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EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Connectivity for conservation: a framework to classify network measures

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Abstract. Graph theory, network theory, and circuit theory are increasingly being used to quantify multiple aspects of habitat connectivity and protected areas. There has been an explosive proliferation of network (connectivity) measures, resulting in over 60 measures for ecologists to now choose from. Conceptual clarification on the ecological meaning of these network measures and their interrelationships is overdue. We present a framework that categorizes network measures based on the connectivity property that they quantify (i.e., route-specific flux, route redundancy, route vulnerability, and connected habitat area) and the structural level of the habitat network to which they apply. The framework reveals a lack of network measures in the categories of "route-specific flux among neighboring habitat patches" and "route redundancy at the level of network components." We propose that network motif and path redundancy measures can be developed to fill the gaps in these categories. The value of this framework lies in its ability to inform the selection and application of network measures. Ultimately, it will allow a better comparison among graph, network, and circuit analyses, which will improve the design and management of connected landscapes.

Key words: circuit theory; conservation management; corridors; fragmentation; graph theory; habitat resistance; inter-patch movement; landscape connectivity; least-cost path; network theory.

INTRODUCTION

The ability of plants, animals, and their genes to move among habitat patches and populations is being undermined by ongoing habitat fragmentation, land-use intensification, and biotic homogenization (Fischer and Lindenmayer 2007). Reduced and impeded movements have significant consequences for biodiversity conservation (Damschen et al. 2006). Maintaining movements of individuals in the short to medium terms enables juvenile dispersal, recolonization of unoccupied habitat patches, seasonal migration, and metapopulation persistence (Hanski 1998), while in the long term it enables range shifts in response to climate change and conserves genetic diversity required for evolutionary adaptation (Minor and Urban 2008). Quantifying the degree to which a landscape promotes or hinders movements among patches of habitat for a given species

(hereafter, habitat connectivity; Fischer and Lindenmayer 2007), is therefore essential to inform conservation management decisions (Calabrese and Fagan 2004).

The use of graph theory as a means of estimating habitat connectivity is rapidly increasing in popularity in ecology and conservation biology (Fig. 1). This popularity can be attributed to three primary strengths of the graph-theoretic approach: (1) its efficiency in characterizing connectivity at broad spatial scales in landscapes with many habitat patches (Urban et al. 2009); (2) its ability to balance data requirements with information content (Calabrese and Fagan 2004); and (3) its flexibility to incorporate additional information about relevant aspects of a species' biology into connectivity assessments (Fall et al. 2007, Minor and Urban 2008, Dale and Fortin 2010). The graph-theoretic approach represents the connectivity of a set of habitat patches as a "habitat graph," a collection of nodes (habitat patches) and links that connect pairs of nodes (representing the potential or frequency of movement between habitat patches). The way in which nodes and links are defined will determine whether the habitat graph
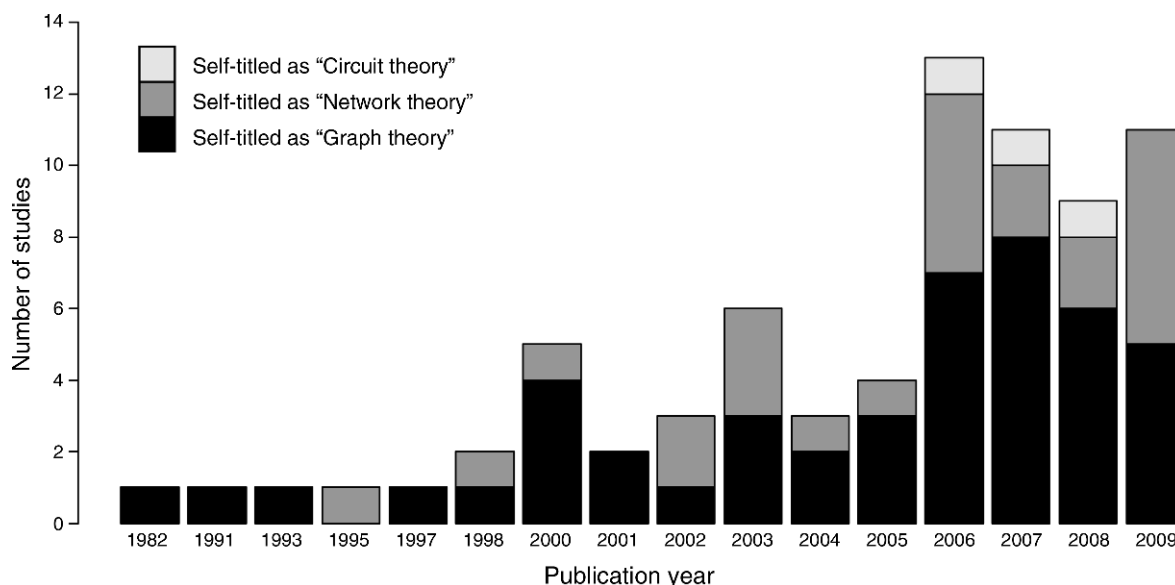
FIG. 1. Number of published studies that use graph, network, or circuit theory to quantify habitat connectivity. The studies are ordered by their year of publication and include five review articles, three conference proceedings, and a user manual. Studies have been categorized based on their self-ascribed method of analysis: graph theory, network theory, or circuit theory. Note that these self-ascribed labels have been inconsistently applied and do not necessarily correspond to our definitions (see *Background terminology: habitat graphs, networks, and circuits*).

represents structural, potential, or functional connectivity among habitat patches (Fagan and Calabrese 2006). Representing structural connectivity requires, for example, that links simply encode information about the physical adjacency of habitat patches or the physical distances among them. Additional information about the focal species' dispersal abilities, such as its maximum dispersal distance threshold, may be used to eliminate links that exceed that threshold distance and produce a representation of potential connectivity for the focal species (e.g., Brooks et al. 2008). Finally, if data are available on actual movement patterns of individuals among habitat patches, then links can be defined based on these observed movements and the corresponding habitat graph would represent functional connectivity. Regardless of the degree of functional connectivity encapsulated in a habitat graph, it is important to evaluate a variety of graph attributes, because species and individuals will differ in their responses to graph characteristics. Hereafter, we use the term habitat network as an intuitive, general reference to a graph-based model of the potential or functional connectivity among habitat patches.

Over the past decade there has been a proliferation of graph-based measures (hereafter referred to as network measures) emanating from the related fields of graph, network, and circuit theory (over 60 network measures; see Appendix A). These network measures were either developed specifically for the application to habitat connectivity assessments (e.g., Pascual-Hortal and Saura 2007) or were adapted from other fields such as social sciences, transportation theory, communication theory,

and epidemiology (e.g., Fortuna et al. 2006). In the absence of any selection guidelines, this wealth of network measures poses a challenge for ecologists trying to select one or a few measures for their connectivity assessments. The result is that most studies use different network measures, making the results difficult to interpret and compare. A framework that classifies network measures is therefore necessary to inform decisions regarding the appropriate measures for any particular assessment of habitat connectivity; developing a framework of network measures is the goal of this paper.

First we review graph, network, and circuit theories with an emphasis on the ways in which they incorporate spatial information about the habitat patches and the surrounding matrix in the definition of nodes and links. We then present a framework that categorizes network measures based on the structural levels of the graph to which they apply (i.e., element, neighborhood, component, and network levels) and the connectivity properties that they quantify (i.e., route-specific flux, route redundancy, route vulnerability, and connected habitat area). We conclude by proposing novel network measures for the underrepresented categories in the framework.

BACKGROUND TERMINOLOGY: HABITAT GRAPHS, NETWORKS, AND CIRCUITS

The terms *graph*, *network*, and *circuit* are often used interchangeably in different disciplines, yet some distinctions can be drawn based on their underlying models and methods of analysis. In general, networks and
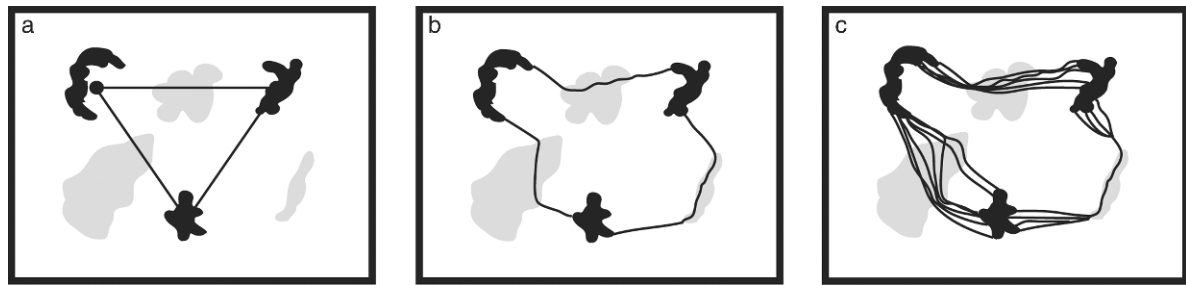
FIG. 2. Representations of habitat connectivity that differ with respect to the amount of ecological information that they incorporate. Habitat patches (black polygons) are connected by links (black lines) that cross hospitable (gray) and inhospitable (white) matrix cover types. (a) A habitat graph connects patch centroids without incorporating a lot of spatial and ecological information about nodes and links. (b) A habitat network connects patch edges by least-cost links that incorporate information about matrix heterogeneity. Additional node and link attributes may also be included by assigning weights. (c) A habitat circuit connects patches with multiple links, thereby incorporating additional spatial information about the matrix.

circuits can be thought of as special types of graphs with restricted definitions and applications. In its most basic form, a graph is a set of *nodes*, some pairs of which are joined by *links* (Harary 1969, Fig. 2a). The term *network* should refer to *weighted* graphs based on either node size or link weight (Fig. 2b; Gross and Yellen 2004, Diestel 2006; Appendix A). A circuit (based on analogy with an electrical circuit) is a network (Fig. 2c) in which nodes are connected by special links made up of one or more resistors (electrical components that each conduct a precise amount of current; McRae et al. 2008).

Graph theory is the branch of mathematics concerned with connections among discrete objects (Harary 1969). Network theory applies graph theory with a focus on properties of real-world networks (e.g., social networks, transportation systems, communication networks, and epidemiology; Brandes and Erlebach 2005), their structural dynamics, and the relationship between their structure and function (Newman et al. 2006). As such, it provides a formal foundation for studying the effects of habitat network structure on functional dispersal processes. Circuit theory applies network theory to quantify connectivity in circuited systems that respond positively to the presence of alternative pathways (or resistors, in the case of electrical circuits; McRae 2006, McRae and Beier 2007, McRae et al. 2008). The relationship between circuit theory and random walk theory facilitates its application to habitat connectivity analyses for species with random dispersal patterns. Specifically, the fates of random walkers on circuits can be predicted by measures derived from circuit theory: voltage can predict the probability of successful random walkers, current can predict the probability of dispersal along a given link as a function of current, and resistance can predict commute times between nodes (reviewed in McRae et al. 2008).

HABITAT NETWORKS

Developments of analytic methods to identify and analyze habitat networks have been made primarily using the language of graph theory (Table 1; see Urban and Keitt 2001, Fall et al. 2007, Pinto and Keitt 2009).

Initially, the application of graph theory to quantify habitat connectivity was based on very simple graph models (Marcot and Chinn 1982, Cantwell and Forman 1993, Forman 1995, Keitt et al. 1997, Marcot 1998). These simple habitat graphs were nondirected, unweighted graphs (Appendix A) in which habitat patches were represented as dimensionless nodes and links were represented as lines connecting nodes. Any information about the spatial location, length, shape, and quality of habitat patches and of links was disregarded. Therefore, estimates of habitat connectivity based on these habitat graphs considered only the presence or absence of connections between habitat patches (topology; Appendix A) instead of the strength of connections.

Further developments of habitat network analyses have resulted from the inclusion of more information about habitat suitability, landscape permeability, and movement behavior into habitat graphs (van Langevelde and van der Knaap 1998). The most straightforward means of including additional information into simple habitat graph models is to assign weights to the nodes and links. Nodes can be weighted to reflect habitat patch properties that may influence immigration and emigration, such as patch area (e.g., Estrada-Pena 2002, Miller and Russell 2003) or patch quality (e.g., Minor and Urban 2007). Links can be weighted to reflect link properties that may affect dispersal, such as the geometric length of the link or the effective length of the link based on estimated movement costs of underlying land cover types (e.g., Halpin and Bunn 2000, Rothley and Rae 2005, O'Brien et al. 2006). Link weights have also been used to describe the dispersal probability between two nodes (e.g., Urban and Keitt 2001, Brooks et al. 2008, Treml et al. 2008). These weighted habitat graphs (habitat networks) have been described using the language of both graph theory (e.g., Bunn et al. 2000, Brooks 2006) and network theory (e.g., Keitt 2003, Bodin and Norberg 2007). More sophisticated means of incorporating additional information into habitat networks focus on maintaining spatial referencing of nodes and links during the construction of habitat networks (Theobald 2006, Fall et al. 2007).

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These more sophisticated methods explicitly account for habitat patch shape and landscape structure in two ways: (1) nodes are treated as two-dimensional patches with georeferenced locations; and (2) links between nodes connect patch perimeter to patch perimeter and follow georeferenced least-cost routes. Connectivity of these habitat networks has been measured in terms of the probability of movement among habitat patches and the area of habitat connected (Saura and Pascual-Hortal 2007).

The most recent development of habitat networks has been to treat links and pathways as multiple routes instead of single, least-cost routes (McRae 2006, Theobald 2006, McRae and Beier 2007, McRae et al. 2008, Pinto and Keitt 2009; reviewed in Urban et al. 2009). In landscapes represented by grid maps, each grid cell can be treated as a node where edges linking adjacent cells can have weights (McRae 2006, Pinto and Keitt 2009). Habitat patches in the landscape can be made up of one or more grid cells and may have multiple pathways connecting them through the grid. Two methods have been proposed for identifying multiple routes between habitat nodes: the conditional minimum transit cost method (CMTC method; Theobald 2006, Pinto and Keitt 2009) and the multiple shortest paths method (MSP method; Pinto and Keitt 2009). Both of these methods identify a large set of routes between a pair of habitat patches, but only retain the subset that is within a given length of the least-cost route. The CMTC method identifies a set of routes such that each path minimizes the CMTC through a different location on the landscape. The CMTC is measured as the least-cost distance between two habitat nodes, contingent upon the least-cost path crossing a given location on the landscape (i.e., a given grid cell in a raster map). The MSP generates a set of paths between two nodes by repeated permutation of the least-cost route. Route segments are randomly deleted and the least-cost route is recalculated in an iterative fashion. These methods allow us to create multi-route habitat networks (or multi-graphs or circuits; Appendix A) that provide important spatial information about movement options through the matrix and allow for increased flexibility in connectivity conservation planning (Urban et al. 2009).

Quantifying Connectivity in Habitat Networks

Due to the large size and complexity of habitat networks, it is necessary to condense and summarize the relevant information via the use of network measures (Appendix A). A network measure is either a single number or a set of numbers that quantifies some property of a network (Brinkmeier and Schank 2005). Through the years, a wide variety of network measures have been proposed to quantify the connectivity of habitat networks. We reviewed the literature covered by the ISI Web of Knowledge Science Citation Index database using the following word combinations in a topic search: graph, network, or circuit in combination with habitat connectivity or landscape connectivity (database *available online*).[5] We found 51 relevant articles dating from January 1982 to May 2009 that have cumulatively proposed 61 network connectivity measures for quantifying habitat connectivity at a single point in time. These network measures have been assembled in Appendices B and C.

Many of these measures have been imported or adapted from other disciplines. For example, the gamma index (i.e., the number of links in a network divided by the number of links in the corresponding planar network; Appendix B) was first imported from transportation geography by Ricotta et al. (2000) to quantify the connectivity of different vegetation types in a landscape, and was later modified by Acosta et al. (2003) to include qualitative differences in the conservation values of vegetation types. Other measures have been developed specifically for ecological applications, such as the integral index of connectivity (Appendix C; Pascual-Hortal and Saura 2006), which was proposed as a means of integrating habitat area and habitat connectivity in a single measure.

Network measures that quantify habitat connectivity can be divided broadly into topological indices (Appendix B) and weighted indices (Appendix C). Topological network measures only consider the presence or absence of a link between nodes during their calculation. They characterize the basic structure of a network based on the qualitative pattern of connections among nodes (Appendix B). Weighted network measures consider the variation and strength of connections between nodes by including node and link weights during their calculation. They characterize connectivity patterns in the network based on ecological characteristics of nodes and links (Appendix C).

Framework of Network Measures

We designed two criteria to classify this large number of network measures: (1) the structural level at which they can be applied (i.e., element, first-order neighbors, component, and network; Fig. 3); and (2) the specific connectivity properties that they measure (Table 1). The connectivity properties are simplified into four primary categories: route-specific flux, route redundancy, route vulnerability, and connected habitat area. Our framework stresses the parallels that exist between connectivity properties that can be measured at different structural levels of the habitat network.

Structural levels of analysis

Distinct structural levels of analysis exist within networks (Fig. 3; see Wasserman and Faust 1994, Brandes and Erlebach 2005) and network measures have been developed for each of the levels. While these

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TABLE 1. Summary of network measures that quantify habitat connectivity.

Connectivity property	Structural level			
	Element	First-order neighbor	Component	Network
Route-specific flux	betweenness centrality; closeness centrality; eccentricity; node degree; node degree correlation; node depth; node in degree; node out degree; node influx; node outflux; reachability index		average path strength; characteristic path length; component order; component size; diameter; Harary index; path strength; Wiener index	asymmetry; connectance; coefficient of variation of component order; degree distribution; diameter of largest component; gamma index; mean component size; mean or SD of node degree; no. components; network order; network size; order of largest or smallest component; recruitment; traversability meshedness
Route redundancy	commute time; effective resistance; network flow; (link) redundancy	clustering coefficient		
Route vulnerability	current density	connectivity correlation	reliability; no. cut nodes; no. cut links	total no. cut nodes; total no. cut links
Connected habitat area	dispersal flux; node area; modified incidence function; quality-weighted area	ecologically scaled connectivity	component area	area index; class coincidence probability; correlation length; expected component size (area); expected dispersal flux; integral index of connectivity; landscape coincidence probability; max. connected local population size; probability of connectivity

Note: Network measures are defined and referenced in Appendices B and C.

distinct levels of analysis do indeed exist, they are not strictly independent. That is, structure at a particular network level is both constrained by lower levels and embedded within higher levels. For instance, network measures pertaining to the elements of the network themselves (i.e., nodes and links) do not exclusively focus on the elements independently, but may also describe their role in the context of the whole network. Hence, at this "element level," network measures can focus on properties such as the number of links per node (i.e., node degree) or the importance of a node based on its position within the network (i.e., node centrality). "First-order neighbor-level" measures assess the connectivity among a set of nodes that are directly connected to a focal node (first-order neighborhoods include spatially adjacent nodes that may or may not be joined by a link or a path to a focal node; Appendix A). For example, a neighborhood analysis could examine the relationship between the degree of a node and the degrees of its neighbors (i.e., connectivity correlation; Appendix B). "Component-level" or "Cluster-level" measures examine groups of interconnected nodes made up of both direct and indirect connections (clusters are linked transitively by paths; Appendix A). These measures could focus on the number of nodes connected (i.e., component order) or the average length of the shortest path connecting node pairs (i.e., characteristic path length). Finally, "network-level" measures focus on the patterns of connectivity among all nodes and links in the network (e.g., the mean node degree or the number of components). Higher levels of analysis, such as the component and network levels, often summarize the distribution of connectivity properties at lower levels with frequency plots or measures of central tendency and spread. These high-level network descriptors can be either single values or distributions (Brinkmeier and Schank 2005). Basic transformations can be performed among single-valued measures and distributions for different levels in the network (for descriptions of
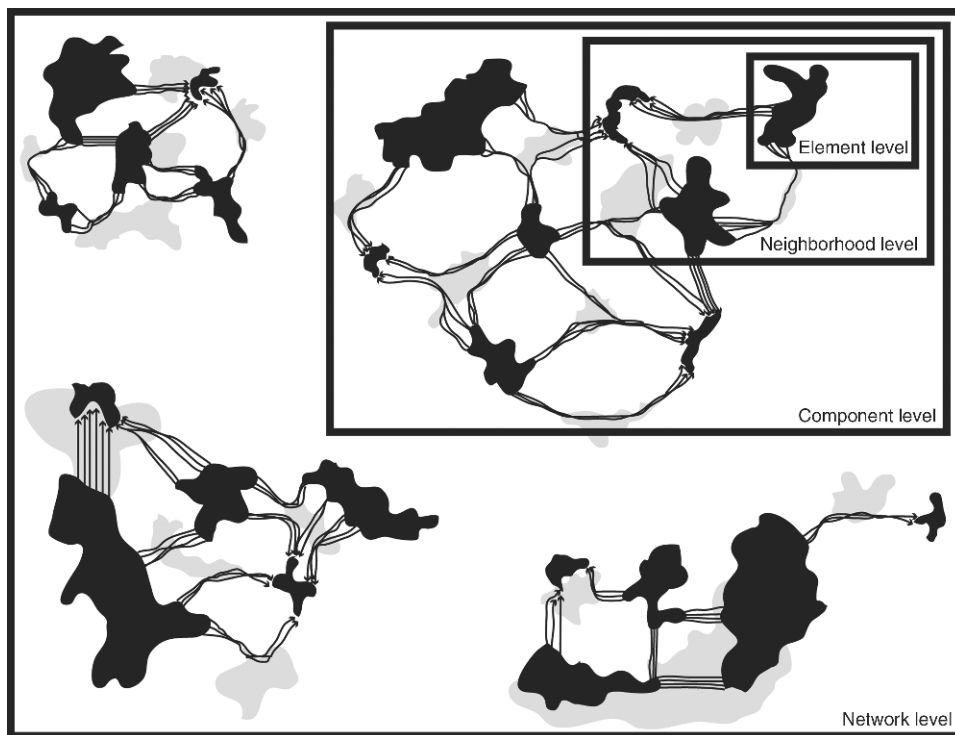
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FIG. 3. Examples of different structural levels of analysis within a habitat network. Habitat patches (black polygons) are connected by multi-route, directional links (black lines) that cross hospitable (gray) and inhospitable (white) matrix cover types. Source–sink motifs are illustrated as a connected pair of habitat patches in which movement is directional from source to sink patches. Note that a single sink patch may receive immigrants from several source patches and vice versa.

possible transformations, see Brinkmeier and Schank [2005]).

These structural levels of analysis are based on network topology rather than a priori definitions of the scale of habitat patches. A habitat patch could be identified prior to the network analysis based on the contiguity of a group of habitat grid cells in a raster map (Gardner 1999), in which case it would be represented as a single node in the network. Alternatively, the identification of habitat patches could emerge at coarser scales from the network analysis itself if a habitat patch consisted of multiple nodes connected into neighborhoods and components (O'Brien et al. 2006).

Connectivity properties

For the purpose of our framework, we have identified four important connectivity properties that are assessed by the different network measures: (1) route-specific flux, (2) route redundancy, (3) route vulnerability, and (4) connected habitat area. These are not direct measures of functional habitat connectivity per se, but they provide important information on the different properties of the species–landscape interaction, including different degrees of spatial contextual information, which result in functional habitat connectivity. Specifically, connected habitat area fully integrates movement

potential and thus is more of an outcome than a cause of connectivity.

The first connectivity property, *route-specific flux*, accounts for movements among habitat patches but takes a relatively narrow view of the strength of connections among habitat patches (e.g., measures are based on the existence, length, or cost of a single route). Route-specific flux depends on the source strength of donor habitat patches, the attraction strength of recipient habitat patches, and the probability of dispersal through the matrix (Hanski 1999b, Tischendorf and Fahrig 2000). Network measures range from simple measures of habitat patch source strength, such as "node out-degree" (Appendix C; Schick and Lindley 2007, Treml et al. 2008), to integrated measures of source strength and dispersal probability, such as "dispersal flux" (Appendix C; Urban and Keitt 2001). Route-specific flux occurs across a multitude of spatial and temporal scales (Mueller and Fagan 2008) requiring the use of scale-specific measures based on levels of analysis within the network. For example, at the scale of movement between a pair of habitat patches or the element level, "dispersal flux" focuses on the recruitment potential of each patch (estimated by area or quality-weighted area) and the probability of dispersal between two patches (based on a dispersal kernel and/or properties of the intervening matrix). At the neighbor-

hood level, "connectivity correlation" (Appendix B) measures the tendency of links to connect nodes with similar degrees and identifies neighborhoods with high levels of mixing. At the component level, "diameter" (Appendices B and C) measures the inter-patch distance that an organism would have to traverse in order to span the component. At the network level, "gamma index" (Appendix B) measures the number of directly connected pairs of habitat patches in the network.

The connectivity property *route redundancy* accounts for the presence of multiple, alternate movement routes among habitat patches, and so broadens the view of the strength with which habitat patches are connected or for which options are available to individuals moving (e.g., measures are based on the number and length/cost distributions of routes). Including multiple movement routes into connectivity analyses acknowledges that individuals rarely use a single optimal route, due to variability in behavior and perception (Bélisle 2005, Driezen et al. 2007). Multiple routes may also be used, either because the theoretical optimal route is unattainable or because there exist multiple ways to disperse optimally (or near optimally) among habitat patches in a landscape (Wiens 2001). An example of the latter is provided by Farmer and Wiens (1998), who modeled long-distance migration of shorebirds and showed variability in individuals' migration patterns even when all individuals were making optimal decisions about when and where to refuel. Route redundancy is desirable to maintain in a habitat network from a conservation planning perspective because it produces more stable connections among habitat patches in the event that natural or anthropogenic disturbances compromise one or more routes (Moilanen et al. 2006, Urban et al. 2009). Redundant movement routes between a pair of habitat patches may be quantified using measures from circuit theory that specialize in measuring cumulative flux between habitat patches distributed over multiple connections (routes). "Resistance distance" (Appendix C) is one such measure (McRae et al. 2008); it measures the opposition to movement of a set of dispersal routes between a pair of habitat patches and decreases with the addition of more movement routes. Redundancy at the first-order neighbor level can be investigated as the fraction of triangles present in the network or "clustering coefficient" (Appendix B). Triangular network topology means that for each pair of directly connected nodes, there exists at least one more indirect path connecting the nodes through a mutual neighbor. A similar measure at the network level is "meshedness" (Appendix B), which compares the actual number of links in the network to the number in the corresponding triangulated planar graph (to which no additional links can be added without creating a nonplanar graph; Forman 1995).

The connectivity property *route vulnerability* accounts for the degree to which the landscape structure funnels or scatters the movements of a particular species (Lees and Peres 2008, Pinto and Keitt 2009). Route vulnerability includes interactions and dependencies among alternate paths, and so expands the view beyond solely considering the number or quality of individual routes (i.e., route redundancy). Parallel paths, bottlenecks, and other spatial aspects of the pattern of links further broaden our perception of the strength of connections. When movements are funneled through particular locations on the landscape, then maintenance of habitat connectivity hinges on protecting those areas as movement passageways. An element-level analysis of vulnerability can identify areas (grid cells) in the intervening matrix surrounding habitat patches through which dispersers are likely to move when traveling from one habitat patch to another (e.g., "current density"; Appendix C). Pinto and Keitt (2009) showed that dispersal bottlenecks in the matrix emerge when the quality of different land cover types in the matrix is spatially autocorrelated and hence there are large clumps of high-quality matrix land cover types to attract dispersers. At higher levels of analysis, vulnerability can be measured by the presence of "cut nodes" and "cut links" (Appendix B) that act as funnels for movements through the network. If these nodes or links are removed, they will disconnect a component to create two or more smaller components and thereby decrease connectivity at both the component and network levels. Note that route vulnerability as we have defined it pertains to structural vulnerability of a route within a network and does not incorporate additional vulnerability due to threatening processes such as development, wildfire, or climate change.

The connectivity property *connected habitat area* accounts for net connected habitat by integrating all pathways to produce a description of effective habitat patches from the perspective of the organism (rather than delineating patches based purely on geometry). At its base, the area of connected habitat considers the area inside a patch of habitat as a space where connectivity occurs in addition to inter-patch movements (Hanski 1999a, Pascual-Hortal and Saura 2006). It recognizes that habitat connectivity may result either from a spatial configuration of habitat patches that promotes inter-patch movements or from large tracts of contiguous habitat (Ferrari et al. 2007). Network measures often include information about the area of habitat patches at different levels of analysis such as node area and component area. Quantifying connectivity based on component area or size is rooted in bond percolation theory, which formally describes component structure in random graphs (Keitt et al. 1997). At the network level, percolation theory relates connectivity to the average size of components in measures such as "correlation length" (Appendix C; see Keitt et al. 1997) and "expected cluster size" (Appendix C; see O'Brien et al. 2006). Pascual-Hortal and Saura (2006) have proposed that measures of habitat and component area be integrated with measures of inter-patch movements.

They have developed two new network-level connectivity metrics, "integral index of connectivity" and "probability of connectivity" (Appendix C; see Pascual-Hortal and Saura 2006, Saura and Pascual-Hortal 2007), which take on low values either if habitat patches are poorly connected by inter-patch movements or if habitat patches are well connected but the amount of habitat is low.

Missing network measures in some categories

Our framework of network measures (Table 1) reveals a striking imbalance in the distribution of measures across different levels of network analysis and among the different properties of habitat connectivity. It is evident that most network measures apply at the level of the entire network or individual elements and indeed these are the network levels that are most commonly measured in habitat connectivity assessments. Network-level analyses are often of interest to conservation planners because they correspond to the scale of conservation planning set by biogeographical or geopolitical boundaries and may reveal landscape-level changes due to climate change (Pearson and Dawson 2005). Element-level analyses are commonly used to identify and prioritize specific patches and corridors for conservation or restoration. Analyses at the level of components are represented by network measures for most connectivity properties and have been identified as an important intermediate scale at which to measure connectivity (Urban 2005, Urban et al. 2009). For example, the area of connected components of habitat patches has been correlated with the spatial distribution of woodland caribou (*Rangifer tarandus caribou*; O'Brien et al. 2006). However, component-level measures that quantify route redundancy are lacking. This omission could be attributed to, first, the importation of measures from other disciplines that prioritized network efficiency over network redundancy and, second, a focus on optimal movement routes between habitat patches rather than the inclusion of alternative pathways. Recent advances in modeling the spatial structure of habitat networks (Fall et al. 2007, Dale and Fortin 2010) and quantifying element-level redundancy via the use of circuit (McRae 2006, McRae et al. 2008) may inspire measures of spatial redundancy at higher structural levels within habitat networks. Circuit analyses have emphasized the redundancy of multi-route links that connect pairs of neighboring habitat patches with a series of routes through the matrix (Theobald 2006, Pinto and Keitt 2009).

Redundancy also exists at the level of components between nodes that are not first-order neighbors. Multiple paths of varying lengths indirectly connect non-neighboring nodes by traversing along a series of connected intermediate links and habitat nodes (Appendix A). We hypothesize that this intermediate scale of connectivity will be important for maintaining metapopulations (Ferreras 2001) and increasing foraging success in landscapes with patchy resource distributions (Wiens 1989). Hence, we propose the use of "path redundancy," which reflects the number of possible paths between pairs of indirectly connected nodes (Kim et al. 2003), as a measure of redundancy at the component level. Enumerating all possible paths between a pair of indirectly connected nodes is nontrivial: hence, an alternative measure of path redundancy is the sum of the "redundancy degrees" of intermediate nodes in the shortest path (Kim et al. 2003). A node's redundancy degree is the number of links incident to that node apart from the incoming and outgoing links involved in the shortest path. A higher number of redundancy degrees would indicate a route consisting of intermediate nodes with relatively more neighboring nodes and hence the potential for more redundant paths toward the destination (Kim et al. 2003). When redundant paths can be identified, they may be further analyzed by applying circuit analyses at the level of habitat nodes rather than grid cells. Effective resistance between indirectly connected habitat nodes could then be assessed by the number and individual resistances of multiple paths (consisting of intermediate links). "Pinch points" identified by circuit analyses applied at this level would then directly correspond to cut nodes and cut links rather than grid cells through which there is a high likelihood of moving (Appendix B; see McRae et al. 2008).

Our framework highlights a dearth of network measures at the neighborhood level despite the prominence of this level of analysis in other disciplines applying network theory (dyadic and triadic levels in Wasserman and Faust 1994, Newman 2003, Proulx et al. 2005). The importance of neighborhoods in a particular habitat network will probably depend on the distances among habitat patches relative to the perceptual range of a species. The connectivity structure of neighborhoods presumably will be more important if the neighborhood level corresponds more closely to the scale of the sensory information window to which an animal can respond (Lima and Zollner 1996). Fortuna et al. (2006) provide an elegant example of the importance of the neighborhood-level measure "clustering coefficient" (Appendix B) in a dynamic network of temporarily flooded ponds. In their system, a high clustering coefficient provided the opportunity for an amphibian, which had moved from a dry to a flooded pond, to move again to another flooded pond if the conditions of the former were not suitable for reproduction.

Another means of quantifying neighborhood topology in networks is through the identification of "network motifs" (Milo et al. 2002, Proulx et al. 2005). Network motifs are small, repeated patterns or subgraphs that occur significantly more often than expected from random networks. A wide variety of biotic and abiotic networks have been found to contain motifs, some of which are common across networks derived from

biochemistry, neurobiology, ecology, and engineering (Milo et al. 2002, Milo et al. 2004). For example, seven separate food webs contained a four-node motif in which two species shared a common predator and prey; this motif was also found in *Caenorhabditis elegans* neuronal network and five technological networks (Milo et al. 2002). The presence, number, and distribution of network motifs has been linked to the functioning of biological networks such as gene regulatory networks (Becskei and Serrano 2000, Shen-Orr et al. 2002) and transcription networks (Mangan and Alon 2003). To identify motifs in a network, it is possible to search and count all possible configurations of subgraphs with a fixed number of nodes (e.g., all three- and four-node subgraphs; Milo et al. 2002) or to restrict the search to specific motifs that are hypothesized to be important for functionality.

Motifs have yet to be identified in habitat networks. We propose that the presence and number of source–sink motifs could indicate ongoing route-specific flux from sources to neighboring sinks (Fig. 3). This motif is rooted in Pulliam's (1988) source–sink model, which has also been invoked as a potential conceptual foundation for habitat networks (Urban et al. 2009). A source–sink motif could be defined as a connected pair of habitat patches in which the source and sink habitat patches have positive and negative net reproduction, respectively. We assume that, all else being equal, net dispersal would be higher between a pair of source–sink patches than between patches that are both sources or both sinks (Pulliam 1988, 1996). To detect source–sink motifs, the habitat network must be delineated with directional links (i.e., as a digraph; see Appendix A) differentiating the outward dispersal from sources and the incoming dispersal into sinks (Fig. 3). Source–sink motifs may exist at a local structural level (i.e., two-node subgraphs) where a single source patch has a single sink patch. Source–sink motifs may also exist at a neighborhood level (i.e., higher-order subgraphs). For example, several patches may act as sources for a single sink or several patches may act as sinks for a single source (Fig. 3; see Tittler et al. 2006 for empirical evidence). These different source–sink motifs may imply different levels of route-specific flux rates and may have different impacts on the long-term persistence of populations occupying sink patches in the habitat network.

Selecting network measures

The network measures discussed here (Table 1) range from reductionist measures of the basic features of a network to integrated measures that simultaneously measure multiple aspects of network structure. Some of these measures may be correlated either because they represent the same basic aspect of network structure (e.g., class coincidence probability and landscape coincidence probability; Appendix B) or because different aspects of the network structure are correlated for the particular landscape under investigation. Presum-

ably, a relatively small subset of all possible network measures would suffice to quantify habitat connectivity for a particular study system, as is the case with other landscape pattern metrics (Riitters et al. 1995, Cushman et al. 2008). It is unlikely, however, that the exact same set of network measures will be appropriate for all studies that differ with regard to location, data models (vector/raster), scale (grain and extent), and objectives. The choice of measures should explicitly reflect a hypothesis about the observed habitat network and how the structure of the habitat network affects key ecological processes. Our framework provides researchers and practitioners who are faced with this choice some much-needed clarification on the ecological meaning of existing network measures and the relevant levels of analysis at which they can be applied.

Multiple measures exist within single categories of our framework (e.g., 12 network measures quantify route-specific flux at a local level). Selecting among measures within a given category remains challenging and we argue for the use of empirical data on species distributions and dynamics to compare the performance of network measures (e.g., O'Brien et al. 2006, Saura and Pascual-Hortal 2007, Magle et al. 2009). It would also be useful to evaluate the behavior of network measures in response to changing spatial landscape pattern scenarios generated by neutral landscape models to establish their consistency and predictive potential (e.g., Tischendorf 2001). Pascual-Hortal and Saura (2006) and Saura and Pascual-Hortal (2007) have provided a useful method to compare network measures based on 13 desirable properties such as their sensitivity to different types of landscape change that affect habitat connectivity (e.g., complete or partial loss of habitat or corridors). Within a given category, several measures may be functions of the same basic network parameters. For example, five of the measures that quantify route-specific flux at the network level are functions of the total number of nodes (n) and links (l): network order (n), network size (l), mean node degree ($2(l/n)$), connectance (l/n^2), and gamma index ($l/(3(n - 2))$). These measures would appear to be alternative ways of representing the same basic information; hence, we recommend the simplest measures that quantify basic ratios between n and l, such as mean node degree or connectance. More complicated measures should be justified with explicit reference to ecological theory. Good examples of this include dispersal flux (Urban and Keitt 2001) and the modified incidence function (Magle et al. 2009), which are derived from metapopulation theory, and effective resistance (McRae et al. 2008), which is expressly linked to random walk theory. Until network measures have been tested empirically, we feel that composite measures (i.e., measuring more than one property or structural level of the network) such as Reachability (Appendix C) should be avoided due to difficulties associated with their interpretation.

CONCLUSIONS

The number of network measures presents a daunting task in selecting among them for any particular assessment of habitat connectivity. Categorizing measures according to (1) their level of analysis within the network and (2) the property of habitat connectivity that they quantify allows for an ecologically meaningful choice of measures grounded in hypothesis testing. One of the major advantages of network thinking is that it encourages ecologists to focus on multiple levels of analysis and ask multi-scale questions (Kotliar and Wiens 1990) about how habitat patches are embedded within a habitat network and how the network structure emerges from local connections between habitat patches. The importance of local patterns on overall landscape connectivity has been stressed in static (Bascompte and Solé 1996, With and King 1999) and dynamic (Matlack and Monde 2004, Wimberly 2006) landscapes. Ultimately, the goal of network connectivity analyses is to determine how the connectivity structure of habitat networks constrains and enables ecological and evolutionary processes at various levels of biological organization (genes, individuals, populations, and communities). An important step toward this goal will involve determining how well measures of structural and potential connectivity can predict functional connectivity. Separately quantifying the four connectivity properties at different structural levels can help to decompose the relationship between potential and functional connectivity to move toward identifying the most important aspects of habitat network structure to maintain.

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APPENDIX A

Definitions of network terminology (*Ecological Archives* E092-073-A1).

APPENDIX B

Topological network measures that have been applied to quantify connectivity in habitat networks (*Ecological Archives* E092-073-A2).

APPENDIX C

Node and link weighted network measures that have been applied to quantify connectivity in habitat networks (*Ecological Archives* E092-073-A3).

CONCEPTS & SYNTHESIS