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Landscape connectivity: A conservation application of graph theory

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We use focal-species analysis to apply a graph-theoretic approach to landscape connectivity in the Coastal Plain of North Carolina. In doing so we demonstrate the utility of a mathematical graph as an ecological construct with respect to habitat connectivity. Graph theory is a well established mainstay of information technology and is concerned with highly efficient network flow. It employs fast algorithms and compact data structures that are easily adapted to landscape-level focal species analysis. American mink (Mustela vison) *and prothonotary warblers* (Protonotaria citrea) *share the same habitat but have different dispersal capabilities, and therefore provide interesting comparisons on connections in the landscape. We built graphs using GIS coverages to define habitat patches and determined the functional distance between the patches with least-cost path modeling. Using graph operations concerned with edge and node removal we found that the landscape is fundamentally connected for mink and fundamentally unconnected for prothonotary warblers. The advantage of a graph-theoretic approach over other modeling techniques is that it is a heuristic framework which can be applied with very little data and improved from the initial results. We demonstrate the use of graph theory in a metapopulation context, and suggest that graph theory as applied to conservation biology can provide leverage on applications concerned with landscape connectivity.*

Keywords: landscape ecology, graph theory, connectivity, modeling, metapopulations, focal species, American mink, *Mustela vison*, prothonotary warblers, *Protonotaria citrea*.

Introduction

The current trend in ecological research and land management is to focus on large biogeographic areas, which leaves the researcher and manager searching for landscape-scale data (Christensen *et al.*, 1996; Noss, 1996). Indeed, the interpretation of large spatial data, conceptually and technologically, can be the limiting factor in making conservation biology and ecosystem management a tangible goal. Because the internal heterogeneity of landscapes makes habitat-conservation planning a formidable challenge, modeling the spatial aspects of landscapes is a critical key to understanding. Until now, the varied approaches to building these models have focused primarily on two types of spatial data, coverages of vectors (polygons) or raster grids. We demonstrate the utility of a less familiar type of lattice, the graph (Harary, 1969), in determining landscape connectivity using focal-species analysis in an island model. A graph represents a binary landscape of habitat and non-habitat, where patches are described as nodes and the connections between them as edges.

Graph theory is a widely applied framework in geography, information technology and computer science. It is primarily concerned with maximally efficient flow or connectivity in networks (Gross and Yellen, 1999). To this end, graph-theoretic approaches can provide powerful leverage on ecological processes concerned with connectivity as defined by dispersal. In particular, graph theory has great potential for use in applications in a metapopulation context. Urban and Keitt (2000) have introduced landscape-level graph-theory to ecologists, and here we build on that work by examining habitat connectivity for two species that share the same habitat but have different dispersal capabilities. Specifically, we ask how American mink (*Mustela vison*) and prothonotary warblers (*Protonotaria citrea*)

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perceive the same landscape. We explore the sensitivity of landscape connectivity through graph operations concerned with edge definition. We also examine each habitat patch's role in maintaining landscape connectivity in terms of source strength (Pulliam, 1988) and long-distance traversability (den Boer, 1968; Levins, 1969) using graph operations concerned with node removal. This type of analysis is done very efficiently with graph theory. We also present an ecologically appealing way to calculate the functional distance between habitat patches using least-cost path modeling. Graph theory as applied to landscapes represents an important advance in spatially explicit modeling techniques because it is an additive framework: analysis of a simple, preliminary graph can prioritize further data collection to improve the graph model.

Study area and methods

Study area

Our study focuses on the Alligator River National Wildlife Refuge (NWR) and surrounding counties on the Coastal Plain of North Carolina (35°50′N; 75°55′W). It is a riverine and estuarine ecosystem with an area of almost 580 000 ha and over 1400 km of shoreline. The area is rich in wildlife habitat, dominated by the Alligator River NWR, the Pocosin Lakes NWR, Lake Mattamuskeet NWR, Swanquarter NWR, and a variety of other federal, state, and private wildlands (Figure 1).

The vegetation is characterized by the Southern Mixed Hardwoods forest community. The area has many diverse vegetation types, including fresh water swamps, pine woods and coastal vegetation. In the upland community, dominant species include many types of oak (*Quercus* spp.), American Beech (*Fagus grandifolia*), and evergreen magnolia (*Magnolia grandiflora*). Mature stands may have five to nine codominants. The wet lowlands are dominated by bald cypress (*Taxomodium distichum*). The pine woods are dominated by longleaf pine (*Pinus palustris*), but loblolly pine (*P. taeda*) and slash pine (*P. elliottii*) are also important (Vankat, 1979).

Focal species

Because connectivity occurs at multiple scales and multiple functional levels (Noss, 1991), we have chosen two focal species to apply a graph-theoretic approach to connectivity. Focal species analysis is an essential tool for examining connectivity in a real landscape, as individual species have different spatial perceptions (O'Neill *et al.*, 1988). The American mink and the prothonotary warbler are appropriate candidates for focal species analysis as they share very similar habitat but have different ecological requirements, and fall into different categories as focal species. Both species are wetland dependent and indicators of wetland quality and abundance in a landscape. Both are charismatic. Furthermore, as meso-predators mink have small but important roles as a keystone species (Miller *et al.*, 1998/1999).

American mink are meso-level, semiaquatic carnivores that occur in riverine, lacustrine and palustrine environments (Gerell, 1970). In chief, they are nocturnal and their behavior largely depends on prey availability. They have a great deal of variation in their diet according to habitat type, season and prey availability (Dunstone and Birks, 1987). Muskrats (*Odantra zibethicus*) are a preferred prey item (Hamilton, 1940; Wilson, 1954), but mink diets in North Carolina are composed of aquatic and terrestrial animals, as well as semiaquatic elements (e.g. waterfowl; Wilson, 1954). In the southeast they have home ranges on the order of 1 ha and a dispersal range of roughly 25 km (Nowak, 1999).

Prothonotary warblers are neotropical migrants that breed in flooded or swampy mature woodlands. They have two very unusual traits in common with wood warblers in that they are cavity nesters and prefer nest sites over water. They are forest interior birds that experience heavy to severe parasitism by brown-headed cowbirds (*Molothrus ater*); (Petit, 1999). They are primarily insectivorous, occasionally feeding on fruits or seed (Curson *et al.*, 1994). Preliminary data indicate that natal dispersal ranges from less than 1 km to greater than 12 km (Petit, 1999). Although this is formulated from a small sample, it is on the same order as other song bird dispersal (e.g. Nice, 1933; Sutherland *et al.*, 2000). Here, we posit warbler dispersal

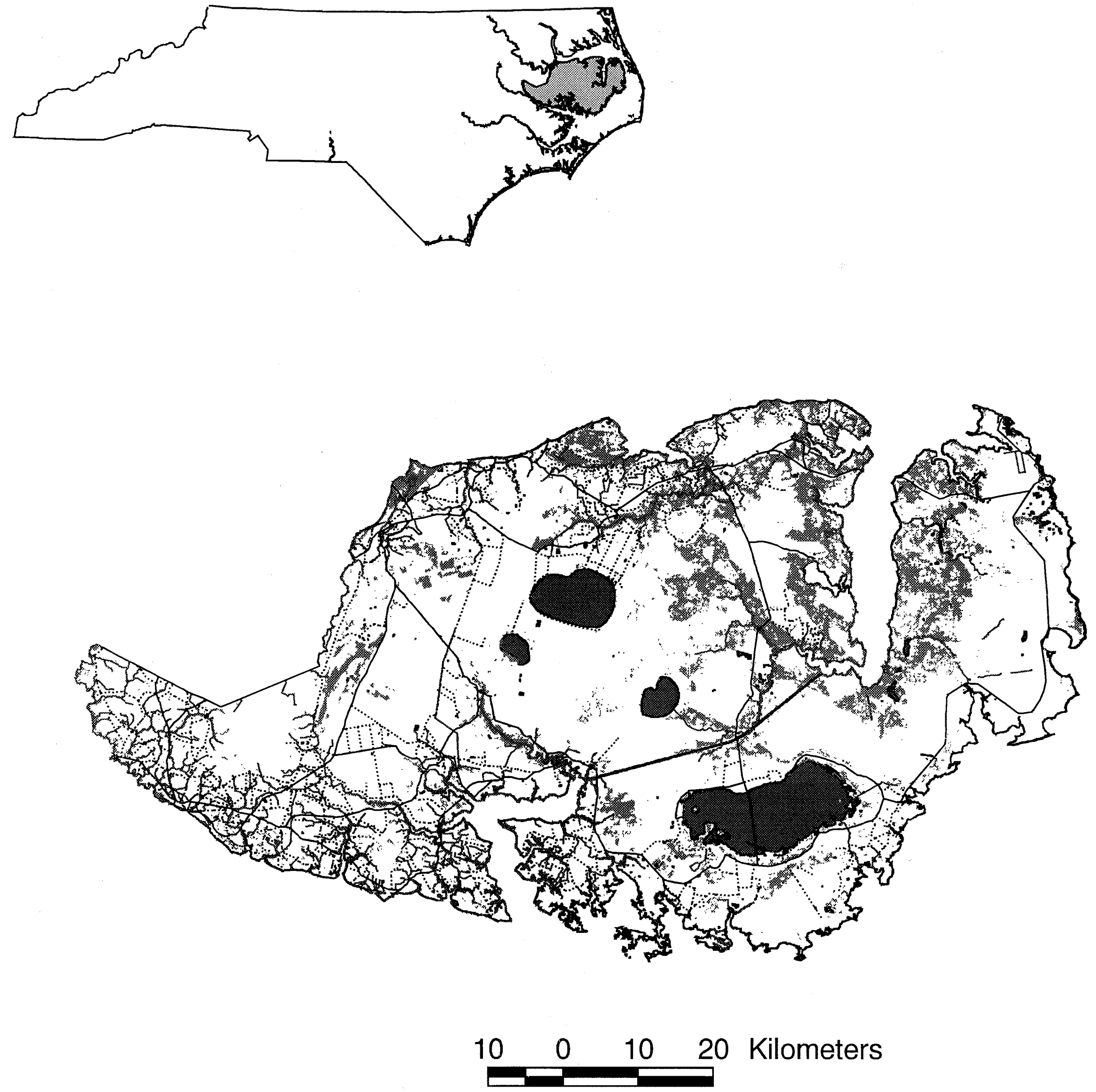

Figure 1. Study area in North Carolina with major roads and streams shown along with bottomland hardwood forest (focal species habitat) identified using GIS analysis.

to be 5 km and return to the uncertainty of this statement later.

Geospatial data

To our knowledge there are no current data on the spatial distribution of the focal species in our study area. The decline in trapping of the mink has perversely led to a decline in good biological information on the species. We are unaware of any work done with mink in the study area since Wilson's (1954) study. The Breeding Bird Survey indicates that this study area contains one of the highest concentrations of prothonotary warblers in the Southeast (Price *et al.*, 1995). Finer scale spatial information is not readily available.

Mink and prothonotary warblers are habitat specialists that use the same habitat. To identify habitat patches in the landscape we combined data from the US Fish and Wildlife Service's National Wetlands Inventory (http://wetlands.fws.gov) and a 1996 land-use coverage from the National Center for Geographic Information and Analysis (http://www.negia.ucsb.edu). Both were derived from Landsat 7 Thematic Mapper imagery with 30-m cells. Cells that were defined as being bottomland hardwood swamp or oak gum cypress swamp, and riverine, lacustrine, or palustrine forested wetland were selected as habitat. These cells were then aggregated into regions using an eight-neighbor rule, and the intervening matrix was described as non-habitat. We also used zonal averaging techniques in an attempt to account for functional scaling in the habitat and found that the patch definition was robust. Transportation and hydrography digital line graphs were obtained for the study area from the US Geological Survey (http://www.usgs.gov) at 1:100 000 resolution.

Graph theory

Urban and Keitt (2000) give a general description of ecological applications of graph theory and readers should refer to any number of excellent texts on graphs as a primer (e.g. Gross and Yellen, 1999). However, this section describes the graph operations and definitions used in this study. While there are numerous excellent texts on the formalisms of graph theory (e.g. Gross and Yellen, 1999), the following largely conforms to Harary's (1969) classic text. A graph G is a set of nodes or vertices $V(G)$ and edges $E(G)$ such that each edge $e_{ij}=v_i v_j$ connects nodes v_i and v_j. A path in a graph is a unique sequence of nodes. The distance of a path from v_l to v_n is measured by the length of the unique set of edges implicitly defined by the path. A path is closed if $n_l=v_n$. Three or more nodes in a closed path is called a cycle. A path with no cycles is a tree. A tree that includes all the vertices in the graph is a spanning tree. The minimum spanning tree is the spanning tree in the graph with the shortest total length. The minimum spanning tree in effect represents the parsimoniously connected backbone of the graph.

A graph is connected if a path exists between each pair of nodes. An unconnected graph may include several connected components or subgraphs. A graph's diameter, $d(G)$, is the longest path between any two nodes in the graph, where the path length between those nodes is itself the shortest possible length. If nodes i and j are not adjacent, then the shortest path between them cannot be the distance between them but must use stepping-stones. Here, we use graph diameter (or diameter of the largest component) as an index to overall traversability of the habitat mosaic.

A graph is defined by two data structures: one that describes its nodes and one that describes its edges. We defined the nodes (habitat patches) by their spatial centroid and size (x, y, s). We defined the edges by a distance matrix $\mathbf{D}$ whose elements d_{ij} are the functional distances between patches i and j. For n patches $\mathbf{D}$ is n by n but because $d_{ij}=d_{ji}$ and $d_{ii}=d_{jj}=0$, it is sufficient to compute the lower triangle of the matrix.

Although the spatial array of nodes is simple to produce from a GIS, the other matrices are not as easy to define. Distance between patches can be measured in several different ways: edge to edge, centroid to centroid, centroid to edge, etc. However, measuring these as Euclidean distance makes little sense when the variance in mortality cost associated with traversal of the intervening habitats is large, and cost associated with traversal of the intervening habitats is large and spatially heterogeneous. Few organisms or even ecosystem processes, such as groundwater movement or wildfire spread, move in this way. To differing extents they are all constrained by the landscape. Good multidimensional models exist to predict some ecosystem processes (e.g. pollution plumes; Bear and Verruit, 1987) but not others. Spatially explicit models that simulate the dispersal of animals have been explored in some depth but the process is still poorly understood (Gaines and Bertness, 1993). Most are complex parametric models which are data-hungry. They require specific information and are hard to parameterize (Gustafson and Gardner, 1996).

For this reason, we have computed $\mathbf{D}$ not as Euclidean distances but as a series of least-cost paths on a cost surface appropriate to the organisms in question. These paths are designed to approximate the actual distance the focal species (or any other landscape agent, e.g. fire) covers moving from one patch to the next. For instance, in this riverine ecosystem, the path a mink might take from one side of a river delta to the other would likely involve traversing the shore for 10 km under cover, rather than a 5-km swim across open water. This allows the animal to use stepping-stones of other habitat (low cost) along the way rather than set off into an unknown habitat matrix (high cost). The least-cost modeling combines habitat quality and Euclidean distance in determining d_{ij}.

Cost was defined in 90-m cells (aggregated up from 30-m cells to improve processing time) by a surface comprised of x, y and z, where z was a uniform impedance that represented the cost of moving through that cell, i.e. its resistance to dispersal. Weights were approximated, based on perceived traversability. Cells corresponding to areas of habitat were given a weight of 0·5, all other forest types were given a weight of one. Cells classified as riverine/estuarine herbaceous were given a weight of two. Shrubland was given a weight of three. Sparsely vegetated cells (cultivated, managed herbaceous) were given a weight of four. Areas of development and large water bodies were given a weight of five. Streams were defined with a weight of one. We used grid functions inside a macro in ArcInfo 7.2.1 (ESRI, 1998) to iteratively loop through the array of patches and compute d_{ij} for each unique pair of nodes in the array. The macro uses area-weighted distance functions to calculate least-cost paths. These functions are similar to Euclidean distance functions, but instead of working in geographical units they work in cost units.

We explored alternative methods for constructing **D**, including Euclidean distance and resistance-weighted distance between nodes. We found that the topology of the graph is robust and not sensitive to the difference between least-cost path distance and Euclidean distance except at the scale of large obstacles in the landscape. For instance, least-cost paths in our model did not cross the 5-km mouth of the Alligator river when moving from the eastern side of the study area but chose a route through habitat instead. In this case Euclidean distance and least-cost path distance were quite different. The least-cost path technique is useful to land managers as the surface can be parameterized based on best available data. Thus, the surface can be tailored to features in the landscape for which the manager has knowledge. The surface can be refined as data becomes available, e.g. in the form of radio tracking.

Gustafson and Gardner (1996) found that dispersal routes are difficult to predict in even slightly heterogeneous landscapes. We have kept that in mind by building a simple cost surface that avoids committing the animals to movement patterns that are not readily possible to predict at 90-m resolution. We are not suggesting that the organisms modeled move purely according to least-cost paths. We use the framework because the distance of the least-cost path is a better approximation of the actual distance covered than a straight line between patches. Our goal has been to get a better estimate of distance traveled using least-cost and not to predict corridors. This modeling technique can be applied in a GIS, with limited spatial data, making it accessible to land managers and conservation practitioners. Despite these advantages, cost-surface analysis has been only occasionally used by ecologists (Krist and Brown, 1994; Walker and Craighead, 1997), but widely used in computer science which is concerned with optimal route planning (e.g. McGeoch, 1995; Bander and White, 1998). This type of analysis is also common in applications of artificial intelligence (e.g. Xia *et al*., 1997).

To focus on scaling between the two focal species we chose to explicitly incorporate only patches greater than 100 ha in our analyses, as prothonotary warblers are not likely to persist in forest patches less than 100 ha (Petit, 1999). Using habitat patches greater than 100 ha results in 83 patches, roughly 83% of the 53 392 ha of possible habitat. Because all habitat patches, regardless of size, are given the lowest value on the cost surface, they are implicitly included in all analyses in that the species can traverse them easily as stepping-stones, accruing minimal cost.

We further defined edges by a dispersal probability matrix **P** that expresses the probability that an individual in patch i will disperse at least the distance between patch i and j. We computed the elements of **P** as negative exponential decay:

$$p_{\mathrm{ij}} = -e^{(\theta \cdot d_{\mathrm{ij}})} \tag{1}$$

where θ is an extinction coefficient greater than 0. This way dispersal functions can be indexed by noting the tail distance corresponding to $P=0{\cdot}05$ is $-\ln(0{\cdot}05)\cdot\theta^{-1}$. The tail distance for mink and prothonotary warbler are indexed as 25 km and 5 km, respectively. The tail distance is the distance to a selected point on the flat tail of the dispersal-distance function. Other curves are possible and Clark *et al*. (1999) provide a discussion of alternate dispersal kernels.

The graphs are described most succinctly by an adjacency matrix $\mathbf{A}$ in which $a_{ij}=1$ if nodes i and j are connected and 0 if not. We set $a_{ij}=1$ if $d_{ij}\leq 25$ km for mink and $d_{ij}\leq 5$ km for prothonotary warbler.

We can also define the graph's edges in terms of dispersal fluxes. Combining $\mathbf{P}$ and $\mathbf{s}$ allows us to compute dispersal flux from i to j:

$$f_{ij}=\frac{s_i}{s_{tot}}\cdot p'_{ij} \tag{2}$$

where s_i is relativized as the proportion of the total habitat area s_{tot} in i and p'_{ij} is p_{ij} normalized by the row sum of i in $\mathbf{P}$. Because dispersal flux is asymmetrical ($f_{ij}\neq f_{ji}$) when $s_i\neq s_j$ we average the directions between nodes to give area-weighted dispersal flux w_{ij}:

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

Subtracting from 1 allows the flux value to have the smaller fluxes at greater distances. The area-weighted dispersal flux matrix allows us to compute a version of a minimum spanning tree with more dispersal biology incorporated.

Graph operations

With graph construction complete we performed two types of graph operations relating to connectivity: edge thresholding and node removal. Edge thresholding allows us to determine connectivity for mink and prothonotary warblers based on their tail dispersal distances. It also allows us to gauge the importance of variation of the tail distance. We removed edges from the graph iteratively with a edge distance thresholded at 100 m to 50 000 m in 100 m increments. At each iteration the number of graph components, the number of nodes in the largest component and the diameter of the largest component were recorded.

Node removal is a way to examine the relative importance of habitat area and connectivity in the landscape. We used node removal to tell us about the dynamics of the entire landscape under different habitat-loss scenarios. Nodes were removed from the graph iteratively. We began with the entire graph and removed nodes randomly (with 100 repetitions), by minimum area, and by endnodes with the smallest area (Urban and Keitt, 2000). An endnode in a graph is a leaf in the spanning tree (here based on area-weighted flux) that is adjacent to only one other node. All edges incident to the removed node were also removed. At each iteration of the removal process the graph was analyzed to determine the importance of the patch to the graph's area-weighted dispersal flux (F), and traversability (T). Area-weighted dispersal flux was indexed as:

$$F=\sum_{i}^{n}\sum_{j,i\neq j}^{n}p_{ij}s_i \tag{4}$$

where s_i is the size of node i and p_{ij} is from Equation (1) above.

Traversability was indexed as the diameter of the largest component in the graph formed by the removal of the node:

$$T=d(G') \tag{5}$$

where G' is the largest component of G. We use F as an index of a patch's source strength, after Pulliam (1988). We use T in the sense of spreading-of-risk or rescue from catastrophe, after den Boer (1968) and Levins (1969).

Finally, we determined the importance of individual nodes to the entire landscape by assessing their individual contribution to area-weighted dispersal and traversability in the graph by computing F and T for the entire landscape, and then recomputing each with a single node removed from the graph. That node's impact is the difference between the intact metric and the metric that its removal elicited. Furthermore, we sought to determine the landscape's overall sensitivity to scale by repeating this process with edge definition thresholds from 2·5 km to 25 km, increasing in 2·5-km increments. We assessed the robustness of the patches' sensitivity rankings on F and T with Spearman's rank correlation, using the middle edge distance of 12·5 km to as the reference case.

Results

The mean distance between patches in the 83×83 matrix is 62·7 km. The study area and habitat patches are illustrated in Figure 1.

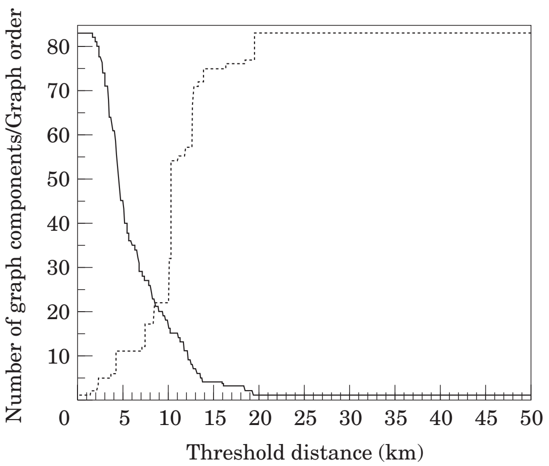

Figure 2. Number of graph components (-----) and graph order (—·—) as a function of effective edge distance.

Edge thresholding

The graph begins to disconnect and fragment into subgraphs at a 19 km edge distance, and quickly fragments into numerous components containing only a few nodes (Figure 2). The diameter of the largest component increases quickly with threshold distance, peaking at 20 km and declining slightly at greater thresholding distances (Figure 3). The edges are drawn as straight lines between patch centroids with 5, 10, 15 and 20 km thresholding distances in Figure 4, even though the actual paths are computed by least-cost and are circuitous.

The distinct threshold at a 19-km functional edge distance (Figures 2–4) implies that the landscape as it stands now is perceived as being connected for species with

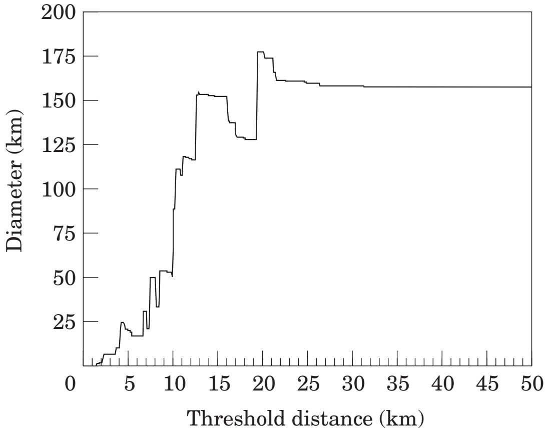

Figure 4. Diameter of the largest component remaining in the graph with increasing thresholding distance.

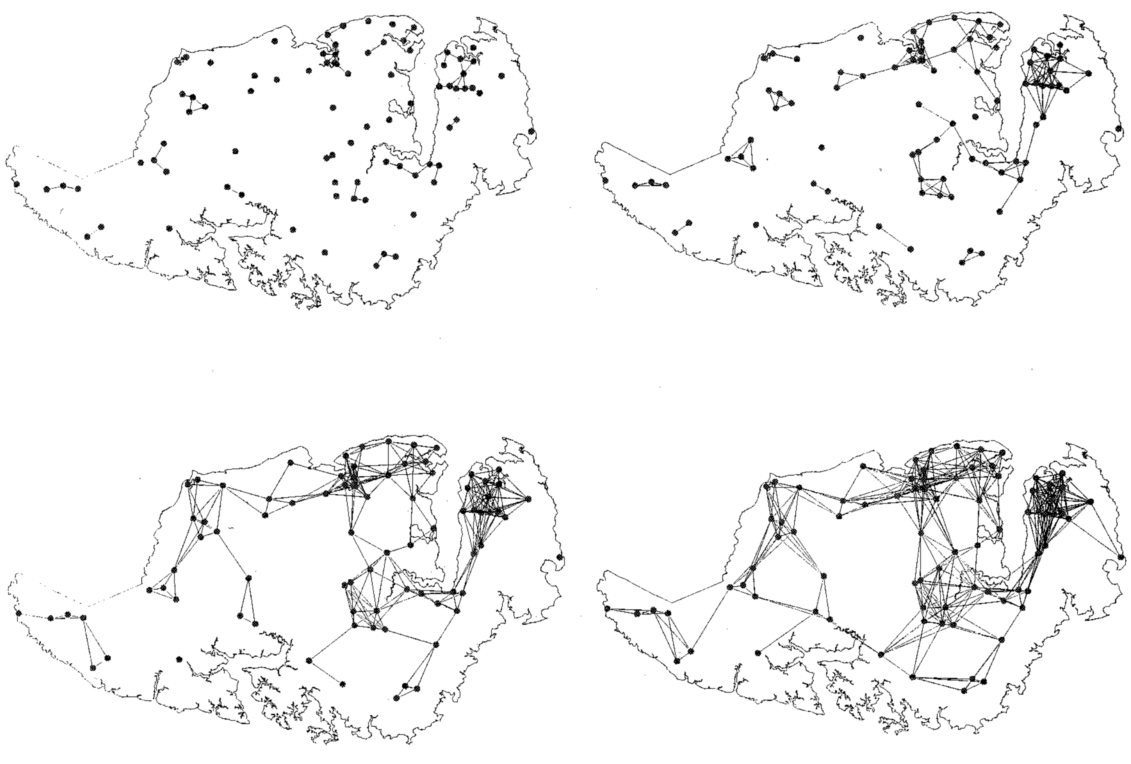

Figure 3. All graphs edges with increasing thresholded distances from 5 to 20 km.

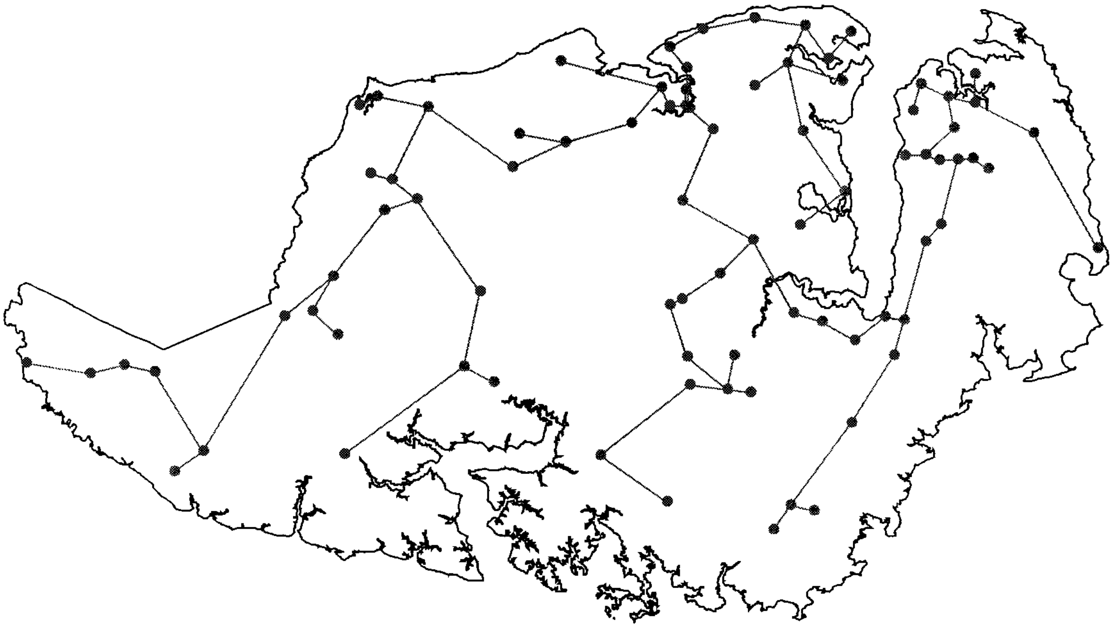

Figure 5. Minimum spanning tree for mink and prothonotary warbler based on distance.

a dispersal range of at least 20 km, and unconnected for species with a dispersal range of less than 20 km. Using this edge-thresholding scenario, and the language of percolation theory, the landscape percolates for mink but not for prothonotary warblers (Gardner *et al.*, 1987, 1992). Another way to envision this landscape is that prothonotary warblers may have a tendency to act as many discrete populations, while the robust connectivity of the landscape indicates that mink will act as one patchy population (Harrison, 1994).

For organisms with a 5-km dispersal distance, like the prothonotary warbler, the landscape graph divides into subgraphs. The implications from edge-thresholding operations are that some portions of the landscape have natural units to partition for management. Edge thresholding also indicates nodes that are easily isolated. This can serve as an early blueprint for decisions regarding habitat acquisition or enhancement. For instance, this analysis indicates useful areas for patch creation via wetland restoration.

This preliminary exploration of edge thresholding can provide some idea of landscape connectivity relative to the dispersal capabilities (however uncertain) of mink and warblers. Using this framework it is easy to highlight important nodes and edges under different dispersal distances.

For mink, the minimum spanning tree on distance (Figure 5) is an excellent first look at habitat-specific connectivity in the landscape. The minimum spanning tree represents the backbone of the habitat in the matrix. The minimum spanning tree based on area-weighted dispersal flux (Figure 6) is very different. Couched in the mainland-island model of Harrison (1994), the tree is now weighted by larger patches which are expected to produce a larger number of propagules. The largest patch now radiates spokes which illustrates the spatial effect on dispersal under these kernels.

Node removal

Node removal is habitat removal. We measured the effects of node removal in two ways which can indicate a landscape's potential to provide conditions that foster metapopulations. Flux (F), as governed by area and dispersal potential, measures a node's influence to a landscape-level metapopulation. Flux can measure the patch's potential to act as a source in a source-sink metapopulation model (Pulliam, 1988). Traversability (T) is a function of the graph's diameter. In this light it can be thought of as a proxy for spreading-of-risk or long distance rescue (den Boer, 1968; Levins, 1969). T has the possibility to point

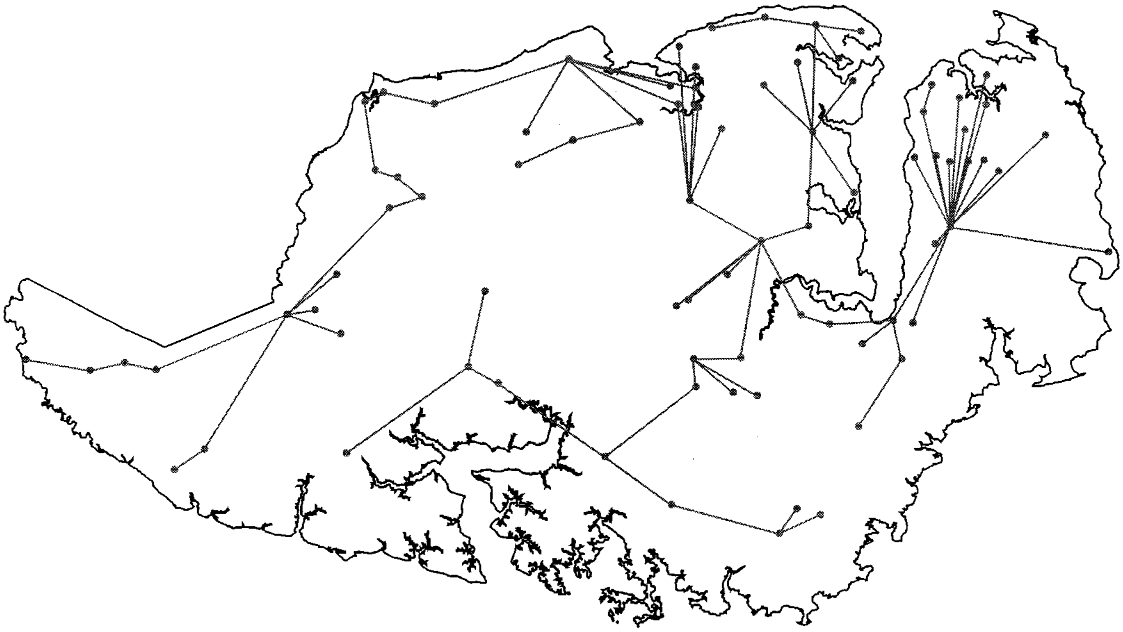

Figure 6. Area-weighted minimum spanning tree for mink with 25-km tail dispersal.

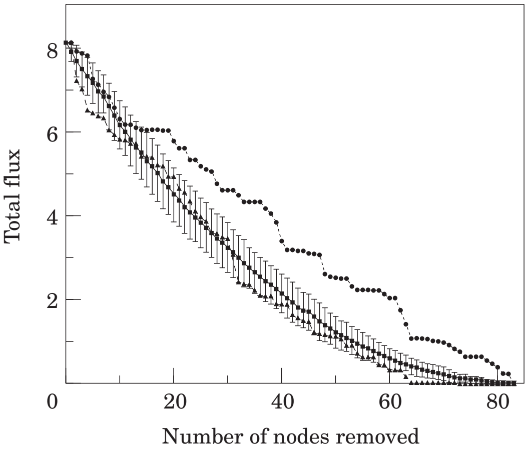

Figure 7. Area-weighted dispersal flux (*F*) as a function of three different node pruning scenarios. (–■–), random; (··▲··), minnode; (··●··), endnode. Graph defined with 25 km adjancency threshold.

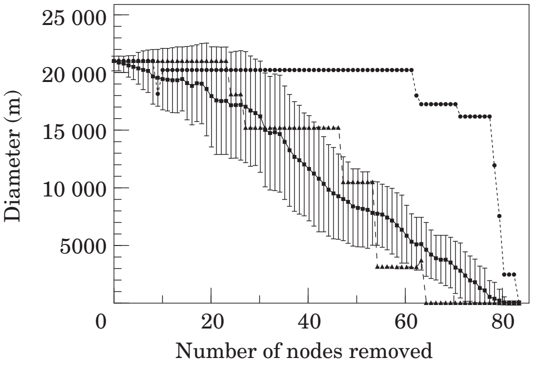

Figure 8. Traversability (*T*) of the largest graph component as a function of three different node prunning scenarios. (–■–), random; (··▲··), minnode; (··●··), endnode. Graph defined with 5 km adjancency threshold.

out important stepping-stone patches in the landscape. Source strength and long-distance rescue are well established in conservation biology. *F* and *T* are codified versions of those that fit into the graph context.

The different node removal scenarios give different pictures of the landscape. The better performance of endnode pruning over random or minimum area pruning for *F* indicates the tendency for endnodes to be less connected to the landscape (Figure 7). The advantage of endnode pruning is clear in its effect on *T* in the graph (Figure 8). Traversability of the graph is maintained with a majority of the graph nodes removed. The effect of endnode pruning on this landscape may indicate that this riverine ecosystem has a high degree of natural connectivity that an ecosystem not comprised of linearly connected features may not posses.

Area-weighted dispersal flux relies on **P** and **s** and is functionally similar for mink and prothonotary warblers under random, endnode, and minimum area pruning. The three thinning procedures produce similar results, although endnode pruning resulted in slightly higher flux values (Figure 7). The effect of different types of patch removal on traversability is markedly different for mink and prothonotary warblers. For mink, with a 25-km functional adjacency threshold, the three removal methods produce very similar results. For prothonotary warblers, with 5 km functional adjacency threshold, the random and minimum area pruning produce similar linear results but the effect of endnode pruning is substantially different. Traversability of the graph is not effected until ~75% of the nodes are removed (Figure 8).

Node sensitivity

The spatial arrangement of habitat patches in a landscape in combination with scale can influence measures of connectivity (Keitt *et al.*, 1997). Our two main metrics for connectivity, F and T, show differing responses to scale. Traversability, T, is indexed independently of patch area and is quite scale-dependent, showing little to no rank correlation between scales (Figure 9). Conversely, F is calculated explicitly with patch area and is very robust across scales. This is likely to be a function of patch area, and illuminates interesting management and ecological aspects of the landscape. In a Levins metapopulation model, T is analogous to spreading-of-risk and is sensitive to scale. In the more commonly used Pulliam model, F is analogous to source-sink strength and is not sensitive to scale because it is influenced most by close patches (short distance).

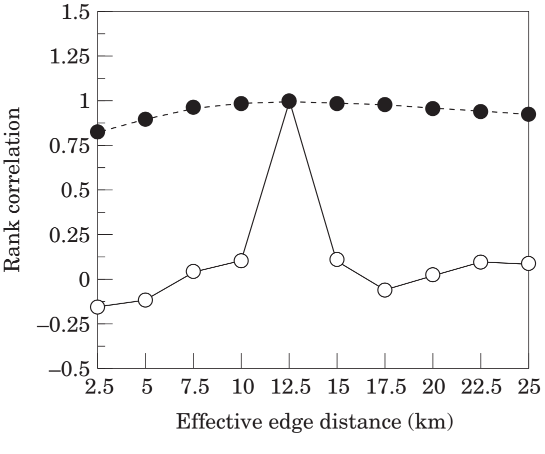

Figure 9. Correlation length of the vectors for area-weighted dispersal (F; --●--) and traversability (T; -○-) at varying scales. Reference variables are respective vectors at 12·5 km edge distance. Filled symbols are significant at $P<0{\cdot}005$.

We have chosen two focal species defined by extremes in dispersal. In our model, mink can disperse five times farther than warblers through the landscape. Our results indicate that the high degree of connectivity for the mink and low connectivity for the warbler do not cause meaningful interpretation of node sensitivity at that scale. However, the great flexibility of the graph approach is the ability to instantly posit other degrees of dispersal based on edge distance. Figures 2–4 illustrate that the landscape begins to fragment seriously with a functional distance threshold between 10 and 15 km. These distances become important if we are concerned with issues of connectivity, as this is the scale that the landscape begins to meaningfully connect. Figure 10 shows a false-color composite of patch sensitivity at 12·5-km effective edge-distance that displays each patch's sensitivity to flux and traversability. We separated the metric F used above into recruitment potential (R) and dispersal flux (F'). Here, F' is a dispersal flux coefficient not influenced by area and computed only with $\mathbf{P}$ ($F=\sum p_{ij}$) so as to separate it from area. R is a neutral model of connectivity that is computed as a function of patch size alone ($R=\sum s_{ij}$). Each patch in the landscape was tested for sensitivity, and scored for the three metrics. This allows us to send R, F', and T to the red, green and blue color guns respectively. When the patches are displayed in a false-color composite (Figure 10), some interesting patterns emerge. In this image, patches that register high on metrics R, F', and T, saturate on all the colors and show up as white. Conversely, patches that show up as a dark color have registered low on every metric. Various other shades are readily interpretable for each patch. Thus, node sensitivity analysis can illuminate nodes that have contextual importance. For instance, the blue patch indicated by the arrow in Figure 10 contributes to T but could be easily dismissed by a land manager as being unimportant because it is small and somewhat isolated. This type of view on the landscape can indicate crucial linkages or bottlenecks to connectivity.

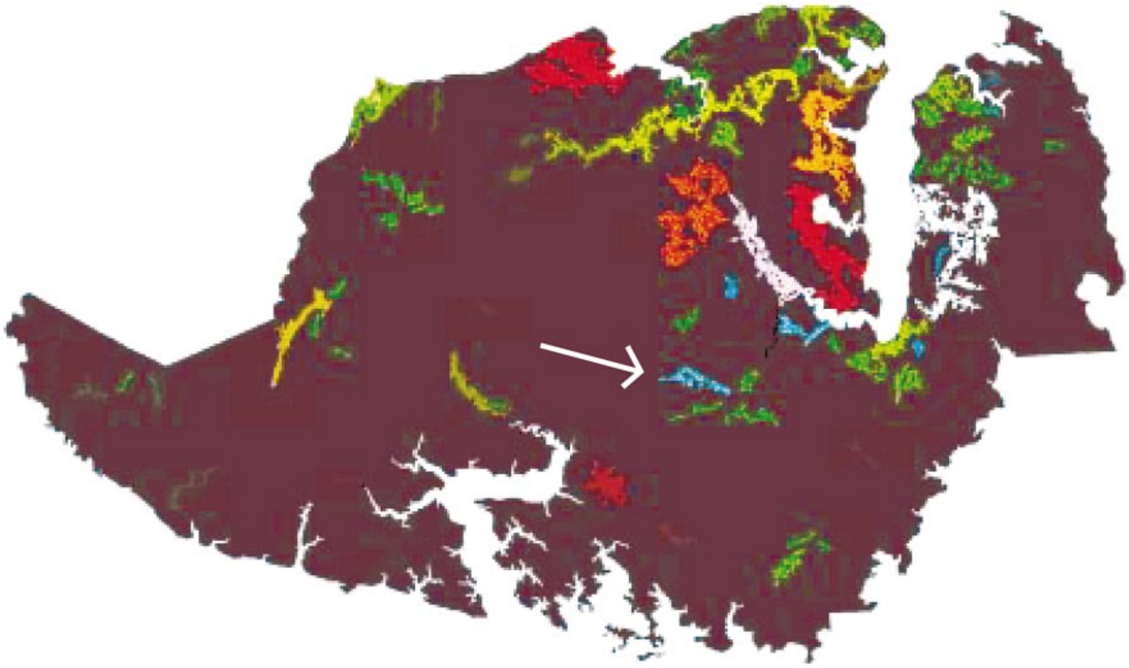

Figure 10. False-color composite of node sensitivity with 12·5 km functional edge distance. Red, recruitment potential (*R*); green, dispersal flux (*F′*); and blue, Traversability (*T*). For instance, the white arrow points to a patch with a high score for *T* and low scores for *R* and *F*.

Discussion

We found that mink and warblers perceived this landscape differently, as a function of their dispersal capabilities. For instance, Figures 2–4 show that the landscape has a great variability in connectivity depending on dispersal distance. According to the dispersal estimates used, we found that mink perceive this landscape as connected, while prothonotary warblers do not. Given a single patchy environment for mink we are able to exercise the graph and highlight the minimum spanning trees based on distance and area-weighted distance (Figures 5 and 6). These represent the parsimoniously connected backbone of the landscape. For the warbler, which experiences this landscape as fragmented components, these graph structures are not as meaningful, but minimum spanning trees based on connected subgraphs can provide utility in examining connectivity on a finer scale (not shown). The edge-thresholding operations serve as a continuous picture of connectivity in the landscape, and can be applied to other focal species.

In contrast to edge-thresholding procedures, which highlight mink and warbler spatial perceptions, the various habitat-removal scenarios allow us to determine patch function in reference to both species. Specifically, they allow us to envision, and then prioritize, habitat loss in the landscape. Habitat fragmentation and loss is one of the greatest threats to biodiversity and a great deal of management decisions focus around minimizing the impact of habitat reduction (Burgess and Sharp, 1981; Harris, 1984). In this landscape, like many others, habitat is managed by many different agencies and private landowners. Conflicting management paradigms virtually guarantee habitat alteration and loss. Given this, node removal also allows us to quickly gauge the tendency of a species to act like a metapopulation. For instance, we found that individual patches have different functions based on their size and position in the landscape. In the node removal graph perturbations, we found a tendency for endnodes to be poorly connected and therefore contribute weakly to dispersal flux and traversability. These results held for mink (Figure 7) and prothonotary warblers (Figure 8).

The node-sensitivity results show that patches also have contextual importance. Figure 10 is a powerful depiction of each patch's contribution to landscape connectivity, describing the landscape based on an edge threshold of 12·5 km. Given our dispersal estimates, this is an intermediate dispersal threshold not of direct importance to mink or warblers. However, this distance serves two pertinent functions in this landscape. First, it is approximately the distance at which the landscape begins to meaningfully connect. Second, it highlights the important versatility of the graph-theoretic approach and lets us instantly posit a gradient of dispersal thresholds. Given the overwhelming complexity of dispersal biology, the node sensitivity analysis provides an initial estimate of the relative importance of individual patches in the landscape. These preliminary analyses can also marshall further study by identifying those patches where field studies should be concentrated. For example, the blue patch highlighted in Figure 10, and surrounding green patches, offer themselves as likely candidates to determine the effectiveness of T and F.

Challenges persist in developing macroscopic landscape models. Although focal species analysis can enrich macroscopic approaches by producing a species-specific perspective to the analyses (O'Neill *et al.*, 1988; Pearson *et al.*, 1996), reliable habitat definition from relatively coarse spatial data (e.g. 30-m cells) is challenging for many species, and limited to habitat specialists. The use of the intervening non-habitat matrix is especially important, as this affects the functional scale at which patches are defined. Edge definition in a graph calls for dispersal biology that is often difficult to parameterize. However, well chosen focal species in a landscape can provide ecological and political effectiveness in issues of connectivity.

When appropriate species such as mink and warblers are available in a landscape, then focal species analysis is particularly well-suited to graphic representation, because ecological flux is a primary concern. The graph-theoretic approach differs from most focal species analyses as it allows one to use surrogates as a rapid assessment tool without long-term population data, although population data can (and should) be incorporated as knowledge of the system improves. It is a heuristic framework which is a robust way to represent connectivity in the landscape. The utility of applying graph theory to landscapes is that it allows managers and researchers to take an initial, but thorough, look at the spatial configuration of a landscape. It is applicable at any scale.

Another benefit of a graph-theoretic approach is that dispersal biology does not need to be fully understood for the graphs to be interpretable. To give context to the graph framework, we have postulated that dispersal for mink is 25 km and for prothonotary warblers, 5 km. We used a conservative negative exponential decay curve for dispersal probability, matrix $\mathbf{P}$. An advantage of the graph-theoretic approach is that gaming with alternative kernels is easy, and will affect dispersal in the landscape based on the spatial arrangement of patches. Dispersal biology is incredibly complex, and precise distances are virtually always unknown. Here our results and their interpretation are largely interpretable despite this uncertainty and can be immediately tailored to different dispersal estimates. Edge thresholding and node removal, as well as node sensitivity, are graph descriptors that are useful macroscopic metrics when dispersal can only be estimated (see Keitt *et al.*, 1997 for an additional example). From a management perspective, the graph can provide a powerful visualization of connectivity when used in conjunction with dispersal estimates such as those based on allometric relationship to body mass (see Sutherland *et al.*, 2000).

Prospectus

Land and conservation management is increasingly concerned with regional-scale habitat analyses. The development of graph theory in an ecological framework represents a promising step forward in that regard. Graph theory rests on a foundation of intensive study for computer networks which must be efficient. Therefore, the theory and algorithms are well developed; many are computationally optimal. Like metapopulation theory, the graph can merge landscape configuration and focal species biology to arrive at process-based measures of connection (Hanski, 1998; Urban and Keitt, 2000). The advantage of graph-theoretic approaches to conservation planners and researchers is that, while reasonable quality spatial data are required, long-term population data are not.

The conservation potential of graph theory is far from realized. The existing body of ecological work that considers landscape graphs is slim (Cantwell and Forman, 1993; Keitt *et al.*, 1997; Urban and Keitt, 2000). The most appealing feature of graph theory as applied to ecology is that it is a heuristic framework for management which is necessarily perpetual. With very little data, one can construct a graph of loosely-defined habitat patches and then explore the structure of the graph by considering a range of threshold distances to define edges. It is important that as more ecological information is collected it can be infused into the graph and consequently add more precision and confidence to the analyses. Graph theory can provide initial processing of landscape data and can serve as a guide to help develop and marshall landscape-scale plans, including the identification of sensitive areas across scales. This does not mean that graph theory should displace alternative approaches. We suggest graph theory as a computationally powerful adjunct to these other approaches. The simplicity and flexibility of graph-theoretic approaches to landscape connectivity offers much to land practitioners and can increase the scope and effectiveness of resource management.

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