (Matlack, 1993b). Thus, changes in forest conditions due to human activities may permeate the forest interior as far or further than microclimatic changes. The influence of a suburban development on adjacent, native habitat may be visually subtle but may extend far beyond property line boundaries, and such significant influences must be an important consideration in the design and planning of suburban developments in continuous, native habitat.

### 3.2. Fragment size / area

The size of a particular habitat fragment markedly influences the ecological processes occurring therein, partly due to the changes induced by the creation of habitat edges discussed above. Because edge effects in a particular habitat permeate a constant distance from the border to the center of a habitat fragment,

### Fragment size

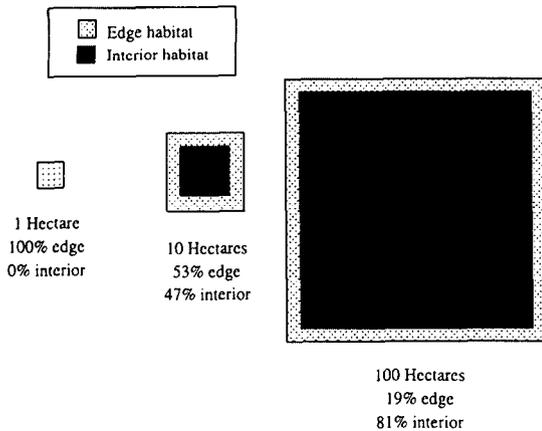


Fig. 2. Relationship between habitat fragment size and edge effects. As fragment size increases, the relative proportion of edge habitat decreases, and interior habitat increases. Edge width is assumed to be 50 m. Light areas are edge habitat, dark areas are interior habitat.

smaller fragments will contain a higher proportion of edge habitat than will larger fragments (e.g. Forman and Godron, 1986; Soulé, 1991; Chen et al., 1992; Groom and Schumaker, 1993). For example, if altered edge conditions extend 50 m into a deciduous forest habitat, then a deciduous forest remnant of 1 ha will be entirely edge habitat (100%) and will have no interior habitat conditions, a 10-ha fragment will have 5.3 ha of edge (53%) and 4.7 ha of interior (47%), while a forest remnant of 100 ha will have 19 ha of edge (19%) and 81 ha of interior habitat (81%) (Fig. 2).

Ecological investigations relating habitat fragment size to the number of plant and/or animal species occurring in fragments are common. Most well-studied are the birds of temperate and tropical forests. In general, the research demonstrates that the number of bird species remaining within isolated forest fragments decreases as fragment area decreases (Forman et al., 1976; Whitcomb et al., 1981; Lovejoy et al., 1984, 1986; Verner et al., 1986; Lynch, 1987; Blake and Karr, 1987; Freemark, 1990; Blake, 1991; Newmark, 1991; Opdam, 1991), with the commonly noted interpretation that the probability of local extinction increases as fragment size decreases. For example, a study of grassland bird communities showed that approximately 79% of the grassland bird species

were present in a 1000 ha grassland fragment, while only 31% of the bird species occurred in 10-ha grassland fragments (Herkert, 1994). This habitat fragment species–area pattern has been documented in other habitats, as well, for mammals (Picton, 1979; Newmark, 1986; Verner et al., 1986; Bennett, 1990; Verboom and Van Apeldoorn, 1990; Cutler, 1991; Bierregaard et al., 1992), insects (Webb and Hopkins, 1984; Powell and Powell, 1987; Klein, 1989; Ås, 1993), amphibians (Dodd, 1990; Laan and Verboom, 1990), and herbaceous plants (Simberloff and Gotelli, 1984; Webb and Vermaat, 1990). These results are consistent with patterns predicted from island biogeographic theory relating island size to species richness (MacArthur and Wilson, 1967).

Some species are more tolerant of reductions in habitat fragment size than others, however, based on particular life history attributes (Terborgh, 1986; Lovejoy et al., 1986; Laurance, 1991; Webb and Thomas, 1994). For example, primate species with especially large home ranges disappeared from 10- and 100-ha isolated tropical forest reserves, while species with smaller home ranges persisted on the 100-ha, but not the 10-ha reserves (Lovejoy et al., 1986). Insects with poor dispersal abilities persisted in large heathland fragments compared with small fragments (Hopkins and Webb, 1984), presumably because small fragments were insufficient to maintain viable populations and these insects were unable to disperse to more suitable habitat. Rare species, which tend to be more specialized in their feeding habits than common species, have been shown to be particularly sensitive to decreases in habitat fragment size (Terborgh and Winter, 1980; Laurance, 1990, 1991). Clonal plant species, which reproduce primarily by vegetative growth and therefore move gradually across the landscape, were more likely to persist in large, old-field fragments than in smaller fragments, where colonization was limited by habitat disruption (Robinson et al., 1992).

The decline in species richness in small habitat remnants results from decreases in population sizes of particular species, and eventually, local extinction of those populations (e.g. Gilpin and Soulé, 1986; Soulé, 1987; Porneluzi et al., 1993; Remmert, 1994; Kindvall, 1996). Populations decline due to direct effects of habitat loss, or to indirect effects, for example, modified interspecific interactions associ-

ated with habitat isolation and edge effects. Increased incidence of avian nest predation and brood parasitism in small forest remnants has caused decline of songbird populations (Brittingham and Temple, 1983; Wilcove, 1985; Gibbs and Faaborg, 1990), and parasitism by arthropods may increase substantially in fragmented habitats to threaten the persistence of certain bird populations (Loye and Carroll, 1995). Fragmentation may lower the searching efficiency of predators, leading to prey insect outbreaks (Kareiva, 1987). Finally, lower rates of pollinator visitation in fragmented habitats has resulted in decreased seed production in certain plant species (Powell and Powell, 1987; Jennersten, 1988; Aizen and Feinsinger, 1994).

### 3.3. Fragment connectivity

Landscape connections play an important role in ecological dynamics within and between habitats (Forman and Godron, 1986; Bennett, 1990; Saunders and Hobbs, 1991; Taylor et al., 1993). The preservation of vegetated corridors among otherwise isolated habitat remnants (Fig. 3) is predicted to moderate the negative effects of habitat fragmentation by maintaining landscape connectivity (Diamond, 1975; Forman and Godron, 1981; Noss, 1987; Harris and Scheck, 1991; Lindenmayer and Nix, 1993; Lindenmayer, 1994). In the context of ecological studies of habitat fragmentation, the term 'corridor' generally refers to a linear landscape element composed of native vegetation which links patches of similar, native vegetation (Forman and Godron, 1986; Bennett, 1990; Harris and Scheck, 1991).

The integrity of riparian corridors, in particular, is of critical importance in preventing soil erosion and maintaining high water quality (Johnson, 1989; Bennett, 1990; Binford and Buchenau, 1993; Naiman et al., 1993). It is well documented that vegetation in riparian zones provides bank stability and water flow control, regulates light and temperature characteristics of the adjacent water bodies, and provides habitat for aquatic life in the form of coarse and fine woody debris (Binford and Buchenau, 1993; Naiman et al., 1993).

Vegetated corridors are predicted to facilitate the movement of plants and animals among habitat fragments, which may allow more species to exist and/or

#### Fragment connectivity

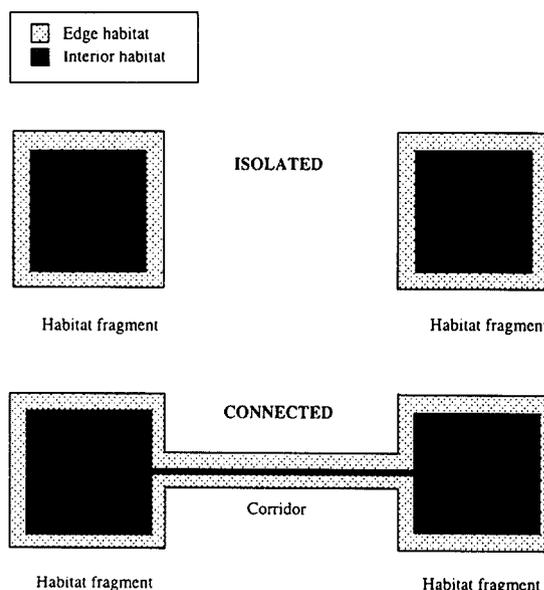


Fig. 3. Diagrammatic representation of two isolated habitat fragments contrasted with two habitat fragments connected by a vegetated corridor, showing edge effects of fragments and corridor. Light areas are edge habitat, dark areas are interior habitat.

populations to persist longer than would be expected based solely on fragment size (Wegner and Merriam, 1979; Bennett, 1990; Henein and Merriam, 1990). For example, computer simulations have suggested that populations of the white-footed mouse, *Peromyscus leucopus*, have higher growth rates and thus lower probabilities of local extinction in woodlots connected by fencerows than in isolated woodlots (Fahrig et al., 1983; Fahrig and Merriam, 1985). A recent experimental field study in an agricultural landscape showed that vole dispersal was greater between old-field fragments connected by vegetated corridors than in completely isolated fragments (La Polla and Barrett, 1993).

Animal use of corridors may vary depending upon their foraging patterns, body size, home range size, degree of dietary specialization, mobility and social behavior (Harrison, 1992; Lindenmayer and Nix, 1993). Interestingly, Lindenmayer and Nix (1993) noted that linear remnants of montane forest harbored several species of large, arboreal marsupials, while smaller species were absent. These authors

suggested that species occurrence in these corridors was largely determined by foraging behavior and social behavior rather than body size. The large animals foraged singly and fed on readily available leaves, while the smaller species foraged in social groups and fed on more widely dispersed arthropods.

The perception and use of corridors by animals may also differ according to the physical dimensions and landscape context of the corridor (Lindenmayer and Nix, 1993; Harrison, 1994; Ims, 1995). For interior habitat specialists, the typically long, narrow dimensions of a corridor may be perceived as largely edge habitat and avoided (Fig. 3). For example, in a study of the role of linear strips of Australian tropical rain forest in promoting animal dispersal (Hill, 1995), individuals of two of the four forest interior species, a butterfly and a beetle, were observed in the rain forest corridor but not in the adjacent cultivated land. This suggests that dispersal for these two species may be enhanced by the presence of the corridor. However, two other forest interior species were not observed in the rain forest corridor, suggesting that its physical dimensions or habitat characteristics were insufficient to facilitate dispersal. Hence, the suitability of corridors as habitat and possible dispersal routes will vary among species.

Moreover, how such movements via vegetated corridors might translate into population persistence and community composition of native habitats is not well understood (Hunter, 1990; Lindenmayer and Nix, 1993). The existence of vegetated corridors between otherwise isolated habitat fragments may modify patterns of species richness and composition by increasing the effective size of the fragments. Thus, connected remnants would be predicted to maintain the attributes of continuous habitat, and support a greater biological diversity than completely isolated remnants (Noss, 1987; Bennett, 1990; Saunders and Hobbs, 1991). For example, the presence of unmown grassland corridors connecting grassland fragments lowered the probability of species loss for some insect species, but only for fragments of an intermediate size (Collinge, 1995). Moreover, the grassland corridors appeared to enhance the rate of recolonization of otherwise-isolated fragments by some species, but not others (Collinge, 1995). More information is needed regarding the efficacy of vegetated corridors in reducing the probability of species

loss in habitat fragments, as well as in enhancing the probability of recolonization of those fragments in the event of a local extinction (Brown and Kodric-Brown, 1977).

Animal movement across continuous habitat is often disrupted by the presence of roads (Harris and Gallagher, 1989; Brocke et al., 1990; Schonewald-Cox and Buechner, 1992; Beier, 1993; Foster and Humphrey, 1995). For example, the density of black bears in the Adirondack mountains decreased 10-fold with a 10-fold increase in road density, due both to hunter access and to road kills (Brocke et al., 1990). Losses of road-sensitive species may be mitigated by road closures (Brocke et al., 1990), or by the implementation of highway underpasses or overpasses (Harris and Scheck, 1991; Foster and Humphrey, 1995). Highway underpasses appear to be particularly effective in facilitating the movement of panthers across southern Florida, as long as underpasses and associated fences are designed and maintained properly (Foster and Humphrey, 1995). The likelihood of animal use of highway underpasses or overpasses will depend heavily on effective designs which incorporate an in-depth understanding of behavior and dispersal characteristics of the target animal species (Lima and Zollner, 1996), as well as the quality and quantity of suitable habitat on either side of the structure.

### 3.4. *Fragment shape*

As described for fragment size above, the geometric shape of a discrete habitat fragment influences the extent to which edge effects permeate the habitat interior (Diamond, 1975; Game, 1980; Forman and Godron, 1986; Schonewald-Cox and Bayless, 1986). Size and shape thus interact to influence the amount of interior area remaining in a particular habitat fragment. Shape can be described most simply by calculation of the perimeter/area ratio of a habitat fragment (Groom and Schumaker, 1993). For example, a square, 100-ha habitat fragment will have a lower perimeter/area ratio and a greater proportion of interior conditions than will a rectangular fragment of equal area (Fig. 4) and would seem to be preferable in maintaining pre-isolation conditions for native species which require interior habitat conditions (Diamond, 1975; Forman and Godron, 1981,

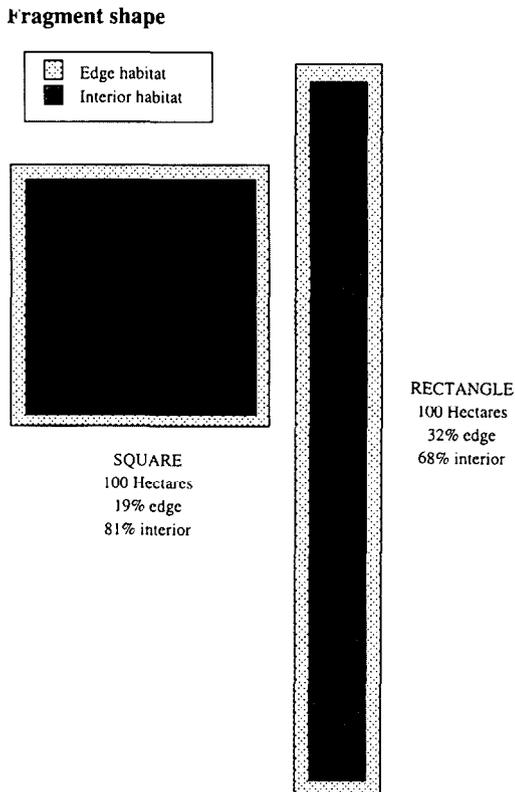


Fig. 4. Relationship between habitat fragment shape and edge effects. A square habitat fragment maintains a greater proportion of interior habitat than does a rectangular fragment of equal area. Edge width is assumed to be 50 m. Light areas are edge habitat, dark areas are interior habitat.

1986; Schonewald-Cox and Bayless, 1986; Soulé, 1991). Interestingly, most areas reserved for nature protection in the United States have relatively high perimeter/area ratios, suggesting vulnerability to the negative consequences of edges (Schonewald-Cox and Bayless, 1986).

Because of the responses of the plant and animal communities induced by abiotic changes at forest edges, Harris (1984) estimated that a stand of old-growth Douglas fir forest would have to be 11 ha, and circular, in order to contain a single point where forest interior conditions existed. Furthermore, a similarly shaped, 80-ha old-growth stand would have only 25% of its area represented by forest interior conditions, and an isolated, circular forest remnant would have to be 2850 ha in order to have 90% of its area represented by forest interior conditions (Harris,

1984). The size and shape of a habitat remnant must therefore be considered when estimating the area of interior habitat available for those plant and animal species which thrive only in continuous habitat and are absent from edges (Forman et al., 1976; Harris, 1984; Soulé, 1991).

The perimeter/area ratio can also provide clues as to the degree of interaction of the fragment with the surrounding habitat matrix, e.g. the probability that nutrients, seeds, or animals will encounter a particular fragment and cross the boundary (Game, 1980; Forman and Godron, 1986; Stamps et al., 1987; Buechner, 1989). For example, migrating birds encountered and built nests in riparian forest fragments which were elliptical and which were oriented perpendicular to their northerly migration route more frequently than in other suitable fragments which were oriented parallel to their migration path (Gutzwiller and Anderson, 1992). Provided that the size of a fragment is sufficiently large to maintain interior habitat conditions, design of the particular shape and orientation may be used as a tool to enhance species richness and persistence (Gutzwiller and Anderson, 1992).

Human activity tends to linearize boundaries between habitats and simplify the complex shapes of habitat fragments (Forman and Godron, 1986; O'Neill et al., 1988; Rex and Malanson, 1990). Our empirical understanding of the ecological consequences of such simplification is minimal (Rex and Malanson, 1990; Hansen and di Castri, 1992). However, recent ecological studies suggest that the linearization of boundaries between habitats may significantly influence the flow of organisms between those habitats. Convolutional boundaries between deciduous forest and strip mines enhanced woody plant colonization of the reclaimed strip mines (Hardt and Forman, 1989). Similarly, in the pinyon-juniper/sagebrush-grassland habitat of northern New Mexico, deer and elk crossed curvilinear habitat boundaries more frequently than straight boundaries (Forman et al., in preparation).

### 3.5. Fragment context

The context in which a remnant of native habitat is situated will undoubtedly influence the degree and type of interaction between the fragment and the

surrounding landscape (Beissinger and Osborne, 1982; Wilcove, 1985; Freemark, 1987; Ambrose and Bratton, 1990; Lindenmayer and Nix, 1993; Åberg et al., 1995). The assertion of Janzen (1983) that “no park is an island” emphasized the influence of surrounding habitat types and human activities on the ecological integrity of areas reserved for conservation. The type, intensity, and degree of dissimilarity of habitat types, land uses and human activities adjacent to habitat fragments may markedly influence the flow of nutrients and materials, and the persistence of plant and animal species in the fragments (Forman and Godron, 1986; Stamps et al., 1987; Buechner, 1989). For example, hazel grouse in Swedish forest fragments dispersed over much greater distances when the surrounding matrix was forested habitat than when it was open fields (Åberg et al., 1995). The relative importance of these adjacent land uses on ecological processes will depend upon other spatial characteristics discussed above, such as fragment size and shape (Janzen, 1983).

The boundary between a habitat fragment and its surrounding matrix may be relatively impervious, with a low tendency for the exchange of materials and organisms between the remnant and the matrix. Alternatively, the boundary may be highly porous, in which case there are frequent and abundant boundary crossings (Wiens et al., 1985; Stamps et al., 1987; Buechner, 1989; Wiens, 1992; Hansen and di Castri, 1992). Boundary permeability and the perimeter/area ratio may both influence the rate and extent of flows across the boundary. For example, computer simulations of animal dispersal across habitat boundaries suggested that for a relatively impassable boundary, the rate of flow across the boundary would be most significantly limited by its permeability. However, for a highly permeable boundary, the models predicted that the rate of flow across the boundary would be more strongly influenced by the perimeter/area ratio (Stamps et al., 1987).

The supply and flow of nutrients, materials, and energy within habitat fragments, as well as between fragments and the surrounding landscape, will likely differ depending on the adjacent land use or activity. For example, a forest fragment adjacent to an active strip mine will probably experience a different set and intensity of impacts from one adjacent to a residential neighborhood (Matlack, 1993b). In an

urban–suburban–rural gradient in central New York state, air temperatures increased within deciduous forest fragments in urban settings, e.g. in Central Park, relative to forests in suburban or rural areas (McDonnell et al., 1993). The authors documented poorer air quality in urban compared with rural forests, and urban forest soils harbored higher levels of lead, copper, and nickel than did similar soils in rural sites (McDonnell et al., 1993).

The unique contributions of varied, adjacent land uses is perhaps best understood for aquatic ecosystems, particularly lakes and streams (Likens et al., 1970; Peterjohn and Correll, 1984; Pringle, 1991; Binford and Buchenau, 1993). For example, the relative inputs of nitrogen and phosphorus to a stream has been shown to vary according to the relative proportion of cultivated cropland versus riparian vegetation adjacent to the stream (Peterjohn and Correll, 1984). Some investigators are currently focusing on how the specific spatial configuration of land uses influences and modifies these flows and inputs to adjacent water bodies (M. Binford, 1994, personal communication). In the midwestern United States, planted riparian buffer strips composed of herbaceous and woody species have effectively reduced the input of agricultural pollutants from crop fields into adjacent streams (Colletti et al., 1995).

Adjacent habitat types, land management regimes, and intensity of human activities may influence plant and animal species persistence in habitat fragments as well (Harris, 1984; Wilcove, 1985; Foppen and Reijnen, 1994). In the urban to rural forest transect described above, soil invertebrates, which are crucial recyclers of nutrients in forest ecosystems, occurred in fewer numbers in the leaf litter of urban forests than in the suburban and rural forests sampled (McDonnell et al., 1993). Bird species composition within isolated tropical rain forest fragments in Brazil varied according to the treatment of adjacent cleared forest (Stouffer and Bierregaard, 1995). *Cecropia* trees primarily colonized cleared land which was abandoned after cutting, while forest areas which were burned following clearing were colonized by a different tree species, *Vismia*. Interestingly, bird species composition of the intact rain forest remnants was determined primarily by the type of secondary growth surrounding the fragments, rather than by fragment size (Stouffer and Bierregaard, 1995).

### 3.6. Fragment heterogeneity

A factor shown to be partially responsible for the relationships found between species composition and fragment spatial characteristics is the degree of habitat heterogeneity within isolated fragments. Large fragments are more likely to contain a greater variety of soil types, greater topographic variation, greater microclimatic variation, and a greater number of habitat types than small fragments (Pickett and Thompson, 1978; Picton, 1979; Boecklen, 1986). Fragments of approximately equal size which are relatively heterogeneous tend to support a greater number and variety of species than those which are more homogeneous (Picton, 1979; Simberloff and Gotelli, 1984; Boecklen, 1986; Newmark, 1986; Freemark and Merriam, 1986; MacDonald and Johnson, 1995; Maehr and Cox, 1995).

Populations of plants or animals in heterogeneous habitat fragments may be less susceptible to local extinction than those living in more homogeneous habitats (Den Boer, 1981; Kindvall, 1996). For example, populations of bush crickets in Sweden were more likely to persist if they occurred in an area which contained several vegetation types than in an area which contained only a single or small number of vegetation types (Kindvall, 1996). This result was largely due to the existence of greater microclimatic variation in the more heterogeneous habitats, which allowed some individuals to persist even under severe weather conditions. In contrast, areas with little vegetational diversity also exhibited little microclimatic variation; thus in severe weather, these cricket populations went extinct. This result suggests that maintenance or restoration of a high diversity of vegetation types within habitat remnants may be integral to long term population persistence.

An analysis of temperate zone, forest birds demonstrated that the structural diversity of forest vegetation significantly influenced bird species composition, in addition to forest fragment size (Boecklen, 1986). Habitat heterogeneity may be more significant for certain species than others. For example, diversity of plant species and forest vertical structure was most closely linked with the distribution of forest edge bird species in an agricultural landscape, and was secondarily important to forest interior species (Freemark, 1990). Species richness of mam-

mals in western North American national parks is strongly influenced by environmental heterogeneity, as well as park size (Newmark, 1986).

## 4. Spatial sequences of land transformation

Spatial and ecological characteristics of habitat fragments interact to influence abiotic processes and biotic processes within and between fragments in many types of landscapes. An integrated view of these spatial characteristics and their ecological consequences improves our ability to predict the outcomes of particular spatial patterns of land conversion (Franklin and Forman, 1987; Harris and Silva-Lopez, 1992; Hansen et al., 1992; Zipperer, 1993; Collinge, 1995; Forman, 1995) and to determine which patterns will likely be most favorable in maintaining ecological processes over the long term. Recent ecological modeling efforts in the context of forestry practices have investigated the consequences of fragment spatial characteristics on ecological processes, and provide clues for minimizing the negative effects of habitat fragmentation in future land conversion scenarios (Franklin and Forman, 1987; Hansen et al., 1992; Li et al., 1993; Spies et al., 1994; Wallin et al., 1994).

Franklin and Forman (1987) determined the geometric properties of clear-cut harvests of Douglas fir forests on federal lands in the Pacific Northwest, and predicted the ecological consequences of such a spatial distribution. The pattern of relatively small, dispersed clear-cuts drastically changed the spatial structure of these forested landscapes. In particular, dispersed cutting decreased the size of intact forest patches, increased the amount of edge habitat in these forests, and increased susceptibility of intact forest patches to wind-throw, fires, and pest outbreaks. Based on these changes in the spatial characteristics, the authors predicted that the richness of old-growth interior species would continue to decline in these forests if this pattern of cutting persisted (Franklin and Forman, 1987). Hence, they proposed alternative cutting regimes which would minimize these negative effects of forest fragmentation on plant and animal species composition.

Their proposed alternatives were modified slightly and recently evaluated quantitatively through com-

puter simulation (Li et al., 1993); the results were consistent with the predicted outcomes. The 'ecologically optimum' spatial pattern appears to involve aggregation of larger, clear-cut patches, which results in the least amount of forest fragmentation (Franklin and Forman, 1987; Li et al., 1993). While these results demonstrate the advantages of such an approach in the context of timber harvest practices, the emphasis on particular spatial patterns of land conversion which minimize habitat reduction and isolation is applicable to other types of land conversion, including development of roads, housing and agriculture, in many kinds of landscapes.

### 5. Importance to landscape architecture and planning

Incorporation of an understanding of the ecological consequences of particular fragment spatial characteristics increases the environmental benefit of landscape architecture and planning proposals. Landscape architects and planners are increasingly involved in projects explicitly aimed at using the principles of landscape ecology to preserve, restore and enhance biological diversity. For example, the restoration of three major wooded areas in New York's Central Park proposed by Andropogon Associates (Rogers, 1987; Cramer, 1993; Sauer, 1993) focused on maintaining large, intact forest patches within currently wooded areas of the park, connecting these patches to enhance movement of birds and mammals, and reducing exotic plant invasion and sedimentation caused by disturbed forest edges. To address these issues, Andropogon Associates devised a habitat corridor network for the park which included a continuous, 32 m (100 ft.) wide, wooded corridor connecting the three woodland areas, a 32 m (100 ft.) margin on woodland areas to ameliorate edge effects, and a 32 m (100 ft.) wide habitat corridor all along the park perimeter.

Although the Central Park habitat corridor scheme may seem an unlikely solution for a park in the midst of such an intensely urbanized area, the second-growth woods of the park are approximately 150 years old, and provide important food resources and a rest-stop for many species of migratory birds (Rogers, 1987). Bird species observed in Central

Park include the ovenbird and the woodthrush (Knowler, 1984), both of which are considered to require interior forest habitat for successful breeding (Gibbs and Faaborg, 1990; Porneluzi et al., 1993).

Recent ecological field research demonstrates that species loss and recolonization may be affected by vegetated corridors (see references above), but that the benefit of corridors may depend upon fragment size (Collinge, 1995). The potential implication for Central Park's woodlands is that the proposed habitat corridor network may be very effective in enhancing species persistence of the intermediate-sized forest fragment (The Ramble), but may be less effective in enhancing habitat values of the relatively small, 4-acre Hallett Nature Sanctuary (Sauer, 1993). Because there may be differences among species in their response to fragment size and connectivity, it would be revealing to evaluate the effectiveness of the corridor network scheme for the movement and maintenance of specific animal populations and communities within Central Park as the restoration project proceeds.

A recent proposal for the new town of Avalon Park, Florida, similarly addressed issues of habitat fragment size and connectivity. The proposal included residential and commercial development for 25 000 inhabitants adjacent to the Econlockhatchee River and associated wetlands near Orlando (Dunlop, 1990, 1992; Kreiger, 1991; Post, 1994). The town planners, DPZ Associates, considered the importance of habitat area and connectivity in their proposal, which included continuous greenbelts between the small villages located along the river. The centerpiece of the scheme was the Econ River preservation area, which included the river and its associated wetlands, and addressed concerns by local citizens regarding the potentially negative impacts of the proposed development on water quality and biological diversity.

Close examination of the proposed scheme revealed that the roadless portion of the Econ River preservation zone was approximately 254 ha. If residential development induces changes at the edges of this habitat, such as increased nest predation or shifts in microclimatic conditions, which are conservatively assumed to extend 50 m (suburban edge effects may extend as far as 80 m; Matlack, 1993b), then the total amount of interior area is reduced to

223 ha. Particularly in the urban/suburban context of the greater Orlando area, it is doubtful that this area would represent a preservation area in terms of maintaining source populations of animals over the long term.

The Avalon Park proposal assertively addressed the importance of maintaining large, connected fragments, but would be improved by considering explicitly the ways in which edge effects reduce effective patch size. Fragment size may exert a much greater influence on species richness than fragment connectivity. Thus, effort devoted to maintaining the integrity of large patches of native habitat should take precedence over connecting smaller habitat patches. Moreover, consideration of the context in which this remnant habitat will be situated might have revealed an opportunity for linkages with existing large, undeveloped areas of native vegetation in this region of central Florida.

Recently, a group of landscape architects at the University of Florida (Carr et al., 1994) identified areas with the highest potential to form a continuous biological corridor through the Central American isthmus, in order to benefit the region's biodiversity, reduce soil erosion, improve water quality and quantity, and reduce flooding. Existing protected areas in the region were categorized according to their size, degree of protection, extent of intact forest, and human population densities (Carr et al., 1994). Large areas with a high proportion of intact forest were considered particularly suitable as the basis for the chain of preservation areas. Based on these characteristics, the proposal recommended the Caribbean coast as the best hope for a continuous corridor through the region. This project creatively incorporated the spatial characteristics of habitat fragment size, connectivity, and the particular spatial context (i.e. proximity to areas of high human population densities) of potential protected areas.

The assumption that the Central American Corridor will maintain biological diversity by allowing movement among protected areas should next be verified by characterizing individual movement patterns of particularly important animal species. Vegetated corridors may provide habitat and facilitate movement of some animal species, but individual movement pathways do not always follow vegetated corridors. Moreover, corridors may modify patterns

of species loss and recolonization for particular species, but not for others. For example, rare species recolonized grassland fragments slowly, regardless of whether or not a corridor was present (Collinge, 1995). The implication is that not all species will be equally affected by the presence of a corridor which links suitable areas of native habitat.

## 6. Conclusion

Ecologists are increasingly able to understand and predict the consequences of human-induced loss and isolation of native habitats due to the concepts of island biogeography and metapopulation dynamics, combined with empirical field studies in fragmented habitats. The primary ecological consequences of habitat fragmentation are (1) loss of native plant and animal species, (2) invasion of exotic species, (3) increased soil erosion, and (4) decreased water quality. The magnitude and extent of these alterations induced by landscape change are influenced by the size, connectivity, shape, context, and heterogeneity of habitat fragments. Moreover, the particular spatial arrangement of habitat fragments may strongly influence ecological phenomena.

It is widely accepted that edge effects induced by human activities are negative. Newly created edges cause significant reductions in native plant and animal populations, alteration of community composition, and changes in ecosystem processes, and should thus be minimized in landscape interventions. Ecological evidence clearly shows that fragment size or area largely determines the extent to which a habitat remnant resembles continuous habitat. When possible, conservation or restoration of large expanses of native habitat is always desirable. The maintenance of riparian vegetation along streams and rivers is critically important to prevent soil erosion, maintain high water quality and provide habitat for riparian specialists. Corridors of native vegetation which link remnants of similar vegetation may provide habitat and facilitate movement of plants and animals. Corridors should be viewed as one of a suite of strategies in planning projects aimed at habitat conservation or restoration, because some species will not be affected by the presence of corridors. Both the shape and size of habitat fragments determine the degree of

interaction of the fragment with the surrounding habitat matrix. When possible, shape and/or orientation of conserved or restored habitat fragments may be readily manipulated to promote certain ecological processes. Because the context in which a remnant of native habitat is situated significantly influences interactions with the adjacent landscape, it must be an important consideration in landscape architecture and planning proposals. The degree of heterogeneity of a habitat fragment influences species richness and the likelihood of population persistence. Conservation or restoration of highly heterogeneous habitats is preferable to those which are more homogeneous. Processes of land conversion vary spatially; those which maintain large, connected patches of native vegetation with minimal edge will likely be more effective in protecting and preserving native species than those which produce small, widely scattered habitat patches.

Ecological investigations continue to focus on relationships between the spatial structure of the landscape and ecological processes. Further research is needed which tests specific hypotheses regarding the mechanisms by which plants and animals respond to landscape spatial structure. Elucidation of these mechanisms will yield greater precision and accuracy in our predictions of species responses to changes in landscape structure. Critical research topics include (1) comparisons of the permeability of habitat boundaries to various ecological phenomena, e.g. seed dispersal, nutrient flow, animal movement; (2) the importance of edge effects in habitats other than forests; (3) how particular species perceive the spatial structure of the habitat, and at what scale they respond to fragment spatial characteristics; (4) the importance of fragment context and heterogeneity for maintaining ecological processes; (5) the influence of particular spatial arrangements of native and disturbed habitats.

The fields of landscape ecology and landscape architecture and planning converge in their emphasis on the spatial structure of the landscape. Landscape architecture as a discipline is uniquely situated to integrate results of ecological studies of landscape spatial structure with social, cultural, and aesthetic concerns into the design of landscapes at many spatial scales. Because landscape architecture is a discipline focused on landscape change, as human

population growth continues, creative design of the spatial configuration of landscapes will become increasingly important in sustaining the integrity of ecological systems.

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### References

- Åberg, J., Vansson, G., Swenson, J.E. and Angelstam, P., 1995. The effect of matrix on the occurrence of hazel grouse (*Bonasa bonasia*) in isolated habitat fragments. *Oecologia*, 103: 265–269.
- Aizen, M.A. and Feinsinger, P., 1994. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology*, 75: 330–351.
- Ambrose, J.P. and Bratton, S.P., 1990. Trends in landscape heterogeneity along the borders of Great Smoky Mountains National Park. *Conserv. Biol.*, 4: 135–143.
- American Heritage Dictionary, 1979. Houghton-Mifflin, Boston, MA.
- Ås, S., 1993. Are habitat islands islands? Woodliving beetles (Coleoptera) in deciduous forest fragments in boreal forest. *Ecography*, 16: 219–228.
- Beier, P., 1993. Determining minimum habitat areas and habitat corridors for cougars. *Conserv. Biol.*, 7: 94–108.
- Beissinger, S.R. and Osborne, D.R., 1982. Effects of urbanization on avian community organization. *Condor*, 84: 75–83.
- Bennett, A.F., 1990. Habitat corridors: their role in wildlife management and conservation. Department of Conservation and Environment, Melbourne, Australia, 37 pp.

- Bierregaard, R.O., Jr., Lovejoy, T.E., Kapos, V., Augusto dos Santos, A. and Hutchings, R.W., 1992. The biological dynamics of tropical rainforest fragments. *BioScience*, 42: 859–866.
- Binford, M.W. and Buchenau, M., 1993. Riparian greenways and water resources. In: D.S. Smith and P.C. Hellmund (Editors), *Ecology of Greenways*. University of Minnesota Press.
- Blake, J.G., 1991. Nested subsets and the distribution of birds on isolated woodlots. *Conserv. Biol.*, 5: 58–66.
- Blake, J.G. and Karr, J.R., 1987. Breeding birds of isolated woodlots: area and habitat relationships. *Ecology*, 68: 1724–1734.
- Boecklen, W.J., 1986. Effects of habitat heterogeneity on the species–area relationships of forest birds. *J. Biogeogr.*, 13: 59–68.
- Brittingham, M.C. and Temple, S.A., 1983. Have cowbirds caused forest songbirds to decline? *BioScience*, 33: 31–35.
- Brocke, R.H., O’Pezio, J.P. and Gustafson, K.A., 1990. A forest management scheme mitigating impact of road networks on sensitive wildlife species. In: R.M. DeGraaf and W.M. Healy (Compilers), *Is Forest Fragmentation a Management Issue in the Northcast?* Gen. Tech. Rep. NE-140, US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, PA, pp. 13–17.
- Brothers, T.S., 1993. Fragmentation and edge effects in central Indiana old-growth forests. *Nat. Areas J.*, 13: 268–275.
- Brothers, T.S. and Spingarn, A., 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Conserv. Biol.*, 6: 91–100.
- Brown, J.H., 1971. Mountaintop mammals: nonequilibrium insular biogeography. *Am. Nat.*, 105: 467–478.
- 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.
- Carr, M.H., Lambert, J.D. and Zwick, P.D., 1994. Mapping of continuous biological corridor potential in Central America. Final Report, Paseo Pantera, University of Florida, Gainesville, FL.
- Chen, J., Franklin, J.F. and Spies, T.A., 1990. Microclimatic pattern and basic biological responses at the clear-cut edges of old-growth Douglas-fir stands. *Northwest Environ. J.*, 6: 424–425.
- Chen, J., Franklin, J.F. and Spies, T.A., 1992. Vegetation responses to edge environments in old-growth Douglas-fir forests. *Ecol. Appl.*, 2: 387–396.
- Colletti, J., Schultz, D., Faltonson, R. and Isenhardt, T., 1995. Creating a buffer. *Iowa Conserv.*, July/August.
- Collinge, S.K., 1995. Spatial arrangement of patches and corridors in the landscape: consequences for biological diversity and implications for landscape architecture. Ph.D. Dissertation, Harvard University, Cambridge, MA.
- Cramer, M., 1993. Urban renewal: restoring the vision of Olmsted and Vaux in Central Park’s woodlands. *Rest. Manage. Notes*, 11: 106–116.
- Cutler, A., 1991. Nested faunas and extinction in fragmented habitats. *Conserv. Biol.*, 5: 496–505.
- Den Boer, P.J., 1981. On the survival of populations in a heterogeneous and variable environment. *Oecologia*, 50: 39–53.
- Diamond, J., 1975. The island dilemma: lessons of modern biogeographic studies for the design of nature reserves. *Biol. Conserv.*, 7: 129–146.
- Diamond, J. and May, R.M., 1976. Island biogeography and the design of natural reserves. In: R.M. May (Editor), *Theoretical Ecology*. Saunders, Philadelphia, PA, pp. 163–186.
- Doak, D.F. and Mills, L.S., 1994. A useful role for theory in conservation. *Ecology*, 75: 615–626.
- Dodd, C.K., Jr., 1990. Effects of habitat fragmentation on a stream-dwelling species, the flattened musk turtle *Sternotherus depressus*. *Biol. Conserv.*, 54: 33–45.
- Dunlop, B., 1990. Breaking the code. *Architecture*, April.
- Dunlop, B., 1992. Community quest. *SF*, February: 72–77.
- Fahrig, L. and Merriam, G., 1985. Habitat patch connectivity and population survival. *Ecology*, 66: 1762–1768.
- Fahrig, L., Lefkovitch, L.P. and Merriam, G., 1983. Population stability in a patchy environment. In: W.K. Lauenroth, G.V. Skogerboe and M. Flug (Editors), *Analysis of Ecological Systems: State-of-the-Art in Ecological Modeling*. Elsevier, New York, pp. 61–67.
- Federowick, J.M., 1993. A landscape restoration framework for wildlife and agriculture in the rural landscape. *Landscape Urban Plann.*, 27: 7–17.
- Foppen, R. and Reijnen, R., 1994. The effects of car traffic on breeding bird populations in woodland. II. Breeding dispersal of male willow warblers (*Phylloscopus trochilus*) in relation to the proximity of a highway. *J. Appl. Ecol.*, 31: 95–101.
- Forman, R.T.T., 1995. *Land Mosaics: The Ecology of Landscapes and Regions*. Cambridge University Press, Cambridge.
- Forman, R.T.T. and Collinge, S.K., 1996. The ‘spatial solution’ to conserving biodiversity in landscapes and regions. In: R.M. DeGraaf and R.I. Miller (Editors), *Conservation of Faunal Diversity in Forested Landscapes*. Chapman and Hall, New York, pp. 537–568.
- Forman, R.T.T. and Godron, M., 1981. Patches and structural components for a landscape ecology. *BioScience*, 31: 733–740.
- Forman, R.T.T. and Godron, M., 1986. *Landscape Ecology*. John Wiley, New York.
- Forman, R.T.T., Galli, A.E. and Leck, C.F., 1976. Forest size and avian diversity in New Jersey woodlots with some land use implications. *Oecologia*, 26: 1–8.
- Foster, M.L. and Humphrey, S.R., 1995. Use of highway underpasses by Florida panthers and other wildlife. *Wildl. Soc. Bull.*, 23: 95–100.
- Franklin, J.F. and Forman, R.T.T., 1987. Creating landscape pattern by forest cutting: ecological consequences and principles. *Landscape Ecol.*, 1: 5–18.
- Freemark, K.E., 1987. Agricultural disturbance, wildlife and landscape management. In: M.R. Moss (Editor), *Landscape Ecology and Management*. Polyscience Publications, Inc., Montreal, Canada, pp. 77–84.
- Freemark, K.E., 1990. Landscape ecology of forest birds in the

- northeast. In: R.M. DeGraaf and W.M. Healy (Compilers), *Is Forest Fragmentation a Management Issue in the Northeast?* Gen. Tech. Rep. NE-140, US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, PA, pp. 7–12.
- Freemark, K.E. and Merriam, G., 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. *Biol. Conserv.*, 36: 115–141.
- Game, M., 1980. Best shape for nature reserves. *Nature*, 287: 630–632.
- Gardner, R.H., O'Neill, R.V. and Turner, M.G., 1993. Ecological implications of landscape fragmentation. In: M.J. McDonnell and S.T.A. Pickett (Editors), *Humans as Components of Ecosystems*. Springer, New York, pp. 208–226.
- Gibbs, J.P. and Faaborg, J., 1990. Estimating the viability of ovenbird and Kentucky warbler populations in forest fragments. *Conserv. Biol.*, 4: 193–196.
- Gilpin, M.E. and Soulé, M.E., 1986. Minimum viable populations: processes of species extinction. In: M.E. Soulé (Editor), *Conservation Biology*. Sinauer Associates, Sunderland, MA, pp. 19–34.
- Groom, M.J. and Schumaker, N., 1993. Evaluating landscape change: patterns of worldwide deforestation and local fragmentation. In: P.M. Kareiva, J.G. Kingsolver and R.B. Huey (Editors), *Biotic Interactions and Global Change*. Sinauer Associates, Sunderland, MA, pp. 24–44.
- Gutzwiller, K.J. and Anderson, S.H., 1992. Interception of moving organisms: influences of patch shape, size, and orientation on community structure. *Landscape Ecol.*, 6: 293–303.
- Hansen, A.J. and di Castri, F. (Editors), 1992. *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows*. Springer, New York.
- Hansen, A., Urban, D.L. and Marks, B., 1992. Avian community dynamics: the interplay of landscape trajectories and species life histories. In: A.J. Hansen and F. di Castri (Editors), *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows*. Springer, New York, pp. 170–195.
- Hanski, I., Pakkala, T., Kuussaari, M. and Lei, G., 1995. Metapopulation persistence of an endangered butterfly in a fragmented landscape. *Oikos*, 72: 21–28.
- Hansson, L., Fahrig, L. and Merriam, G. (Editors), 1995. *Mosaic Landscapes and Ecological Processes*. Chapman and Hall, London.
- Hardt, R.A. and Forman, R.T.T., 1989. Boundary form effects on woody colonization of reclaimed surface mines. *Ecology*, 70: 1252–1260.
- Harris, L.D., 1984. *The Fragmented Forest: Island Biogeography Theory and the Preservation of Biotic Diversity*. University of Chicago Press, Chicago, IL.
- Harris, L.D. and Gallagher, P.B., 1989. New initiatives for wildlife conservation: the need for movement corridors. In: G. Mackintosh (Editor), *Preserving Communities and Corridors. Defenders of Wildlife*, Washington, DC.
- Harris, L.D. and Scheck, J., 1991. From implications to applications: the dispersal corridor principle applied to the conservation of biological diversity. In: D.A. Saunders and R.J. Hobbs (Editors), *Nature Conservation 2: The Role of Corridors*. Surrey Beatty and Sons, Chipping Norton, Australia, pp. 189–220.
- Harris, L.D. and Silva-Lopez, G., 1992. Forest fragmentation and the conservation of biological diversity. In: P.L. Fiedler and S.K. Jain (Editors), *Conservation Biology*. Chapman and Hall, New York, pp. 198–237.
- Harrison, S., 1992. Toward a theory of inter-refuge corridor design. *Conserv. Biol.*, 6:293–295.
- Harrison, S., 1994. Metapopulations and conservation. In: P.J. Edwards, R.M. May and N.R. Webb (Editors), *Large-Scale Ecology and Conservation Biology*. Blackwell Scientific Publications, London, pp. 111–128.
- Henein, K. and Merriam, G., 1990. The elements of connectivity where corridor quality is variable. *Landscape Ecol.*, 4: 157–170.
- Herkert, J.R., 1994. The effects of habitat fragmentation on midwestern grassland bird communities. *Ecol. Appl.*, 4: 461–471.
- Hill, C.J., 1995. Linear strips of rain forest vegetation as potential dispersal corridors for rain forest insects. *Conserv. Biol.*, 9: 1559–1566.
- Hopkins, P.J. and Webb, N.R., 1984. The composition of the beetle and spider faunas on fragmented heathlands. *J. Appl. Ecol.*, 21: 935–946.
- Hunter, M.L., Jr., 1990. *Wildlife, Forests, and Forestry*. Prentice-Hall, Englewood Cliffs, NJ.
- Ims, R.A., 1995. Movement patterns related to spatial structures. In: L. Hansson, L. Fahrig and G. Merriam (Editors), *Mosaic Landscapes and Ecological Processes*. Chapman and Hall, London, pp. 85–109.
- Janzen, D.H., 1983. No park is an island: increase in interference from outside as park size increases. *Oikos*, 41: 402–410.
- Jennersten, O., 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. *Conserv. Biol.*, 2: 359–366.
- Johnson, A.S., 1989. The thin green line: riparian corridors and endangered species in Arizona and New Mexico. In: G. Mackintosh (Editor), *Preserving Communities and Corridors. Defenders of Wildlife*, Washington, DC, pp. 35–46.
- Kareiva, P., 1987. Habitat fragmentation and the stability of predator–prey interactions. *Nature*, 326: 388–390.
- Kindvall, O., 1996. Habitat heterogeneity and survival in a bush cricket metapopulation. *Ecology*, 77: 207–214.
- Klein, B.C., 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology*, 70: 1715–1725.
- Knaapen, J.P., Scheffer, M. and Harms, B., 1992. Estimating habitat isolation in landscape planning. *Landscape Urban Plann.*, 23: 1–16.
- Knowler, D., 1984. *The Falconer of Central Park*. Karz-Cohl, New York.

- Kreiger, A., 1991. *Andres Duany and Elizabeth Plater-Zyberk: Towns and Town-Making Principles*. Rizzoli Publications, New York.
- Kruess, A. and Tscharntke, T., 1994. Habitat fragmentation, species loss, and biological control. *Science*, 264: 1581–1584.
- Laan, R. and Verboom, B., 1990. Effects of pool size and isolation on amphibian communities. *Biol. Conserv.*, 54: 251–262.
- Lankester, K., van Apeldoorn, R., Meelis, E. and Verboom, J., 1991. Management perspectives for populations of the Eurasian badger (*Meles meles*) in a fragmented landscape. *J. Appl. Ecol.*, 28: 561–573.
- La Polla, V.N. and Barrett, G.W., 1993. Effects of corridor width and presence on the population dynamics of the meadow vole (*Microtus pennsylvanicus*). *Landscape Ecol.*, 8: 25–37.
- Laurance, W.F., 1990. Comparative responses of five arboreal marsupials to tropical forest fragmentation. *J. Mammal.*, 71: 641–653.
- Laurance, W.F., 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. *Conserv. Biol.*, 5: 79–89.
- Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.*, 15: 237–240.
- Lewis, P.H., Jr., 1969. Upper Mississippi River Comprehensive Basin Study. Appendix B. Aesthetic and Cultural Values. Department of the Interior, United States National Park Service, Northeast Region.
- Li, H., Franklin, J.F., Swanson, F.J. and Spies, T.A., 1993. Developing alternative forest cutting patterns: a simulation approach. *Landscape Ecol.*, 8: 63–75.
- Likens, G.E., Bormann, F.H., Johnson, N.M., Fisher, D.W. and Pierce, R.S., 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. *Ecol. Monogr.*, 40: 23–47.
- Lima, S.L. and Zollner, P.A., 1996. Towards a behavioral ecology of landscapes. *Trends Ecol. Evol.*, 11: 131–135.
- Lindenmayer, D.B., 1994. Wildlife corridors and the mitigation of logging impacts on fauna in wood-production forests in south-eastern Australia: a review. *Wildl. Res.*, 21: 323–340.
- Lindenmayer, D.B. and Nix, H.A., 1993. Ecological principles for the design of wildlife corridors. *Conserv. Biol.*, 7: 627–630.
- Lovejoy, T.E., Rankin, J.M., Bierregard, R.O., Jr., Brown, K.S., Jr., Emmons, L.H. and van der Voort, M.E., 1984. Ecosystem decay of Amazon forest remnants. In: M.H. Nitecki (Editor), *Extinctions*. University of Chicago Press, Chicago, IL, pp. 295–325.
- Lovejoy, T.E., Bierregard, R.O., Jr., Rylands, A.B., Malcolm, J.R., Quintela, C.E., Harper, L.H., Brown, K.S., Jr., Powell, A.H., Powell, G.V.N., Schubart, H.O.R. and Hays, M.B., 1986. Edge and other effects of isolation on Amazon forest fragments. In: M.E. Soulé (Editor), *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, MA, pp. 257–285.
- Loye, J. and Carroll, S., 1995. Birds, bugs and blood: avian parasitism and conservation. *Trends Ecol. Evol.*, 10: 232–235.
- Lyle, J.T., 1985. *Design for Human Ecosystems*. Van Nostrand Reinhold, New York.
- Lynch, J.F., 1987. Responses of breeding bird communities to forest fragmentation. In: D.A. Saunders, G.W. Arnold, A.A. Burbidge and A.J.M. Hopkins (Editors), *Nature Conservation: The Role of Remnants of Native Vegetation*. Surrey Beatty and Sons, Chipping Norton, Australia, pp. 123–140.
- MacArthur, R.H. and Wilson, E.O., 1963. An equilibrium theory of insular zoogeography. *Evolution*, 17: 373–387.
- MacArthur, R.H. and Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- MacDonald, D.W. and Johnson, P.J., 1995. The relationship between bird distribution and the botanical and structural characteristics of hedges. *J. Appl. Ecol.*, 32: 492–505.
- Maehr, D.S. and Cox, J.A., 1995. Landscape features and panthers in Florida. *Conserv. Biol.*, 9: 1008–1019.
- Matlack, G.R., 1993a. Microenvironment variation within and among forest edge sites in the eastern United States. *Biol. Conserv.*, 66: 185–194.
- Matlack, G.R., 1993b. Sociological edge effects: spatial distribution of human impact in suburban forest fragments. *Environ. Manage.*, 17: 829–835.
- McDonnell, M.J., Pickett, S.T.A. and Pouyat, R.V., 1993. The application of the ecological gradient paradigm to the study of urban effects. In: M.J. McDonnell and S.T.A. Pickett (Editors), *Humans as Components of Ecosystems*. Springer, New York, pp. 175–189.
- McHarg, I.L., 1969. *Design with Nature*. Natural History Press, New York.
- McHarg, I.L. and Sutton, J., 1975. Ecological plumbing for the Texas coastal plain. *Landscape Arch.*, January: 78–89.
- McNeely, J.A., Miller, K.R., Reid, W.V., Mittermeier, R.A. and Werner, T.B., 1990. *Conserving the World's Biological Diversity*. IUCN, Gland, Switzerland; WRI, CI, WWF-US, and The World Bank, Washington, DC.
- Miller, K. and Tangley, L., 1991. *Trees of Life: Saving Tropical Forests and their Biological Wealth*. Beacon Press, Boston, MA.
- Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. *Trends Ecol. Evol.*, 10: 58–62.
- Naiman, R.J., Décamps, H. and Pollock, M., 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecol. Appl.*, 3: 209–212.
- Newmark, W.D., 1986. Mammalian richness, colonization, and extinction in western North American national parks. Ph.D. Dissertation, University of Michigan, Ann Arbor, MI.
- Newmark, W.D., 1991. Tropical forest fragmentation and the local extinction of understory birds in the eastern Usambara Mountains, Tanzania. *Conserv. Biol.*, 5: 67–78.
- Noss, R.F., 1987. Corridors in real landscapes: a reply to Simberloff and Cox. *Conserv. Biol.*, 1: 159–164.
- O'Neill, R.V., Krummel, J.R., Gardner, R.H., Sugihara, G., Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M.G., Zygmunt, B., Christensen, S.W., Dale, V.H. and Graham, R.L., 1988. Indices of landscape pattern. *Landscape Ecol.*, 1: 153–162.

- Opdam, P., 1991. Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. *Landscape Ecol.*, 5: 93–106.
- Peterjohn, W.T. and Correll, D.L., 1984. Nutrient dynamics in an agricultural watershed: observations on the role of a riparian forest. *Ecology*, 65: 1466–1475.
- Pickett, S.T.A. and Thompson, J.N., 1978. Patch dynamics and the design of nature reserves. *Biol. Conserv.*, 13: 27–37.
- Picton, H.D., 1979. The application of insular biogeographic theory to the conservation of large mammals in the northern Rocky Mountains. *Biol. Conserv.*, 15: 73–79.
- Porneluzi, P., Bednarz, J.C., Goodrich, L.J., Zawada, N. and Hoover, J., 1993. Reproductive performance of territorial ovenbirds occupying forest fragments and a contiguous forest in Pennsylvania. *Conserv. Biol.*, 7: 618–622.
- Post, N., 1994. Putting brakes on suburban sprawl. *Eng. News-Rec.*, 9: 32–38.
- Powell, A.H. and Powell, G.V.N., 1987. Population dynamics of male euglossine bees in Amazonian forest fragments. *Biotropica*, 19: 176–179.
- Pringle, C.M., 1991. U.S.–Romanian environmental reconnaissance of the Danube delta. *Conserv. Biol.*, 5: 442–445.
- Ranney, J.W., Bruner, M.C. and Levenson, J.B., 1981. The importance of edge in the structure and dynamics of forest islands. In: R.L. Burgess and D.M. Sharpe (Editors), *Forest Island Dynamics in Man-Dominated Landscapes*. Springer, New York, pp. 68–95.
- Remmert, H. (Editor), 1994. *Minimum Animal Populations*. Springer, Berlin.
- Rex, K.D. and Malanson, G.P., 1990. The fractal shape of riparian forest patches. *Landscape Ecol.*, 4: 249–258.
- Robinson, G.R., Holt, R.D., Gaines, M.S., Hamburg, S.P., Johnson, M.L., Fitch, H.S. and Martinko, E.A., 1992. Diverse and contrasting effects of habitat fragmentation. *Science*, 257: 524–526.
- Rodiek, J.E. and DelGuidice, G. (Editors), 1994. *Wildlife habitat conservation: its relationship to biological diversity and landscape sustainability*. *Landscape Urban Plann.*, Special Issue, 28.
- Rogers, E.B., 1987. *Rebuilding Central Park: A Management and Restoration Plan*. MIT Press, Cambridge, MA.
- Sauer, L., 1993. The North Woods of Central Park. *Landscape Arch.*, March: 55–57.
- Saunders, D.A. and Hobbs, K.H. (Editors), 1991. *Nature Conservation 2: The Role of Corridors*. Surrey Beatty and Sons, Chipping Norton, Australia.
- Saunders, D.A., Hobbs, R.J. and Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. *Conserv. Biol.*, 5: 18–32.
- Schonewald-Cox, C.M. and Bayless, J.W., 1986. The boundary model: a geographical analysis of design and conservation of nature reserves. *Biol. Conserv.*, 38: 305–322.
- Schonewald-Cox, C.M. and Buechner, M., 1992. Park protection and public roads. In: P.L. Fiedler and S.K. Jain (Editors), *Conservation Biology*. Chapman and Hall, New York, pp. 373–395.
- Simberloff, D.S. and Gotelli, N.J., 1984. Effects of insularization on plant species richness in the prairie–forest ecotone. *Biol. Conserv.*, 29: 27–46.
- Soulé, M.E. (Editor), 1987. *Viable Populations for Conservation*. Cambridge University Press, Cambridge.
- Soulé, M.E., 1991. Land use planning and wildlife maintenance. *J. Am. Plann. Assoc.*, 57: 313–323.
- Soulé, M.E., Bolger, D.T., Alberts, A.C., Wright, J., Sorice, M. and Hill, S., 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv. Biol.*, 2: 75–92.
- Spies, T.A., Ripple, W.J. and Bradshaw, G.A., 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. *Ecol. Appl.*, 4: 555–568.
- Stamps, J.A., Buechner, M. and Krishnan, V.V., 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. *Am. Nat.*, 129: 533–552.
- Stouffer, P.C. and Bierregaard, R.O., Jr., 1995. Use of amazonian forest fragments by understory insectivorous birds. *Ecology*, 76: 2429–2445.
- Taylor, R.D., Fahrig, L., Henein, K. and Merriam, G., 1993. Connectivity is a vital element of landscape structure. *Oikos*, 68: 571–573.
- Terborgh, J., 1986. Keystone plant resources in the tropical forest. In: M.E. Soulé (Editor), *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, MA, pp. 330–344.
- Terborgh, J. and Winter, B., 1980. Some causes of extinction. In: M.E. Soulé and B.A. Wilcox (Editors), *Conservation Biology: An Evolutionary-Ecological Perspective*. Sinauer Associates, Sunderland, MA, pp. 119–133.
- Thorne, J., Huang, C-S., Hatley, M.T., III and Mathur, A., 1991. Applying the landscape ecological aesthetic to land acquisition planning in the Upper Schoharie Watershed, Catskill Mountains, New York. CELA Conference Proceedings, Vol. III. Landscape Architecture Foundation, Washington, DC.
- Turner, M.G., 1989. Landscape ecology: the effect of pattern on process. *Annu. Rev. Ecol. Syst.*, 20: 171–197.
- Verboom, B. and van Apeldoorn, R., 1990. Effects of habitat fragmentation on the red squirrel, *Sciurus vulgaris* L. *Landscape Ecol.*, 4: 171–176.
- Verner, J., Morrison, M.L. and Ralph, C.J. (Editors), 1986. *Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates*. University of Wisconsin Press, Madison, WI.
- Wales, B.A., 1972. Vegetation analysis of north and south edges in a mature oak–hickory forest. *Ecol. Monogr.*, 42: 451–471.
- Wallin, D.O., Swanson, F.J. and Marks, B., 1994. Landscape pattern response to changes in pattern generation rules: land-use legacies in forestry. *Ecol. Appl.*, 4: 569–580.
- Webb, N.R. and Hopkins, P.J., 1984. Invertebrate diversity on fragmented *Calluna* heathland. *J. Appl. Ecol.*, 21: 921–933.
- Webb, N.R. and Thomas, J.A., 1994. Conserving insect habitats in heathland biotopes: a question of scale. In: P.J. Edwards, R.M. May and N.R. Webb (Editors), *Large-Scale Ecology and Conservation Biology*. Blackwell Scientific Publications, Oxford, pp. 129–151.

- Webb, N.R. and Vermaat, A.H., 1990. Changes in vegetational diversity on remnant heathland fragments. *Biol. Conserv.*, 53: 253–264.
- Wegner, J.F. and Merriam, G., 1979. Movements by birds and small mammals between a wood and adjoining farmland habitats. *J. Appl. Ecol.*, 16: 349–357.
- Whitcomb, R.R., Robbins, C.S., Lynch, J.F., Whitcomb, B.L., Klimkiewicz, M.K. and Bystrak, D., 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. In: R.L. Burgess and D.M. Sharpe (Editors), *Forest Island Dynamics in Man-dominated Landscapes*. Springer, New York, pp. 125–205.
- Whitney, G.G. and Somerlot, W.J., 1985. A case study of woodland continuity and change in the American Midwest. *Biol. Conserv.*, 31: 265–287.
- Wiens, J.A., 1992. Ecological flows across landscape boundaries: a conceptual overview. In: A.J. Hansen and F. di Castri (Editors), *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows*. Springer, New York, pp. 217–235.
- Wiens, J.A., Crawford, C.S. and Gosz, J.R., 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos*, 45: 421–427.
- Wilcove, D.S., 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology*, 66: 1211–1214.
- Wilcove, D.S., McLellan, C.H. and Dobson, A.P., 1986. Habitat fragmentation in the temperate zone. In: M.E. Soulé (Editor), *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, MA, pp. 237–256.
- Wilcox, B.A., 1980. Insular ecology and conservation. In: M.E. Soulé and B.A. Wilcox (Editors), *Conservation Biology: An Evolutionary-Ecological Perspective*. Sinauer Associates, Sunderland, MA.
- Wilcox, B.A. and Murphy, D.D., 1985. Conservation strategy: the effects of fragmentation on extinction. *Am. Nat.*, 125: 879–887.
- Wright, S.J. and Hubbell, S.P., 1983. Stochastic extinction and reserve size: a focal species approach. *Oikos*, 41: 466–476.
- Yahner, T.G., Korostoff, N., Johnson, T.P., Battaglia, A.M. and Jones, D.R., 1995. Cultural landscapes and landscape ecology in contemporary greenway planning, design and management: a case study. *Landscape Urban Plann.*, 33: 295–316.
- Young, A. and Mitchell, N., 1993. Microclimate and vegetation edge effects in a fragmented podocarp–broadleaf forest in New Zealand. *Biol. Conserv.*, 67: 63–72.
- Zipperer, W.C., 1993. Deforestation patterns and their effects on forest patches. *Landscape Ecol.*, 8: 177–184.
- Zube, E., 1986. The advance of ecology. *Landscape Arch.*, March/April: 58–67.