Contributed Paper

A Graph-Theory Framework for Evaluating Landscape Connectivity and Conservation Planning

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Abstract: *Connectivity of habitat patches is thought to be important for movement of genes, individuals, populations, and species over multiple temporal and spatial scales. We used graph theory to characterize multiple aspects of landscape connectivity in a habitat network in the North Carolina Piedmont (U.S.A). We compared this landscape with simulated networks with known topology, resistance to disturbance, and rate of movement. We introduced graph measures such as compartmentalization and clustering, which can be used to identify locations on the landscape that may be especially resilient to human development or areas that may be most suitable for conservation. Our analyses indicated that for songbirds the Piedmont habitat network was well connected. Furthermore, the habitat network had commonalities with planar networks, which exhibit slow movement, and scale-free networks, which are resistant to random disturbances. These results suggest that connectivity in the habitat network was high enough to prevent the negative consequences of isolation but not so high as to allow rapid spread of disease. Our graph-theory framework provided insight into regional and emergent global network properties in an intuitive and visual way and allowed us to make inferences about rates and paths of species movements and vulnerability to disturbance. This approach can be applied easily to assessing habitat connectivity in any fragmented or patchy landscape.*

Keywords: dispersal, fragmented landscapes, graph theory, habitat connectivity, habitat network, network theory, spread of disturbance

Un Marco de Referencia Teórico-Gráfico para Evaluar la Conectividad del Paisaje y Planificar Conservación

Resumen: *Se piensa que la conectividad de los parches de hábitat es importante para el movimiento de genes, individuos, poblaciones y especies en múltiples escalas temporales y espaciales. Utilizamos la teoría de gráficos para caracterizar múltiples aspectos de la conectividad del paisaje en una red de hábitats en el Pie de Monte en Carolina del Norte (E.U.A.). Comparamos este paisaje con redes simuladas con topología, resistencia a la perturbación y tasa de desplazamiento conocidas. Introdujimos medidas gráficas como la compartimentación y el agrupamiento, que pueden ser utilizados para identificar localidades en el paisaje que pueden ser especialmente resilientes al desarrollo humano o áreas que pueden ser más adecuadas para la conservación. Nuestros análisis indicaron que la red de hábitats en el Pie de Monte estaba bien conectada para las aves. Más aun, la red de hábitats tenía características en común con las redes en planicies, que exhiben desplazamiento lento y con redes sin escalas, que son resistentes a las perturbaciones aleatorias. Estos resultados sugieren que la conectividad en la red de hábitats fue suficiente para prevenir las consecuencias negativas del aislamiento pero no para permitir la rápida dispersión de enfermedades. Nuestro marco de referencia teórico-gráfico proporcionó entendimiento de las propiedades regionales y globales de las redes de manera intuitiva y visual y nos permitió inferir las tasas y direcciones de los movimientos de las especies y su vulnerabilidad a la perturbación. Este método se puede aplicar fácilmente a la evaluación de la conectividad del hábitat en cualquier hábitat fragmentado.*

Introduction

Connectivity of habitat patches is thought to be important for movement of genes, individuals, populations, and species over multiple time scales. Over short time periods connectivity affects the success of juvenile dispersal and thus recolonization of empty habitat patches (Clergeau & Burel 1997). At intermediate time scales it affects migration and persistence of metapopulations (Hanski & Gilpin 1991; Ferreras 2001). At the largest time scales it influences the ability of species to expand or alter their range in response to climate change (Opdam & Wascher 2004). Habitat connectivity is especially important when habitat is rare, fragmented, or otherwise widely distributed (Flather & Bevers 2002; King & With 2002) and can be a critical component of reserve design. Nevertheless, the definition and measurement of connectivity has been controversial (e.g., Tischendorf & Fahrig 2000; Moilanen & Hanski 2001; Tischendorf & Fahrig 2001) because connectivity can be measured either at the patch scale (Uezu et al. 2005) or at the landscape scale (Hutchinson & Vankat 1998) and can be defined either structurally or functionally (Belisle 2005).

Graph theory provides a simple solution for unifying and evaluating multiple aspects of habitat connectivity, can be applied at the patch and landscape levels, and can quantify either structural or functional connectivity. Although graph theory has only recently been introduced to the field of landscape ecology (Urban & Keitt 2001; Jordan et al. 2003; Rhodes et al. 2006), there is a well-developed body of research from computer and social sciences that quantifies connectivity and flow in networks. Graph theory offers insight into regional and emergent network properties in an intuitive and visual way, provides a framework for cross-scale analysis, and allows spatially explicit representation of dynamics. We propose that conservation theory and practice would benefit from viewing habitat patches within a graph-theory or network framework.

Although other methods of measuring habitat connectivity may be more appropriate for specific research questions (e.g., metapopulation capacity [Hanski & Ovaskainen 2000] for predicting population persistence across an entire landscape), graph theory may be preferable for many applications. Graph-theoretic approaches may possess the greatest benefit-to-effort ratio for conservation problems that require characterization of large-scale connectivity, due to their ability to provide a detailed picture of connectivity with modest data requirements (Calabrese & Fagan 2004). An additional strength of graph models lies in their flexibility. Although graph theory does not require knowledge of behavior, fecundity, or mortality parameters, these data can be incorporated and used to create an ecologically rich graph model. Empirical occupancy and movement data can also be used (but are not required) to build a graph that shows actual connectivity for a given species (e.g., Rhodes et al. 2006). Alternatively, the graph can be built with connectivity estimates from a dispersal model, such as a spatially structured diffusion model (Ovaskainen 2004). Rare long-distance dispersal events can be included by creating connections with very low probabilities. That these models can contain species-specific biology is another compelling argument for their use because simple measures of habitat pattern are usually insufficient to predict the process of animal movement (Winfree et al. 2005).

Graph theory is well suited to patch-level analyses of fragmented landscapes (Minor & Urban 2007), but here we applied it to larger-scale ecological questions about a network of forest patches in the Triangle region of North Carolina (U.S.A.). With a focus on forest songbirds, we described landscape topology and made inferences about rates and paths of movement, vulnerability to disturbance, and conservation strategies. Our goals were to (1) characterize the connectivity of our study site in an ecologically meaningful way, and (2) provide a useful framework for thinking about habitat connectivity in a variety of landscapes. To this end we compared the North Carolina habitat network with 2 simulated networks with recognized properties.

Graph Theory

A graph or network is a set of nodes and edges, where nodes are the individual elements within the network and edges represent connectivity between nodes (Fig. 1). Edges may be binary (connected or not) or contain additional information about the level of connectivity (i.e., flux of individuals moving between nodes; Minor & Urban 2007). Networks surround us in both the natural and anthropogenic world. For example, societies are networks of people connected by family, friendship, and professional ties (Kossinets & Watts 2006), and landscapes can be viewed as a network of habitat patches connected by dispersing individuals (Bunn et al. 2000). Network topology is especially interesting because it is an emergent property that affects qualities such as spread of information and disease, vulnerability to disturbance, and stability (Albert & Barabasi 2002; Melian & Bascompte 2002; Gastner & Newman 2006).
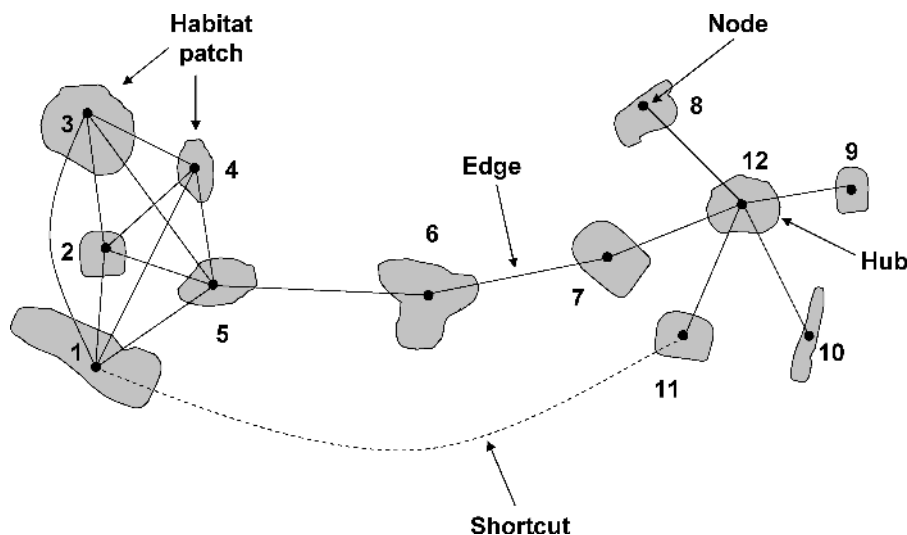
Figure 1. Illustration of some network terms. See examples column in Table 1 for an explanation of habitat patch numbers.

Graph Terminology

Node degree refers to the number of other nodes connected to a node; this is ecologically equivalent to the number of patches within a given distance or patch density (e.g., van Dorp & Opdam 1987). A *hub* is a node that is connected to many other nodes (a high-degree node). A *path* is a route through a graph from one node to another. If 2 nodes are not nearest neighbors, the path between them will contain one or more intermediary nodes. There are often many alternative paths between 2 nodes and perhaps even several shortest paths when alternative paths are the same length. *Shortcuts* may be inserted into a network so that 2 nodes that were previously separated by more than one node become directly linked to one another. Graph *diameter* is the longest of all the shortest paths between any 2 nodes in a network. *Characteristic path length* (CPL) is the average shortest path length between all pairs of nodes in the network. Graph *diameter* is indicative of speed of movement through a network, whereas CPL describes the density of the network. Both diameter and CPL are most revealing when considered relative to the number of nodes in a graph because the larger of 2 random graphs will tend to have longer paths.

Network *components* are sets of nodes connected to each other but separated from the rest of the landscape. Movement can occur between any 2 nodes in a component but cannot occur between nodes in different components. *Clustering* refers to the probability that 2 nearest neighbors of the same node are also mutual neighbors (a common analogy is that one's friends also tend to be friends with each other). A *compartmentalized* network consists of a series of highly connected nodes (i.e., hubs) that are not directly connected to each other, so high-degree nodes tend to have low-degree nodes as neighbors. *Compartmentalization* is the correlation between node degree and average degree of the node's neighbors. This metric is also called *connectivity corre-*

lation (Melian & Bascompte 2002). Table 1 provides a quick reference for these terms along with other graph terminology used in this paper.

Kinds of Networks

The topology of any given network may fall into one or more nonexclusive categories: planar, regular, random, or complex (which includes small-world and scale-free topology) (Fig. 2). Regular networks may be more of a heuristic concept than a naturally occurring phenomenon and will not be discussed further. Each other kind of network displays predictable characteristics with interesting ecological implications.

Planar networks (Fig. 2a) are two-dimensional—the edges do not cross each other. In other words, a node may only be connected directly to its geographical neighbors (i.e., adjacent nodes) and must connect to more distant nodes by passing through stepping-stone nodes. A real-world example of this kind of network is an urban street network with intersections as nodes and streets as edges. If 2 intersections are separated by more than 1 block, a traveler must pass through all intervening intersections to reach one from the other. Conversely, the air-transportation network is not planar in that one can board a plane and arrive at one's destination without passing through every city in between. Whether or not a habitat network is planar depends on the movement behavior of the focal organism. Birds resemble airplanes in that they can fly over or around intervening habitat patches. Nevertheless, a dispersing bird may not exhibit this behavior because it is searching for new territory and may examine each neighboring patch before moving away from its natal territory. For this reason planar networks may be suitable null models in some cases for landscape connectivity. Planar networks can have long path lengths (i.e., slow movement) because there are no shortcuts and they may or may not have a high clustering coefficient.

Table 1. Definitions, ecological relevance, and examples of graph terminology used in text.

Graph term	Definition	Ecological relevance	Examples
Characteristic path length (CPL)	A network attribute measuring the average shortest path length over the network	If CPL is short, all patches tend to be easily reachable. This implies a patchy population rather than a metapopulation or subpopulations.	
Clustering coefficient	A node attribute measuring the average fraction of the node's neighbors that are also neighbors with each other	Highly clustered nodes facilitate dispersal and spread of disturbances. They may be more resilient to patch removal due to many redundant pathways.	Nodes 1–5 (Fig. 1) are highly clustered, whereas nodes on the right side of the graph are not clustered.
Compartmentalization or connectivity correlation	A network attribute measuring the relationship between node degree and average node degree of its neighbors	High compartmentalization slows movement through a network and may isolate the potentially cascading effects of disturbance.	
Component	A set of nodes that are connected to each other	Patches in the same component are mutually reachable. There is no movement between different components, implying eventual genetic divergence.	Figure 1 shows a single graph component that contains all the nodes in the network.
Degree	A node attribute measuring the number of edges (or neighbors) adjoining a node	Low-degree patches may be vulnerable to extinction if neighboring patches are developed. High-degree patches may be population sources or sinks, depending on size and quality of patch.	Node 2 has a node degree of 4, whereas node 6 has a node degree of 2 (Fig. 1).
Diameter	A network attribute measuring the longest shortest path joining any two nodes in the network; there may be more than one	Short diameter implies fast movement through the network. This could be beneficial (dispersal is easy) or detrimental (spread of disease) for the focal organism.	Ignoring the shortcut, one diameter in Fig. 1 is from node 3 to 11 (along the path 3→5→6→7→12→11). There are multiple diameters in this network.
Path	A sequence of consecutive edges in a network joining any two nodes	Represents the possible routes an individual may take while traveling across the landscape.	In Fig. 1, there are multiple paths between nodes 3 and 1: some alternatives include 3→2→1 and 3→4→2→1. The shortest path is 3→1.

Random networks (Fig. 2b) consist of nodes with randomly placed connections. In these networks, a plot of node-degree distribution is often bell shaped, with most nodes having approximately the same number of edges (i.e., there are no hubs). They typically do not display clustering and may or may not be planar. In fact, the U.S. highway system has been described as random (Barabasi & Bonabeau 2003). In the past science theory treated all complex networks as random, although it has been recognized recently that most self-forming networks are more complex (e.g., scale free or small world) (Albert & Barabasi 2002; Proulx et al. 2005).

A scale-free network (Fig. 2c) is characterized by preferential attachment to certain nodes, so there are a few high-degree nodes (i.e., hubs), whereas the majority of nodes are low-degree nodes (Barabasi & Bonabeau 2003).
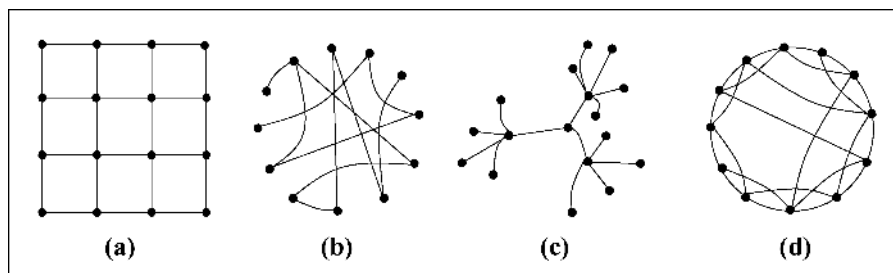

Figure 2. Kinds of networks: (a) planar, (b) random, (c) scale free, and (d) small world. Black dots are nodes; lines are edges.

The result is that the node degree distribution follows a continuously decreasing function. This is evident in the World Wide Web, in which a few highly connected pages (e.g., google.com) have millions of connections and are responsible for holding the entire Web together. In highly fragmented landscapes, conservation efforts may result in the formation of one or more landscape hubs such as national or state parks connected to many smaller and scattered habitat patches such as undeveloped lots and city parks. Scale-free networks are highly resistant to random disturbances but vulnerable to deliberate attacks on the hubs (Barabasi & Bonabeau 2003). In a scale-free habitat network, if a disease or invasive species were introduced into a random habitat patch it would probably not spread far or quickly because most patches have few connections. Nevertheless, if the introduction was made into a hub, the invasion would quickly spread throughout the network. Similarly, network connectivity would show little change if most of the smaller patches were removed but would quickly break apart if hubs were removed. Consequently, conservation and monitoring efforts would be best spent on hub patches.

A *small-world network* (Fig. 2d) is characterized by shortcuts that allow rapid and direct movement between distant nodes (Fig. 1), which results in a small diameter relative to the number of nodes (Watts & Strogatz 1998). In habitat networks, these shortcuts are likely to be the result of natural disturbances or human intervention. For example, hurricane-force winds may carry a bird much farther than it would fly on its own. Alternatively, people often intentionally or unknowingly transport organisms over long distances. Small-world networks are much more vulnerable to random disturbance than scale-free networks because the shortcuts make spreading through the network relatively quick and easy. Small-world networks also tend to have a high clustering coefficient compared with random graphs, so that a node's neighbors are often connected to each other (Watts & Strogatz 1998).

Habitat Networks

Important features in a habitat network include connectivity and resilience to disturbance (Peterson 2002; Opdam et al. 2003), both of which are affected by network topology. An intermediate level of connectivity is most desirable—too little and patches will be isolated from each other, too much and disease or other disturbance will spread rapidly (Jules et al. 2002). We use *resilience* to refer to the number of patches that can be removed without altering network connectivity. In the network literature, these 2 features are sometimes referred to as *network robustness* (i.e., robustness to the spread of a deleterious mutation and to the fragmentation of the network as an increasing number of nodes are deleted) (Albert et al. 2000; Sole & Montoya 2001; Dunne et al.

2002). Network robustness depends strongly on node-degree distribution; thus, networks with significant variance in node connectivity are most robust to random removal of nodes (Albert et al. 2000). A compartmentalized pattern of nodes may also increase overall network robustness by isolating deleterious effects of disturbances (Maslov & Sneppen 2002; Melian & Bascompte 2002). In addition, a highly compartmentalized network may confer a higher resistance to fragmentation if a fraction of the nodes is removed (Melian & Bascompte 2002), offering an alternative form of robustness. Compartmentalization is not a distinguishing feature of any of the types of networks described above, but it does require that node degree be somewhat heterogeneous. The scale-free network in Fig. 2 displays a fairly high level of compartmentalization.

From a conservation standpoint, the ideal habitat network might resemble a scale-free network with several large hubs connected to multiple smaller patches. This would create a landscape with heterogeneous node degree and resilience to patch removal. The hubs would be protected areas, such as parks or reserves, so that there would be no threat of removal (i.e., development). The hubs could be managed and/or monitored to prevent spread of invasive species, disease, or other disturbances. Widely scattering the hubs across space would create a compartmentalized landscape, isolating disturbances while allowing dispersal across the landscape.

Alternatively, clustering might also be desirable in habitat networks because highly clustered areas have many redundant connections and can probably lose more nodes without losing connectivity. Clustering is common in small-world networks but not in scale-free networks. Clustering may also confer stability to populations (Minor & Urban 2007)—yet another desirable attribute in a habitat network.

It is not generally known whether habitat networks tend to display the qualities described above or even what the topology of a typical habitat network might be. Recently, a network of bat-roosting trees was shown to have scale-free topology (Rhodes et al. 2006). Nevertheless, a single landscape can have very different connectivity characteristics when examined from the perspective of different organisms (Bunn et al. 2000). We examined landscape connectivity from the perspective of songbirds—a relatively mobile taxon. We measured the network characteristics described above and determined whether our study area resembled other naturally occurring networks by displaying scale-free or small-world topology or whether it fit the simpler null model of a planar network. Analyzing landscapes within this framework allows assessment of multiple aspects of connectivity and subsequently can lead to more informed conservation plans.
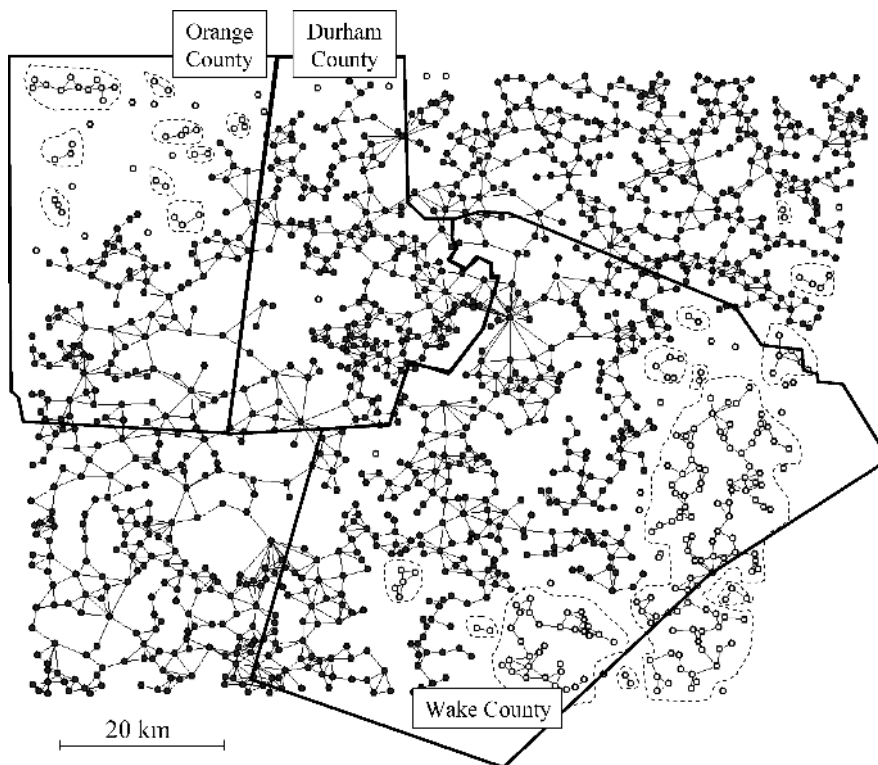
Figure 3. The Triangle habitat network in North Carolina. Nodes in the large component are black. Smaller components containing more than one node are outlined with dashed lines.

Methods

Study Area

Our study area comprised an entire Thematic Mapper image (~7700 km²) of the North Carolina Piedmont and included all of Orange, Wake, and Durham counties and much of Chatham, Johnston, Granville, and Vance counties (hereafter referred to as the Triangle; Fig. 3). Hardwood-forest pixels were identified and grouped with a 4-neighbor rule and patches >25 ha were retained for the analysis. The resulting map contained 1382 habitat patches. Due to computational limitations for data sets of this size, distance between patches was calculated from radius-corrected centroids rather than patch boundaries. The radius-corrected centroid (similar to radius of gyration [Keitt et al. 1997]) is the average distance from each cell in the patch to the centroid. This method adjusts centroid-to-centroid distance between patches by subtracting the radius of each patch to approximate distance between patch boundaries.

Creation of the Networks

Each habitat patch was represented by a node, which was located at the patch centroid. Edges were defined based on a typical dispersal distance for a small songbird (1500 m; Sutherland et al. 2000) so that patches closer than 1500 m were connected by an edge (Fig. 3).

Two simulated networks were also created for comparison in Pajek 1.12 (Batagelj & Mrvar 1996). Both networks had the same number of nodes (1382) and approximate mean node degree of the Triangle network. We generated the first, a random network, with the Erdos-Renyi random network algorithm, which creates random graphs that preserve only the number of nodes and edges of the real network. We generated the second, a scale-free network, with an algorithm modified from Pennock et al. (2002) in which a new node is added at each step of growth and edges are randomly attached according to a power law. We did not draw artificial networks because they do not have x,y coordinates assigned to their nodes and can be difficult to display visually.

Analyses

All network analyses were done with Pajek and were repeated for each network. First, we identified general patterns of connectivity by distinguishing separate components in each of the networks. Second, we measured the diagnostic network characteristics described above: diameter, CPL, node-degree distribution, clustering coefficient, and network compartmentalization. The goal was to compare our real-world habitat network to the artificial networks and subsequently to draw conclusions about the implications of our network topology for conservation.

Results

In the Triangle network, there were 55 components ranging in size from 1 to 1148 nodes (Table 2). The random

Table 2. Graph metrics used to assess connectivity for each network.

	Triangle network[a]	Random network[b]	Scale-free network[b]
Number of components	55	43	306
Size of largest component	1148	1337	1054
Diameter	60	14	12
Diameter/size of largest component	0.05	0.01	0.01
Characteristic path length	22.1	5.8	4.6
Clustering coefficient	0.08	0.0004	0.002
Connectivity correlation	0.47	0.00	0.48

[a]*Forest-habitat network in the Triangle region of North Carolina (U.S.A.).*
[b]*Simulated networks.*

and scale-free networks had 43 and 306 components, respectively. All 3 networks contained a single giant component and multiple smaller components, many of which consisted of only one patch.

The diameter and CPL were longer in the Triangle network than in either one of the simulated networks. In the Triangle network, the diameter was 60 nodes and the CPL was 22.1 nodes (Table 2). The diameter and CPL were 14 and 5.8 in the random network and 12 and 4.6 in the scale-free network. Because diameter is related to the size of the largest component, it may be more meaningful to examine the ratio of diameter to the size of the largest component (Watts & Strogatz 1998). This ratio was 0.05 for the Triangle and 0.01 for both the random and the scale-free networks.

Mean node degree was 3.7 in the Triangle network, and node-degree distribution was somewhat skewed to

the right (skewness = 1.0; Fig. 4). By design, mean node degree was similar in the random and the scale-free networks (3.6 and 3.7 respectively), but the random node-degree distribution was close to normal (skewness = 0.5), whereas the scale-free node-degree distribution had a skewness of 2.0.

The clustering coefficient was higher in the Triangle network than in either of the simulated networks by at least one order of magnitude (Table 2). The clustering coefficient was 0.08 in the Triangle network, 0.0004 in the random network, and 0.002 in the scale-free network. Finally, connectivity correlation (i.e., compartmentalization) values were positive for both the Triangle network and the scale-free network and zero for the random network (Table 2, Fig. 5).

Discussion

The Triangle Network

Even by our conservative standards (1500 m dispersal distance, only patches > 25 ha), the Triangle was very connected for forest songbirds. Eighty-three percent of patches (1148 out of 1382 patches) were contained in a single component that stretched from the southwest corner to the northeast corner of the map, indicating that it was possible for a bird to move across the entire landscape in small dispersal bouts.

This connectivity has some positive implications for conservation in the study area. Few patches were isolated so there should not be problems with permanent patch extinction or lack of gene flow. Depending on
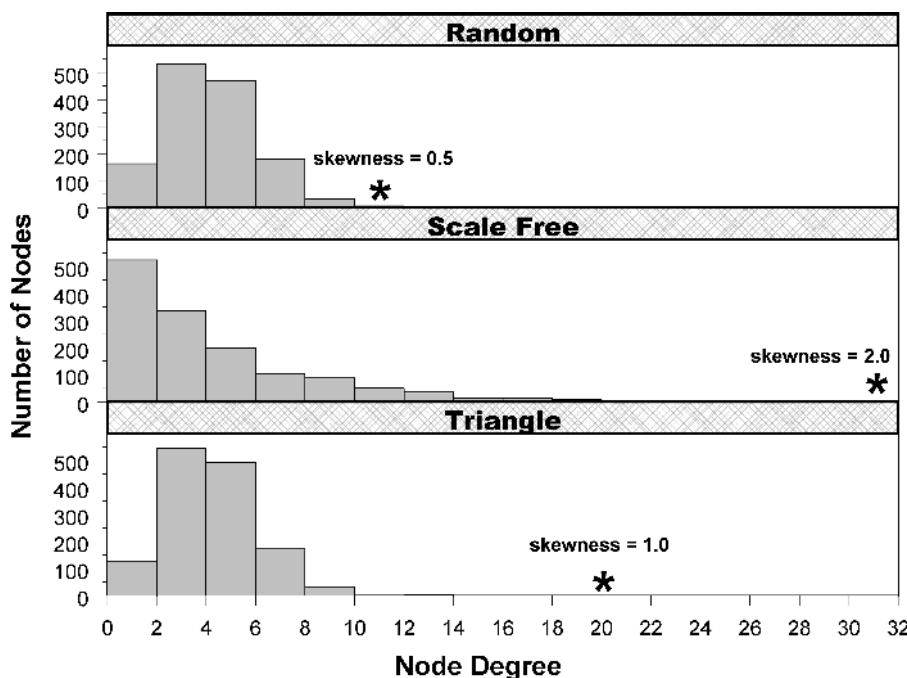

Figure 4. Node-degree distribution for the Triangle network (a forest habitat network) and the random and scale-free networks (simulated networks). The higher the node degree, the more neighbors connected to each node. An asterisk (∗) indicates maximum node degree for each network.
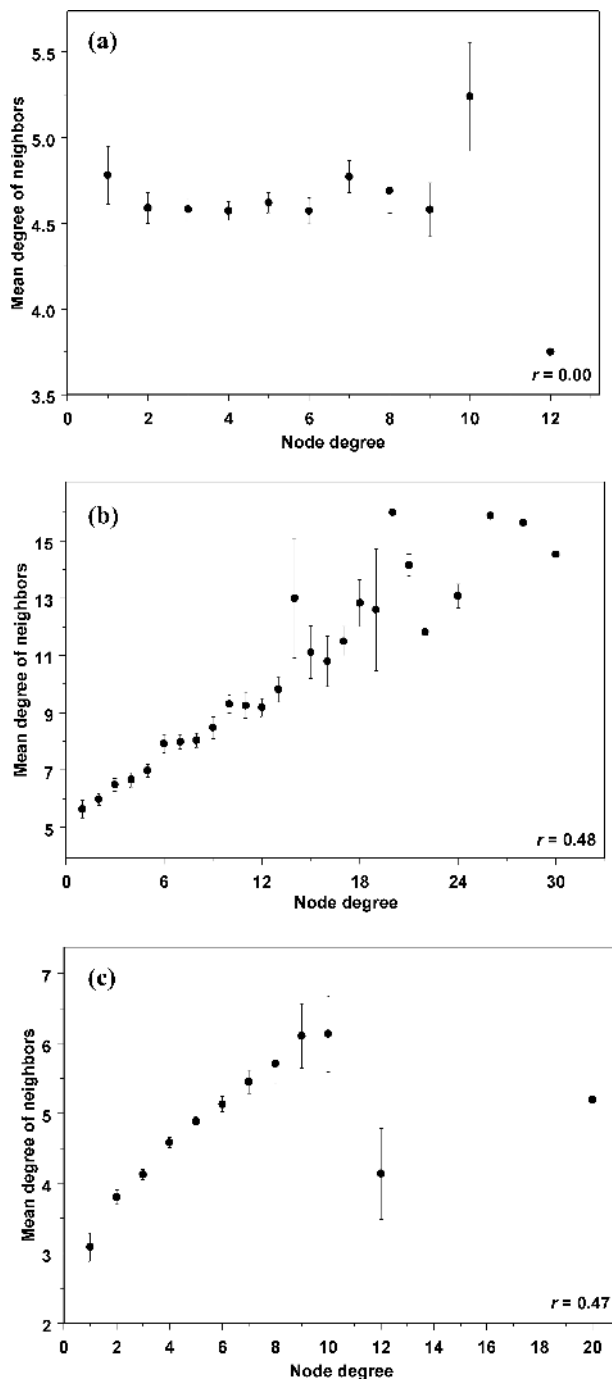
Figure 5. Connectivity correlation (i.e., compartmentalization) for (a) a random network, (b) a scale-free network, and (c) the habitat network in the Triangle region of North Carolina. Refer to Table 1 for an explanation of node degree.

network topology, however, this level of connectivity could also have negative consequences. For example, West Nile virus or Avian Flu could spread rapidly across the Triangle, leaving few (if any) patches unaffected. To better understand the likely rate of spread of any such disturbance, it was necessary to further characterize the topology of the Triangle network.

The Triangle network had a much larger diameter than either of the simulated networks. This implied there were few shortcuts, and rate of movement through the Triangle will be slow. In other words, the Triangle seemed to display the desirable characteristic of intermediate connectivity that would allow dispersal and gene flow while slowing the spread of disease or other disturbance. The large diameter of the Triangle network relative to both the random and scale-free networks suggested the possibility of planar network topology.

A lack of empirical data dictated that our description of movement be qualitative rather than quantitative, but we expected that bird dispersal and gene flow would occur at the same rate as spread of a bird-dispersed pathogen. Although this movement should be slow due to the relatively large diameter of the landscape, the landscape topology indicated that both birds and pathogens could cross the landscape given enough time. Nevertheless, the slow rate of pathogen spread may allow managers to intervene or, over longer time periods, it may allow bird species to adapt. Calculating the exact level of landscape connectivity that balances "desirable" movement (e.g., dispersal and gene flow) with "undesirable" movement (e.g., spread of pathogens or exotic species) is no small task. These ideas have been touched on, particularly in the context of spatially autocorrelated phenomena and reserve design (Hof & Flather 1996), but graph theory holds promise for additional insight or even an analytic solution to this problem.

Node-degree distribution was more skewed in the Triangle network than in the random network and less skewed than the scale-free network. The skewness showed a heterogeneous node degree, which is thought to provide resilience against node removal or disturbance. As long as hubs are protected from development, networks with heterogeneous node degree can sustain random loss of many nodes before connectivity is compromised (Urban & Keitt 2001; Barabasi & Bonabeau 2003). In addition, if management efforts are focused on hubs and disturbances are quickly identified and contained or eliminated, the network is not likely to succumb to disturbance.

The clustering coefficient was quite a bit higher in the Triangle than in either of the simulated networks, which indicated the presence of many redundant pathways across the landscape. Redundant or alternative pathways confer resilience to random patch removal because they help maintain connectivity through the landscape when routes are deleted. High clustering coefficients are characteristic of small-world networks and uncharacteristic of random networks. Planar and scale-free networks may or may not show clustering. The skewed node-degree distribution and long path lengths revealed that the Triangle network did not have small-world network
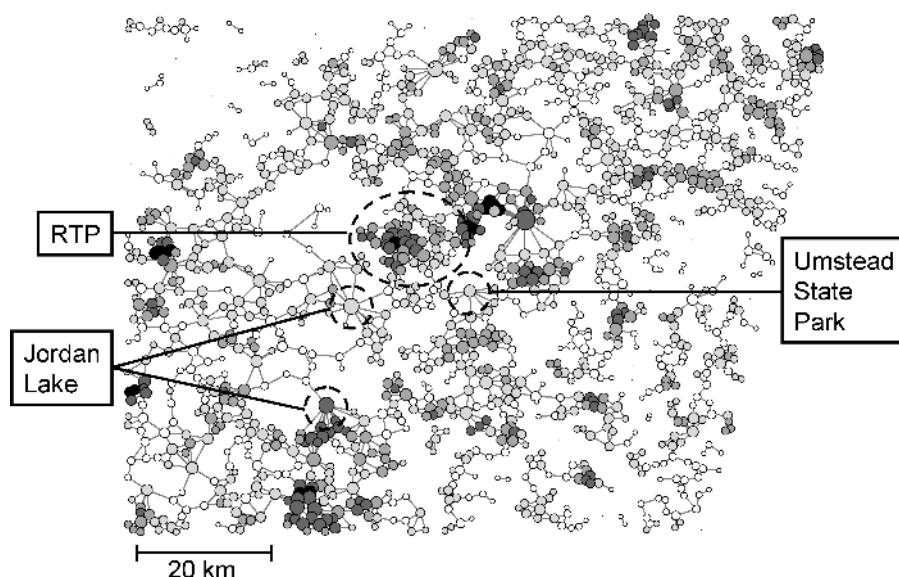
Figure 6. Node degree and clustering in the Triangle region of North Carolina (circles, habitat patches, size of which is proportional to node degree and intensity of shading is proportional to clustering; RTP, Research Triangle Park in Durham County).

topology, but it was not clear whether it resembled a planar or scale-free network.

The connectivity correlation in the Triangle network was positive, indicating the inverse of compartmentalization—hubs tend to be clustered next to each other on the landscape. High-degree nodes (larger circles) tended to be grouped together and separated from groups of low-degree nodes (smaller circles) (Fig. 6). These groups also tended to be in highly clustered areas (darker colors), resulting in many darkly colored large circles and pale-colored small circles. This occurred because there were large regions on the landscape with high forest cover and many patches (e.g., Chatham county—the southwestern portion of the map) and other regions with low forest cover and few patches (e.g., Wake and Johnston counties—the southeastern portion of the map). Conservation strategy in the Triangle might focus on these highly clustered regions. On one hand, they may be desirable areas for many forest interior species because of their high forest cover and densely connected patches, which facilitate dispersal. On the other hand, however, their highly interconnected nature makes them vulnerable to spread of disease. Furthermore, some might argue that because clustering confers resilience to patch removal, these regions can withstand development more than other regions in the Triangle and development would be better concentrated in these areas than in more vulnerable, less-clustered areas, where connectivity may be easily severed.

Figure 6 highlights some areas of conservation interest in the Triangle network. Research Triangle Park, a research park in southeastern Durham County, is a heavily forested area that is undergoing rapid development. It currently contains many hubs that are also highly clustered, perhaps making this a safe choice for additional well-planned development. Umstead State Park is located in Wake County adjacent to the international airport. The

park is a large (2201 ha) protected area and appears to be more compartmentalized than clustered, potentially conferring some protection from disturbances in the outside landscape. Finally, Jordan Lake State Recreation Area is a large (1585 ha) protected area contained mostly in Chatham County that is composed of several smaller forest patches, two of which appear to be large hubs. The southern hub is much more clustered than the northern one, and this variation may provide an interesting opportunity to test some of the concepts discussed in this paper, such as the effect of clustering on population stability or spread of disease.

For forest birds, the Triangle network appears to be somewhere between a planar network and a scale-free network, although network topology might change completely if a different organism were under consideration. For example, if the focal organism was Norway Maple (*Acer platanoides*), an exotic tree commonly used in residential landscaping, the average edge might be much shorter than for birds because seed dispersal is more limited. Nevertheless, the network would also contain many shortcuts radiating from plant nurseries to locations across the Triangle. This network would more closely resemble a small-world network and would display the small diameter and fast spread of disturbance characteristic of this topology.

Applications and Future Work with Graph Theory

Graph theory may be well suited for selecting habitat reserves (Opdam et al. 2006; Pascual-Hortal & Saura 2006; Minor & Urban 2007). Our results, however, do not suggest a formula for reserve design because each landscape and conservation problem is different. Despite these differences, the importance of considering landscape connectivity when designing reserves is becoming widely acknowledged (e.g., Briers 2002; Nikolakaki 2004;

Moilanen & Wintle 2007). Here, we presented some new tools for measuring aspects of connectivity that might be important to consider in conservation planning. At times a high level of connectivity is desirable (Jordan et al. 2003), whereas at others it can be detrimental (Condeso & Meentemeyer 2007). Difficult choices must sometimes be made, such as whether it is more important to have a network that is robust to spread of disturbance or one that maximizes population stability. If the former is preferred, a highly compartmentalized reserve might be appropriate. If the latter is preferred, a highly clustered reserve might be the better design. Graph theory cannot make these decisions, but it does provide tools that make these decisions easier.

The next step in developing graph-based conservation theory might be to use simulation models to identify the topological characteristics that are most important to network resilience and connectivity. For example, is a large diameter or network compartmentalization more likely to slow spread of a disturbance? What is the interaction between the two? Also of interest are the relative effects of clustering and node-degree heterogeneity on resilience to node removal, which can be tested with node removal simulations. It may be even more enlightening to relate empirical population trends to network topology across a variety of landscapes—data from the Breeding Bird Survey could be ideal for this kind of analysis. An increased understanding of the ecological consequences of network topology would allow managers and conservationists to make better decisions about land acquisition and reserve design and to make predictions about the consequences of a variety of anthropogenic or natural disturbances for a variety of species.

Acknowledgments

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