

Is Landscape Connectivity Necessary and Sufficient for Wildlife Management?

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Landscape connectivity is a central issue in conservation and wildlife management. Nevertheless, connectivity has eluded a precise definition and has been difficult to quantify and implement in practice. Neutral landscape models, derived from percolation theory, have been presented as a quantitative tool for defining landscape connectivity. In this framework, landscape connectivity is defined by the likelihood of having a connected cluster of habitat that spans the landscape (the *percolation cluster*). Connectivity emerges as a consequence of the scale at which organisms interact with the scale of fragmentation (e.g., a species' gap-crossing abilities). Thus, habitat need not be adjacent to be considered connected if the organism has good gap-crossing abilities. I analyzed species' perceptions of landscape connectivity for different forest management scenarios modeled with fractal neutral landscapes. Although all landscapes with >40% forest were perceived to be connected, gap-sensitive species (incapable of crossing non-forest gaps) actually perceived fragmented landscapes (timber harvest conducted at fine scales) to be more connected than clumped landscapes (timber harvest conducted at a coarse scale) when half (40-60%) of the landscape was forested. A percolation cluster was more likely to form on fragmented landscapes because of the more dispersed habitat distribution. Nevertheless, these landscapes had less suitable habitat (connected habitat meeting the MAR of the species) and supported smaller populations than clumped landscapes. Landscape connectivity (or habitat connectivity at some scale) may thus be a necessary, but not sufficient condition, for wildlife management. Assessment of connectivity is further complicated by the fact that species may exhibit different scales of movement in response to different scales of patchiness on the landscape. Maintenance of connectivity at a variety of scales will ultimately be necessary for successful conservation and wildlife management.

Key words: connectivity, dispersal, forest fragmentation, fractal landscapes, gaps, habitat corridors, hierarchy, movement, neutral landscape models, perceptual resolution, percolation theory, scale

1. INTRODUCTION

With the recognition that forestry and wildlife management must be implemented at a broader ecosystem or landscape scale

(Salwasser, 1991; Franklin, 1993; Petit et al., 1995; Beattie, 1996; Thomas, 1996) has come the challenge of maintaining or restoring the integrity of landscapes and their associated ecosystems. A disruption in the structural integrity of landscapes, owing to disturbances such as anthropogenic habitat loss and fragmentation, is expected to impede ecological flows of wa-

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ter, nutrients, energy, and the movement (dispersal) of organisms across the landscape (Gardner et al., 1993). Subsequently, a disruption in landscape structure may compromise its functional integrity, by interfering with the critical ecological processes necessary for population persistence and the maintenance of biodiversity and ecosystem health. *Landscape connectivity* thus involves both a structural component (the amount and spatial distribution of habitat on the landscape) and a functional component (the interaction of ecological flows with landscape pattern). A landscape that is structurally connected is assumed to be functionally connected. For example, dispersal should occur freely within contiguous habitat or among patches connected by corridors, and as a result, populations are well connected and the species is able to persist on the landscape. The principal concern facing wildlife and land managers in today's increasingly fragmented forests, however, is whether a landscape can maintain its functional integrity even if it is not structurally connected.

In this chapter, I review issues related to the definition and quantification of landscape connectivity, particularly as these apply to the management of the structural and functional integrity of forested landscapes. I present an analysis of different forest management scenarios to evaluate how species that differ in their minimum area requirements and gap-crossing abilities are affected by different intensities and patterns of timber harvest that fragment the landscape. This permits a species-centered assessment of the suitability and connectivity of landscapes, which is a necessary perspective if we are to implement successful strategies for wildlife and conservation management in fragmented forests.

2. PERSPECTIVES ON LANDSCAPE CONNECTIVITY

Although connectivity is considered a "vital element of landscape structure" (Taylor et al., 1993), it has eluded a precise definition and has been difficult to quantify and implement in practice. Two perspectives have emerged, however, which reflect different conceptualizations of landscape structure (Wiens, 1994;

1995). The first derives from island biogeographic theory, in which habitat fragments are viewed as analogues of oceanic islands in an inhospitable sea or ecologically neutral matrix (e.g., forest fragments in an agricultural matrix). The second is the landscape mosaic perspective, in which landscapes are viewed as spatially complex, heterogeneous assemblages of habitats, which can not be simply categorized into discrete elements such as patches, matrix and corridors.

2.1 Habitat Corridors: Lifelines or Landmines?

Strategies for conservation management and reserve design tend to consider connectivity in a very literal sense, by advocating the creation of habitat corridors between isolated habitat fragments or between reserves in a regional reserve network (Noss, 1991). Corridors are intended to facilitate movement or dispersal of organisms between habitat patches in the hopes that metapopulation dynamics will be maintained on the landscape (Hansson, 1991). Corridors are clearly a legacy of an island biogeographic or patch-based view of the world. Landscape structure is viewed in simple terms of habitat patches embedded within an inhospitable matrix, such that habitat corridors are required to facilitate dispersal among isolated fragments (Figure 1). Emphasis is placed on the structural component of connectivity, but the expectation (or hope) is that corridors will also restore the functional integrity of landscapes.

Although intuitively appealing, evidence in support of corridors is equivocal (Simberloff and Cox, 1987; Simberloff et al., 1992; Hobbs, 1992; Mann and Plummer, 1995). Some species use them, others do not. Species documented to use corridors are generally those that are unable or unwilling to cross gaps of unsuitable habitat (i.e., the inhospitable matrix). Small mammals, such as chipmunks (*Tamias striatus*), white-footed mice (*Peromyscus leucopus*) and voles (*Microtus pennsylvanicus*), use corridors in the form of fencerows connecting woodlots (chipmunks, deer mice) or experimentally created vegetative strips among old-field patches (voles), presumably because corridors provided increased cover and safety from

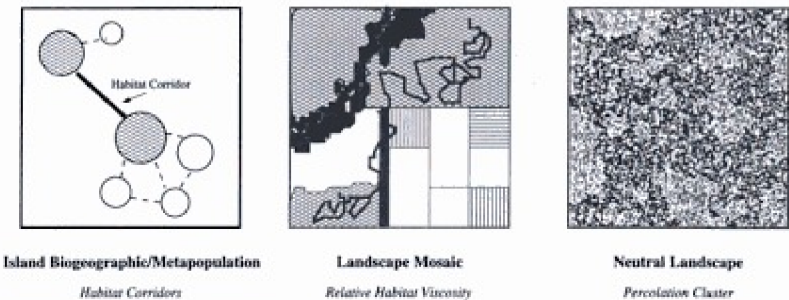


Figure 1. Different perspectives on landscape connectivity. The Island Biogeographic/Metapopulation perspective views landscape structure in terms of discrete elements such as patches, habitat corridors, and an "inhospitable matrix." Habitat corridors are deemed necessary to facilitate dispersal between isolated fragments to maintain metapopulation dynamics [dashed lines indicate dispersal between adjacent populations, some of which act as sources (shaded) or sinks]. The Landscape Mosaic perspective represents landscape structure as a spatially complex mosaic of different habitat types and landscape elements (rivers, roads). Connectivity is defined on the basis of the differential movement of organisms through habitat. Habitat may differ in its "viscosity" or resistance to movement, facilitating movement through certain elements of the landscape and impeding it in others. The solid, convoluted line represents the movement pathway of a hypothetical organism through this landscape mosaic. Note that it is deflected by certain habitat boundaries (e.g., agricultural fields). Neutral Landscapes offer a means of quantifying landscape connectivity, based on the movement responses (gap-crossing abilities) of species. Transitions in landscape connectivity can be determined by the presence or absence of a single cluster of habitat that spans the entire landscape (percolation cluster shown in black; additional habitat not part of the percolation cluster shown in gray).

predators relative to the surrounding matrix (Wegner and Merriam, 1979; Henderson et al., 1985; La Polla and Barrett, 1993).

Even highly vagile organisms, such as birds and large carnivores, which can easily traverse areas of unsuitable habitat may nevertheless be reluctant to do so. Birds, with their prodigious flight capabilities, may nevertheless utilize corridors to locate patchily distributed food resources or isolated patches of breeding habitat on a landscape (Haas, 1995; Machtans et al., 1996). Cougars (*Felis concolor*) may also benefit from well-placed corridors on the landscape (Beier, 1993; 1996). Urban sprawl has resulted in the increasing isolation of cougar populations among the mountain ranges of southern California. Persistence of this metapopulation is critically dependent upon maintaining dispersal among populations, which is facilitated by riparian corridors or by freeway under-

passes which minimize traffic-related mortality.

Wolves (*Canis lupus*), however, traverse fragmented landscapes without benefit of corridors, as evidenced by the recolonization in recent years of areas in Montana where they had been extirpated (Forbes and Boyd, 1997). Wolves are such effective dispersers, barring human persecution or interference, that discrete corridors connecting populations (e.g., reintroduced wolf packs in Idaho and Yellowstone National Park) may not be necessary as long as the overall structural integrity of the landscape is maintained ("broad landscape linkages already in use by wolves;" Forbes and Boyd, 1997).

Reliance upon corridors may be influenced by the surrounding landscape context (Anderson and Danielson, 1997). Bachman's Sparrow (*Aimophila aestivalis*) was primarily a

forest species prior to the logging of open, mature pine forest in the southeast, but now nests in open habitats of early pine regeneration that contain the open shrub and understory conditions preferred by this species (4-7 years post-harvest; Dunning et al. 1995). Subsequently, most of the forest now represents unsuitable habitat and colonization of clearcuts of suitable age, which are distributed as isolated patches, is facilitated by dispersal along corridors of early-successional habitat such as utility right-of-ways.

Habitat specialists do not necessarily require corridors to locate suitable breeding habitat in fragmented landscapes, however. The northern Spotted Owl (*Strix occidentalis aurina*) requires old-growth forest for breeding, but is able to traverse nonforest habitat during juvenile dispersal (Gutiérrez and Harrison, 1996). Other studies have demonstrated, both theoretically and empirically, that habitat quality of the corridor itself may influence whether the corridor is ultimately used (Henein and Merriam, 1990; Bennett et al., 1994).

As these examples illustrate, it is difficult to predict whether species will utilize corridors, because this is not simply a function of body size or vagility. We lack basic information on species' gap-crossing abilities and thus their potential reliance on corridors for most vertebrates, especially amphibians and reptiles (Lidicker and Koenig, 1996). Direct observation or "tenacious tracking" of radio-tagged individuals has provided the strongest evidence of corridor use in some species, but is obviously time intensive, especially considering that corridor use may be infrequent (Haas, 1995; Beier, 1996). If a species can cross gaps of unsuitable habitat, corridors may not be necessary. Innovative approaches to measuring species' responses to gaps have recently been conducted in birds by quantifying the extent to which individuals can be lured into different matrix habitats or across gaps of varying sizes using taped playbacks of territorial songs or mobbing calls (Sieving et al., 1996; Rail et al., 1997; Desrochers and Hannon, 1997).

Thus, the jury is still out on the efficacy of corridors. Corridors are costly to construct if they are deemed necessary to maintain patch connectivity, and potentially costly to conser-

vation efforts if they also serve as conduits for predators, competitors or disease (e.g., Hess, 1994). The debate over the utility of corridors will probably never be resolved because it depends upon the nature of the target species and the structure of the landscape. In the meantime, it is assumed that a landscape connected by corridors is better than a fragmented landscape that is not (Beier and Noss, 1998). Landscape connectivity can be assessed and realized in other ways, however.

2.2 The Landscape Mosaic Perspective

A newly emerging perspective on landscape connectivity represents a departure from the traditional island biogeographic/metapopulation view of patches, matrix and corridors and instead characterizes landscapes as complex, heterogeneous mosaics comprised of multiple habitat types (Wiens, 1994; Wiens, 1995). This approach focuses on the differential responses of organisms to landscape structure. Landscape connectivity is assessed by the extent to which movement is facilitated or impeded through different habitat types across the landscape (Taylor et al., 1993; With et al., 1997; Pither and Taylor, 1998). Highly connected landscapes are those in which organisms can move easily among habitats, and landscapes with low connectivity contain habitats or configurations of habitat that resist the movement of organisms across the landscape (Figure 1).

Apart from its representation of the landscape, this perspective on landscape connectivity differs from the island biogeographic/metapopulation view in another important way: it explicitly incorporates an organismal or species-centered view of landscape structure (Pearson et al., 1996). We must guard against viewing landscapes purely in anthropocentric terms, or as a level of organization in the conventional ecological hierarchy that lies beyond the ecosystem level, but below that of the biome, both of which imply an area of broad spatial extent (King, 1997). Given that landscapes must be defined relative to the scale at which the organism or ecological process of interest operates (Wiens, 1989; With, 1994), it follows that connectivity of a given landscape must also be determined by how organisms

perceive and respond to landscape structure. Boundaries (e.g., habitat edges) that deflect some species will be readily traversed by others (Lidicker and Koenig, 1996). Thus, a landscape is not inherently connected or fragmented; the same landscape may in fact be both from the perspective of two different species that differ in their gap-crossing abilities or movement responses to landscape structure.

This perspective represents a more holistic view of landscapes, in that connectivity is an emergent property of landscapes resulting from the interaction of species with landscape structure. Note that this approach does not require the a priori dissection of the landscape into discrete elements, such as patches and corridors, because patch structure emerges from how, and at what scales, organisms interact with landscape heterogeneity (the abundance and distribution of habitat types). Patches are seldom discrete in nature, and the hierarchical patch structure characteristic of environmental heterogeneity is resolved differently by species depending upon the spatial grain and extent of their activities (Kotliar and Wiens, 1990). The perceptual resolution of an organism is defined by its grain, the finest scale of patchiness to which an organism responds, and its extent, the broadest scale of patchiness that it perceives and to which it responds (Kotliar and Wiens, 1990; With, 1994). This is analogous to the concept of an "ecological neighborhood" (Addicott et al., 1987) or "ambit" (Hutchinson, 1953), which define the appropriate spatial and temporal scales that bound a particular process (e.g., movement). Subsequently, corridors need not be discrete structures on the landscape (linear elements connecting patches), but may emerge from particular configurations of habitat that facilitate movement (Gustafson and Gardner, 1996).

How can this species-centered definition of landscape connectivity be operationalized and put into practice? How can we assess whether a given landscape is connected from the perspective of species that differ in their scale of interaction with landscape structure, in terms of their minimum area requirements and gap-crossing abilities? Neutral landscape models, developed in the field of landscape ecology, provide a means of quantifying landscape

connectivity based on species-specific movement rules.

3. A PRIMER TO NEUTRAL LANDSCAPE MODELS

Neutral landscape models are grid-based (raster) maps in which complex landscape patterns are created using theoretical spatial distributions (e.g., With, 1997; With and King, 1997). They are thus "neutral" to the biophysical processes that structure real landscapes. Neutral landscape models were inspired by *percolation theory*, which concerns the flow of liquids through material aggregates (percolation) and provides a quantitative means for describing connectivity in heterogeneous systems (Stauffer and Aharony, 1991). Robert Gardner and his colleagues (Gardner et al., 1987; Gardner and O'Neill, 1991) were quick to see the potential application of percolation theory for modeling ecological flows in heterogeneous landscapes. Neutral landscapes provide a useful null model for assessing the effect of spatial pattern on ecological processes, and for quantifying when landscape connectivity becomes disrupted (With and King, 1997; Pearson and Gardner, 1997).

In the framework of neutral landscape models, habitat connectivity is first determined by the ability of organisms to move among habitat cells, which is a function of the ability or willingness of a species to cross gaps of unsuitable or less-preferred habitat. The willingness to cross gaps may be further modified by the nature of the intervening matrix habitat; an organism may be willing to cross certain habitats and not others. Species' gap-crossing abilities are then used to identify whether a cluster of habitat spans the entire landscape (Figure 1). Such a landscape is considered to be connected because organisms moving among habitat cells within this percolation cluster would at least be able to disperse freely. Thus, the functional response of species to landscape pattern (gap-crossing ability) is used to identify a structural feature of the landscape that confers overall connectivity (percolation cluster). The use of percolation theory to identify regions of the landscape, such as percolation clusters, that facilitate dispersal for a given

species is a potentially powerful tool in the management and restoration of landscape connectivity.

At what point does the landscape become "disconnected?" Percolation theory predicts that this will occur abruptly, as a critical threshold, over a small range of habitat loss. Imagine a completely forested landscape. As habitat is destroyed, there is a decreasing probability that a landscape will remain connected with each subsequent loss (e.g., 10%) of forest cover. Habitat loss compromises the structural integrity of the percolation cluster, until finally only one or a few cells of habitat are holding the entire structure intact. These cells serve as critical links between regions of the percolation cluster, and once severed, abruptly fragment the percolation cluster into two or more segments; the landscape is no longer connected. As the threshold level of habitat loss is reached, the probability of having a connected landscape rapidly goes to zero when the percolation cluster is fragmented (i.e., the relationship between habitat loss and landscape connectivity is not linear). Thus, while landscape connectivity is a probabilistic function of habitat loss, the non-linear nature of this relationship makes it convenient to refer to landscapes as being either "connected" or "disconnected" (fragmented) with respect to this threshold.

The threshold level of habitat loss at which landscapes become disconnected depends on the scale at which organisms interact with the scale of patchiness on the landscape (i.e., a species' gap-crossing or dispersal ability relative to the gap-size distribution on the landscape; Dale et al., 1994; With and Crist, 1995; Pearson et al., 1996; With et al., 1997). For example, Pearson et al. (1996) used hierarchical random neutral landscapes, in which habitat abundance is varied at different levels in a nested fashion (the habitat distribution at the broader scale constrains the distribution at the next, finer scale) to model the hierarchical patch structure that exists in nature (Kotliar and Wiens, 1990; Figure 8.3 in Pearson and Gardner, 1997). A hypothetical species that lacked gap-crossing abilities (movement through adjacent habitat cells only; "Rule 1," Plotnick and Gardner, 1993) was very sensitive to the pattern of habitat loss. Fine-scale habitat

loss was more disruptive to dispersal in this species than if habitat loss occurred at a coarser scale. Although coarse-scale habitat loss created large gaps (e.g., clearcuts in a forested landscape), the remaining habitat was also distributed as large blocks which facilitated dispersal (at least within the forest stand). Thus, landscape connectivity was maintained across a greater degree of habitat loss under this scenario for a gap-sensitive species; that is, the critical threshold occurred at lower levels of remaining habitat when habitat was destroyed in large tracts than if fine-scale habitat loss (e.g., selective logging) occurred throughout the landscape.

Neutral landscape models have the advantage of permitting the unlimited exploration of how spatial pattern (e.g., owing to habitat loss and fragmentation) affects dispersal or some other ecological process across a wide range of landscape scenarios. Although most neutral landscape applications have been binary maps of habitat vs. non-habitat, heterogeneous landscape mosaics comprised of multiple habitat types can be generated (With and Crist, 1995; With et al., 1997). Real landscape maps (e.g., land-cover map layer within a GIS) can also be used. An example of such an application (albeit with binary maps of forest and agriculture) is an analysis of how current and projected patterns of land-use change in the central Amazon are expected to impact rainforest species that differ in their gap-crossing abilities and area requirements (minimum amount of connected habitat an organism requires; Dale et al., 1994). Species in this analysis were as diverse as jaguars (*Felis onca*; large area requirements and high gap-crossing ability), three-toed sloths (*Bradypus variegatus*; small area requirements and low gap-crossing ability), and insects (e.g., Euglossine bees, which forage over a broad area and thus have large area requirements, but very limited gap-crossing abilities); all of these species need to be considered in the development of a comprehensive management strategy. Gap-sensitive species with large area requirements (i.e., insects) were most sensitive to the different scenarios of deforestation; suitable habitat for such species was perceived to be lost at a much faster rate than the actual rate of forest loss. This study did not quantify landscape connectivity per se, but the authors rec-

ommended maintaining connectivity of forest patches particularly to prevent the extirpation of species with low gap-crossing abilities and large area requirements.

Although maintenance of landscape connectivity has become a central issue in conservation and wildlife management, organisms clearly require a certain amount of connected habitat to meet their minimum area requirements, as the Dale et al. (1994) study illustrates. Is habitat connectivity necessary and sufficient for assessing landscape suitability for a particular species? How is the amount of suitable habitat available to the organism (connected habitat meeting the minimum area requirements of the species) affected by habitat fragmentation? How does this affect assessment of landscape connectivity? To address these questions, I performed a spatial analysis similar to that conducted by Dale et al. (1994), but with fractal landscapes to provide a more general assessment of how habitat fragmentation affects the connectivity and suitability of landscapes for different species.

4. CONNECTIVITY OF SPECIES-DEFINED LANDSCAPES

The procedure used to assess the suitability and connectivity of species-defined landscapes follows that of Dale et al. (1994), but a general overview is presented here and detailed below for completeness. The gap-crossing ability of the species is used to determine whether individual cells of habitat are connected. The minimum area requirement (MAR) of the species imposes a filter on the landscape by identifying habitat that is not only connected, but also of sufficient area to support individual territories. The resulting *species-defined landscape* can then be analyzed for connectivity, based on the species' gap-crossing abilities.

4.1 Spatial Analyses

4.1.1 Generation of Forested Landscapes

Neutral landscape maps were generated as 256 x 256-cell grids (i.e., raster maps) using the midpoint displacement algorithm to produce fractal distributions of habitat (see With et al., 1997, With 1997 for details). Spatial contagion

(clumping) of habitat can be adjusted by altering the value of a single parameter (H). For a given level of habitat abundance, landscape patterns can be produced that are clumped ($H = 1.0$) or extremely fragmented ($H = 0.0$; Figure 2). For this application, it will be assumed that these fractal landscapes are forested landscapes undergoing different intensities and patterns of timber harvest. Clumped fractal landscapes represent timber harvest conducted at a coarse scale by clearcutting extensive forested areas, whereas fragmented fractal landscapes represent fine-scale timber harvest (selective logging). While the absolute size of neutral landscapes is arbitrary, it is necessary to assign units of measurement in this application because the availability of habitat on the landscape will ultimately be based on the MAR (ha) of a given species. I will therefore consider the resolution of individual grid cells (pixels) to be 30 m, which is consistent with the resolution of widely available remotely sensed data (e.g., Landsat Thematic Mapper Imagery). Thus, each pixel is 0.09 ha (30 x 30 m) and the overall landscape is ~5900 ha or ~60 km². Again, the size of the landscape is not important for the objectives of this analysis; larger landscapes can be generated easily. My primary interest here is in understanding how the scale(s) at which species operate *relative* to the scale of landscape pattern affects assessment of habitat suitability and landscape connectivity. The results of this analysis should therefore not be taken literally, as applying to a particular species in a given landscape, but is useful to wildlife and land managers by analogy.

A total of 16 management scenarios were created by generating fractal neutral landscapes across eight levels of forest cover ($p = 0.01, 0.1, 0.2, \dots, 0.7$) and two levels of fragmentation (Clumped vs. Fragmented; Figure 2). Forest cover represents the intensity of harvest or degree of land transformation. Previous studies have demonstrated that landscapes with >70% habitat are well connected regardless of the spatial configuration of habitat or the gap-crossing abilities of the species (Gardner et al., 1989; With and Crist, 1995; Pearson et al., 1996; With et al., 1997; With and King, 1999a). Therefore, habitat levels above this were not analyzed. Forested landscapes with <10% cover have obviously undergone extensive transfor-

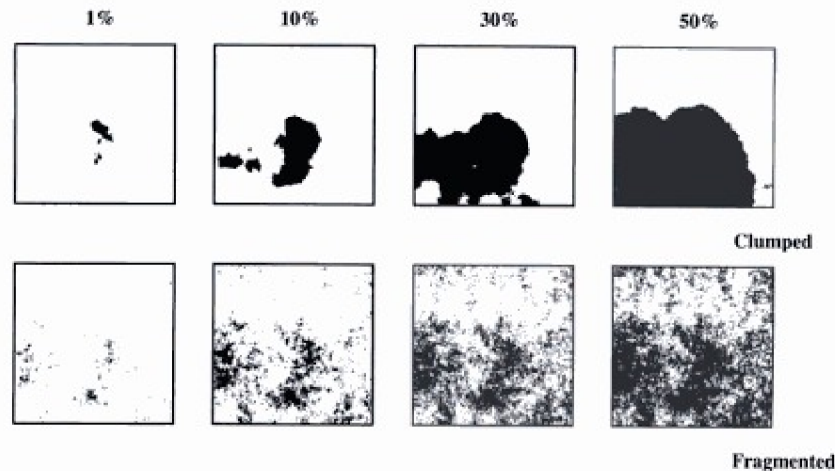


Figure 2. Fractal neutral landscapes at different levels of habitat abundance. These landscapes can be used to model different forest management scenarios. Timber harvest is conducted at either a coarse scale to create extensive clearcut areas so as to preserve large forest stands (Clumped), or at a fine scale via selective logging, producing an extensively fragmented forest (Fragmented).

mation, such as has occurred in the central hardwoods forest of the Midwest. While such landscapes may no longer be a concern from a forest management perspective, they nevertheless are a land management concern and serve to illustrate the extreme case. Five replicate landscapes were generated for each of the 16 management scenarios, resulting in a total of 80 landscape maps which served as the basis for this analysis of habitat suitability and connectivity in species-defined landscapes.

4.1.2 Species Characteristics

To explore a wide range of species' responses to landscape structure, I analyzed habitat suitability and connectivity from the standpoint of a suite of hypothetical species that differed in their gap-crossing abilities and MAR. Species differed in their MAR by four orders of magnitude (1, 10, 100, 1000 ha). Most forest passerines have territory sizes <1 ha, and small forest-dwelling mammals, such as deer mice and red-backed voles (*Clethrionomys californicus*) likewise have home ranges on the order of 1 ha or less (e.g., Nowak, 1991). Porcupines

(*Erethizon dorsatum*) and opossums (*Didelphis virginianus*) are examples of species with home range sizes around 10 ha, and mesopredators such as racoons (*Procyon lotor*) and striped skunks (*Mephitis mephitis*) may have home ranges in the vicinity of 100 ha (Nowak, 1991). Northern spotted owls require unusually large tracts of old-growth forest for breeding habitat (800 ha; Gutiérrez and Harrison, 1996). Pine martens (*Martes americana*) may likewise require suitable forested habitat on the order of 1000 ha (Nowak, 1991).

Gap-crossing abilities indicate the size of the non-forest gap the species is able or willing to cross. Species were either unable to cross gaps (gap-sensitive species) or could cross gaps of 1 cell (30 m) or 3 cells (90 m) in this analysis. In their search for forested cells, gap-sensitive (Gap = 0 cells) species were able to move among the eight neighboring cells (four adjacent cells, plus diagonals; "Rule 2" movement; Plotnick and Gardner, 1993). A species capable of crossing 1 cell of unsuitable habitat had a movement neighborhood of 24 cells (a 5 x 5-cell block centered on the individual's current

location), and a species capable of crossing 3 non-forested cells had a movement neighborhood of 80 cells (a 9 x 9-cell block).

The combinations of MAR and gap-crossing abilities give rise to 12 species-types (e.g., species with small area requirements and high gap-crossing abilities). Although terrestrial vertebrates with large area requirements also tend to be highly vagile and have good gap-crossing abilities, certain forest insects may need to cover large areas to find suitable food resources but are strongly influenced by microclimatic changes of forest openings which would prevent them from crossing gaps (large area requirements and limited gap-crossing ability; Dale et al., 1994).

4.1.3 Analytical Procedure

Analysis of species-defined landscapes for each management scenario ($n = 80$ maps) entailed the following steps:

- 1) Identify clusters of forested cells that are connected. A "cluster" is defined as a group of forested cells that can be accessed by an individual, based on its gap-crossing abilities. Thus, forested cells need not be adjacent within a cluster if the species can cross gaps;

- 2) Measure the size of each cluster on the landscape. The number of forested cells comprising each cluster identified in (1) is counted;

- 3) Assess suitability of clusters. Suitable forest clusters are those large enough to meet the area requirements of the species. Thus, forest clusters considered suitable for a species with an area requirement of 10 ha are > 111 forested cells in size in this application;

- 4) Produce species-defined landscape map. Only the suitable forest clusters (connected habitat meeting the MAR of the species) that were identified in (3) are retained. The amount of forest habitat remaining on the landscape and the total number of territories (units of minimum area) that can be supported (suitable habitat area/minimum area) are calculated; and,

- 5) Analysis of connectivity for species-defined landscapes. The species-defined landscape map generated in (4) was then surveyed for the presence of a percolation cluster (forest cluster that spans the landscape) using the species' gap-crossing abilities to quantify whether landscapes are connected.

To illustrate the implementation of this approach, consider a landscape with 10% forest cover (Figure 2). For a species with a MAR of 100 ha, most (99.6%) of the available habitat is suitable for this species if the forest cover is clumped (total suitable forest cover on species-defined landscape = 9.9%; Figure 3). Three of the patches on the original landscape are sufficiently large to meet the area requirements of this species; only a few isolated cells of forest on the periphery of the larger patches and one small patch are not suitable (compare Figures 2 and 3). In fragmented landscapes, however, less than half (46.2%) of the available habitat is suitable if the species lacks gap-crossing abilities (total forest cover on species-defined landscape = 4.6%; Figure 3). If the species has gap-crossing abilities, however, nearly twice as much forest cover is now suitable (total forest cover on species-defined landscape = 8.9%; Gap = 3, Figure 3). For gap-sensitive species, the clumped forested landscape is clearly the preferable management scenario, given that it supports nearly twice as many territories (or units of minimum area) as the fragmented landscape and 40% more territories than expected for a species with good gap-crossing abilities on the same fragmented landscape (Figure 3). Population sizes are thus likely to be greater on the clumped forested landscape. This does not indicate whether landscapes with such limited forest cover will actually be able to support viable populations of this species, however.

4.1.4 Overview of analyses

Analyses were conducted for gap-sensitive species (Gap = 0 cells) on clumped and fragmented landscapes, because differences were expected to be greatest between forest management scenarios for these species (80 landscapes x 4 levels of MAR = 320 species-defined landscapes analyzed). Initial analyses revealed that gap-crossing ability had a greater effect on the suitability and connectivity of fragmented landscapes than on clumped landscapes. Therefore, subsequent analyses focused on fragmented landscapes (40 landscapes x 4 levels of MAR x 3 levels of gap-crossing ability = 480 species-defined landscapes analyzed).

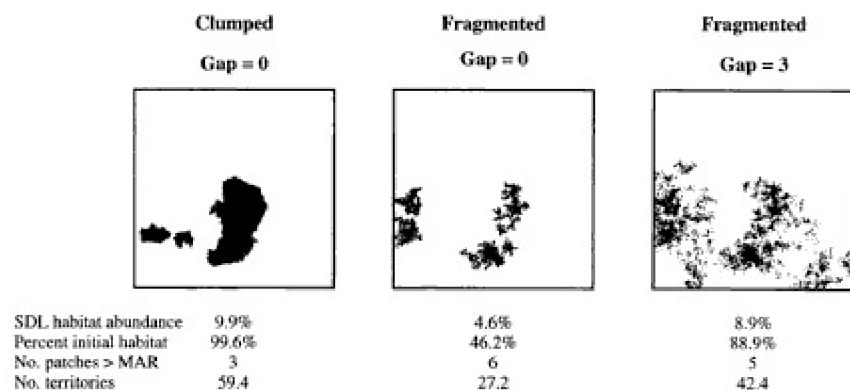


Figure 3. Species-defined landscapes. Landscapes are either 10% clumped or fragmented landscapes (see Figure 2). The suitability of forest cover is affected by the scale at which the species interacts with landscape pattern (i.e., its gap-crossing abilities). For a species requiring a minimum area of 100 ha, most of the forest cover on the clumped landscape is available even to a species incapable of crossing gaps of unsuitable habitat ("gap-sensitive species"). Only half of the available forest cover is suitable for gap-sensitive species on the fragmented landscape. If the species has good gap-crossing abilities, however, most of the forest can be utilized, although fewer territories can be supported on the fragmented landscape.

4.2 Results

Gap-sensitive species (Gap = 0 cells) were able to utilize nearly all of the available habitat when forest management preserved large tracts of forest (Clumped landscapes, Figure 4). The proportion of suitable habitat on the landscape exhibited a precipitous decline for gap-sensitive species with large area requirements (MAR = 100, 1000 ha), however. This is because the total amount of habitat on the landscape was less than the MAR of the species ($\leq 1\%$ for species with MAR = 100 ha; $\leq 10\%$ for species with MAR = 1000 ha). In contrast, gap-sensitive species on fragmented landscapes perceived a much faster rate of habitat loss relative to the actual percentage of forest cleared (Figure 4). Fragmentation significantly reduced the amount of suitable forest for gap-sensitive species if more than 40% (MAR = 100, 1000 ha) or 50% (MAR = 1, 10 ha) of the forest was cleared. The difference between management scenarios (effect of fragmentation) is greatest when habitat is limiting (e.g. 1-20%). Note, for

example, that a species with large area requirements (MAR = 1000 ha) could not be supported on a fragmented landscape with only 20% forest cover, but nearly 80% of available habitat would be deemed suitable (0.8 x 20% available = 16% suitable) if the landscape was managed to create large forest tracts (Figure 4). This is not to suggest that this will be sufficient habitat to support viable populations of this species, however.

Gap-crossing abilities clearly mitigated the effects of fragmentation (Figure 5). Even if a species was only able to cross a single cell of non-forest (30 m; Gap = 1 cell), a greater proportion of available forest cover was perceived to be suitable than for gap-sensitive species on fragmented landscapes. Species with good gap-crossing abilities (Gap = 3 cells) were generally able to use most of the available habitat on fragmented landscapes (Figure 5). At low levels of habitat abundance ($<30\%$), however, less of the available habitat is suitable for these species on fragmented landscapes than for gap-sensitive species on clumped landscapes

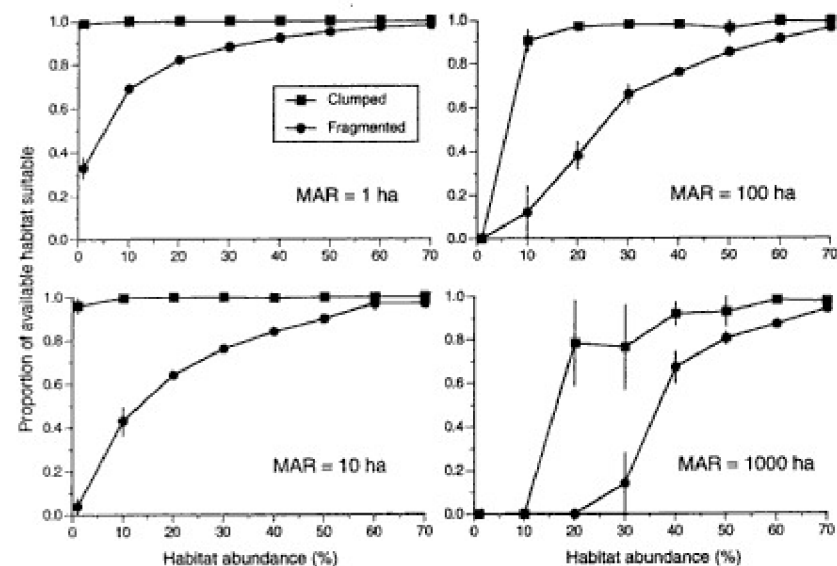


Figure 4. Effect of forest fragmentation on the suitability of available habitat for gap-sensitive species (incapable of crossing gaps of unsuitable habitat) that differ in minimum area requirements. If all of the available habitat on the landscape can be utilized by the species, then the proportion of available habitat that is suitable is 1.0. "Clumped" and "Fragmented" refer to the different forest management scenarios depicted in Figure 2. Error bars are ± 1 SE.

(compare Figures 4 and 5). Still, the number of territories that could be supported on a clumped and fragmented landscape at a given level of habitat abundance was about the same if the species has good gap-crossing abilities (Gap = 3 cells; Figure 6). Fragmented landscapes support smaller populations of gap-sensitive species, however, especially for species with moderate to large area requirements (Gap = 0 cells; Figure 6).

All landscapes containing at least 40% forest cover were connected, if we adopt the convention of defining connectivity as a $>50\%$ probability that a percolation cluster occurs on the landscape (Figure 7; Pearson and Gardner, 1997). The critical threshold at which landscapes became disconnected was influenced by the degree of forest fragmentation and the species' gap-crossing abilities. Gap-sensitive species on fragmented landscapes perceived a disconnected landscape when forest cover decreased to about 40%, whereas such species

on clumped landscapes perceived a connected landscape until 30% forest cover (Figure 7A). Note, however, that there is a higher probability that fragmented landscapes will be connected than clumped landscapes in the range of 40-60% habitat cover (Figure 7A). Habitat is more dispersed on fragmented fractal landscapes, and thus it is more likely that a single cluster of forest cover that spans the landscape will emerge at this range of habitat abundance. If the organism possesses gap-crossing abilities, all landscapes with $>20\%$ cover are connected (e.g., Fragmented landscape, Gap = 3 cells; Figure 7B). Thus, fragmented landscapes are functionally connected, if not physically connected, for species with gap-crossing abilities. Such species are able to integrate forest cover across areas of unsuitable habitat to fulfill their MAR.

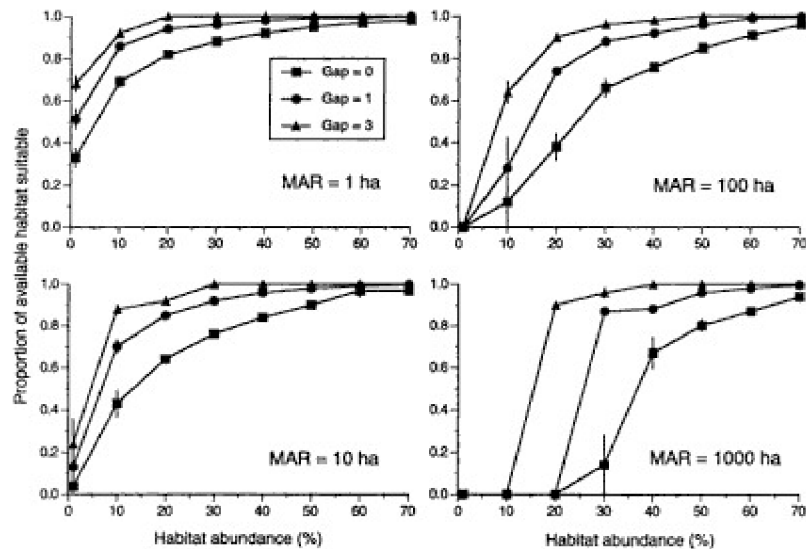


Figure 5. Effect of gap-crossing abilities on the suitability of available habitat on fragmented landscapes for species that differ in minimum area requirements. Gap-crossing ability refers to the "movement neighborhood" of the organism; that is, the ability or willingness to cross gaps of unsuitable habitat (e.g., Gap = 1 is a 24-cell neighborhood in which the species is able to cross gaps 1-cell wide). Error bars are ± 1 SE.

4.3 Discussion

It may seem surprising at first that a fragmented landscape can be connected, or that it could have a higher degree of connectivity than landscapes with more intact habitat distributions. Our surprise should serve as a reminder that landscapes are neither inherently fragmented nor connected. Assessment of landscape connectivity is based on the scale at which organisms interact with the scale of fragmentation. In this analysis, species with good gap-crossing abilities, which therefore operate at a broader spatial scale than the fine-scale pattern of timber harvest depicted in the fragmented fractal landscapes, perceived all fragmented landscapes as connected until only about 10-20% forest remained. Such landscapes are considered to be *functionally connected*, because the organism is able to connect disjunct habitat patches via dispersal. Gap-sensitive species, however, were more affected

by the scale of fragmentation, which complicated the assessment of landscape connectivity. Fragmented landscapes (timber harvest conducted at fine spatial scales) were *more likely* to be perceived as connected than clumped landscapes (timber harvest conducted at coarse spatial scales) if about half (40-60%) of the forested landscape was cleared (Gap = 0, Clumped vs. Fragmented; Figure 7).

Habitat clusters appear to coalesce sooner, forming larger patches, on fragmented fractal landscapes than on clumped fractal landscapes within this particular range of available habitat (Figure 5 in With and King, 1999a). This is a consequence of the more dispersed habitat distribution on fragmented landscapes, which makes it easier for patches to coalesce into a percolation cluster (the defining characteristic of a connected landscape in the neutral landscape/percolation framework). At 30% habitat, however, gap-sensitive species no longer perceived fragmented landscapes to be connected, although most clumped landscapes were still

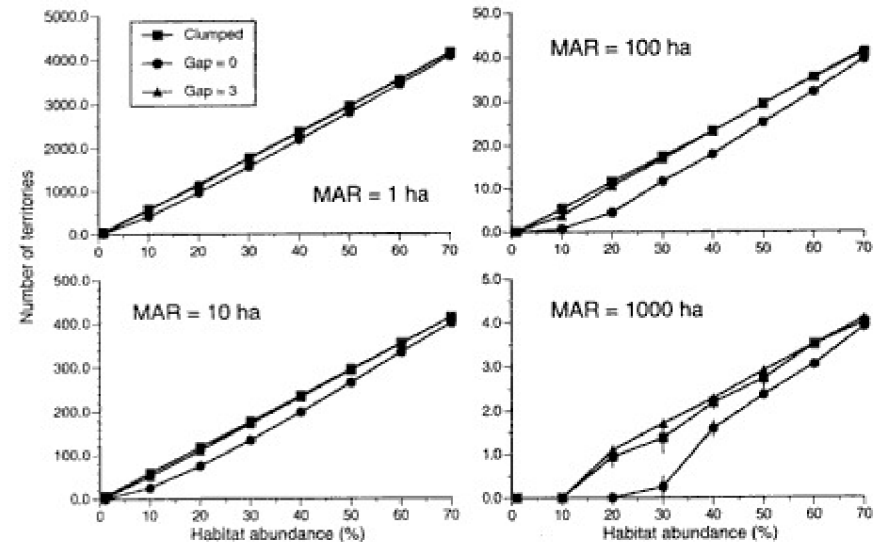


Figure 6. Effect of forest fragmentation and gap-crossing abilities on the number of territories that can be supported on the landscape. Population sizes are expected to be lower for gap-sensitive species (Gap = 0) on fragmented landscapes, then for such species on "Clumped" landscapes. Species with good gap-crossing abilities (Gap = 3) are able to utilize most of the available habitat, and thus fragmented landscapes support as many territories as for gap-sensitive species on clumped landscapes. Error bars are ± 1 SE.

connected at this level. In addition, the disruption of landscape connectivity occurred more precipitously (i.e., as a threshold) in fragmented landscapes than in clumped landscapes (Figure 7).

While landscape connectivity (or habitat connectivity at some scale) is a necessary condition for wildlife management, is it sufficient? Consider a scenario where half of the landscape is slated for timber harvest. If forest management is concerned solely with the maintenance of connected landscapes, then one might interpret the results of this analysis to suggest that fine-scale fragmentation would be preferable to a coarser scale of deforestation. Gap-sensitive species would then be assured of a connected landscape. [Note that this is a different recommendation than presented by Pearson et al. (1996) because a different neutral landscape model (fractal vs. hierarchical random) and movement rule (Rule 2 vs. Rule 1) is being used to assess landscape connectivity for

gap-sensitive species.] However, the amount of suitable habitat (connected habitat meeting individual area requirements), and thus the number of territories that can be supported, is substantially reduced on fragmented landscapes relative to clumped landscapes, particularly for gap-sensitive species with large area requirements (MAR = 100, 1000 ha; Figures 5-7). Fewer territories presumably equates to smaller populations, and smaller population sizes should enhance extinction risk for species in fragmented landscapes. This was borne out in a recent modeling synthesis that coupled a generalized metapopulation model with fractal neutral landscapes to predict extinction thresholds for species that differ in dispersal ability and life-history traits (With and King, 1999b). Species on clumped fractal landscapes either did not go extinct, or persisted longer across a greater range of habitat loss, than species on fragmented fractal landscapes.

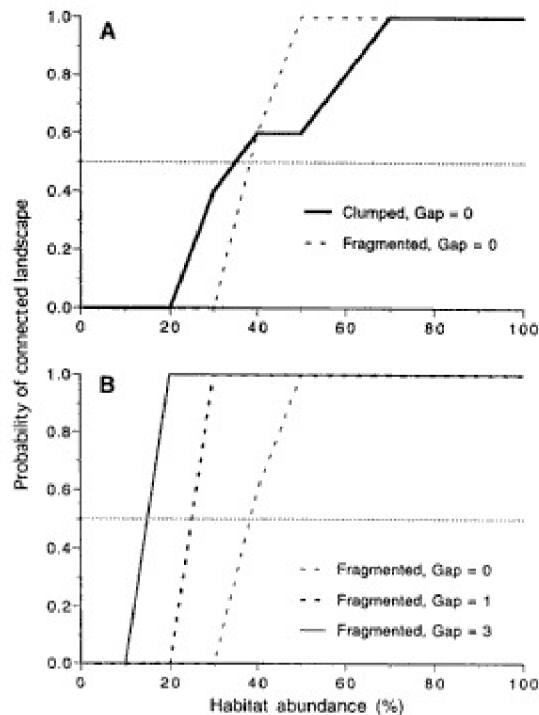


Figure 7. Landscape connectivity in different forested landscapes (Clumped vs. Fragmented), as assessed by species with different gap-crossing abilities. Connectivity is defined as a >50% probability that a percolation cluster (a single cluster of habitat that spans the landscape) occurs on the landscape (see Figure 1). Thus, all landscapes are connected if forest cover >40%. A. Comparison of landscape connectivity in clumped and fragmented forests for species without gap-crossing abilities (Gap = 0). B. Comparison of landscape connectivity in fragmented forests for species that differ in gap-crossing ability.

Thus, landscape connectivity may not be sufficient for wildlife management. Fragmented landscapes may be functionally connected, but support smaller, less viable populations than clumped landscapes that lack overall connectivity. This apparent paradox can be resolved by considering the scale at which connectivity is assessed. In this analysis, landscape connectivity is being inferred from the scale at which organisms are able to integrate forest cover (based on gap-crossing ability) to meet their MAR. Thus, the suitability of available habitat on the landscape for a given species is defined as the amount of connected

habitat that meets the area requirements for individuals of that species. This is accomplished by identifying patches of connected habitat that are at least as large as the MAR for that species. If a patch of connected habitat spans the landscape, the overall landscape is considered to be connected (i.e., habitat connectivity implies overall landscape connectivity).

Is this an appropriate scale at which to assess landscape connectivity, however? Strictly speaking, percolation measures the resistance of the overall landscape to movement. Theoretically, an individual could traverse the en-

tire landscape on the percolation cluster of a connected landscape (Gardner et al., 1989). This definition of landscape connectivity would have little relevance to a territorial vertebrate or to organisms bounded by physiological and energetic constraints that limit their foraging range, however. Such organisms are unlikely to operate at the spatial extent of the entire landscape, which is the scale at which connectivity is being defined. Such scale mismatches in how connectivity is defined relative to the process being studied may explain why thresholds in landscape connectivity (i.e., percolation thresholds) often do not coincide with thresholds in ecological responses to habitat fragmentation (e.g., Wiens et al. 1997, With and King 1999a, b).

Does this represent a failure of percolation theory to define landscape connectivity in a meaningful way for wildlife management? Not necessarily. The key is to define connectivity at a level appropriate to the scale at which movement or dispersal occurs. However, assessment of connectivity is complicated further by the fact that many species may exhibit different scales of movement in response to different scales of patchiness on the landscape (Kotliar and Wiens, 1990; Pearson et al., 1996). For example, birds are able to fly across extensive regions of the landscape in search of suitable habitat, but are often very specialized in their foraging requirements such that habitat edges, roads and waterways may be barriers to movement at a finer scale within territories (Lidicker and Koenig, 1996). Thus, the scale at which connectivity is assessed at one level (connected habitat that will fulfill breeding requirements) may be inappropriate for assessing connectivity at another level (connected patches of breeding habitat required for population persistence).

Connectivity thus needs to be assessed at multiple scales. At the finest scale, gap-crossing abilities could be used to quantify the amount of suitable connected habitat that is capable of fulfilling the individual area requirements of the species (this study). Dispersal distances, the ability and propensity of individuals to move between suitable habitat patches, might then be used to assess the connectivity of the overall landscape, and also to evaluate the need for habitat corridors or "stepping stones" to con-

nect isolated fragments. Connectivity should be evaluated within a hierarchical framework (e.g., King, 1997). For example, Reed Noss (1991) identified three scales of connectivity that might be necessary in species management: 1) fencerow scale, which is the connection of close habitat patches by corridors, such as hedgerows connecting isolated woodlots; 2) landscape mosaic scale, which are larger corridors connecting major landscape features, such as riparian vegetation along rivers; and 3) regional scale, in which broad-scale landscape corridors connect nature reserves. Although these recommendations are based on a very literal definition of connectivity (i.e., corridors), they nevertheless demonstrate how connectivity can be assessed and maintained at different scales. Maintenance of connectivity at a variety of scales will ultimately be necessary for the successful conservation and management of wildlife.

4.4 Management Considerations

The analysis of species-defined landscapes presented in this chapter should not be misconstrued as endorsement for a particular landscape management scenario as being superior over another in maintaining habitat or landscape connectivity. Such was not the intent of this analysis. Instead, this analysis illustrated the application of neutral landscape models to demonstrate how connectivity (defined by percolation clusters) can be quantified from the perspective of species that operate at different scales on the landscape, highlighted some of the difficulties inherent in assessing landscape connectivity, and provided some general guidelines regarding the definition and management of landscape connectivity. Some general recommendations that emerge from this analysis are as follows:

1) *Landscape connectivity needs to be assessed from an organismal perspective.* A landscape is not inherently connected or fragmented. Assessment of connectivity is based on the scale at which organisms interact with the scale of fragmentation on the landscape;

2) *Connectivity is a necessary, but not sufficient, condition for evaluating landscape suitability.* A fragmented landscape may be connected, and yet have less suitable habitat (connected

habitat meeting the individual area requirements for the species) and support smaller populations than a more clumped habitat distribution;

3) *Connectivity needs to be assessed across multiple scales and species.* A species may exhibit different scales of movement which may influence its response to different scales of patchiness that exist on the landscape. Thus, connectivity perceived at a broad scale does not guarantee that patch structure at a fine scale will also be perceived as connected, and vice versa. Furthermore, various species on the same landscape will likely have different perceptions as to whether the landscape is connected at a particular scale;

4) *Connectivity must be maintained across a variety of scales and for a variety of species.* A hierarchical approach to the maintenance and management of landscape connectivity must be adopted to ensure connectivity at the different levels necessary to sustain minimum viable populations and to ensure the regional persistence of the species (e.g., connected habitat to fulfill MAR at the level of the individual, connected habitat patches at the level of the population, and connected populations at the level of the metapopulation); and,

5) *Habitat corridors may not be strictly necessary to achieve connectivity.* Percolation theory may facilitate the identification of critical regions on the landscape that facilitate dispersal (percolation clusters), and which need to be maintained or restored to promote landscape connectivity (e.g., Keitt et al., 1997). Because habitat patches within the percolation cluster may be functionally connected by dispersal for species with gap-crossing abilities, this argues more for the protection of habitat "stepping stones" rather than continuous strips of habitat (corridors). Nevertheless, corridors may enhance dispersal success for even vagile species by reducing mortality incurred during dispersal (e.g., cougars; Beier 1993, 1996).

The analytical approach presented here, founded on percolation theory, can be implemented for real species on actual landscapes to assess connectivity, to identify regions of the landscape essential in preserving connectivity, or to evaluate how different scenarios of forest management may disrupt connectivity. Nevertheless, it should be obvious that the assess-

ment of landscape connectivity, from whatever perspective and at whatever scale, is dependent upon information on species' movement responses to patch structure, the gap sizes they are willing to cross, or the distances they can disperse. Such basic information is unavailable for most vertebrates (Lidicker and Koehnig, 1996). While innovative approaches have recently been developed to obtain these data (e.g., Sieving et al., 1996; Rail et al., 1997; Desrochers and Hannon, 1997; Zollner and Lima, 1997), this continues to be a research priority. In the meantime, neutral landscape models may at least permit a general assessment of how patterns of deforestation affect landscape connectivity from the perspective of different species, which is a necessary vista if we are to adopt meaningful conservation strategies (Hansen and Urban, 1992).

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