

REVIEW AND
SYNTHESIS

Graph models of habitat mosaics

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Abstract

Graph theory is a body of mathematics dealing with problems of connectivity, flow, and routing in networks ranging from social groups to computer networks. Recently, network applications have erupted in many fields, and graph models are now being applied in landscape ecology and conservation biology, particularly for applications couched in metapopulation theory. In these applications, graph nodes represent habitat patches or local populations and links indicate functional connections among populations (i.e. via dispersal). Graphs are models of more complicated real systems, and so it is appropriate to review these applications from the perspective of modelling in general. Here we review recent applications of network theory to habitat patches in landscape mosaics. We consider (1) the conceptual model underlying these applications; (2) formalization and implementation of the graph model; (3) model parameterization; (4) model testing, insights, and predictions available through graph analyses; and (5) potential implications for conservation biology and related applications. In general, and for a variety of ecological systems, we find the graph model a remarkably robust framework for applications concerned with habitat connectivity. We close with suggestions for further work on the parameterization and validation of graph models, and point to some promising analytic insights.

Keywords

Connectivity, conservation, graph theory, habitat, landscape, metapopulation, network analysis.

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INTRODUCTION

Ecology and conservation biology are much invested in habitat connectivity and its implications for populations (Tischendorf & Fahrig 2000; Fahrig 2003; Calabrese & Fagan 2004; Chetkiewicz *et al.* 2006; Crooks & Sanjayan 2006; Beier *et al.* 2008). Graph theory (also called network theory) is a branch of mathematics concerned explicitly with connectivity. Graph theory has been around for centuries but recently the theory and its applications have been undergoing explosive growth in many disciplines including, finally, landscape ecology and conservation biology (Bunn *et al.* 2000; Urban & Keitt 2001; Keitt 2003; Rothley & Rae 2005; Fall *et al.* 2007; Estrada & Bodin 2008; McRae *et al.* 2008). A graph is a set of nodes (points) connected by links (lines); a link between two points indicates a functional connection between the two nodes. In landscape ecology, the nodes typically represent habitat patches and links indicate dispersal potential or frequency between patches.

This representation invokes a metapopulation model of the habitat mosaic (Hanski & Gilpin 1991; Urban & Keitt 2001).

Graphs are *models* of landscapes – that is, simplifications of a more complicated reality – and so it is appropriate to consider the application of these models in the same way we might evaluate other models used in ecology. This invites a series of very pragmatic questions: What is the underlying conceptual model of the system? How might we formalize and implement (codify) this conceptual model? How will the model be parameterized? Which parameters are most sensitive, most uncertain? What insights might be garnered from a formal analysis of the model? Can the model be extended to applications beyond those used to build it initially, and how might these extensions be validated with independent data? Importantly, can graph models provide predictions about landscapes that are not available from other models we already use?

Here we review recent applications of graph theory to habitat mosaics, focusing on applications in landscape

ecology and conservation biology. In particular, we consider the match between the ecology of interest and its abstraction as a graph, and review the sorts of insights that can be obtained from graphs or network models. We offer suggestions to reduce uncertainties concerned with model implementation and parameterization, and emphasize potential means for verifying or validating graph models empirically. Finally, we point to promising avenues for the analysis of graph models and their application to conservation planning.

Networks and graph theory: definitions

Graph theory dates back to Euler (300+ years ago) and it persists now as a multithreaded discipline in natural sciences, social sciences, engineering, and mathematics. Because of this, the theory and applications have evolved a rich vocabulary that sometimes is not consistent across disciplines. Graph definitions are reviewed from an ecological perspective by Urban & Keitt (2001), Fall *et al.* (2007), and Minor & Urban (2008). Here we define concepts and terms that will be used in the discussion that follows.

A graph G is a set of nodes (also called vertices) V and links (or edges) E (Fig. 1). A graph with n nodes and p links has *order* n and *value* (or *size*) p . The nodes may be annotated with additional attributes such as their spatial coordinates, size, and quality or productivity. A link ab between nodes a and b indicates some functional connection; in the case of a network of habitat patches, this connection is typically related to dispersal. The links might be of various kinds: binary adjacencies (connected/not), or they might represent distance, or the likelihood or the rate of dispersal. In a graph in which the links represent distance or other quantities, the links are *weighted*. Links by convention are

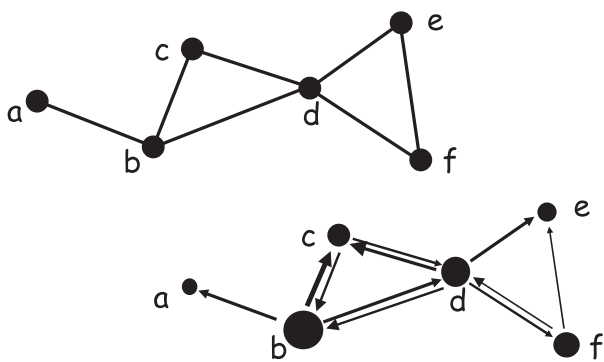


Figure 1 Schematic of a simple graph, to illustrate key definitions. Top: a simple (unweighted) graph. Bottom: a weighted digraph, with nodes attributed with their sizes, arrows on arcs indicating the direction of movement and line thicknesses indicating magnitude of fluxes.

bidirectional (i.e. link ab implies the symmetric back-link ba). Alternatively, the connections might be directional, in which case the links are by convention called *arcs* and the graph is *directed*, a *digraph*. Because these fluxes are often asymmetric for biophysical reasons (gravity, air or water currents) or for biological reasons (e.g. to reflect the population sizes of the donor nodes), habitat graphs are often weighted digraphs. In some instances, it might make sense for there to be more than one link between a pair of nodes. Such parallel links give rise to a *multigraph*; these links might represent alternative dispersal routes between a pair of nodes, or connections of qualitatively different types (and see below). Of course, the same ecological system can be represented by a variety of graphs of differing complexity – and these alternative formulations will be appropriate to different applications.

We should point out at the outset that ‘graph theory’ is a much larger subject than ‘network theory’ or ‘network analysis’. Graph theory includes algebraic analysis of graphs, geometric problems, and a lot of ‘pure math’ that is not directly relevant here. Network analysis (or theory) is concerned with topological or functional relationships among nodes in a graph. While this usage might not be universal, we will attempt to adhere to this convention in this discussion. In particular, we will use ‘graph’ to refer to the general data structure and use ‘network’ to connote topological relationships on graphs.

A *walk* on a graph is a sequence from node to node along links or arcs; a *path* is a walk in which no node (and hence no link) is revisited. The *length* of a path is the sum of the weights of all the links (or arcs) in the path; for an unweighted graph, this is simply the number of links. A graph in which each node can be reached via some path from any other node is *connected*, while an unconnected graph consists of multiple (connected) subgraphs or *components*.

A central task in network analysis is to find the *shortest path* between any pair of nodes in a graph; shortest path algorithms are well developed and some popular algorithms have been known for decades (e.g. Dijkstra 1959), although many are still being improved in terms of computational performance. For an undirected graph of order n , there are $(n - 1)$ shortest paths from each node. The longest shortest path between any pair of nodes is the graph’s *diameter*. A graph with long shortest paths is comparatively slow to traverse, while one with very short paths is faster. In some cases, it is convenient to index this by simply averaging the shortest paths, referred to as the graph’s *characteristic path length*.

A *tree* in a graph is a path without cycles and with only one link between any pair of nodes, and a *spanning tree* is a tree that visits every node in a graph. There might be several of these for any given graph. A *minimum spanning tree* is a

spanning tree with the lowest total weight (there also might be more than one of these, if there are ties among shortest paths). A minimum spanning tree provides an easy representation of the skeleton of the graph, a quick visualization of its topology. Other indices provide a richer illustration of the same concept. In particular, various *centrality* indices highlight the backbone of the graph. For example, *node betweenness* tallies the number of shortest paths in a graph that pass through a given node; that node has high centrality because it is between many pairs of nodes. Alternatively, *degree centrality* tallies the number of neighbours for each node, while *closeness centrality* is the inverse of the average path lengths from a node to each of its neighbours (Freeman 1978).

Graphs can exhibit various levels of *clustering* or *community structure*. Here, a community refers to a group of nodes that are highly connected: a cluster is correctly evoked by the adage 'Friends of friends are also friends', which implies 'triangles' among members of a community or cycles in a graph. Not surprisingly, social network theory is a branch of graph theory much invested in community structure (Wasserman & Faust 1994; Girvan & Newman 2002; Freeman 2004).

METAPOPULATION MODELS AND IMPLEMENTATION AS GRAPHS

Graph models of habitat mosaics implicitly or explicitly invoke metapopulations as a conceptual foundation. There are at least two versions of this conceptual model. One is Pulliam's (1988) source/sink model. In this, source habitat patches are those with positive net reproduction (i.e. births > deaths), which then are capable of exporting surplus individuals to nearby patches. By contrast, sink patches have negative net reproduction and so depend on nearby source patches for long-term persistence. A well-documented example concerns forest birds subject to nest predation and brood parasitism in forest edges. In this example, sink patches are small or have a high proportion of forest edge, and so vulnerable bird species often fail to fledge young successfully (Donovan *et al.* 1997; Thompson *et al.* 2002). Source patches, by comparison, are large or productive and have core areas well buffered from patch edge effects. The source–sink model is framed in terms of local dispersal, especially the one-way dispersal flux from sources to sinks. In terms of graph theory, this would invite implementations in terms of weighted digraphs: sources would have high dispersal outward (large weights on out-arcs) whereas sinks would have a high dispersal subsidy (negligible out-flux but high weights on in-arcs).

The other model of metapopulations is older but less formally described in current applications; this is the

spreading-of-risk (den Boer 1968) or the long-distance rescue (Brown & Kodric-Brown 1977) model. The spreading-of-risk model is evoked by the adage 'Don't put all of your eggs in one basket' and is readily envisioned for patchy systems subject to disturbance: we hope that a single disturbance would not destroy the entire system but, rather, that distal regions would escape local disturbance and provide dispersers to recolonize the patches suffering local extinctions. This conceptual model invites graph implementation in terms of measures of the overall traversability of the graph – metrics such as graph diameter or characteristic path lengths.

It is worth emphasizing these alternative – but not competing – conceptual models of metapopulations because most applications concerned with connectivity do not specify which model is being invoked. We make the distinction because graph models provide straightforward methods to invoke either model. Urban & Keitt (2001) illustrated these two models, underscoring the likelihood that patches important in Pulliam's model (i.e. strong sources) need not be the same patches important to long-distance traversability of the network (e.g. stepping-stones). Estrada & Bodin (2008) suggested a similar distinction about the role of nodes in network connectivity, based on different indices of centrality (and see below). It is worth noting that the 'original' metapopulation model, that of Levins (1969), is not much invoked in network applications – perhaps because it is not explicit about the role each patch might play in the network.

Graphs provide a simple but effective means of depicting the overall structure of a habitat mosaic in terms of metapopulation structure. For example, a highly connected graph might function as a single patchy population (*sensu* Harrison 1994), while a largely unconnected graph might effectively be a set of isolated populations; intermediate cases or various regions or components of a graph would be obvious on inspection.

As an overall summary of the graph, the leading eigenvalue of the link weight matrix (with weights estimated as area-weighted dispersal probabilities) is the *metapopulation capacity* of the landscape as defined by Hanski & Ovaskainen (2000) – explicitly linking metapopulation theory to graph data structures. Coincidentally, in social network theory, the eigenvector corresponding to the dominant eigenvalue of this matrix summarizes the contribution of each node to network connectivity – its eigenvector centrality (Borgatti 2005).

Implementation and parameterization

Implementing a graph model essentially consists of defining the nodes and links ecologically. A graph model typically represents discrete elements of habitat as graph nodes,

essentially collapsing the landscape into a binary ‘habitat/non-habitat’ world. Further, the model invokes an ‘island’ view of habitats: discrete habitat islands in a ‘sea’ of non-habitat (MacArthur & Wilson 1967). In this model, the patches are often clustered as like-valued cells in a raster data layer in a geographical information system (GIS), or equivalently, as polygons in a vector representation. Patches are connected by links if they are within some species-specific dispersal distance (Bunn *et al.* 2000; Urban & Keitt 2001; D’Eon *et al.* 2002). An alternative formulation represents each cell of the raster dataset as a node, with links connecting neighbouring cells (4, 8, or more, depending on the application). In either case, node definition implies an explicit definition of ‘habitat’ for the application. This might be extracted from vegetation or land cover types from a GIS (e.g. O’Brien *et al.* 2006), or it could involve a more nuanced statistical model of potential habitat for a focal species (e.g. Minor & Urban 2007).

It should be noted that there are other alternatives for node definition. O’Brien *et al.* (2006, see also Fall *et al.* 2007) defined habitat nodes by creating a Delaunay tessellation of their study area, ensuring that any location could be unambiguously associated with a reference habitat node. In this case, the focal species was the woodland caribou (*Rangifer tarandus caribou*), a species that uses ‘habitat’ patches but also ranges beyond these patches into ‘non-habitat’. The tessellation also provides for a parsimonious *planar graph* (illustrated, via a Delaunay tessellation, in Fig. 2g). In a planar

graph, links can be drawn without crossing each other; in a minimum planar graph (Fall *et al.* 2007), each node is connected only to its topological neighbours – a nicety that facilitates graph creation and some subsequent analyses. Ecologically, insisting on a minimum planar graph dictates that organisms dispersing from a given node can only traverse the graph via stepping-stone paths through topological neighbours (i.e. a bird could not fly directly to a nearby habitat patch even if that patch was within the dispersal capacity of the species). This represents a trade-off between ecology and computational efficiency, as with other ecological models.

For habitat graphs, links typically represent dispersal rates or likelihoods. Even so, these can be specified at varying levels of precision. As the simplest case, links can be represented as binary (0/1). More typically, links are represented by distances or functional distances between nodes. Simple Euclidean distances, in map units, can be computed either between node centroids or between the edges of patches; this might be a matter of computational convenience, but it does have some implications about how we presume species dispersal actually occurs. Recently, applications have become more invested in functional distances instead of simple Euclidean distances. Functional distances are weighted to reflect the relative navigability or resistance to dispersal of matrix habitats between focal habitat patches. In a GIS, these distances are computed as ‘least-cost paths’ using standard routing algorithms. In this,

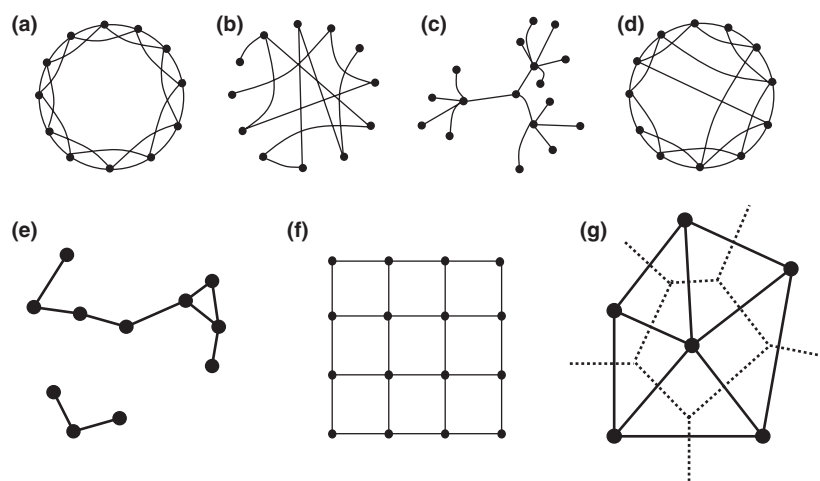


Figure 2 Examples of graphs. Top panel: well-studied ‘theoretical graphs’ – (a) regular, (b) random, (c) scale-free and (d) small-world. Bottom panel: graphs more typical of landscapes – (e) a graph in which nodes are linked if they are less than some threshold distance apart (this example includes two separate components), (f) a regular planar graph representing a raster grid (each cell joined to its four cardinal neighbours) and (g) a minimum planar graph defined by a Delaunay tessellation (DT, dashed lines) from a Voronoi diagram (VD, solid lines). The VD connects the nodes. The DT is defined by lines that bisect the links of the VD; the intersections of the DT lines outline polygons that tile the surface parsimoniously. The DT/VD pair is a *dual graph*. Note that the regular graph (f) is also a dual graph, as an underlying raster grid is represented computationally as a graph with nodes at the centre of each cell and links to its four cardinal neighbours.

the algorithm finds the shortest route between two nodes (patches) through a 'cost surface' defined to represent the relative resistance of the intervening matrix.¹ Although these algorithms have been known for some time – Urban & Shugart (1986) suggested their use for spatially explicit metapopulation models – it has only recently become computationally feasible to compute least-cost links for a large graph with hundreds of nodes (Bunn *et al.* 2000; Larkin *et al.* 2004; Theobald 2006) and it remains largely infeasible to do this analysis for several thousand nodes. It is worth emphasizing that this means that *constructing* a graph can be a computational bottleneck, if this entails computing least-cost links between all pairs of nodes. Actually *analysing* extremely large graphs is currently not a problem computationally; available software packages can handle millions of nodes.

Best *et al.* (unpublished) devised a method to implement least-cost links for large networks in a GIS environment. They convert the raster cost surface to a triangulated irregular network (TIN), and embed the habitat patches into this TIN. Because the TIN is itself a graph, they can then use extremely efficient graph algorithms to find the least-cost paths (LCPs) for all pairs of nodes, extracting only the habitat nodes as the final graph. The analyses are performed using graph routines from the NetworkX module in Python (networkx.lanl.gov). Using this approach, graphs with thousands of nodes can be constructed and displayed in ArcGIS (ESRI, Redlands, CA, USA).

Note that while least-cost links are appealing conceptually, it has proven remarkably difficult to parameterize these directly; indeed, link definition in general seems as much a working hypothesis as an actual parameterization. Promising developments that should facilitate the implementation of least-cost links (i.e. by parameterizing cost surfaces) include telemetry data with high spatiotemporal resolution (e.g. McDonough & Paton 2007) or field experiments that allow animals to 'choose' among cover types and so quantify resistances (Ovaskainen 2004; Belisle 2005), and genetic data (Cushman *et al.* 2006; Arens *et al.* 2007; McRae & Beier 2007) or isotopic analysis (Cook *et al.* 2007), which can verify inferences about movement.

In many applications, link weights (actual or weighted distances) are truncated relative to some maximum

dispersal distance for the target species. This requires an empirical estimate of the dispersal capacity, if not an actual dispersal kernel or distance-decay function. New methods mentioned above in relation to calibrating resistances might also be useful in estimating maximum effective dispersal ranges.

McRae and colleagues (McRae 2006; McRae & Beier 2007; McRae *et al.* 2008) have promoted circuit theory as a way to model connectivity. Circuits are graphs, defined in terms of resistances between nodes (i.e. based on a cost surface as above). Founded in random walk theory, circuit theory provides intuitive analytic analogues for resistance, conductance, and flow over networks depicted as 'wiring diagrams'. In terms of dispersal, circuits offer the advantage that multiple pathways may be modelled between pairs of nodes, with these paths quantified in terms of relative flow rates; the effective conductance of the connection between two nodes can be integrated over all possible paths. A slight disadvantage of this approach is that circuit links cannot be directional (McRae *et al.* 2008).

In a marine application concerned with connectivity among coral reefs, Treml *et al.* (2008) simulated larval dispersal via modelled ocean currents to estimate dispersal likelihoods among reefs, generating a weighted digraph for the Tropical Pacific. Similar approaches could be developed for terrestrial systems using models of dispersal based on appropriate life-history data. For example, Gustafson & Gardner (1996) developed a dispersal simulator based on correlated random walks by 'virtual' animals subject to behavioural rules and physiological constraints. They used the model to estimate the likelihoods (rates) with which organisms dispersing from each patch might successfully arrive at each other patch.

While graphs are often abstractions of real systems, some network models are rather straightforward to implement, as the ecosystem is already structured as a network. Schick & Lindley (2007) developed a graph model for salmonid populations in streams in the Sierra Nevada of California. In this, stream segments (reaches partitioned by elevation zones) were defined as nodes, and arcs were parameterized based on return rates from the ocean, with some small chance that fish would return to streams other than their natal reach based on empirically observed 'straying' rates.

It might be useful here to comment on 'structural connectivity' as sometimes used to describe physical features of landscapes such as forest patches, hedgerows, and other elements obvious to the human eye. While it might be tempting to represent these as graph models, this raises the difficulty that, unless the graph model is implemented to represent some actual target species (i.e. 'functional connectivity'), there is no way to estimate link weights meaningfully: all graph models should represent functional connectivity.

¹This analysis invites some confusion. The GIS-based algorithm actually finds a least-cost path between two habitat patches by finding the shortest path between them based on a raster cost surface, which is itself a regular graph. The result is a single link between two nodes, a least-cost link. Done for all pairs of nodes, the result is a graph of least-cost links. One might then find shortest paths between these nodes, based on the computed link weights. Thus, this analysis is nested: least-cost paths for the habitat graph are computed as least-cost paths on the graph representing the cost surface. We will try to distinguish least-cost links from shortest paths in the larger graph.

An alternative method to define a graph invokes a slightly different conceptual model. In this, nodes represent habitat patches that tile the landscape (e.g. as in a tessellation), and the links represent the likelihood that individuals moving within the patch might encounter the boundary to an adjacent patch and 'pass through'. This model echoes the 'boundary dynamics' conceptualization of Wiens *et al.* (1985), which considers the balance of within- and between-patch movements as a function of patch size and the permeability of the boundaries between patches. Behavioural responses to habitat boundaries have been explored for a variety of taxa (reviewed by Ries *et al.* 2004), which would seem to provide an empirical basis for this model. A compelling feature of this conceptual model is that it invites estimates of the permeability of the shared boundaries between adjacent habitat patches – a rather straightforward implementation in a GIS. For example, one might assign a permeability to each land cover type in a GIS, and compute link weights based on the relative permeability of land covers at shared borders between patches. This implementation, while subject to the same uncertainties about habitat (boundary) resistances that apply to least-cost links, also would force a more formal consideration of the likely shift in the proportion of within-patch dispersal as patch size increases (Fagan & Lutscher 2006). To our knowledge, this conceptual model has not been developed in graph applications. Cantwell and Forman (1993) explored the topology of graphs defined by the juxtaposition of different patch types, but they did not focus on boundary permeability explicitly. Margosian *et al.* (in press) approximated this approach in a graph-based analysis of agricultural pests in counties of the American Great Plains. In this, links were drawn as lines connecting county centroids, and link weights were assigned based on the amount of agricultural land cover intersected by these lines (regions with high agricultural land cover were considered less resistant to pest transmission). Note that this approach is very similar to the Voronoi diagram used to generate a Delaunay tessellation of a landscape (Fall *et al.* 2007; and see Fig. 2g), and is rather straightforward to implement in a GIS.

Additional behavioural ecology might be incorporated into link weights. For example, one might estimate link weights based on the viewshed of dispersing organisms, in which dispersal likelihoods are based on patches visible from a focal vantage point (the donor node). Graf *et al.* (2007) modelled the effects of topographic interference in the viewsheds of the caercaillie (*Tetrao urogallus*) in central Europe.

In short, ecologists have explored a variety of ways to implement spatially articulated ecosystems as graphs. We have been quick – perhaps too quick – to adopt least-cost links as a means for constructing graphs. It might be fruitful

to explore alternative conceptual models of species dispersal as this effects connectivity.

MODEL VERIFICATION AND VALIDATION

Modellers sometimes distinguish two kinds of model tests. Model *verification* refers to tests of model output against data used to build the model. This is a necessary test, as it establishes the extent to which the model does what it was designed to do. But the test is not independent of the data, and so this is a comparatively weak test – after all, the model *should* do as it was designed. A more stringent test, model *validation*, tests the model against data that were not used in model development. This independent test provides a cleaner test of the model; indeed, the farther removed from the development case, the stronger the test. While verification demonstrates that the model successfully implements basic assumptions about the system, validation establishes that the assumptions themselves are reasonable. Continued validation tests establish the domain within which the model can 'safely' be applied, its domain of applicability.

Applied to graphs, we might consider model testing at multiple levels. Here, we might use verification to refer to tests of the construction of the graph itself. That is, can we adequately represent habitat patches and dispersal fluxes with appropriate nodes and links? Model validation might then consider whether network-level implications of the graph model are reasonable and consistent with available data.

Some steps have already been taken in this direction. McRae & Beier (2007) tested their circuit-theory models using genetic data from two distinct taxa: big-leaf mahogany (*Swietenia macrophylla*, a tropical hardwood tree) and the wolverine (*Gulo gulo*, a North American carnivorous mammal). Their verification tests showed that circuit theory was better able to predict genetic differentiation between populations than were conventional gene flow models. Driezen *et al.* (2007) used telemetry data to verify least-cost links estimated for the hedgehog (*Erinaceus europaeus*). They found that the animals selected routes that were better than random but that fell somewhat short of least-cost routes.

Variations on Mantel tests can be used to select among alternative formulations of network connections. A Mantel test is a correlation or regression on distance matrices (Legendre & Legendre 1998). In this case, one distance matrix would be a candidate set of graph distances (shortest paths or link weights) between pairs of patches, and the other matrix would be ecological (species composition) or perhaps genetic distances. A simple test would require that the Mantel correlation be higher for cost-weighted distances than for simple Euclidean distances. Treml has found some

success in this approach with marine systems (E.A. Treml, unpublished data, and see Hedgecock *et al.* 2007). This approach might also be used to select among alternative path weights or cost surfaces (Cushman *et al.* 2006).

Urban (2005) suggested that, if networks are an appropriate model for metapopulations, then we should be able to observe emergent behaviours at the level of the graph component, a level of organization between the single patch and the entire landscape. In this, graph component membership could be entered into a regression as a dummy variable; a significant partial on this variable would indicate that the components share ecological function. Minor *et al.* (in press) used this approach and found the composition of exotic plants was more similar within graph components than among components, validating the network model.

Ultimately, the criterion for judging a graph model is based on how well graph metrics correspond to measures obtained from the represented system. Minor & Urban (2007) compared the performance of a graph model to that of a spatially explicit population model (SEPM) in selecting important patches for wood thrush (*Hylocichla mustelina*) conservation. Both models used the same habitat and dispersal distance but the SEPM employed at least nine additional life-history and behavioural parameters in order to simulate complicated population dynamics. Their model tests showed that the graph model made predictions very similar to the complicated SEPM and – in its simplicity – even offered insights about network structure not easily obtained from the simulator; this was because the SEPM made predictions at the level of the single patch while the graph model could assess the entire network.

An appealing feature of graph models is the ease with which they can be used to refine our knowledge of species biology, develop better parameter estimates, and feed back to improve themselves in an iterative, targeted sampling approach. In this, the model itself provides a sampling frame, and the aim is to use model uncertainty as a guide to tactical field studies (Urban 2002). For example, we might be uncertain about the dispersal capacity of a focal organism. We can tackle this uncertainty by creating two graphs that bracket the range of possible dispersal distances. Each graph (one with shorter links than the other) will highlight habitat patches that are isolated from the rest of the landscape; isolated patches in the longer-distance graph will be a subset of isolated patches in the shorter-distance graph. The key is to focus sampling efforts on the habitat patches that are isolated in the short-distance graph but not in the long-distance graph. If these patches are occupied, we might conclude that the dispersal distance of our organism is closer to our longer estimate than to our shorter estimate; the opposite holds true as well.

MODEL ANALYSIS

Model analysis includes several techniques geared to understanding the qualitative and quantitative implications of the model as implemented and parameterized (reviewed by Gardner & Urban 2003). Here we review applications based on (1) visualization and interpretation; (2) analytic or theoretic results from graph theory; (3) methods for evaluating alternative model scenarios; (4) sensitivity and uncertainty analysis; and (5) ‘engineering solutions’ aimed at optimizing particular network properties, especially connectivity.

Visualization and interpretation

One of the compelling features of a graph model is that they tend to be intuitive and accessible on inspection. Illustrations of graphs, overlaid onto a GIS map, provide an immediate summary of patterns of connectivity in a landscape and provide an easy means to visually explore the implications of assumptions about link weights or dispersal biology (Bunn *et al.* 2000; Urban & Keitt 2001). One particularly informative representation of a landscape graph is a series of figures that show how connectivity varies with different assumptions about dispersal capacity for the target species (Bunn *et al.* 2000; D’Eon *et al.* 2002). A general result of this analysis is that landscape connectivity (measured as graph diameter) typically shows a strongly nonlinear threshold response to increasing dispersal capacity (illustrated by Urban & Keitt 2001; Fig. 3). In this, graph diameter increases rapidly as the graph coalesces into a large component; the diameter then decreases as long stepping-stone paths are replaced by direct connections. This curve implies that habitat graphs have a connectivity level at which the network is fully connected but slow, because the paths are indirect stepping-stone routes. At lower dispersal capacities, the graph is less connected (leaving some nodes isolated), while at higher capacities the graph is much ‘faster’ because the connections are direct. This threshold in connectivity is exactly analogous to the percolation threshold in raster lattices (themselves a special form of graph; Stauffer 1985; Keitt *et al.* 1997), and provides a convenient index by which to assess the dispersal capacity of a target species relative to the landscape – termed ‘scale-matching’ by Brooks (2003). Along with this illustration of connectivity thresholds, the same analysis also highlights separate graph components as a function of dispersal capacity, as well as any obvious instances of dispersal isolation or highly connected regions in the graph.

Similarly, the results of basic graph measures such as centrality scores can be readily visualized in a GIS environment as an intuitive way to interpret network topology. Betweenness centrality is a measure of the role

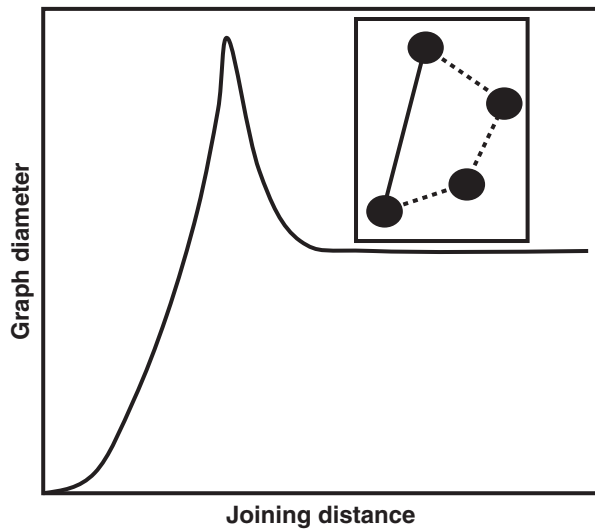


Figure 3 Relationship between landscape connectivity (as diameter of the graph's largest component) vs. joining distance, or the maximum dispersal distance at which two nodes are considered connected (redrawn from Urban & Keitt 2001). Inset: the peak in graph diameter corresponds to the replacement of longer stepping-stone paths with shorter direct links.

each node or link in a graph might play in network traffic as measured in shortest paths. For example, nodes with high betweenness might be deemed crucial to graph connectivity because of the high traffic implied by their position in the network. Bodin & Norberg (2007) used betweenness indices from social network theory to identify well-connected compartments (sub-networks) of habitat patches for the ring-tailed lemur (*Lemur catta*) in southern Madagascar. Mapping betweenness scores in this way can readily emphasize the well-connected backbone of a landscape (Fig. 4). Estrada & Bodin (2008) explored a variety of centrality indices for this purpose. They found that the indices captured conceptually different aspects of connectivity. For example, degree centrality seemed to capture local patterns of connectivity in dense regions of the graph, while betweenness centrality reflected long-distance connectivity over the graph. This result echoes the results of Urban & Keitt (2001), concerning the various roles that nodes might play in network connectivity and inviting reflection on the alternative source/sink compared to spreading-of-risk metapopulation models.

Borgatti (2005) emphasized the mode of transfer of information among nodes in a network and the implications of this for choosing an appropriate index of betweenness. For example, the way that a package is delivered to its target destination is quite different from the way rumours spread through friendship networks. Borgatti (2005) categorized transfers in terms of mode of transmission and allowable trajectories of these transmissions. Modes include parallel

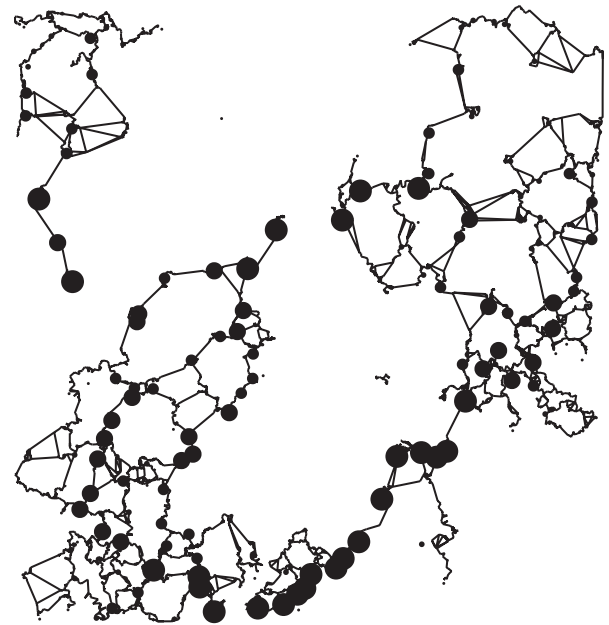


Figure 4 A graph of forest habitat patches in the Piedmont of North Carolina, with nodes sized in proportion to their betweenness centrality. Larger nodes have higher centrality, and highlight the pattern of flow across the landscape (after Bodin & Norberg 2007).

duplication (copies of the information move from one node to many), serial duplication (one to one), or transfer (only one package of information exists at a time). Allowable trajectories include shortest paths (termed *geodesics* in social network theory), paths (with no repeated nodes or links), trails (nodes may be revisited, but links cannot), or walks (any sequence of nodes and links is permitted). Ecologically, these distinctions are important because they evoke different kinds of applications. For example, we might model the dispersal of large mammals as individual packages, each animal choosing a (perhaps least-cost) route during dispersal. This presumes some discriminatory capacity by the animal. By contrast, we might model the dispersal of a cohort of propagules as divisible flow, with various proportions of the pool moving to various patches, and perhaps subsequently moving from these to other patches, and so on; the dispersal flux to any target patch is then the net flux from all paths that end at the target, no matter what the route. This model might apply to active dispersers or to passive ('unthinking') species. Clearly, the underlying conceptual model should inform what mode of transfer the graph links represent. Importantly, the mode of transfer implies a corresponding index of centrality; Borgatti (2005) tabulates appropriate choices.

Least-cost links are conceptually appealing, but these can be limited or even misleading in that they show by definition

the path of minimum cost. This ignores the likelihood that there might be multiple alternative paths, perhaps including some that are nearly as short as the minimum cost. Pinto & Keitt (2008) developed two extensions to least-cost links, conditional minimum transit costs (CMTCs) and multiple shortest paths (MSPs), to facilitate the exploration of redundant paths. $CMTC(V, S, T)$ is defined as the least-cost distance from S to T conditional on that path passing through node V . Analytically this is a relatively straightforward extension of a common shortest-path algorithm. Dijkstra's (1959) algorithm finds the shortest paths from node S to all other nodes in a graph, returning this result as a tree rooted at S . Combining the tree rooted at S with the corresponding tree rooted at T provides the CMTCs for all routes between these two nodes. This analysis can be performed readily in a GIS (Fig. 5), and Theobald (2006) has developed tools for constructing network models in this way. The MSP method relies on randomly deleting links in Monte Carlo fashion. At each iteration, the least-cost path is

identified, and when a link from the actual shortest path is deleted the path is re-routed. The result over many iterations is a set of shortest paths, which can be arbitrarily edited to retain any path shorter than an user-specified threshold. Pinto & Keitt (2008) retained paths within 10% of the true length. Similarly, tools from circuit theory can be used to identify all possible routes and the cumulative flow between graph nodes; this provides a powerfully visual summary of the routing of flows among nodes (McRae 2006; McRae *et al.* 2008).

In practice, these approaches are important for two reasons. First, management agencies might not be poised to pursue optimal least-cost paths, but might instead welcome a set of 'nearly optimal' alternative paths connecting valued habitat patches. Of course, information on whether such alternatives exist would also be welcome. Second, we might desire some degree of redundancy in paths, simply as insurance. Given these goals, analytic approaches to identify multiple, alternative routes invite further exploration. In this, the approaches of Theobald (2006), Pinto & Keitt (2008), or results from circuit theory might be implemented as multigraphs, with multiple links (of varying weights) between pairs of nodes.

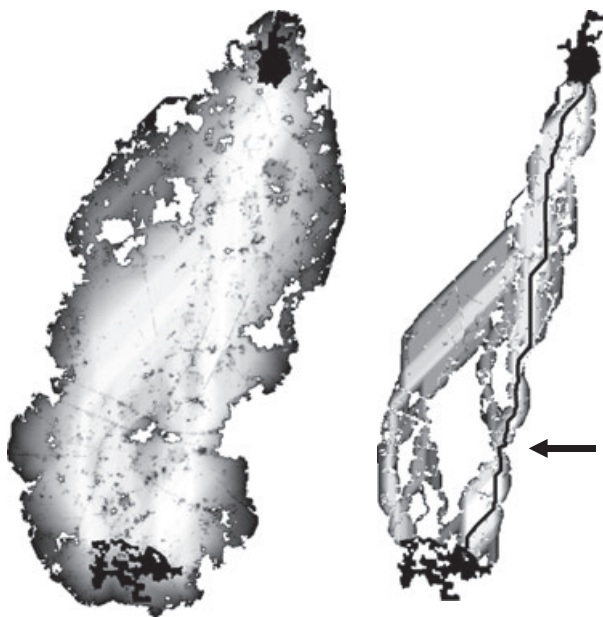


Figure 5 Conditional minimum transit costs between two focal nodes, illustrating all possible routes between the two nodes. Left: cost–distance surface between the two focal nodes (black patches at top and bottom), truncated to a maximum cost–distance of 25 km; darker shades are farther from the target patch at bottom. Right: this cost–distance surface thresholded to 22 km, revealing a 'braided stream' of possible routes. The least-cost path (solid black line) has length 21 663 m. The figure reveals a possible bottleneck (arrow) where the path is highly constrained by nearby development, but also reveals an alternative 'western' route that is only a few hundred metres longer. Figure generated using the *corridor* function in the Spatial Analyst extension to ArcGIS (ESRI, Redlands, CA, USA).

Graphs in theory and practice

An early impetus for applications of graph theory in conservation was the likelihood that existing theory might contribute immediately and powerfully to conservation applications (Urban & Keitt 2001). One goal of model analysis is a search for an 'analytic' solution, which is a general solution to the model expressed in terms of model parameters. A statement of the stability conditions for a population model, expressed explicitly in terms of demographic rates, is one familiar example. This sort of analysis has not been a large part of applications of graph theory to habitat mosaics. In part, this might reflect our lack of familiarity with available analyses. But it might also reflect a separation within graph theory itself, between people who study algorithms and algorithmic solutions to applications, and those who explore graphs as an exercise in pure mathematics (e.g. Chartrand 1977). For the latter, a typical graph problem is an ' n, p, k ' question: Does a graph of order n and size p have some property k ? For example, a theorist might wish to prove that any graph for which the degree of each node is even (i.e. is connected to an even number of nodes) can be visited with a Hamiltonian circuit (a path that visits each node once, never back-tracking, and returns to its starting position – the basis for 'travelling salesman' and 'postman' problems). The solution to this problem is to *prove* that this conjecture about node degrees is true; a person concerned with conservation applications would like to *identify that route*. From this perspective, graph algorithms

would seem to have more to offer to ecology and conservation biology than graph theory itself.

There is, however, a large and growing body of work on generalizations about graphs based on their topology or other statistical properties. For example, there has been a great deal of work recently on random graphs, small-world networks, and scale-free graphs (e.g. Watts & Strogatz 1998; Watts 1999; Strogatz 2001; Barabasi & Bonabeau 2003; Newman 2008). But actual habitat mosaics seem to not quite fit the definitions of these well-studied networks. In particular, the geography of habitat networks – with functional connections based largely on proximity – seems to make habitat mosaics more akin to regular graphs or minimum planar graphs than to small-world or scale-free graphs (Fig. 2). This is because natural adjacencies governed by physical proximity tend to not include the long-distance connections that define small worlds; similarly, geography seems to constrain habitat networks so that these tend not to include the extremely connected nodes (hubs) that characterize scale-free networks (Minor & Urban 2008).

Intriguingly, it is easy to envision anthropogenic connections that defy the natural geometry of landscapes, and so introduce unnaturally long-distance or fast connections. Many examples of invasive species or introduced pests might fit this definition. For example, while natural links (arcs) connecting coral reefs are governed by ocean currents (Treml *et al.* 2008), other connections are made via ballast water from ships following trade routes that are independent of currents. Similarly, many invasives are spread by human-facilitated paths that defy natural adjacencies (via airline connections, ports of call, and other transportation hubs). Thus, there is some potential for posing invasive species issues in terms of natural graphs overlain with anthropogenic ‘short-cuts’ that might impart a predictably unnatural small-world behaviour to human-modified systems. In graph terms, these would be multigraphs, having qualitatively different types of links between nodes (i.e. natural and anthropogenic).

It seems that emerging work with landscape graphs might actually inform this body of work about network topology and graph behaviour. The infusion of social network theory into these analyses seems especially promising.

Evaluating alternative landscape scenarios

Landscapes are large by conventional definitions, and experiments with landscape pattern are logistically difficult. Consequently, landscape ecologists often rely on models to evaluate alternative scenarios about landscape management (Dale 2003). In this, the model provides a form of experimental control, so that alternatives can be assessed within the common framework of the model itself. From this perspective, graph models are especially appealing

because graph analyses tend to be computationally expedient. For example, Keitt *et al.* (1997) developed a patch-deletion algorithm for landscape analysis, in which the ecological value of each patch could be assessed relative to the overall value of the initial (baseline) landscape.² In this case, they computed a measure of landscape connectivity for the baseline landscape, then removed each patch in turn and recomputed the connectivity index. The importance of each patch to connectivity was indexed by the difference in connectivity affected by the loss of that patch. Estrada-Pena (2003) followed a similar approach in northern Spain, using ticks (*Ixodes ricinus*) as indicators for the movements of their hosts; he was able to identify important stepping-stones as well as isolated habitat patches based on relative tick abundances. Urban & Keitt (2001) generalized this approach to multiple indices of patch importance, recognizing that a patch might be important due to its productivity, local connections (source strength, after Pulliam 1988), or role as a stepping-stone in long-distance connectivity (see also Bunn *et al.* 2000). Pascual-Hortal & Saura (2006) extended this approach to explore a larger set of connectivity indices.

Schick & Lindley (2007) reversed the node deletion logic to develop an assessment of restoration potential using graphs. After first documenting the actual fragmentation of the system, they explored several node addition scenarios. They found that adding (restoring) populations with high source strength (i.e. both large and highly connected) first had the highest restorative impact on the populations in the graph.

This general approach is noteworthy because it can be conducted for hundreds to thousands of habitat patches, an otherwise daunting computational demand that is minimized by using efficient graph algorithms.

Sensitivity and uncertainty analysis

Sensitivity or uncertainty analysis are a related set of model analyses, in which the goal is to understand *why* the model behaves as it does – that is, how the model responds to individual parameters, given the model structure. A *sensitive* parameter is one for which a small change in the parameter value elicits a large change in model output. An *uncertain* parameter is one that is sensitive within the range of precision with which it can be estimated. In the context of graph models of metapopulations, sensitivity and uncertainty might apply to the definition of graph nodes (i.e. the habitat model) and the definition of links (based on data about dispersal capacity, and in the case of least-cost paths, knowledge about the relative habitat resistance of

²Not coincidentally, this analysis echoes now-conventional ‘species deletion sensitivity’ in food web analysis (Pimm 1980), which also involves the iterative deletion of nodes from a graph.

various land cover types). To date, this sort of analysis has not been pursued much in ecological applications of graphs. Minor *et al.* (2008, and see Urban *et al.* 2006) developed graph-based simulation models for the wood thrush (*Hyllocichla mustelina*) and explored their sensitivity to alternative definitions of 'habitat' and different assumptions about the dispersal capacity of the bird. Schick & Lindley (2007) tested the sensitivity of all five parameters in their network model of salmonid populations, and found that the results were most sensitive to assumptions about straying and recruitment into the recipient populations. Rayfield *et al.* (2008) have explored the sensitivity of graph solutions to various estimates of dispersal resistances used to compute least-cost links. They found their results reasonably robust to such variation, although local solutions (i.e. paths involving particular nodes or habitat patches) varied in a manner that is probably idiosyncratic to a particular landscape. Given the fundamentally uncertain nature of dispersal data, this sort of analysis warrants further attention by ecologists using graph models. Information on model sensitivity would suggest which parameters dominate model behaviour (i.e. which parameters matter), while uncertainty analysis would marshal further studies to refine estimates of parameters that are sensitive and uncertain.

Network engineering and optimization

A final sort of model analysis might be referred to as 'engineering solutions' for graphs. In particular, this would include formal network optimization, such as to maximize connectivity. Little work has been carried out on network optimization for habitat mosaics. This is despite the reality that in many areas of network applications – for example, communications – the explicit goal is optimization. One analysis with clear potential for habitat mosaics is the so-called maximum-flow/minimum-cut optimization (Phillips *et al.* 2008). This analysis seeks a set of 'cuts' (link removals) from the network that would disconnect a donor node from a target node. The solution takes advantage of the fact (from Menger's theorem) that this minimum cut also represents the maximum flow between the two nodes. The analysis effectively identifies the dispersal bottlenecks between the two focal nodes.

The task of optimizing a habitat network would seem especially compelling for the design of nature reserve systems. Phillips *et al.* (2008) used network optimization for a conservation application in the Cape province of South Africa, to find optimal connections between existing habitat patches for this flora and the modelled locations where these species might need to live in a future climate (a connection in time as well as space). Their analysis used linear programming methods to minimize the amount of

habitat area needed to be preserved to maintain an adequate connected area of suitable habitat over time.

PROMISING APPLICATIONS

Once calibrated for a particular species, graph models can offer novel insights into many conservation and ecology questions. Network topology has potentially important implications for population stability and resilience. For example, Minor & Urban (2008) suggest that clustering may improve population persistence on habitat patches, while Melian & Bascompte (2002) indicate that compartmentalization may help isolate deleterious effects of disturbances. Krause *et al.* (2003) showed a strong relationship between compartmentalization and resilience in food webs. An increased understanding of the ecological consequences of network topology is critical for making better conservation decisions and predictions about the consequences of anthropogenic or natural disturbances. Network analysis, as developed in other disciplines, offers a variety of compelling applications. Here we consider a few especially promising cases.

We previously raised the issue of multigraphs, in which natural and anthropogenic links are identified separately. This case is a natural fit for applications concerned with the spread of invasive species, infectious disease or pathogens. One way to consider such cases is to contrast the dynamics of the system as governed by natural when compared to human-mediated connections (empirically, a model selection exercise). As network models are already well developed in epidemiology (Newman 2002; Franc 2004), this seems a fruitful direction for ecological applications.

Maximum flow/minimum cut problems seem especially well suited to applications concerned with migration between two natural endpoints (Phillips *et al.* 2008). Migration corridors between winter and summer ranges are one obvious case. Large-scale corridor projects represent another promising case, as these typically involve a more-or-less linear (if braided) stream of core reserves; examples might include the Yellowstone-to-Yukon corridor, the Meso-American corridor in Latin America, NATURA2000 in Europe, and similar efforts.

Multispecies conservation planning is increasingly common (Nicholson & Possingham 2006), and this invites applications that overlay multiple graphs. Because multiple target species may exhibit different patterns of connectivity based on their dispersal biology, the simplest option may be to construct and analyse graphs independently for several species, and then overlay or intersect the solutions to find locations that are important to several species. This could apply to instances where the habitat nodes are similar across species but the dispersal biology differs

(Bunn *et al.* 2000), or to cases where the nodes themselves vary among species (i.e. the species use different habitats). In addition, we may want to design nature reserve systems that are maximally connected with respect to dispersal of target species while minimally connected in terms of contagious disturbances, invasive species, or pathogens. At the least, we might identify regions within a landscape (subgraphs) that are connected for one target but not the other.

Social network theory offers a few especially compelling applications. Borgatti (2006) has recently introduced the notion of *key players* in social networks. Two instances are relevant. In one case, the task is to identify a set of nodes of order k , whose removal would maximally disrupt communication within the network. The theory is well developed for application such as the disruption of terrorist cells, but the relevance to ecological applications such as invasive species or pathogens is obvious. Reciprocally, one might wish to identify the set of key players who collectively could communicate with most of the members of the network. This case is well developed in human health applications based on the rapid diffusion of new knowledge into a social network or community (e.g. safe sex practices that might curb the spread of HIV). Here, the analogy in conservation might be to identify a set of nodes (nature reserves) that could act as source patches for, and thus connect, the rest of a functional landscape. Importantly, key player analysis is fundamentally different from other graph analyses such as node-removal exercises, in that the number of key players is specified in advance and the solution varies depending on how many players are targeted. This is because connections between potential key players are often redundant ('friends of friends are also friends').

This last case – identifying the minimal set of reserves that might maximally serve a landscape – invites a comparison to the design of computer networks (Albert *et al.* 2000). In this, a few hubs (servers) are protected while a large number of client machines are less so. The design is such that network performance is not compromised by the loss of a client machine; only the loss of a server affects the network. The same is true of the performance of the web: most URLs could be lost with no real impact, but the loss of Google or Yahoo would be dramatic. Implicitly at least, we seem to want to design the nature reserve systems this same way: Parks or protected areas would serve as the hubs, with the implicit assumption that habitat outside the reserve system might be lost with little impact on the network's function to preserve the long-term viability of biodiversity. Network models obviously could have much to contribute to reserve system design. In particular, issues of network resilience as a function of node failure rates and redundancy are well studied for networks in engineering but unexplored by ecologists. Especially, network design might invite us to

consider *resilience* as the relevant goal of reserve network design, when compared to *resistance*. Resilience refers to the ability of the system to recover from perturbation (i.e. to *accept* node failure, while including redundancy in system design), by resistance connotes a system designed to withstand perturbation (i.e. to *deny* node failure). It is perhaps simplistic to argue that reserve design has focused mostly on a resistance model; but it would be equally simplistic to deny the wealth of insights and analytic rigor available by exploring a resilience model for conservation applications.

CONCLUSION

Graph models offer a versatile representation of habitat mosaics and can provide insight into a variety of ecological questions at both the patch and landscape-level. The flexible data requirements and well-developed algorithms make these models accessible and useful to a wide variety of researchers. The simple act of drawing a graph can provide a quick visual assessment of the landscape, which in some cases might be all that is needed; more sophisticated analyses offer added value. A limiting factor, however, is our ability to parameterize these models in an ecologically relevant way. Building graphs from empirical dispersal data, and validating these models with independent data, will take this approach from the hypothetical to the tangible and establish graph-theoretic approaches as a crucial component of the ecologist's toolbox. There remains a wealth of theoretical insight and algorithmic power available to ecologists, and we hope that this review offers useful guidance for further efforts.

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