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Timothy H. Keitt
Deal L. Urban
Bruce T. Milne

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Managing Fragmented Landscapes: A Macroscopic Approach*

Timothy H. Keitt[†], Dean L. Urban[‡] and Bruce T. Milne[§]

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Abstract

Habitat fragmentation is generally thought to be a leading cause of loss of biodiversity. In fragmented landscapes, maintenance of habitat connectivity is an important consideration in conservation planning. In this paper, we develop methods for quantifying habitat connectivity at multiple scales and assigning conservation priority to habitat patches based on their contribution to connectivity. By representing the habitat mosaic as a mathematical “graph” we show that percolation theory can be used to quantify connectivity at multiple scales from empirical landscape data. Our results indicate that connectivity of landscapes is highly scale dependent, exhibiting a marked transition at a characteristic distance and varying significantly for organisms with different dispersal behavior. More importantly, we show that the sensitivity and importance of landscape pattern is also scale dependent peaking at scales associated with the percolation transition. The sensitivity analysis allows us in addition to identify critical “key-stone” patches that when removed from the landscape cause large changes in connectivity. These methods are applied to the distribution of forest habitats throughout the Southwestern U.S. and management implications for the threatened Mexican Spotted Owl (*Strix occidentalis lucida*) are discussed.

1 Introduction

Habitat fragmentation is a primary concern for conservation of biodiversity in human dominated landscapes (Harris 1984, Noss 1987, Saunders et al. 1991, Rich et al. 1994, Simberloff 1995). Human population growth, and the subsequent conversion of landscapes for human use, has lead to a rapid increase in habitat

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[†]University of New Mexico, Department of Biology, Albuquerque NM, 87131. Current address: The Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501; phone: 505/984-8800; FAX: 505/982-0565; email: tkeitt@santafe.edu

[‡]School of the Environment, Levine Science Research Center, Duke University, Durham NC, 27708

[§]University of New Mexico, Department of Biology, Albuquerque NM, 87131

fragmentation and loss of biodiversity in many parts of the world (Noss 1991, Saunders et al. 1993, Pimm et al. 1995).

The threat of habitat fragmentation stems, of course, from the direct loss of the quantity of habitat, and from the subdivision of populations into smaller and increasingly isolated demes. Small populations suffer greater risk of local extinction for a number of reasons. These include environmental and demographic stochasticity (Hanski 1991, Harrison 1991, Verboom and Lankester 1991), genetic stochasticity resulting in a loss of heterozygosity through drift (Gilpin 1991), and from loss of fitness due to inbreeding (Soulé 1980). Habitat fragmentation also reduces dispersal among populations which can lead to extinction of local populations that depend on immigration (Brown and Kodric-Brown 1977, Pulliam 1988), and may cause collapse of an entire metapopulation (Lande 1987, Hanski and Gilpin 1991, Ebenhard 1991, Lamberson et al. 1992). More subtle effects of fragmentation include alteration of microclimate along exposed forest edges (Lovejoy et al. 1986), invasion by disturbance tolerant species (Harris 1984, Villard and Taylor 1994), reduced rates of pollinator visits to flowering plants (Aizen and Feinsinger 1994), and disruption of herbivore population regulation by predators and parasitoids (Kruess and Tscharntke 1994).

Dispersal among habitat patches reduces many of the problems associated with fragmentation and isolation. As a result, many conservation efforts have focussed on maintaining habitat connectivity by preserving “corridors” of habitat linking important populations (Wilson and Willis 1975, Harris 1984, Noss 1987). Preservation of all existing habitats will, of course, be most effective in maintaining connectivity. However, resources for habitat preservation are often limited. Thus, a key step in developing a conservation plan is to identify habitat areas most critical to the species or ecosystem of concern, so that available resource can be used efficiently. Currently, however, there exists no systematic, quantitative methodology for designating critical habitats.

In this paper, we introduce a multi-scaled approach to assigning priority to landscape elements based on a quantitative measure of habitat connectivity. Our approach emphasized measurement of habitat connectivity at multiple scales, defined as a maximum dispersal distance between two patches, and the assignment of importance to habitat patches based on their overall contribution to landscape connectivity.

The emphasis on a multi-scaled approach was important because, in general, landscape patterns are not expressed at a particular scale, but involves a hierarchy of scales (Urban et al. 1987, Delcourt and Delcourt 1988, Rykiel et al. 1989). Furthermore, organisms of different size resolve patterns in the landscape at different scales (Holling 1992). Allometric scaling relations, for example, predict increased territory size with increased body mass (Peters 1983). Thus, a given landscape that appears highly fragmented at one scale may appear relatively connected to organisms that interact with the landscape at another scale (Milne 1992). In the context of ecosystem management (Franklin 1993), measuring connectivity at multiple scales allows for an aggregate measure of patch importance that applies simultaneously to species of different sizes. When the focus is on a particular species, a multi-scaled approach allows one to incorporate uncertainty

in estimates of a species dispersal behavior.

1.1 The Mexican Spotted Owl

Although we are principally concerned with a theory of landscape connectivity across scales, the following analyses were developed in conjunction with the recovery plan for the Mexican Spotted Owl (Block et al. 1995). The Mexican Spotted Owl is a subspecies of the Spotted Owl, and is distributed in a highly fragmented manner across mountain ranges and canyonlands in the southwestern U.S. and Mexico (Ganey and Balda 1989). The subspecies was recently listed as Threatened under the Endangered Species Act because of concerns over potential habitat loss due to current and future timber harvests (Turner 1993). Mexican Spotted Owls appear to depend on old growth forests, at least in part of their range (Ganey and Balda 1991). They nest on ledges in rocky canyons, but only if there are suitable foraging habitats nearby (Ganey and Balda 1994). Mexican Spotted Owls are relatively intolerant to heat stress and may prefer closed canopy forests and steep walled canyons for their cooler microclimates (Barrows 1981).

With a few exceptions (Ganey and Balda 1994), relatively little is known about demographics, dispersal, foraging behavior, and habitat use of the Mexican Spotted Owl. Thus we were confronted with finding an approach that would provide useful information to decision makers despite the lack of precise knowledge about Mexican Spotted Owl life history traits. We focused on habitat pattern because a primary goal of conservation biology is to identify and protect critical habitats. We felt the approach should characterize the landscape at multiple scales, which is useful in two contexts. First, by quantifying landscape connectivity at multiple scales, one can assess the sensitivity of the results to uncertainty about the scale at which individuals disperse among patches. Second, the multiscaled approach allows composite measures applicable to communities of species that operate at a variety of spatio-temporal scales. Thus our results have implications for conservation beyond Spotted Owls and provide a step towards ecosystem management in a spatial context.

2 Methods

Our approach to the study of landscape connectivity derives from graph theory (Harary 1969, Cantwell and Forman 1993) and percolation theory (Stauffer and Aharony 1985, Gardner et al. 1987, Gould and Tobochnik 1988, Creswick et al. 1992). First, we generated a potential habitat map for the Mexican Spotted Owl. We used a digital forest cover map produced by U.S.D.A. Forest Service (Evans and Zhu 1993, Evans et al. 1993) to find areas of suitable owl habitat. The cover map was derived from AVHRR satellite imagery and had a 1 km² grid-cell size. Each grid-cell contained a label identifying it as one of 23 forest types. The forest types were named for dominant or indicator species; each type represented a multispecies plant assemblage. For example, the Douglas-fir

type corresponds to a mixed-conifer forest which may contain white fir (*Abies concolor*) and several species of pine (*Pinus ponderosa*, *P. contorta*). The extent of the image was cropped to the boundaries of Colorado, Utah, Arizona, and New Mexico, to encompass the entire range of the Mexican Spotted Owl within the U.S. Data were not available for Mexico.

Two cover types, Douglas-fir (i.e., mixed conifer) and ponderosa pine types, were chosen to represent potential habitat based on studies of Mexican Spotted Owl habitat requirements (Ganey and Balda 1994). All other cover types were considered “non-habitat.” The resulting map was a coarse-scale approximation of the distribution of habitat which could be used by Mexican Spotted Owls for foraging and nesting. We did not expect to resolve landscape features less than the 1 km cell size of the imagery, even though in some cases those features may have been used by owls, e.g., narrow, rocky canyons in Southwest Utah. However, we were interested in the broad-scale distribution of habitat and, in particular, the distance relationships among habitat patches. Therefore, we were not concerned with fine-scale habitat heterogeneity. Instead, we focused on distances between pairs of habitat patches as indices of inter-patch connectivity.

Second, we identified and labeled each contiguous habitat patch on the map. Two habitat cells were considered to be in the same forest patch if they were adjacent in the four cardinal directions or diagonally (northeast, northwest, and so on). The habitat map contained $> 2,000$ individual patches, most of which were single, isolated habitat cells. Patches of only a few habitat cells may have been the result of errors in the original satellite image classification. We therefore removed patches $< 10 \text{ km}^2$ from the map, retaining only the largest 254 patches. We had no means of determining whether the patches removed represented true habitat patches. Neither was it known if such small, isolated patches are of importance to Mexican Spotted Owl dispersal. However, estimates of Mexican Spotted Owl territory size range from 5 km^2 to 20 km^2 (Ganey and Balda 1994). Therefore, patches of a few grid-cells probably did not represent significant owl habitat. We repeated our analyses on several different potential habitat maps using different combinations of cover types and different minimum patch sizes. In all cases we found qualitatively similar results to those presented here.

In terms of graph theory, each patch or contiguous region of habitat can be considered “node” or “vertex” in a graph. For the purpose of illustration, each vertex was represented by a dot placed at the center of its corresponding patch (see Fig. 1). Connections between patches were represented by lines or “edges” connecting vertices. A set of interconnected patches, separated from the rest of the habitat distribution, was called a “sub-graph.”

Third, we varied an assumed maximum dispersal distance, or the farthest distance a dispersing individual could fly between two patches, and measured landscape connectivity at each maximum distance. Patches of potential owl habitat were joined together if their minimum edge-to-edge distance (i.e., the shortest distance over “non-habitat” a disperser must cross to move from one patch to the other) was less than or equal to the maximum dispersal distance. For each maximum dispersal distance, we grouped sets of habitat patches con-

nected via dispersal into aggregate clusters or sub-graphs. We incremented the maximum dispersal distance from 0 km (all patches independent) to 100 km (all patches connected to form a single large cluster) in 5 km steps.

Aggregation of patches at increasing distances or length scales is equivalent to a bond-percolation problem (Stauffer and Aharony 1985). At each maximum dispersal distance, we measured the connectivity of the resulting habitat distribution. In percolation theory a standard measure of connectivity is the “correlation length”, defined as the weighted average radius of the clusters on the map. The radius of each cluster or sub-graph (sometimes referred to as the “radius of gyration,” Creswick et al. 1992) was given by

$$R_s = 1/n_s \sum_{i=1}^n \sqrt{(x_i - \bar{x}_s)^2 + (y_i - \bar{y}_s)^2} \quad (1)$$

where \bar{x}_s and \bar{y}_s are the mean x and y coordinates of habitat cells in sub-graph s , x_i and y_i are the x and y coordinates of the i th habitat grid-cell in the sub-graph and n_s is the total number of habitat cells in the sub-graph. The average radius is a standardized measure of the length of a habitat cluster. For example, a chain of habitat patches connected in a line would have a relatively long radius, whereas as set of connected patches all located nearby to one another would have a shorter radius. The average radius is a measure of the degree to which a sub-graph spans across the landscape thereby connecting distant habitat patches.

The correlation length (Creswick et al. 1992) was given by

$$\xi = \frac{\sum (n_s R_s)}{\sum n_s} \quad (2)$$

where symbols are as defined in Eq. 1. The correlation length represents the distance away, on average, that an individual is able to disperse from a randomly chosen starting point. Any one individual was not expected to disperse a distance equal to the correlation length, unless its dispersal range approached the extent of the habitat distribution. However, offspring from individuals that successfully disperse to new areas can themselves disperse and so forth, such that over a number of generations, the distance traveled was expected to approach the measured correlation length. Thus, a short correlation length would indicate a disconnected habitat distribution and fragmented populations. A long correlation length (approaching the extent of the habitat distribution) would indicate a connected landscape and highly interconnected populations.

Fourth, we measured the relative contribution of each habitat patch to the connectivity of the landscape. For each maximum dispersal distance, each patch was systematically removed from the landscape and the correlation length was recalculated. The change in the correlation length observed when a patch was removed was used as an index of the patch contribution to connectivity. The normalized importance index for patch p was given by

$$I_p(\delta) = \frac{\xi(\delta) - \xi(\delta, p)}{\xi(\delta)} \quad (3)$$

where $\xi(\delta)$ is the correlation length of the landscape reclustered at distance δ and $\xi(\delta, p)$ is the correlation length after patch p was removed.

Throughout we have assumed that a set of disjunct, isolated populations have a higher risk of extinction than does a metapopulation. Habitat degradation in large, high importance patches is of concern. However, the risk of a large patch being entirely removed from the map is low. Small patches which connect large areas of habitat are of special concern because they have a large effect on landscape connectivity as well as a proportionately higher risk of being lost from the available habitat. For instance, a large fire could engulf an entire habitat patch if it were sufficiently small. We therefore defined a second, area-corrected importance index,

$$R_p(\delta) = \frac{I_p(\delta)}{n_p} \quad (4)$$

where n_p is the number of habitat cells in patch p . The area-corrected index can be interpreted as a measure of the relative risk, per unit area, associated with the loss of a particular habitat patch.

Organisms of different size and dispersal behavior interact with the landscape at different scales (Holling 1992). Therefore, a particular patch may have variable importance across a range of scales or to species of different body size. To incorporate multi-scale dynamics, we defined an overall importance index as the average patch importance across a range of maximum dispersal distances:

$$I_p = \frac{1}{\delta'} \int_0^{\delta'} I_p(\delta) \quad (5)$$

where δ' is the distance at which the all patches are connected. This index orders patches according to their overall contribution to connectivity.

Similarly, we defined an overall, area-corrected index as the average per grid-cell importance over a range of scales:

$$R_p = \frac{1}{\delta'} \int_0^{\delta'} R_p(\delta) \quad (6)$$

Because the overall indices are computed across a wide range of scales, they represent an aggregate measure of patch importance. The indices potentially apply to an entire suite of species that resolve the landscape at different scales. They also provide a multiscale measure of risk associated with the removal of certain habitat patches from the landscape by quantifying the sensitivity of the landscape configuration in terms of loss of connectivity.

Finally, we joined habitat patches together based on a stochastic dispersal function. We assumed that the probability of an owl successfully dispersing between two patches would decrease monotonically as the distance between the patches increased. A simple function that fits this assumption is a negative exponential:

$$p(d) = e^{-kd} \quad (7)$$

where $p(d)$ is the probability of dispersing at least distance d and k is the dispersal coefficient. Dispersal data for the Mexican Spotted Owl are well fit by a negative exponential dispersal function (Block et al. 1995). Notice that the negative exponential is a cumulative probability distribution. It specifies the fraction of individuals that disperse to or beyond a given distance. The function can be indexed conveniently by a tail probability distance, $p_{0.05}$, the distance beyond which 5% of individuals might disperse.

We then used a Monte Carlo procedure to generate multiple landscape configurations. We varied the dispersal coefficient, k , from 1.0 ($p_{0.05} = 3$ km) to 0.01 ($p_{0.05} = 300$ km). For each value of the dispersal coefficient, 100 randomly-connected landscape-configurations were generated and their correlation length recorded. The connections between patches in each configuration were determined by comparing a uniform random number between 0.0 and 1.0 to the probability of dispersal occurring between the patches according to Eq. 7. If the random number was less than the the dispersal probability, the patches were joined into the same sub-graph or cluster, based on the minimum edge-to-edge distance. Thus, the expected frequency, over many random configurations, of two patches being joined was equal the probability of successful dispersal between them. Patches far apart were rarely connected, whereas patches whose edges were in close proximity were often connected, the frequency being determined by the dispersal coefficient.

3 Results

As the maximum inter-patch dispersal-distance was increased, the forest cover map became increasingly and connected and eventually coalesced into a single, large graph that spanned the entire habitat distribution (Fig. 1). At a 20 km joining distance, the landscape was largely composed of independent patches and small habitat clusters. Thus, for organisms capable of dispersing 20 km, the landscape was highly fragmented. At 40 km, larger sub-graphs formed, but the landscape was still divided into several habitat clusters. Above 40 km, most of the habitat distribution was joined, effectively connecting subpopulations into a large metapopulation. Although most of the habitat was joined at 50 km, only a single edge existed between the large subgraphs in the northeast and southwest of the habitat distribution. The vertices at either end of the single connecting-edge are known as “articulation points” because removing either one would bisect the graph (Harary 1969). At a joining distance of 80 km, the graph was highly interconnected and, in general, there were many alternate pathways from any one patch to another.

The sudden transition from a relatively disconnected distribution of habitat to a largely connected map appeared as an inflection in the plot of correlation length versus joining distance (Fig. 2). Between 40 and 45 km the correlation length of the landscape nearly doubled, increasing from 150 km to about 275 km. A sudden change in connectivity at a critical density, or in this case a dispersal distance, is referred to in percolation theory as a geometric “phase transition”

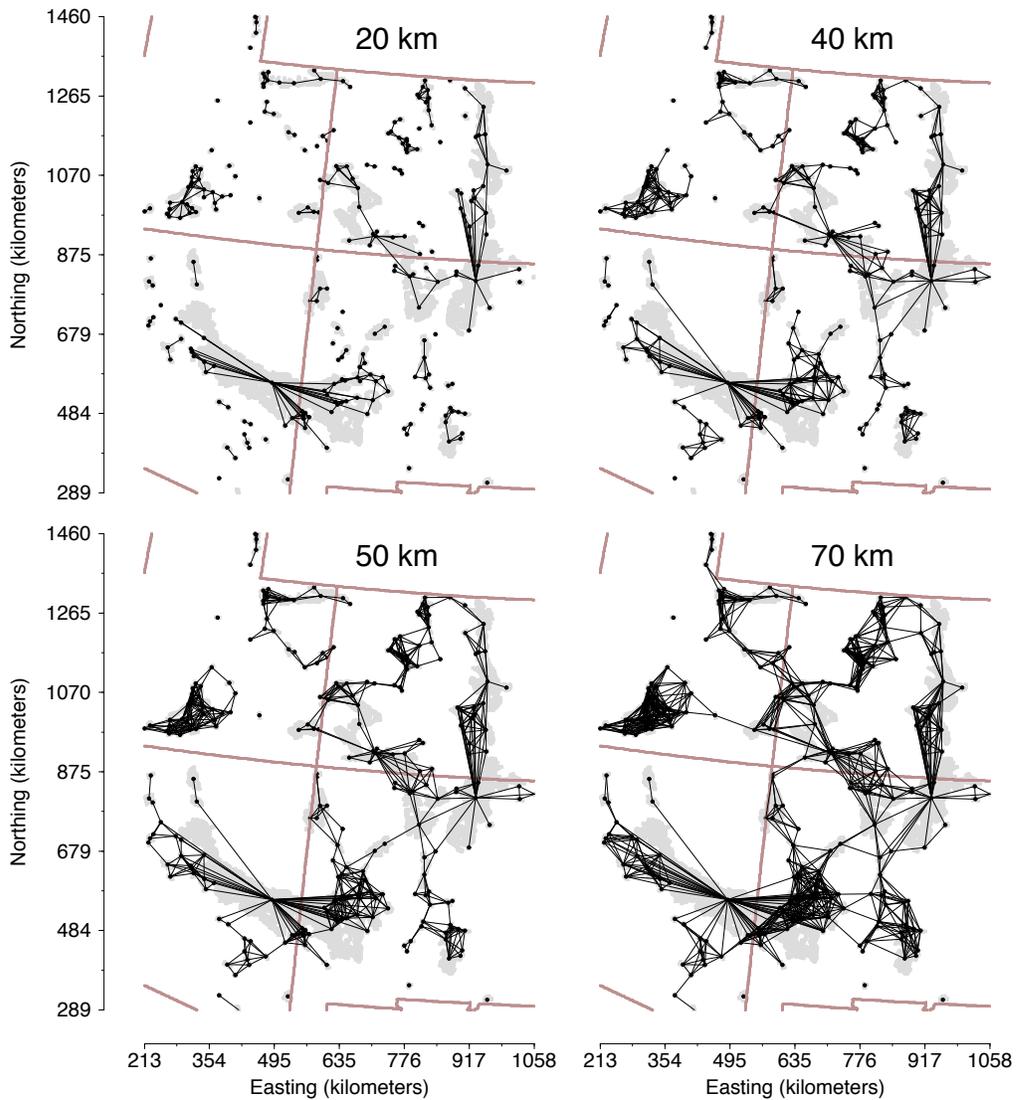


Figure 1: Landscape graphs depicting functional landscape connections at different scales. Dots represent graph vertices and were placed at the center of forest habitat patches. Lines or edges were drawn between vertices if the minimum edge-to-edge distance between patches was less than the maximum dispersal distance.

(Stauffer and Aharony 1985). Thus, the landscape of habitat patches was divided into two separate “phases”: a connected phase and a disconnected phase. Owls which typically disperses less than 45 km would be in the disconnected phase with relatively isolated subpopulations. If however, owls dispersed beyond 45 km, their populations would be interconnected and less subject to stochastic

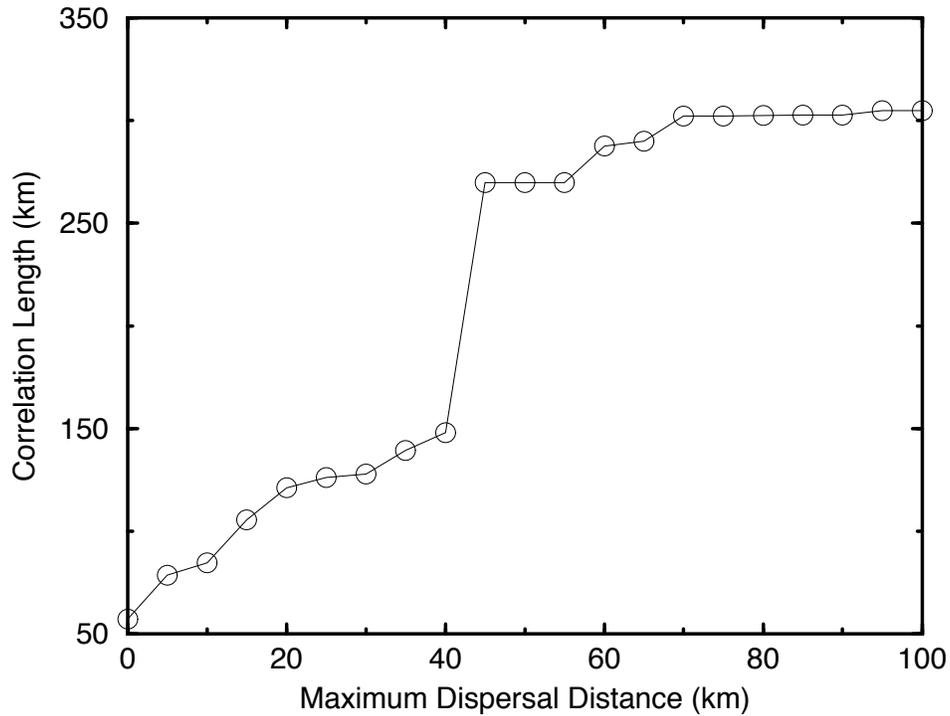


Figure 2: Correlation length of potential owl habitat at different maximum inter-patch dispersal distances.

and other extinction threats associated with isolation.

The inflection in the correlation length not only separated the connected and disconnected phases of the map, but also was related to the sensitivity of the landscape to habitat alterations. When patches were removed from the map, the effect on connectivity was highly scale dependent (Fig. 3). At short joining distances, the effect of removing a patch was largely determined by its size, although shape may have also been important. At a 0 km joining distance (all patches independent), the profile was dominated by the largest patch.

At longer joining distances (30 and 40 km), several of the largest patches caused large deviations in the correlation length when removed. At 30 and 40 km dispersal distances, the second and third largest patches composed the bulk of the graph. Up to this point (0–40 km), the sensitivity profiles were dominated by the largest patches. Thus, the relative position and orientation of patches mattered little: patch size was the most important factor determining importance.

The pattern of landscape sensitivity changed abruptly at 45 and 50 km. Although the largest patch still had a relatively high importance index, the profile (Fig. 3) exhibited several large spikes generated by much smaller patches. The large sensitivity associated with these patches was not due to their size;

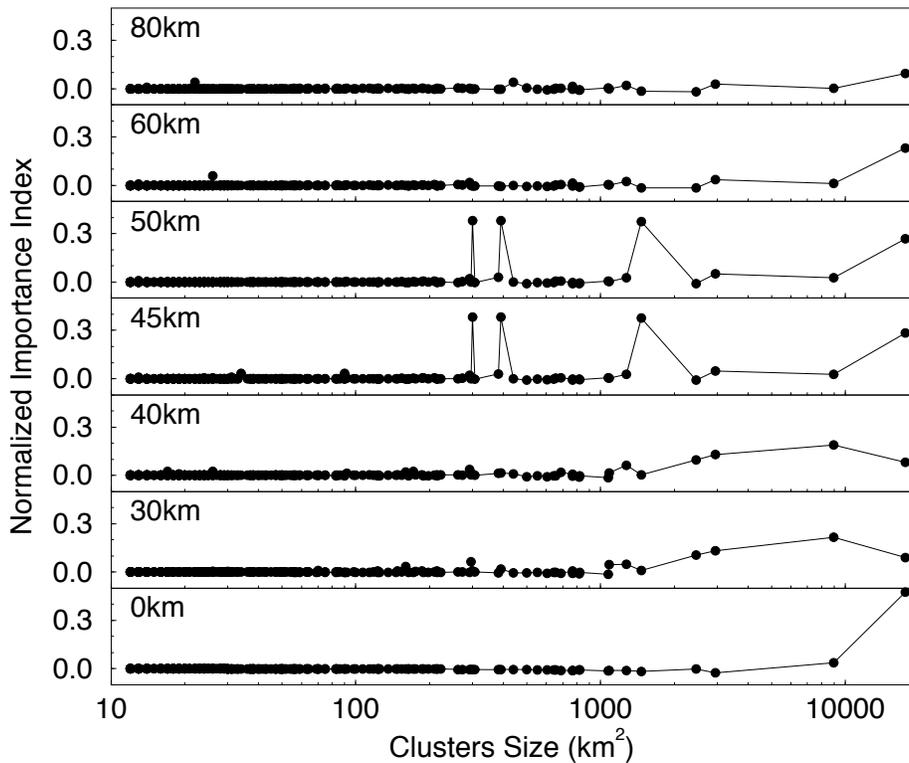


Figure 3: Sensitivity profiles at different scales. From bottom to top, the landscape was reclustered at 0, 30, 40, 45, 50, 60, and 80 km. The normalized importance index is $I_p(\delta)/\xi(\delta)$.

rather it reflected their role as “key-stone” patches connecting large areas of habitat. These key-stone patches corresponded to articulation-points in the graph.

At distances above the transition (60 and 80 km), the sensitivity profile returned to a pattern where the largest patches were most important. However, the overall sensitivity was much lower, particularly at 80 km, because as the maximum-joining distance was increased, the number of alternate pathways between any two patches increased, and the removal of any one patch had little effect on connectivity.

The importance of individual patches was measured by removing each patch and recording the change in connectivity. Importance measures were summed across all dispersal distances to give an overall measure of importance for each patch (Eq. 3). When forest patches were colored according to their importance, a large “habitat core” spanned across the forest cover map (Fig. 4). Patches in the habitat core had a large effect on connectivity at all measured dispersal distances. The importance of core patches stemmed not only from their size,

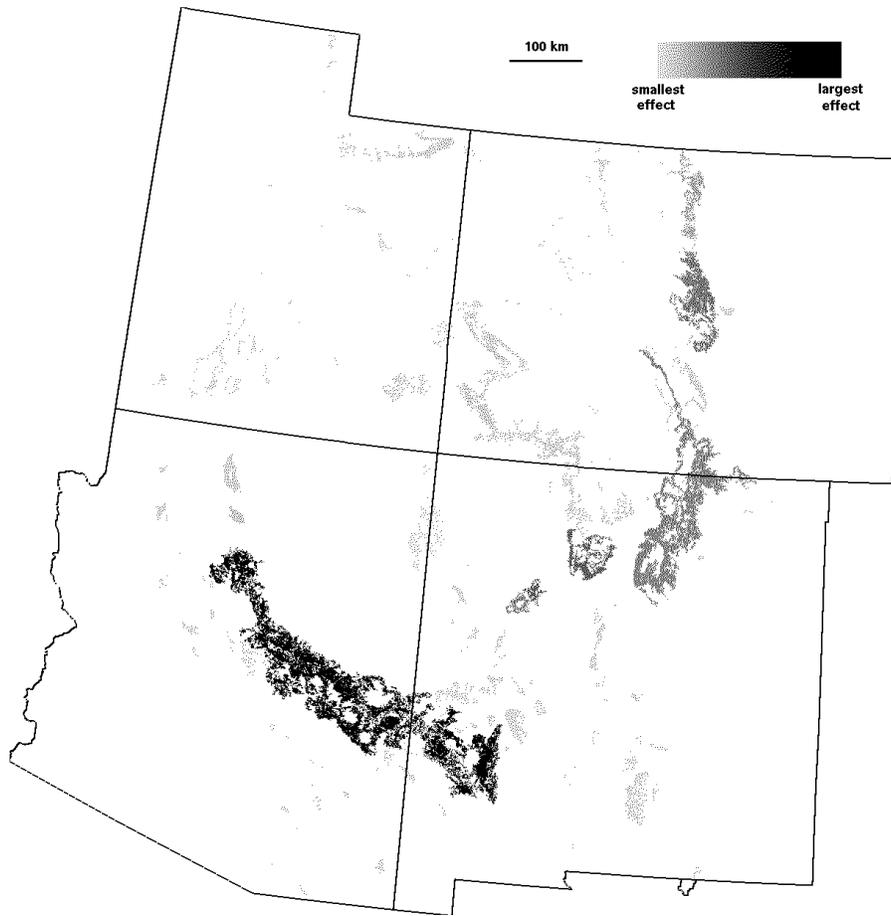


Figure 4: Map of habitat patch importance (I_p) across scales (0–100 km). Numbers indicate the six highest scoring patches.

but also from the fact that they formed a connected corridor across most of the owls range within the U.S.

A different pattern emerged when area-corrected patch importance was used: small key-stone patches appeared scattered throughout the habitat distribution (Fig. 5). Patches with high area-corrected importance values, although small in size, had a large effect on connectivity when removed from the landscape. Key-stone patches typically corresponded to articulation-points in the landscape graph. The most important patches, for example, appear near the middle of the habitat distribution (Fig. 5) and are the same patches that generated a spanning link at a 50 km dispersal distance (Fig. 1). Because the loss of key-stone patches could lead to large changes in landscape connectivity, they may

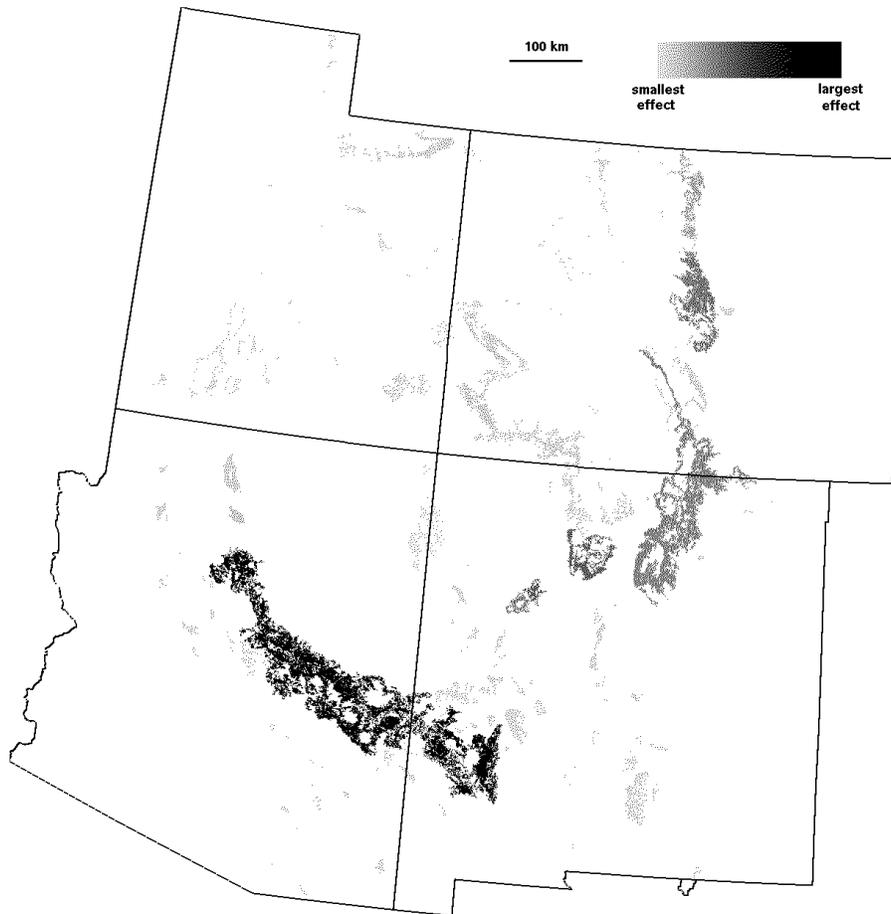


Figure 5: Map of habitat patch importance (R_p) across scales (0–100 km). Numbers indicate the six highest scoring patches.

merit disproportionate concern relative to their size in designations of critical habitat.

3.1 Monte Carlo analysis

Whereas the assumption of a maximum dispersal distance is useful for characterizing the connectivity of landscapes at different scales, it does not consider the stochastic nature of dispersal events. Therefore, we employed a Monte Carlo analysis, based on a dispersal probability function, to characterize the range of connectivities observed for different dispersal coefficients (see Eq. 7).

When the dispersal coefficient was varied between $k = 0.01$ (i.e., long range

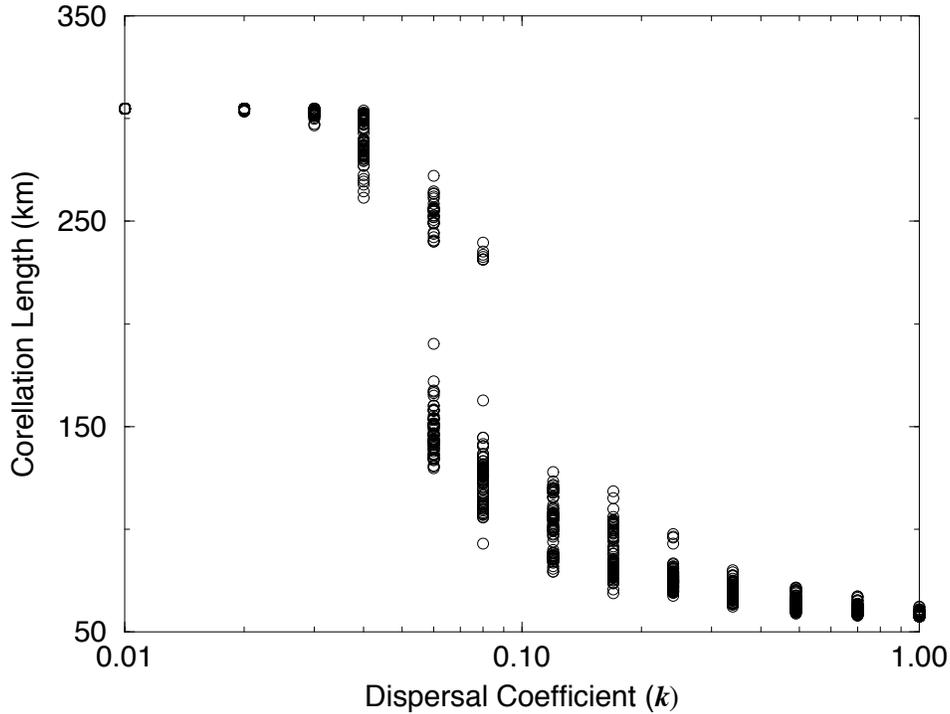


Figure 6: Landscape connectivity for different dispersal coefficients. The coefficient is k in $p(d) = e^{-kd}$ where $p(d)$ is the probability of an individual dispersing at least distance d . Each circle represents a single random landscape configuration.

dispersal) and $k = 1.0$ (i.e., short range dispersal), the relationship between dispersal behavior and connectivity of the landscape was profoundly non-linear, exhibiting a strong inflection at intermediate values (Fig. 6). Furthermore, the distribution of correlation lengths was clearly divided into two distinct phases, higher values indicated the connected phase and lower values a disjoint phase. At intermediate values, both phases existed for the same value of the dispersal coefficient. Thus, the phase transition observed previously for maximum dispersal distances was, in the Monte Carlo analysis, directly related to a particular dispersal coefficient. For forest habitats in the Southwest, the critical dispersal coefficient (k_c) was approximately 0.06–0.07.

The range of connectivities for a given dispersal coefficient also exhibited marked differences across as dispersal distances were increased. At either end of the plot ($k = 0.01$ and $k = 1.0$), the range of connectivity values was minimal. Long-range dispersal resulted in the landscape being connected for every Monte Carlo iteration. For short-range dispersal, the landscape was always fragmented. At intermediate dispersal coefficients, near the percolation transition, the range of connectivity values was much greater. The large range of connectivity values

was again a reflection of the increased sensitivity found near a phase transition.

4 Discussion

We have demonstrated two main results: 1) as potential dispersal distances were increased, the connectivity of Southwest forest habitats exhibits a marked transition from a disconnected or fragmented distribution to a connected distribution; and 2) the sensitivity of the habitat distribution to perturbations was greatest at intermediate dispersal distances, near the percolation threshold. It is well known that random graphs also exhibit phase transitions (Stauffer and Aharony 1985). Thus, we have no reason to believe these results apply only to Southwest forests.

The existence of a transition between connected and disconnected phases has important implications for conservation biology. First, fragmentation of a landscape is not a continuous process. Loss of connectivity can occur suddenly as the landscape passes through the percolation threshold. Thus extinction risks may increase suddenly and unexpectedly as habitats become increasingly fragmented (see also Lamberson et al. 1992).

Second, the scale at which organisms interact with the landscape is an important consideration in evaluating risks associated with fragmentation. When the distance between patches is large relative to the scale at which a species disperses, then the populations in each patch are effectively isolated. Therefore, the loss of any one patch from the landscape will not have an effect beyond the particular patch lost. Similarly, if a species typically disperses a much longer distance than the inter-patch distance, loss of any single patch will not significantly change the connectivity among populations because there are many alternate dispersal routes from one patch to another. It is only when the populations are tenuously connected, near the percolation threshold, that the relationship among patches becomes critical; removal of even a single patch can have a large effect on connectivity and, by inference, extinction risk. One could also consider this a formal definition of a metapopulation: a set of populations that are neither completely connected into a single population, nor fragmented into independent and isolated demes, but instead tenuously connected.

The sensitivity of landscape graphs near the percolation threshold also has implications for the dynamics of metapopulations. In the Monte Carlo analysis, the variance of the connectivities observed increased greatly near the critical dispersal coefficient. The range of connectivities may reflect the range of time-scales involved in metapopulation dynamics. Returning to the Mexican Spotted Owl, if juvenile birds disperse only short distances ($k \rightarrow 1.0$), then the landscape is relatively disconnected. In a single generation, juvenile birds would typically disperse within their natal patch, or, at most, to a nearest neighbor patch. Over many generations, the pattern would be the same: demes would remain isolated because juveniles generally would not disperse far enough to reach other populations. This was reflected in the Monte Carlo analysis by a small variance in connectivity across all randomizations. No matter how many

trials, the landscape remained disconnected.

If juvenile owls disperse long distances ($k \rightarrow 0.01$), then local sub-populations would be completely connected, even over the time-span of a single generation, because juveniles could disperse essentially across the entire habitat range. Thus, the short-term connectivity and long-term connectivity would be the same. Again, this was reflected in the Monte Carlo analysis; the landscape remained connected over all randomizations.

If owls disperse intermediate distances ($k \rightarrow k_c$), populations will be connected across a hierarchy of time and space scales. Because juveniles are dispersing just far enough to reach neighboring patches, nearby patches would be connected within a single generation. However, in order for far away patches to be connected in terms of exchange of alleles, it would require several generations of dispersal events. In other words, it would take a considerable length of time for an allele to diffuse or “percolate” across the landscape before it reached a far distant deme. Thus, the range of connectivity values found in the Monte Carlo analysis can be viewed as an index of the range of time-scales involved in genetic mixing of populations. The rate of dispersal through critically-connected landscapes also has implications for demographic and population dynamics as well as population genetics. It would be important, for example, in determining the rate of population recovery after a local extinction has occurred.

How does Mexican Spotted Owl dispersal behavior relate to the distribution of forest habitats in the Southwest? Available data suggest that a negative exponential function is a good approximation to the owl’s dispersal behavior (Block et al. 1995). We estimated the dispersal coefficient to be approximately $k = 0.06$, a value near the percolation threshold for Southwest forests. Thus, we believe the results shown here are of particular importance to the Mexican Spotted Owl.

Using the results of the perturbation analysis, we can make specific recommendations for habitat preservation. We identified two kinds of important patches: 1) core patches forming a corridor across habitat distribution, and 2) key-stone patches that link large areas but are themselves small. We believe conservation priority should be given first to key-stone patches, then core patches, and finally the remaining patches. Of course, finer-scale habitat properties will also need to be considered, such as land-ownership and habitat quality, in determining which patches to give priority. Nonetheless, our approach can be used in a top-down fashion that first maintains the integrity of the landscape by preserving connectivity, and then suggests where more detailed studies are needed.

Key-stone patches may have importance beyond single species. Because the patch-importance measures were averaged over many scales, key-stone patches may be important components of the landscape for multiple species. Due to the proximity of key-stone patches to large core patches, key-stone patches may receive a larger and more constant influx of dispersing individuals, and therefore maintain higher population densities with lower year-to-year variation in abundance. As a result, key-stone patches may correspond to diversity “hot-spots” (Pimm et al. 1995), an hypothesis which could easily be tested in the field.

Finally, we consider the implications of a critical dispersal distance for evolution of dispersal strategies. Clearly, there are potential fitness advantages to dispersal (Olivieri et al. 1995). In territorial species, such as the Mexican Spotted Owl, juveniles must disperse to find a nesting territory and a mate. Dispersal can also facilitate the spreading of more fit genotypes throughout the population. However, there are costs to dispersal as well. Dispersing individuals experience increased risk of mortality, either by predation or failing to find suitable habitat. Also, if there is too much mixing of populations, locally adapted genotypes would tend to diffuse into the greater population and be lost. Thus, the dispersal behavior may be a tradeoff between advantages of local dispersal and advantages of long-range dispersal. These tradeoffs will be strongly affected the geometry of the landscape in which dispersal occurs.

We are intrigued by the correspondence between the measured dispersal coefficient for Mexican Spotted Owls and the critical coefficient found in the Monte Carlo analysis. We suggest that organisms evolve dispersal behavior in response to landscape patterns and that optimal dispersal strategies may correspond to a critically connected graph. If true, critical dispersal behavior would have important implications for understanding population dynamics in heterogeneous landscapes, as well as providing a framework in which to unite landscape ecology with population biology.

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