Landscape Connectivity: A Graph-Theoretic Perspective

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LANDSCAPE CONNECTIVITY: A GRAPH-THEORETIC PERSPECTIVE

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Abstract. Ecologists are familiar with two data structures commonly used to represent landscapes. Vector-based maps delineate land cover types as polygons, while raster lattices represent the landscape as a grid. Here we adopt a third lattice data structure, the graph. A graph represents a landscape as a set of *nodes* (e.g., habitat patches) connected to some degree by *edges* that join pairs of nodes functionally (e.g., via dispersal). Graph theory is well developed in other fields, including geography (transportation networks, routing applications, siting problems) and computer science (circuitry and network optimization). We present an overview of basic elements of graph theory as it might be applied to issues of connectivity in heterogeneous landscapes, focusing especially on applications of metapopulation theory in conservation biology. We develop a general set of analyses using a hypothetical landscape mosaic of habitat patches in a nonhabitat matrix. Our results suggest that a simple graph construct, the minimum spanning tree, can serve as a powerful guide to decisions about the relative importance of individual patches to overall landscape connectivity. We then apply this approach to an actual conservation scenario involving the threatened Mexican Spotted Owl (*Strix occidentalis lucida*). Simulations with an incidence-function metapopulation model suggest that population persistence can be maintained despite substantial losses of habitat area, so long as the minimum spanning tree is protected. We believe that graph theory has considerable promise for applications concerned with connectivity and ecological flows in general. Because the theory is already well developed in other disciplines, it might be brought to bear immediately on pressing ecological applications in conservation biology and landscape ecology.

Key words: connectivity; conservation biology; dispersal; graph theory; habitat fragmentation; habitat patches and landscape connectivity; habitat pattern; landscape ecology; metapopulation theory; minimum spanning tree; Strix occidentalis lucidus.

INTRODUCTION

Ecological work is being done at increasingly larger scales. For example, conservation biology is necessarily concerned with large biogeographic areas (Noss 1991), and ecosystem management is inherently large scale (Christensen et al. 1996). This has lead us to work with new sorts of data sets summarizing the spatial attributes of landscapes. Indeed, construction and analysis of spatial landscape data is the first step in virtually all habitat conservation planning.

In the development of landscape-scale conservation plans, we typically encounter one of three classes of spatial data (Cressie 1993): (1) spatial point patterns

that comprise a set of locations of entities of interest (e.g., locations or distributional records of species of concern); (2) geostatistical data that represent measurements at locations separated by some distance; and (3) lattices that assign a measurement or value to regions within the landscape. In geographic information systems (GIS) these data classes provide for two alternative conceptual models of landscapes (Goodchild 1994). In the *field* view, a landscape is a continuous surface defined by some variable(s) that can be measured at any point on the surface. Examples of fields would include elevation, surface temperature, or vegetation biomass. Fields that are represented exhaustively (i.e., the entire surface) are lattices, while incompletely sampled representations are geostatistical data. Alternatively, one might view a landscape as *features* or objects, discrete entities that occupy positions in an otherwise undifferentiated space. Elevation benchmarks (points), temperature isopleths (lines), and lakes (polygons) are examples of features.

A lattice often is represented in one of two familiar data structures (other less common structures are used for certain applications, see Goodchild 1994). In vector maps the patches are represented by vectors of coordinates outlining each patch as a polygon. Patches are treated as internally homogeneous. In the class of metapopulation models called "island models," the patches are islands of suitable habitat in a sea of inhospitable matrix (nonhabitat). This modeling approach converts the lattice from a field into a set of features (habitat patches). Raster lattices or mosaics are grids in which each cell is assigned to a discrete state or assumes some value. The size of the grid cells defines the minimum resolution or grain of the mosaic. A raster mosaic is a field model. The island and mosaic data structures have complementary strengths and weaknesses: vector files are compact but sacrifice fine-grain information; mosaics retain this information at the expense of data volume. Ecologists generally are comfortable choosing or converting between these two forms to match the data structure to a particular application. For example, habitat patches might be defined as regions (clusters) of more-or-less similar cells, converting a mosaic into polygon features.

Here we adopt a less familiar lattice data structure, the graph. A graph represents a landscape of habitat patches as a set of *nodes* (points) connected to some extent by *edges* between nodes (these are not the "edges" of field–forest ecotones, although the term might indeed connote a similar sense of adjacency between patches). An edge between two nodes implies there is some ecological flux between the nodes, such as via propagule dispersal or material flow. Graph theory is widely applied in various disciplines (computer science, operations research) for a wide variety of applications concerned with maximally efficient flow or routing in networks or circuits (Harary 1969, Thulasiraman and Swamy 1992, Gross and Yellen 1999). The theory is currently being stretched to even greater algorithmic efficiency through its extension to applications on huge networks such as the worldwide web (Hayes 2000*a, b*). While long used as a framework for food-web theory in ecology (e.g., Pimm 1982), the formalisms of graph theory are not widely appreciated in landscape ecology (Cantwell and Forman 1993). A graph-theoretic perspective would seem to provide powerful leverage on ecological applications concerned with connectivity or ecological fluxes (van Langevelde et al. 1998). In particular, graphs are amenable to applications concerned with metapopulations and conservation biology (Fahrig and Merriam 1985, Verboom and Lankester 1991, Taylor et al. 1993, Schippers et al. 1996). Here we illustrate the power and potential utility of applying graph theory to landscape analysis. We begin with an overview of graphs, and then illustrate this approach with an empirical application to habitat pattern for the Mexican Spotted Owl (*Strix occidentalis lucida*). Our purpose is not to argue
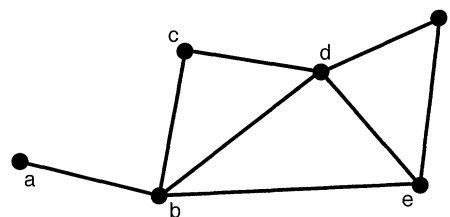

FIG. 1. An example of a graph defined by the sets of p = 6 nodes {a,b,d,c,e,f} and q = 8 edges {ab, bc, be, bd, cd, de, df, ef}.

against other approaches already used in ecology, but rather to present an additional option that has much to offer to large-scale ecological applications.

GRAPHS AND GRAPH THEORY

Definitions

Graph theory has rich vocabulary and some definitions are necessary to the following discussion. The following largely follows Harary's classic (1969) text. A graph G is a set of *nodes* or vertices $V(G)$ and *edges* $E(G)$ such that each edge $e = v_i v_j$ connects nodes v_i and v_j. In this, nodes v_i and v_j are adjacent and each is incident to their shared edge. A graph of m nodes and n edges is $G(m,n)$ and has order m and value n. The graph G is defined by its sets $\{v_i\}$ and $\{e_i\}$, but it is common to represent these sets as a diagram (Fig. 1).

A *path* in this graph is a sequence of nodes—a *walk* from v_0 to v_n, such that each node is unique (i.e., no node is visited more than once). This implies that the edges of a path are also unique. The length of a walk is the sum of the lengths of its edges. A walk is closed if $v_0 = v_n$ (i.e., the node first is revisited), and a closed path of three or more nodes is a *cycle*. A path that includes no cycles is a *tree*. A tree that includes every node in the graph is a *spanning tree*. There might be several of these for any given graph. The spanning tree with the shortest length is the graph's *minimum spanning tree*. The path defined by the edges *ab, bc, cd, df, de* is the minimum spanning tree in Fig. 1.

A graph is *connected* if there exists a path between each pair of nodes, that is, if every node is reachable from some other node. An unconnected graph may consist of several subgraphs. A graph *component* is a connected subgraph, that is, a subgraph in which every node is adjacent to at least one other node in the subgraph. A connected graph that can be disconnected by the removal of a key node has a *cut-node* at that point. The minimum number of nodes that must be removed from a connected graph before it disconnects is its *node-connectivity* $\kappa(G)$. Equivalently, the minimum number of edges that must be removed to disconnect a graph is its *edge-* or *line-connectivity* $\lambda(G)$, and an edge whose removal disconnects a graph is a *cut-edge* or *bridge*. (Ecologists use a variety of terms to connote connectivity. The connectivity terms above have a special meaning in graph theory that does not correspond

to general usage. Rather than confuse things further, we will continue to use "connectivity" in a general sense and use the more specific terms "node-connectivity" or "edge-connectivity" when more precision is needed.)

A graph's *diameter*, $d(G)$, is the longest path between any two nodes in the graph, where the path length between these nodes is itself the shortest possible path. Finding the shortest path between two nodes is a central task in graph theory (Dijkstra's [1959] algorithm is the classic solution). If nodes i and j are adjacent, then the shortest path length l_{ij} is the direct route d_{ij}. If the nodes are not adjacent, any path must be along adjacent stepping-stone nodes in the graph. This requires discovering all possible paths between nodes i and j, and then finding the shortest path length l_{ij}. The longest of these (shortest) lengths l_{ij} as taken over all nodes j is the *eccentricity* of node i, $e(i)$. The diameter of the graph is the maximum eccentricity over all nodes i. In Fig. 1, $e(a)$ is the summed lengths of edges *ab*, *bd*, and *df*; and $d(G) = e(a)$.

Data structures

A graph is defined by two data structures describing its nodes and edges. The nodes are a set provided by an array or list. For particular applications the list also might include additional attributes describing each node. For landscape applications the nodes might be habitat patches, and each patch $i = 1, \ldots, m$ might be located by its spatial centroid (x,y) and described by its area or size s_i, perhaps its core area or carrying capacity, or perhaps some index of its habitat quality or productivity.

Additionally, a graph requires a matrix that summarizes connections between nodes. There are three such matrices: (1) A *distance matrix* **D** has the elements d_{ij} that are the functional distances between patches i and j. These distances might be measured as minimum edge-to-edge or centroid-to-centroid distances; alternatively, distances might be weighted to reflect the navigability or resistance of the intervening matrix between two nodes (Gustafson and Gardner 1996). (2) A flux rate or dispersal *probability matrix* **P** expresses the probabilities that an individual in node i will disperse to node j (or the rate at which some material will undergo such a flux). The matrix **D** might be used to construct a probability matrix **P**. For example, we might assume that dispersal probability can be approximated as negative-exponential decay,

$$p_{ij} = \exp(\theta \times d_{ij}) \qquad (1)$$

where θ is a distance-decay coefficient ($\theta < 0.0$) that determines the steepness of the relationship. This function is convenient because we can index the dispersal function by noting that the tail distance corresponding to $P = 0.05$ is $\ln(0.05)/\theta$, which allows us to compute θ given a known tail distance for a species. Here, "tail distance" is the distance to an arbitrarily selected point

on the flat tail of the dispersal-distance function. Of course, other forms of dispersal-distance functions are possible (Clark et al. 1998, 1999). (3) The edges of a graph are summarized most succinctly in its *adjacency matrix* **A**, a binary matrix in which each element is defined $a_{ij} = 1$ if nodes i and j are connected, otherwise $a_{ij} = 0$. The diagonal of **A**, a_{ii}, is also set to 0 (graphs include no self-loops). In practice, **A** may be generated from either of the matrices **D** or **P** by choosing a threshold distance or probability to define adjacency. Each of these matrices is $m \times m$ and symmetric except in special cases beyond the scope of our current discussion (but see below, Eq. 2). Note that if the geographic locations or other attributes of the nodes are not of interest, all of the information in the graph is contained in the matrices.

These few data structures are central to most operations on graphs. Additional data structures sometimes are defined, typically to lend computational efficiency to numerical algorithms for graph analysis (Buckley and Harary 1990, Thulasiraman and Swamy 1992). Again, we need not attend these complexities now.

Graph operations

There are two general classes of operations on graphs, which we might categorize as being primarily edge related or node related. In landscape applications these correspond to research questions concerning the addition or removal of functional connections between patches (e.g., dispersal corridors), and issues concerning the gain or loss of habitat patches through changes in land use or management. We illustrate some of these relationships using a hypothetical landscape of habitat patches in a nonhabitat matrix. The 50 habitat patches range in size from 1 ha to 32 ha on a doubling scale, with a small amount of Gaussian noise added to each patch size (total area 396 ha). The patches are randomly located in a 10×10 km (10 000-ha) landscape. The mean distance between patches is 5024 m. For illustration, dispersal probabilities are defined by $p_{ij} = 0.05$ for $d_{ij} = 1500$ m. While purely hypothetical, this landscape has a range of patch sizes, patch density, and spatial extent equivalent to that of often-cited Cadiz Township in southern Wisconsin, USA (Curtis 1956, Burgess and Sharpe 1981); the dispersal function is consistent with data collected for the Song Sparrow (Nice 1933). The graph's minimum spanning tree, assembled using Prim's classic (1959) algorithm, is traced in Fig. 2.

To make the edge more relevant to dispersal among patches in a habitat mosaic, we can redefine the graph so that its edges are defined in terms of dispersal fluxes. In this we use the dispersal matrix **P** as well as the patch size array **s**, because dispersal flux depends not only on the probability of dispersal but also on the source strength of the donor patch. Thus, the expected dispersal flux from patch i to node j is:
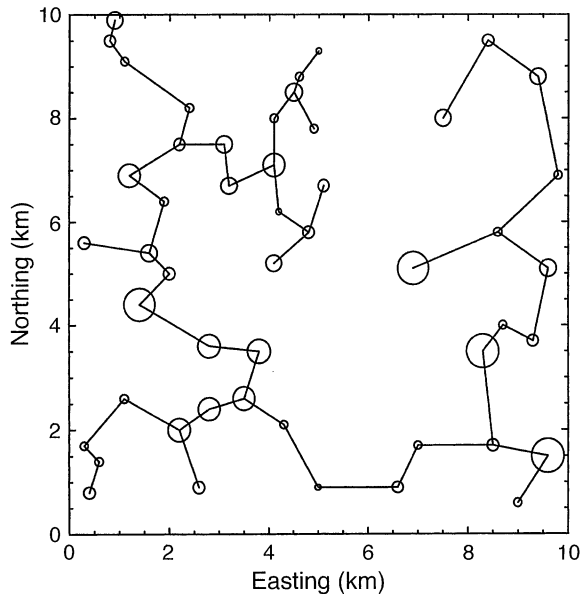
FIG. 2. A hypothetical landscape of 50 circular habitat patches in a 100-km² landscape. Edges drawn comprise the minimum spanning tree of the graph (based on distance).

$$f_{ij} = \frac{s_i}{s_{tot}} \times p'_{ij} \qquad (2)$$

where s_i is relativized as the proportion of total habitat area s_{tot} and p'_{ij} is the probability of dispersal from i to j, normalized by i's row sum in $\mathbf{P}$. The normalization is necessary because each row of $\mathbf{P}$ must sum to 1.0, while relativizing s forces the donor sources to sum to 1.0. Computed this way, the dispersal flux matrix is not necessarily symmetric. This indeed defines a *directed graph* or *digraph*, which has two edges for each pair of nodes, one in each direction. Gustafson and Gardner (1996) have noted the ecological importance of such asymmetries in dispersal probabilities. Here we simplify this graph by averaging the two directions, yielding an area-weighted flux w_{ij} for each pair of nodes. Finally, for convenience this weight is subtracted from 1.0 so that the flux value has the same rank order as distance itself (i.e., smaller fluxes at greater distances). The flux weight w_{ij} is thus

$$w_{ij} = w_{ji} = 1 - \left(\frac{f_{ij} + f_{ji}}{2}\right). \qquad (3)$$

The minimum spanning tree computed for this area-weighted flux matrix (Fig. 3) is different from the distance-based tree (Fig. 2) in an ecologically appealing way, as illustrated by the change in the tree to span across the larger node near the center of the graph instead of the smaller node at the bottom of the figure. Because of its larger size and expected number of propagules, the larger patch is a more likely connection. Similarly, the emergence of edges as "spokes" from larger patches reflects the area effect on dispersal rates,

consistent with a "core–satellite" (mainland–island) model of metapopulations (Harrison 1994).

Edge removal

Clearly the result of adding or removing edges in a graph is to effect its overall connectivity. For example, Fig. 4 illustrates the loss of edges as we successively constrain adjacencies to shorter distances. Here adjacencies are thresholded at distances of 1500 (i.e., $P = 0.05$) 1250, 1000, and 750 m. As the threshold distance decreases, the graph fragments into subgraphs that are themselves further disconnected at shorter threshold distances. The between-node distance in this graph is 5024 ± 2526 m (mean ± 1 SD) while the mean nearest-neighbor distance is 590 ± 346 m. Note that the graph becomes essentially disconnected at distances that are quite short relative to the distribution of all between-node distances. The question thus arises, *Is there a systematic relationship between the connectivity of a graph and the number of edges retained or removed?* Ecologically, this question translates into determining how functional links or corridors should be preserved in order to maintain overall connectivity of the habitat mosaic.

Approach.—We can approach this question by removing edges from a graph systematically and then summarizing overall connectivity in the process. We begin with all edges included in the graph and then systematically remove edges until the graph is arbitrarily sparse.

To summarize the connectivity of the graph, we compute three metrics at each step of the edge-removal
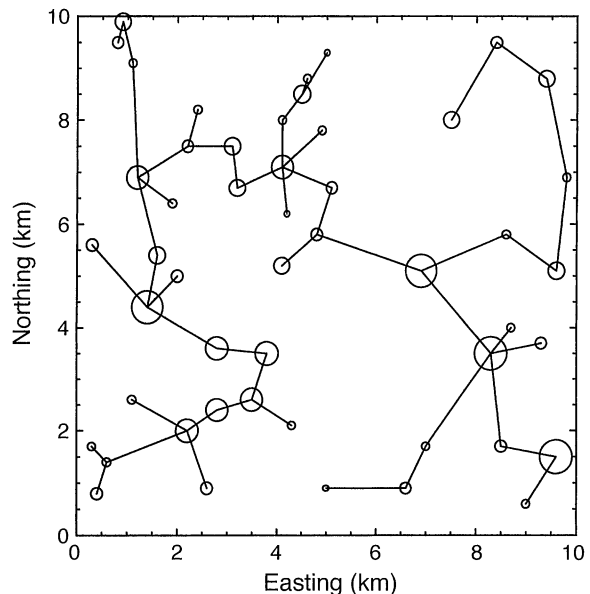

FIG. 3. A minimum spanning tree for the landscape graph, based on area-weighted normalized dispersal probabilities between patches (see *Graphs and graph theory: Graph operations*).
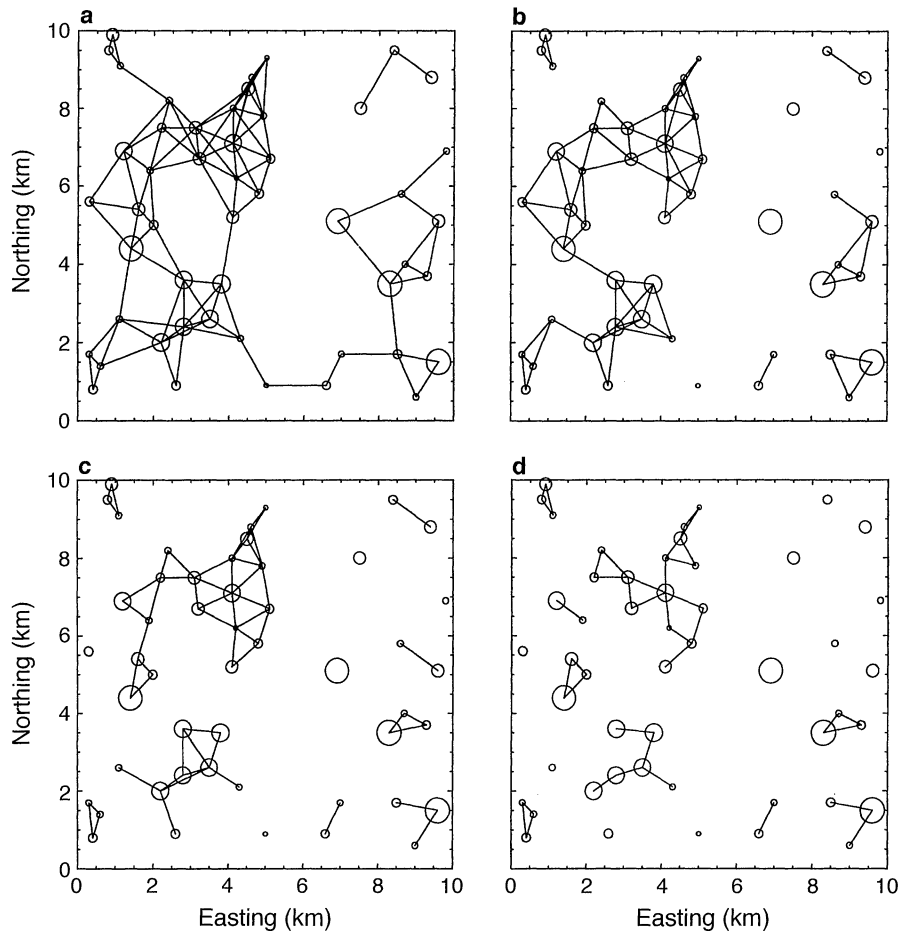
FIG. 4. Edge thinning: Connectivity of the landscape graph as edges are sequentially removed, at threshold distances of (a) 1500 m, (b) 1250 m, (c) 1000 m, and (d) 750 m.
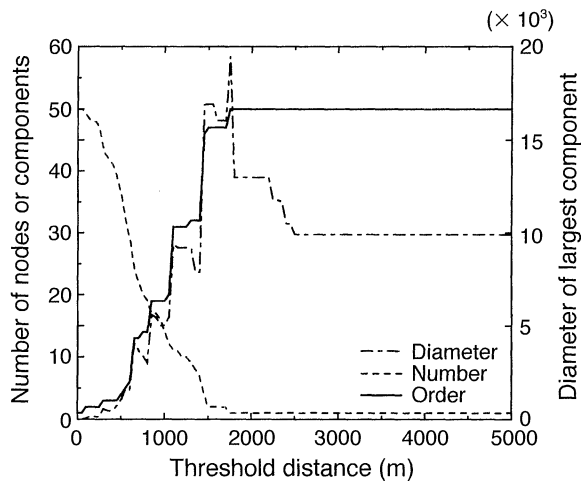

FIG. 5. Edge thinning. Trend in number of nodes, and order and diameter of largest node as edges are sequentially removed from the landscape graph.

sequence. Because the number of components increases as the graph disconnects, the number of graph components is one index of overall graph connectivity. A second metric is the order (number of nodes) of the largest remaining component. But order does not distinguish between linear chains of nodes as compared to compact constellations, and so we compute a third metric, the diameter of the largest component, to summarize the effective size of a graph. (In percolation theory, these last two terms would correspond to the area and radius of gyration of the largest cluster in a raster map; see Stauffer 1985.)

Fig. 5 illustrates the trend in number of components, order of the largest component, and diameter of the largest component as edges are sequentially removed from the graph. The graph shows a rather abrupt transition from connected to disconnected over a narrow range of distances. The trend in graph diameter, perhaps counterintuitive at first glance, shows an initial increase in diameter as direct paths between distant nodes are lost and replaced by longer stepping-stone paths; diameter then decreases as these stepping-stone paths are

lost. This edge-removal scenario also could be performed on edges defined in terms of area-weighted dispersal fluxes. Redefining edges in this way alters the order in which particular edges are removed in an edge-thinning scenario (not shown) but does not alter the shape of the relationships illustrated in Fig. 5.

Ecological implications.—A graph disconnects with a threshold behavior reminiscent of other similar phenomena in landscapes, such as the percolation threshold characteristic of raster lattices (Gardner et al. 1987, 1992). Given this behavior, the questions arise, *At what threshold distance does the graph come unconnected? How does this distance compare to the dispersal capabilities of species of concern?* This determines how a given species might perceive the landscape, i.e., to what extent that species might act as a metapopulation. We would expect different species to experience landscapes in scale-dependent ways, reflecting the scaling laws of allometry as well as species-specific habitat affinities (O'Neill et al. 1988b, Pearson et al. 1996). Thus, the same landscape might appear connected to some species while other species experience it as discrete (isolated) habitat patches; these cases would correspond, respectively, to the "patchy population" or "nonequilibrium" variants of metapopulations (Harrison 1984).

For a landscape that is more-or-less connected, identifying the bridges or cut-edges at particular distances (scales) would be helpful for prioritizing site acquisition or protection, as these sites would be expected to influence overall connectivity the most.

Landscapes comprising multiple connected subgraphs have further management implications that are more logistical or administrative: These regions (subgraphs) might be analyzed or managed separately, as nearly decomposable subsystems of a larger system (Tansley 1935, Allen and Starr 1982, O'Neill et al. 1986).

Node removal

The illustrations thus far have focused on graph edges or, by analogy, functional connections between patches in a landscape. But in many cases our concern is not with edges but rather with the nodes themselves. In particular, the gain or loss of habitat patches is central to landscape change in general and land management in particular. Here we turn our attention to habitat patches. As loss of habitat is probably the central driving force in conservation biology, we focus on the implications of the loss of habitat patches from a landscape. In terms of a graph: *How does the graph change as nodes are removed?*

Approach.—Consider three ways in which a habitat patch can be important to a landscape-scale metapopulation. (1) A patch might influence a metapopulation through its contribution to overall recruitment potential (R) as governed by its local natality, or mortality rates as influenced, perhaps, by patch area or habitat quality.

(2) A patch also might be important to dispersal flux (F), indexed as the flux of individuals or propagules away from their natal patches. A patch can have a high contribution to overall dispersal flux only if it is productive and well connected. Such patches are the "sources" in source–sink models in metapopulation theory (Pulliam 1988). (3) A patch might also contribute to traversability T of the landscape as a means of spreading of risk (den Boer 1968, Levins 1969). In this we are especially concerned with patches that would provide for a long-distance rescue effect, an index of the metapopulation's capability to rebound eventually from a perturbation to a significant portion of its range. A small stepping-stone patch might be important to traversability without contributing substantially to overall productivity or dispersal flux. For a landscape to have high traversability in this sense requires that it be sufficiently disconnected that a disturbance would not affect all patches at once, while still being sufficiently connected that local populations extirpated by such a disturbance eventually could be recolonized from afar.

We index recruitment R for the landscape as

$$R = \sum_{i=1}^{m} s_i \times k_i \qquad (4)$$

where s_i is patch size (fraction of total habitat area) and k_i is some scaling function related to habitat quality as this relates to natality or mortality rates in that patch. In practice this might be based on cover type or other measured environmental variables.

The index of dispersal flux F is

$$F = \sum_{i=2}^{m} \sum_{j=1}^{i-1} p_{ij} \times s_i \times k_i \qquad (5)$$

which includes only dispersal away from the natal patch, and because **P** is symmetric, need only be tallied from the lower triangle of the matrix.

The effect on traversability T is indexed as the diameter of the largest component in the graph formed on the removal of some node(s). Thus, traversability is defined as follows:

$$T = d(G') = Max(e_i, i \in G') \qquad (6)$$

where $e(i)$ is the eccentricity of a node i in the largest component G'.

We begin with the entire graph and iteratively remove nodes in three ways: (1) removal of a random node at each iteration; (2) removal of the smallest node (minimum patch area) remaining in the graph; and (3) removal of the endnode with the smallest area. An *endnode* in a spanning tree is a terminal "leaf" in the tree, that is, is adjacent to only one other node. After each iteration, all edges incident to the removed node are also removed, and so new endnodes emerge as the node thinning proceeds. In this case the spanning tree is based on area-weighted fluxes (Fig. 3). For all three
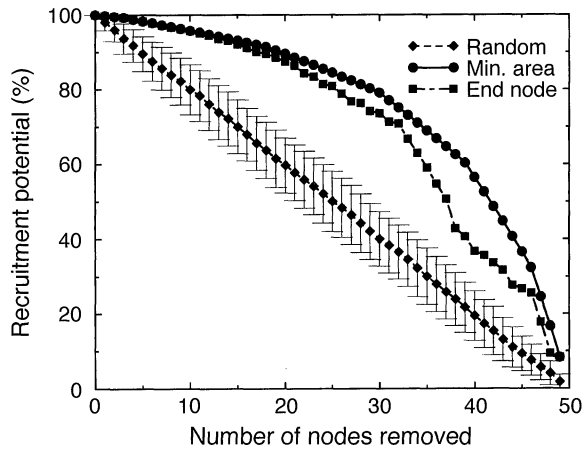
FIG. 6.   Node thinning. The figure shows the trend in over-all recruitment R as nodes are sequentially removed at random (drawn with 1 SD), according to minimum size, and by pruning a flux-weighted minimum spanning tree (see *Graphs and graph theory: Node removal: Approach*).
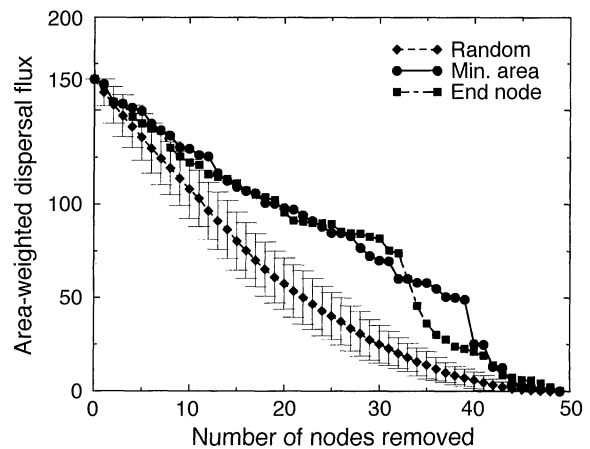

FIG. 7.   Node thinning. The figure shows the trend in dispersal flux F as nodes are sequentially removed at random (drawn with 1 SD), according to minimum size, and by pruning a flux-weighted minimum spanning tree (see *Graphs and graph theory: Node removal: Approach*).

node-thinning scenarios, we began with an adjacency matrix defined on area-weighted dispersal fluxes (Eq. 2), thresholding this value arbitrarily to a level corresponding to the maximum diameter of the initial graph. In the case of random thinning, we generated confidence limits by performing 100 stochastic trials, saving the mean and standard deviation for each thinning sequence.

In this example recruitment is indexed in terms of node area alone, and R exhibits a linear reduction as nodes are removed randomly (Fig. 6). By contrast, both minimum-area thinning and endnode pruning retain much higher recruitment potential because they place a premium on node area. By definition, the minimum-area thinning scenario retains the most recruitment potential as nodes are removed.

Because dispersal flux is defined to include node area, minimum-area and endnode-pruning thinning scenarios produce similar effects on overall dispersal flux (Fig. 7). The slight and inconsistent differences between these two scenarios suggest that area itself is the more important effect.

The advantage of endnode pruning is most evident in its effect on overall traversability of the graph (Fig. 8). In this case ~35 nodes (70%) can be removed before traversability decreases substantially. By contrast, the minimum-area thinning scenario is not very different than random thinning, as neither of these considers node location as a criterion for node removal.

Ecological implications.—The exact shape of these curves is landscape specific and so is not of particular interest in general. Similarly, the noise in the example curves is also landscape specific. What *is* important is the relative differences among the three curves. The discrepancy between these curves, especially for minimum area as compared to endnode pruning, underscores the importance of connectivity as compared to

patch area itself. In cases where the curves are quite different we would expect dispersal to be important, while in landscapes for which the curves are similar, research or management might focus on habitat area. This is a method to infer, in a preliminary way, the relative importance of habitat area and connectivity for a given landscape. The importance of either area or connectivity emerges from the deviation of either curve from the confidence limits generated by random-thinning trials.

Importantly, the result of this analysis will be unique to any particular landscape and so there cannot be any general expectation. We can anticipate, however, that certain kinds of landscape mosaics might be especially
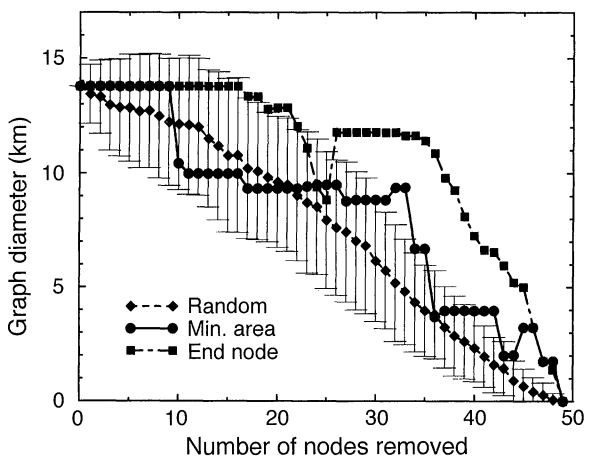

FIG. 8.   Node thinning. The figure shows the trend in traversability T of the largest graph component as nodes are sequentially removed at random (drawn with 1 SD), according to minimum size, and by pruning a flux-weighted minimum spanning tree (see *Graphs and graph theory: Node removal: Approach*).

amenable to this approach. Naturally connected networks such as those constrained by topography (e.g., high-elevation vegetation zones, or riparian habitats) might tend to show a high importance of connectivity because these networks have a strongly linear or chain-like structure that imparts importance to key links in the chain. By contrast, in habitat mosaics that are more centrally arranged as compact constellations, connectivity might not be as crucial an issue. This can be anticipated, perhaps, by examining the minimum spanning tree for the landscape, focusing on the fraction of nodes in the tree that are endnodes or that are adjacent to only two nodes in the tree.

Importance of individual nodes

Presuming that the removal of nodes has a significant impact on overall recruitment, dispersal flux, or traversability of a graph, it is logical to ask, *Which nodes are most important to preserving the graph's structure?* That is, *Which habitat patch(es) are most influential on metapopulation processes within the landscape?* An answer to this question would help researchers or managers to prioritize sites for further study, monitoring, or protection.

Approach.—We index a patch's impact on recruitment, dispersal flux, and traversability by computing the landscape-level index for each metric R, F, and T, and then we systematically remove each node from the graph and recompute the overall metric. The node's impact is the difference in the overall metric that its removal elicits (see Keitt et al. [1997] for a similar approach using raster lattice data structures). Again, we begin with an adjacency matrix defined by a threshold flux value chosen to maximize T for the graph.

In this hypothetical landscape, the three highest-ranked nodes are different for each criterion R, F, and T (Fig. 9). One large patch is ranked fourth in its effect on recruitment and first in its effect on traversability. The four large nodes, of course, are the most important to recruitment potential. Four nodes that are central to clusters of nodes are most important to overall dispersal flux, and in this particular landscape these do not happen to be the largest patches. The most important node for traversability is the one that effectively bridges the left and right sides of the graph. Nodes whose removal substantially prunes a long branch of the spanning tree are similarly important to traversability.

Ecological implications.—Which patches are most crucial to maintaining overall recruitment, flux, and traversability? These might be different patches for each metric, or some patches might be important for all metrics. This will depend on the particulars of a given landscape, including the definition of habitat quality as it effects recruitment, the distribution of patch sizes, and their arrangement within the landscape. In every case, patches identified as important warrant special attention in management or monitoring schemes.

Note that this analysis, even performed from preliminary or inadequate data, can be a powerful guide in marshalling further research or monitoring. For example, even if one merely suspects that dispersal is important, the patches identified as being important are the monitoring sites most likely to provide the data that would confirm (or disprove) that suspicion. Thus, the approach provides a direction in which to proceed even in the absence of sufficient data to make confident predictions.

ECOLOGICAL APPLICATION

The case of the Mexican Spotted Owl

An example system particularly suited to landscape graphs is the spatial population structure of the Mexican Spotted Owl (*Strix occidentalis lucida*). The Mexican subspecies of the spotted owl is distributed from Utah and Colorado south to Central Mexico (USDI 1995). In 1993 the subspecies was listed as threatened under the Endangered Species Act. A graph-theoretic approach was used previously to characterize owl habitat connectivity across four southwestern states (Utah, Colorado, New Mexico, and Arizona [USA]) as part of a federally mandated conservation plan (Keitt et al. 1995, 1997).

The habitat distribution for Mexican Spotted Owls is highly fragmented in the Southwest because suitable foraging and nesting sites are largely determined by topographic relief. Because of the arid climate and orographic effects, much of Mexican Spotted Owl habitat is divided into "sky islands" surrounded by grasslands and desert. Juvenile spotted owls are known to disperse considerable distances in search of vacant nesting territories. Thus it is highly likely that dispersal success plays an important role in the genetic, demographic, and metapopulation structure of the Mexican Spotted Owl.

Since dispersal success depends principally on the time and energy spent searching for suitable sites, the connectivity of suitable habitat patches is a prime concern when making habitat conservation decisions. In a previous study, Keitt et al. (1995, 1997) analyzed distance relationships among hypothesized spotted owl habitat patches. Their analysis identified two kinds of patches that contribute to landscape connectivity. The first were large core patches that provided regional dispersal routes simply because of their size and extent. The second were small stepping-stone patches that despite their small size contributed greatly to potential dispersal because of their location. The spatial analysis was used as a basis for ranking habitat patches and making habitat-conservation recommendations.

Here we use the data of Keitt et al. to demonstrate the application of minimum spanning trees to habitat conservation. Our goal is not to make specific recommendations about spotted owls, but rather to illustrate a general approach of applying graph theory to

habitat-conservation efforts. We assume that the Mexican Spotted Owl is structured as a metapopulation and use Hanski's incidence-function approach (Hanski 1994, 1998) to simulate the effect of different habitat-alteration scenarios.

First, we constructed two potential habitat scenarios based on reported spotted owl habitat preferences (USDI 1995). We used forest type and forest density maps derived from AVHRR (advanced very high resolution radiometer) satellite imagery (Evans et al. 1993, Zhu 1994). The first habitat map, which we refer to as the "island model," was identical to the one used by Keitt et al. (Fig. 10). It consisted of all grid cells in the habitat cover map labeled "ponderosa pine" or "mixed conifer." Mexican Spotted Owls breed principally in mixed conifer forests and forage extensively in adjacent stands of ponderosa pine. Adjacent habitat cells were then joined to form clusters or islands. After removing clusters <10 km² in area (approximate territory size, USDI 1995), the remaining 250 habitat clusters were analyzed with respect to proximity and location.

The second habitat map we refer to as the "mosaic landscape." It was generated from the same landscape coverages, but instead of clustering certain cover types, we combined forest type with forest density to arrive at a measure of habitat suitability. Forest density ranged between 0 (no trees) and 1 (closed canopy) (Zhu 1994) and forest types included mixed conifer, ponderosa pine, and pinyon–juniper (Evans et al. 1993). The forest types were given weights (mixed conifer = 1.0, ponderosa pine = 1.0 and pinyon-juniper = 0.2) and these weights were multiplied by forest density to arrive at a suitability index in each 1-km² grid cell. Suitability was then averaged in 25-km² blocks to arrive at the final mosaic.

The incidence function models a situation in which populations experience stochastic extinction and re-colonization events. In Hanski's formulation, the probability of a local extinction is

$$E_i = \min\left(1, \frac{e}{s_i^x}\right) \qquad (7)$$

where s_i is the effective size of patch i, e is the minimum viable patch area and x is a parameter that scales the intensity of environmental disturbances. (For consistency, we retain our earlier notation rather than adopting Hanski's, which conflicts with terms defined previously in this paper.) Effective size is considered a surrogate for the size of the local population and can be scaled to take into account habitat degradation. For the island landscape, we set s_i equal to the patch area. In the mosaic landscape, s_i was the area (a constant since all patches were of equal size) multiplied by the mean habitat quality within each habitat cell.

Hanski also introduced a colonization function that relates the number of propagules arriving in a patch and the probability of successful establishment. Colonization probability increases as sigmoid function of the dispersal input and is given by

$$C_i = \frac{1}{1 + \left[\dfrac{y}{P_i}\right]^2} \qquad (8)$$

where P_i is the number of propagules arriving in patch i, and y is a parameter that relates to the capacity of a species to successfully establish in a new patch. P_i is estimated as follows:

$$P_i = \sum_j \sigma_j s_j \exp(\theta \cdot d_{ij}) \qquad (9)$$

where σ_j is a switch set to 1 if patch j is occupied and 0 otherwise, θ is the dispersal-distance coefficient, d_{ij} is the distance between patch i and j, and s_j is the size of patch j.

Given probabilities of colonization and extinction, we can then use the incidence function

$$J_i = \frac{C_i}{C_i + E_i} \qquad (10)$$

to compute the long-term quasi-stable equilibrium probability that patch i will be occupied (Diamond and May 1977, Hanksi 1994). Given suitable data, it is possible to estimate the main parameters e, θ, x, and y for a particular species and landscape. To do so requires presence–absence data for many patches, preferably over many population–turnover events. Collecting such data for large vertebrates such as the Mexican Spotted Owl is difficult if not impossible. In this case, however, we are not actually attempting to predict the viability of spotted owls in the Southwest. Rather, we simply wish to illustrate one possible scenario and its consequences for habitat conservation problems. For the simulations reported here, we used $e = 1$, $\theta = 0.05$, $x = 1$ and $y = 5$.

Decisions regarding habitat preservation need to consider future patterns of habitat loss and degradation. If one or a few patches are at risk at any given time, it implies a different planning response than if the landscape is systematically converted into alternative land use. Here we consider a scenario in which available habitat is gradually removed until all the habitat is lost. An important question is, of course, *How much habitat can be removed before a species becomes extinct?* Unfortunately, this question has no generally meaningful answer because of the high uncertainty in any predicted consequence of habitat alteration (Taylor 1995). All habitat is valuable. The question thus becomes, *Which patches should we choose to preserve given limited resources, time, and data?* It is our position that the relative ranking of patches is most useful in the decision process. In the following scenarios, we assume that habitat will be lost, but that we get to choose the order in which patches are lost. We then compare the
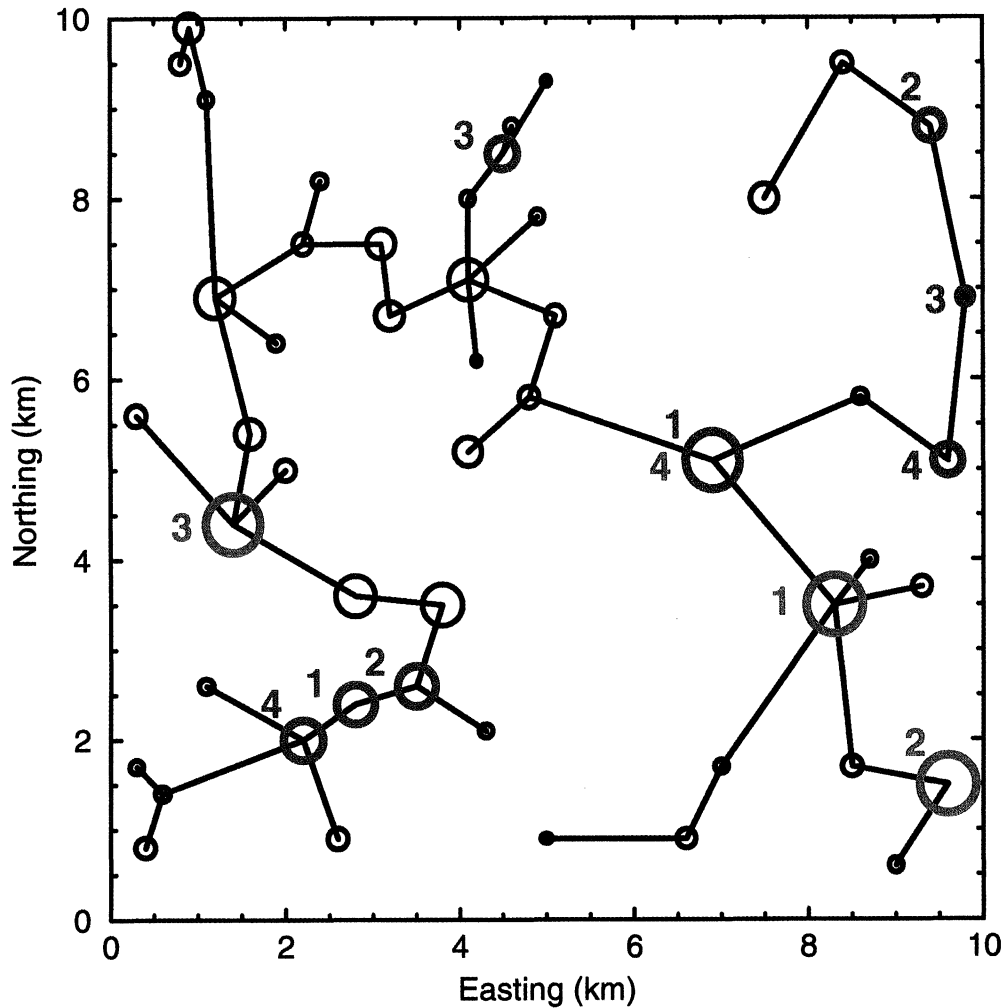
FIG. 9.   Node sensitivity on removal. The figure depicts the relative importance of individual patches to overall recruitment R (in red), dispersal flux F (blue), and traversability T (green) of the landscape graph. The four highest-ranking patches for each metric are labeled 1–4.

success of different methods of ranking patches at equivalent levels of habitat destruction.

The three methods of ranking patches are based on the node-removal algorithms discussed previously (see *Graphs and graph theory: Node removal,* above). We used random removal, minimum patch weight (weight equal to area in the island landscape and to mean habitat quality in the mosaic landscape), and minimum-weight pruning of the minimum spanning tree. For each of the three rankings, we removed an equivalent area of habitat from the landscape and calculated the mean patch occupancy of the remaining patches using the incidence-function model. On each removal step, the model was run for 10 000 iterations and results were averaged over an additional 100 iterations, yielding an index of habitat occupancy at steady state.

When patches were removed in random order and in order of patch weight from the island landscape, occupancy declined dramatically as habitat was removed

(Fig. 11). Removal of least-weight patches exhibited a characteristic signature of a percolation transition: an abrupt change in qualitative dynamics at a critical density of habitat. For these simulations, the transition appeared to occur when about 20% of the landscape area was removed. Once a sufficient number of patches were removed, the least-weight ranking resulted in roughly the same or worse than removing random patches.

When island patches were pruned from the minimum spanning tree, a dramatically different result occurred (Fig. 11). Occupancy actually increased until nearly all the habitat was removed. This results from the fact that pruning the spanning tree maintains the integrity of the landscape by not only providing large core populations, but also by providing dispersal routes between core habitats.

For the mosaic landscape, the results were much less dramatic, although the minimum-spanning-tree ranking
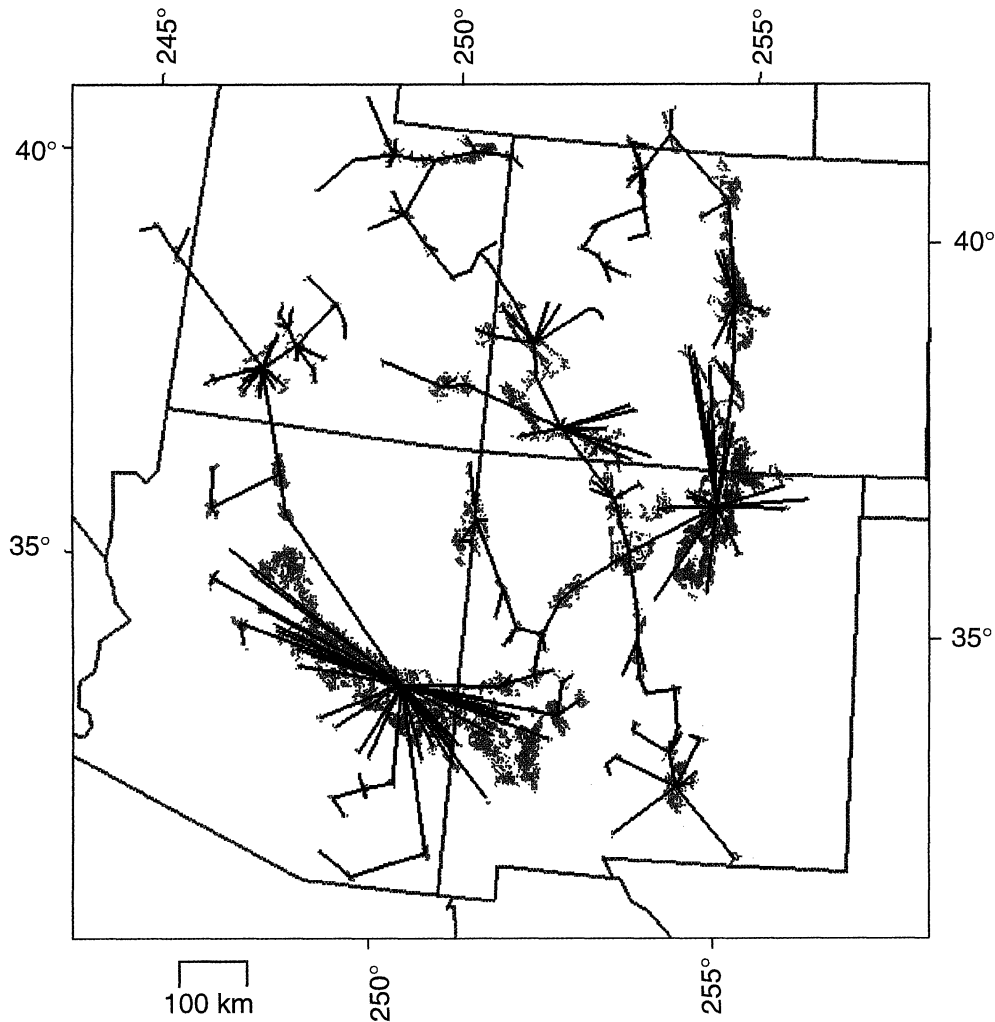
Fig. 10.   Representation of a landscape of potential habitat (green) of the Mexican Spotted Owl (*Strix occidentalis lucida*) in the Southwest (USA) as an island model and a graph (based on data from Keitt et al. [1995, 1997]) The graph's minimum spanning tree is shown.

performed as well or better than patch-weight ranking (Fig. 12). The reason that occupancy remained high even at a high degree of habitat loss has to do with the spatial scale of the modeled disturbance. In the mosaic landscapes, extinctions in habitat cells were spatially independent. Thus, extinctions were localized in space, and, as a result, the importance of traversability was not as large.

An important implication of these simulations is that the landscape graph can provide a useful, static guide to dynamic processes unfolding on the landscape. In particular, this static approximation does not require us to estimate all of the parameters of the metapopulation model, but still provides useful insights into the behavior of the landscape. The correspondence between the graph model and a more complicated dynamic model will, of course, increase as one incorporates more detailed ecological information into the graph in terms of how the nodes and edges are defined (see below).

DISCUSSION

We have presented a general introduction to graph theory as it might apply to conservation applications couched in metapopulation theory. In this, we hope to take advantage of extremely efficient computational algorithms already available for graph operations (Thulasiraman and Swamy 1992, Gross and Yellen 1999). For instance, Keitt et al. (1997) used a raster model and percolation theory to examine connectivity in an application similar to that presented here. They were forced to restrict their analysis to a few hundred habitat patches because of computational limitations even for powerful computers. Using a graph-theoretic framework for the same general problem can extend the analysis to at least an order of magnitude more patches; implementing more efficient coding of these same algorithms (such as those used in computer science) would extend this capability by at least another order
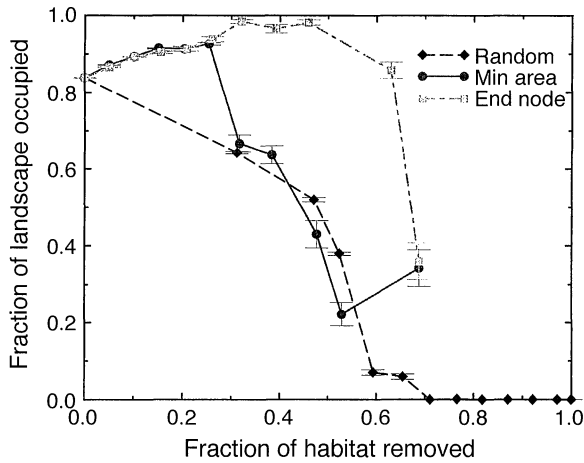
FIG. 11. Metapopulation persistence, based on the island model. Depicted are results of random, minimum-weight, and weighted tree-pruning patch-removal scenarios for the habitat island landscape. For random scenarios, plotted values are means ± 1 SD based on 100 trials.

of magnitude. Moreover, the graph-theoretic framework provides for facile manipulations of landscapes and ready summaries of landscape structure in terms of shortest paths, diameter, subgraphs, and so on. Thus, our purpose is to illustrate a means of *facilitating* landscape analysis. This does not mean that graph theory should subsume other approaches based on alternative approaches; we suggest graph theory as a computationally powerful adjunct to these other approaches.

Graph theory is not appropriate for all landscape applications. It is best suited to landscapes that can be represented reasonably as discrete patches in a matrix that itself can be treated as "nonhabitat." In cases where intervening land covers or habitats do matter, these might be incorporated into the calculation of between-patch distances. For example, by assigning a "resistance" or navigability value to each cover type, the intervening matrix can be accounted for in the distances (Gustafson and Gardner 1996). In some cases the effective distances between patches, and hence their dispersal probabilities, are asymmetric. For example, if gravity matters so that distance uphill is effectively farther that distance downhill, then asymmetries should be preserved in the distance matrix. This would yield a directed graph or "digraph," with two edges between each pair of nodes. Most graph operations can be applied to digraphs as well as to simple graphs; the algorithms are somewhat more complicated but are well developed and readily available.

For some landscapes it may be inappropriate to use a graph representation. If habitat patches are poorly resolved spatially because habitat quality varies continuously and subtly over the landscape, then aggregating this variability into discrete patches would be inappropriate. In such cases a model based on a con-

tinuous surface (a field model) would provide a better rendition of the landscape.

One compelling feature of a graph-theoretic framework is that it can be a heuristic framework for ongoing research. For example, with very little data one can construct a graph of habitat patches (however crudely defined) and then explore the structure of the graph by considering a range of threshold distances to define edges (as in Fig. 4 and 5). This preliminary exploration can provide some idea of landscape connectivity relative to the dispersal capabilities (however uncertain) of a species of interest. Similarly, constructing the minimum spanning tree for the graph can indicate the backbone of the habitat mosaic, and node-removal sensitivity analysis can provide an initial estimate of the relative importance of patches in the landscape. These preliminary analyses also marshall further study by identifying those patches where field studies should be concentrated. For example, the patches highlighted in the node-removal analysis offer themselves as likely candidates for further field studies. Importantly, as more or better data are collected these can be incorporated, infusing more ecological information into the graph and consequently adding more precision and confidence to the analyses. In the examples we have presented, defining edges in terms of dispersal probability rather than simple distance can affect the analyses dramatically. This argues in favor of infusing as much biological information as possible into the graph framework. Ultimately, the graph model might incorporate sufficient biological information that it can provide a bridge to other computational models such as Markov processes (e.g., Norris 1997) or Petri nets (Peterson 1981, Reisig and Rozenberg 1998). Roberts (1976) presents Markov chains as stochastic versions of weighted graphs; in the examples we present, the focus would
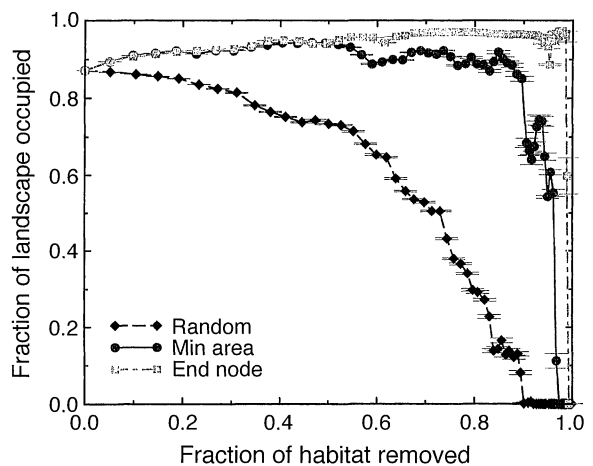

FIG. 12. Metapopulation persistence, based on the mosaic model. Depicted are results of random, minimum-weight, and weighted tree-pruning patch-removal scenarios for the habitat mosaic landscape. For random scenarios, plotted values are means ± 1 SD based on 100 trials.

be on the dispersal probability matrix. Petri nets are bipartite directed multigraphs (bipartite, with two types of nodes; multigraphs, with multiple edges per node) used in computer systems and communication theory. Thus, graph theory can provide a consistent heuristic framework that can begin quite simply but grow in complexity as more information is incorporated.

CONCLUSIONS

The shift from raster and vector-based landscape indices (Gardner et al. 1987, O'Neill et al. 1988a, McGarigal and Marks 1994, Gustafson 1998) to measures of connectivity based on a graph representation is an important step toward making landscape ecology a discipline useful to conservation planners. The graph representation allows us to merge population process (recruitment, dispersal) with landscape pattern (patch size, shape, and location) to arrive at process-based measures of connectivity, both for whole landscapes and for individual patches (Hanski 1998).

There are many other important considerations beyond landscape connectivity to be considered in conservation planning, such as the timing of when particular sites may be acquired and the opportunity costs of adding a site to the reserve network. Our approach to landscape analysis is in no way incompatible with other kinds of risk analysis or cost–benefit analysis. We strongly advocate best current practices for monitoring and modeling threatened populations. These may include both simple analytic models and more complex metapopulation and individual-based models with parameters estimated from known biological constants or from statistical data analysis.

We realize that all too often, managers do not have the luxury of waiting for more or better data, nor do they have the time or resources to apply the latest theoretical models. Managers need results, usually based on inadequate or nonexistent data, and they need them urgently. Graph-theoretic analysis of landscape networks may fill an important niche in this regard. The approach does require spatial habitat data of reasonable quality, but these are increasingly available. More importantly, because our approach does not require long-term population data, it can be used as a kind of rapid landscape-scale conservation assessment tool that allows initial prioritization of habitat resources and can guide the development of data collection and monitoring.

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