

From Graphs to Spatial Graphs

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Abstract

Graph theory is a powerful body of mathematical knowledge, based on simple concepts, in which structural units are depicted as nodes with relationships between them depicted as lines. The nodes may have qualitative and quantitative characteristics, and the edges may have properties such as weights and directions. Graph theory provides a flexible conceptual model that can clarify the relationship between structures and processes, including the mechanisms of configuration effects and compositional differences. Graph concepts apply to many ecological and evolutionary phenomena, including interspecific associations, spatial structure, dispersal in landscapes, and relationships within metapopulations and metacommunities. We review applications of graph theory in biology, emphasizing graphs with spatial contexts. We show how spatial graph properties can be used for description and comparison as well as to test specific hypotheses. We suggest that future applications should include explicit spatial elements for landscape studies of ecological, genetic and epidemiological phenomena.

Node: a dimensionless point, or vertex, shown as a dot in a diagram representing the graph

Graph: a mathematical object consisting of nodes and edges

Aspatial graph: graph in which the positions of the nodes and edges are not interpreted as locations in space

Network: graph in which nodes usually have weights, like abundance, and where edges represent connections like interactions or physical links, also with weights such as rates or capacity

Spatial graph: graph in which the nodes have locations and the edges' end points are defined by those locations

Edge: the line between nodes that represents the relationship between the nodes

Connectivity: a graph is highly connected if either edge connectedness or node connectedness is large

Directed graph (digraph): each edge has a direction, and so the set of nodes reachable from any node depends on the directions of the edges

INTRODUCTION: GRAPHS AND NONSPATIAL APPLICATIONS

Understanding interactions among biological entities from ecological and evolutionary perspectives is crucial given the current dynamic and disturbed global environment (Agrawal et al. 2007). To study these interactions, biological entities can be treated as nodes of a graph and their interactions as the links between the nodes, so that graph theory can be applied (Bang-Jensen & Gutin 2002, Harary 1969, Kolaczyk 2009, Lesne 2006, Mason & Verwoerd 2007, West 2001, Proulx et al. 2005). In ecology, individuals, populations, and habitats are the main objects of interest, with behavior and dispersal as the main processes that link them, maintaining interactions through metacommunity structures (Economo & Keitt 2008, Holyoak et al. 2005) and persistence through metapopulation dynamics (Rozenfeld et al. 2008). In evolution, population genetics, and epidemiology, organisms and Operational Taxonomic Units (taxa, traits, genes, etc.) are the objects, and the links are relationships of descent or similarity; whereas in bioinformatics, proteins and nucleic acids are the objects, and the links are the biochemical interactions (Nikoloski et al. 2008).

Graph theory was first used in biology to model organisms and interactions with aspatial graphs and networks (Aldous & Wilson 2000, Barabási & Oltvai 2004, Bascompte 2007, Brandes & Erlebach 2005, Cowperthwaite & Meyers 2007, Dale 1977, Dunne et al. 2002, Dyer 2007, Joppa et al. 2009, Lieberman et al. 2005, May 2006, Milo et al. 2002, Montoya et al. 2006, Newman et al. 2006, Ohtsuki et al. 2007, Sporns 2006, Strogatz 2001, Wardle 1998). Recently, appropriate software has allowed researchers to analyze the spatial context of data using spatial graphs (Bodin et al. 2006, Dyer 2009, Okabe et al. 2006, Saura & Torne 2009, Theobald 2006). This review is motivated by the importance of graph theory in ecology and evolution, and the realization that spatial structure should be included in graphs of these systems. We emphasize graphs in general, rather than networks in particular, although the two are closely related. We do not discuss functional applications of networks in detail, in part because there are already several very good reviews on that aspect of the topic (Bascompte & Stouffer 2009, Ings et al. 2009, Mason & Verwoerd 2007, Pascual & Dunne 2006, Urban et al. 2009). Instead, we focus on expanding the application of graph theory in biology with spatial graphs (Fall et al. 2007).

Graphs

In graph theory, a graph is a mathematical object consisting of two sets: nodes (points, also called vertices) and edges (lines, also called arcs) that represent connections between pairs of nodes (Harary 1969, West 2001; for a comprehensive list of key graph definitions, see Gross & Yellen 2006) (**Figure 1**). The most basic graph has only these two entities, each with no other characteristics, and it represents structure in the abstract so that the positions of the nodes have no meaning in a diagram that represents it. The edges must have nodes at their ends, so while nodes can have no edges, each edge needs two nodes. Nodes can be linked by edges based on several criteria (see sidebar, How to Join Nodes), which will affect the degree of connectivity.

The edges are usually symmetric, but they can have directions producing a digraph (directed graph). The edges may also have signs (positive or negative) or weights (quantitative magnitude). A network is usually a digraph in which each edge has direction and a value related to capacity (West 2001) or its own dynamics (Strogatz 2001). For example, trophic structure is frequently represented by a digraph with taxa as the nodes (e.g., grasses, hares, lynx, etc.) with directed edges indicating consumption.

Graph theory can quantify many functional and relational characteristics in ecology and evolution, including structural complexity, compositional diversity, dynamic complexity, and the

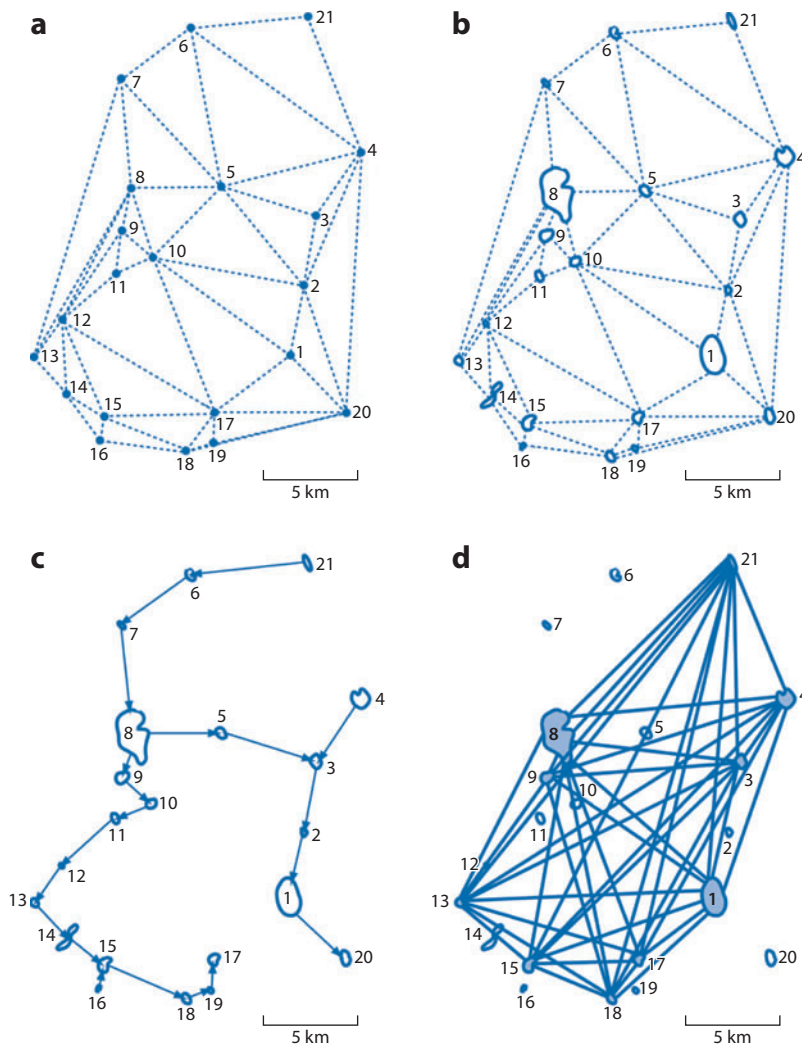


Figure 1

Graph types: (a) aspatial graph (nodes as dots and edges as dashed lines); (b) planar spatial graph (lakes as nodes); (c) directed spatial graph, where edges have direction (water flow); and (d) highly connected spatial graph for a sample of lakes in light blue. (Figure and lake numbers are based on the same system as Dale & Fortin 2005, their figure 2.23)

interactions of these characteristics (Strogatz 2001). Because a graph is about structure, there is a specialized vocabulary for its characteristics. This flexible conceptual model can elucidate the relationships between structure and function in ecological systems, including configuration effects and compositional differences.

In plant ecology, a graph can depict the relative frequencies of each species in the proximity of plants of other species in vegetation (Hopkins 1957). Here, the edges have signs, plus and minus, for positive and negative spatial associations (Dale 1977). The argument is that only plants that are close together interact strongly or respond to the same environment; therefore, associations determined by location can be related to the dynamic processes of dispersal, growth, and mortality.

HOW TO JOIN NODES

There are several algorithms for linking spatial point events as nodes to form a hierarchy of spatial graphs (Fortin & Dale 2005). Each is a subgraph of the next, with increasing expected node degrees (in brackets) through the series:

Mutually nearest neighbors (0.62),
 Nearest neighbors (1.4),
 Minimum spanning tree (2.0),
 Least diagonal neighbors (2.4),
 Gabriel graph (4.0),
 Delaunay triangulation (6.0),
 Complete graph ($n-1$), for n nodes).

Voronoi polygons (Okabe et al. 2000), also known as Dirichlet domains and Thiessen polygons, are the dual of the Delaunay triangulation: Each node in the triangulation graph represents a polygon, and an edge joins two such nodes when the corresponding polygons share a boundary.

In another kind of application, Bebbler et al. (2007) used a weighted planar graph to study nutrient transport in fungi. For investigating the association structures of communities (Dale 1985) and metacommunities (Economo & Keitt 2008), graph theory can be used to evaluate the roles of individual species and to quantify the communities' similarities and differences.

In evolutionary studies, the most familiar graph is the phylogenetic tree, which depicts evolution from an ancestral node by bifurcations at nodes representing evolutionary divergencies, producing a structure with a "leaf" (node of degree 1) at the end of each branch, representing a taxon. Different bases for phylogenetic trees (protein sequences, nuclear genes, mitochondrial sequences) can give rise to different trees. Penny et al. (1982) used graph theory to compare five different phylogenetic trees of 11 mammalian species based on five proteins: The trees were not identical, but they were significantly similar, "showing a relationship between them that is consistent with the theory of evolution" (Penny et al. 1982, p. 200). Other studies use phylogenetic networks, which allow cycles in the structures, reflecting the recombination of branches that once diverged or unresolved structures (Huson & Bryant 2006). The netted structure may also represent a summary of several possible phylogenetic trees (Hall 2008).

Graph theory is also applied in evolutionary trait quantification and in descriptions of speciation. There is a growing body of literature on evolution in the context of game theory, with the games taking place on an underlying graph (see, for example, Lieberman et al. 2005, Taylor et al. 2007, or Wolf & Arkin 2003 among many). Similarly, several studies apply graph theory to epidemiological questions (Keeling 2005, Meyers 2007, Shirley & Rushton 2005).

Planar graph: graph that can be drawn in two dimensions with no edges crossing, and each edge must be continuous but need not be straight

Tree: connected graph that contains no cycles

Cycle: a closed path that begins and ends at the same node, with no node or edge used twice

Subgraph: a subset of a graph's nodes, joined by a subset of edges (possibly "a module" if highly connected)

GRAPH PROPERTIES AND MEASURES

The nodes of a graph can be linked according to different criteria, reflecting the interactions between them (see sidebar, How to Join Nodes). In a dynamic context, a set of edges linking the same nodes can be modified by removing some edges between nodes, creating subgraphs (see also sidebar, How to Form Subgraphs) or graphs with different connectivity properties.

To compare graph structures, many metrics have been developed (Albert & Barabási 2002, Estrada & Bodin 2008, Freeman 1977, Fortin 1994, Oden et al. 1993, Pascual-Hortal & Saura 2006, Urban & Keitt 2001, Wasserman & Faust 1994) to characterize different graph properties

HOW TO FORM SUBGRAPHS

From a graph, one can obtain subgraphs, or modules, by removing edges (cut edges) between nodes. Modularity is the divisibility of a graph into highly connected subgraphs with few edges between them. This may reflect the substructure of any spatial graph. Newman (2006) provides an algorithm for dividing a univariate graph into such subgraphs based on the eigenvectors of a characteristic matrix for the graph. This process of dividing the graph into modules is much like spatially constrained clustering (Fortin & Dale 2005), where the most similar nodes are joined into clusters, but only if they are adjacent in space (as defined by some algorithm; see sidebar, How to Join Nodes).

The process of delimiting modularity is also closely related to the spatial partitioning of a spatial graph using graph boundary detection algorithms: Monmonier's algorithm (Monmonier 1973), and categorical-wombling for qualitative data and triangulation-wombling for quantitative data (Fortin 1994, Jacquez et al. 2000). Edges between nodes that are most different represent the steepest rates of change between adjacent locations and are therefore candidates to be part of a boundary between regions of the graph. Graphs can also be disconnected by removing a node (cut node).

based on nodes [e.g., number of edges per node, degree of node assortativeness (Newman 2002), node importance to overall connectivity, and centrality of a node], based on edges (e.g., shortest path, path diameter), or based on the entire graph [e.g., diameter of a graph, network centrality metrics (Wasserman & Faust 1994)]. Each of these metrics assume that all the nodes have been included, and the metrics are sensitive to missing nodes to different degrees depending of the characteristics being measured; this sensitivity is referred to as the sampling issue (Clauset et al. 2008, Corson 2010, Lee et al. 2005). This sampling issue creates serious limitations for the interpretation of graph metrics when there is no assurance that there is a complete census of the objects depicted in the graph. Further comparisons of these metrics have been conducted by B. Rayfield, M.J. Fortin, and A. Fall (submitted), who proposed a classification framework for them based on the component of connectivity quantified and the structural level (element, neighborhood, cluster, and network) to which they can be applied.

Two graphs having the same nodes can also be compared directly by a simple probabilistic calculation (van Langevelde et al. 1998). Consider two graphs, G_1 and G_2 , with the same n vertices, thus having $k = n(n-1)/2$ positions for edges. The two graphs' edges are E_1 and E_2 . Let c_a be the smaller number of edges in either of the graphs and let c_b be the larger: $c_a = \min(c_1 = |E_1|; c_2 = |E_2|)$; $c_b = \max(c_1 = |E_1|; c_2 = |E_2|)$. Let y be the number of edges common to the two, and z the total number of distinct edges in both:

$$y = |E_1 \cap E_2| \quad z = |E_1 \cup E_2|.$$

A simple measure of the similarity of the two graphs is $S = y/z$. S runs from 0 to 1.0.

The probability that the graphs share as many edges as they do is:

$$P_y = \sum_{j=y}^{c_a} \frac{\binom{c_a}{j} \binom{k-c_a}{c_b-j}}{\binom{k}{c_b}} = P_y = \sum_{j=y}^{c_a} \frac{\binom{c_1}{j} \binom{k-c_1}{c_2-j}}{\binom{k}{c_2}} = P_y = \sum_{j=y}^{c_a} \frac{\binom{c_2}{j} \binom{k-c_2}{c_1-j}}{\binom{k}{c_1}}.$$

As an example, consider the data for subtidal communities in the Deer Group Archipelago presented by Salomon et al. (2006). Compare the graph of the sites that are the most distant (sites 1, 2, 3, and 4 versus 9 and 10) and the graph of the sites that are most taxonomically different

Cut edge (bridge): a single edge, the removal of which disconnects the graph

Cut node (articulation point): a single node, the removal of which disconnects the graph

Centrality of a node: measure of the importance of a node's structural position in the shortest paths between other pairs of nodes

Path: sequence of nodes and edges where each node is attached to the next node in the sequence by an edge and each edge is joined to the next edge by a shared node; nodes or edges may not be used more than once in the same path

Diameter of a graph (path diameter): maximum distance between any two nodes, defined as the number of edges in the shortest path between them

Degree of a node:
number of edges
attached to a node

(1 versus 8 and 10; 2 versus 6; 3 versus 7 and 8; 5 versus 6; 6 versus 8; and 7 versus 10). The numbers are: $n = 10$, $k = 45$, $c_1 = c_2 = 8$, $y = 1$, and $z = 17$. The probability that the graphs share as many edges as they do is 0.993, but the probability that they share as few as they do is 0.021. The two graphs are not similar, but significantly dissimilar. This simple comparison shows that distance is not a good predictor of taxonomic dissimilarity.

Hypothesis Testing Based on Graphs

The application of graph theory is not limited to description and comparison, but plays a critical role in the testing of hypotheses, both by comparing observed graphs with the characteristics of graphs generated from theoretical models, and by using a hierarchical approach to hypothesis testing, often by randomization techniques.

An observed graph can be compared with various models of graph formation or growth (Albert & Barabási 2002, Erdős & Rényi 1960). One such theoretical model is a random graph, which begins with nodes only, and adds edges to randomly chosen pairs of nodes, not yet joined, independent of the positions of other existing edges (Erdős & Rényi 1960). Graphs that are scale free result from the preferential edge attachment that results in a few nodes (hubs) having many edges. The small world graphs are similar in having preferential attachment, but the most important feature is that this results in subgraphs with a high proportion of the possible edges (highly connected). A number of properties differ among these categories of graph (Albert & Barabási 2002), but as far as degrees of the nodes are concerned:

1. A random graph has a binomial or Poisson distribution of node degrees.
2. A scale-free graph has a power law distribution of node degrees.
3. A small world graph has an exponential distribution of node degrees.

The differences among the three models of graphs and their formation provide information about the processes that may have produced them, but also are important characteristics of the graph's structure. For example, how vulnerable is its function to the removal of any particular node (think about airline routes and snowstorms!)?

Graphs are often compared with models by comparing the distributions of node degrees, but this approach cannot detect all differences between graphs (**Figure 2**), and it may be necessary to examine the relationship between the degree of a node and the distribution of degrees of its first order neighbors (those immediately adjacent). For example, there is a big difference between two structures both with a few high-degree nodes and many low-degree nodes, depending on whether the high-degree nodes are directly connected to each other or whether paths between them depend on less connected nodes (**Figure 2**). A combination of graph metrics may be required to compare graphs effectively.



Figure 2

These two graphs have eight nodes, same number of edges, one closed path, and the same distribution of the node degrees (as indicated), but the two graphs have different numbers of edges in the cycles (3 versus 6) and different numbers of edges in the longest path (4 versus 5).

SPATIAL GRAPHS

There is a continuum from the truly aspatial graph, where the positions of its elements have no meaning and cannot be interpreted in a spatial context (**Figure 1a**), to fully and explicitly spatial graphs, in which the nodes have location (and possibly size, shape, etc.) and the edges have end locations and extension (and possibly length, width, shape, etc.) (**Figure 1b,c**). In a spatial graph, the nodes have locations and the edges have lengths, whether or not the location of the edge is explicit along its length. The edges can also have a magnitude or weight, forming a weighted spatial graph or spatial network.

As one example of the application of this approach, Dyer & Nason (2004) depicted the geographic clusters of cactus populations in a spatial graph. The two clusters they identified had significantly few connections between them, and graph theory provided the basis for calculating that significance probability. Insect pollination in *Prunus mahaleb* provides another example (Fortuna et al. 2008), here using the connectance and modularity of a bivariate spatial graph (the nodes are pollen donors or mother trees). Most mother trees had similar numbers of donor trees but modularity showed a significant population substructure of well-defined groups of mother trees and their shared pollen donors. The sidebar, How to Form Subgraphs, presents the similarity between evaluating modularity and delineating subgraphs.

Several algorithms can determine the inclusion of edges between nodes in a spatial graph (see sidebar, How to Join Nodes). A simple hierarchy of graphs can be based on a series of threshold distances: increasing the distance threshold produces a new graph by including more edges. Any evaluation of autocorrelation as a function of distance between samples therefore involves an implicit series of distance-defined spatial graphs (Fortin & Dale 2005, 2009). One ecological illustration is the scale of plant-pathogen association in *Silene latifolia* (Brooks 2006) determined by a bivariate spatial graph with nodes of diseased or healthy plants. The scale of connectivity in the graph was determined by a range of threshold distances using a hierarchical analysis. The mean node number and diameter of the largest connected subgraph showed that most patches were weakly connected but that there were few patches with high connectivity (Brooks 2006).

Spatial Graph Randomization

Because of the complexities of spatial graphs, and because of the possible ranges of hierarchical hypotheses (**Table 1**) that may be of interest, tests based on permutation and randomization, and in particular randomization with restrictions, are the most powerful techniques available (Croft et al. 2008, Fuller et al. 2008).

For example, consider a graph of 6 nodes and 5 undirected edges, with all the edges joining one node with all the others, forming a star. If the null hypothesis is that all 6 nodes are equivalent, we may wish to test whether the maximum observed node degree is unexpectedly high. We proceed to calculate the probability that, under complete randomness, 5 of 5 edges occur at a single node. There are 15 possible positions for undirected edges, and so that probability is $6 \text{ (nodes)} \times (5/15) \times (4/14) \times (3/13) \times (2/12) \times (1/11) = 0.002$. It is highly improbable that, if the nodes are equivalent, a single one would end up with so many edges. Changing the example to be a digraph, now suppose 4 of the 5 edges point outward from the high-degree node. If we ask whether this is highly improbable given the same null hypothesis, the answer is yes because its probability is even less than the 0.002 already calculated. If, however, the question is “Given the positions of the edges, what is the probability that 4 or more of 5 point outward?,” the answer is different. It is then $5 \times (1/2)^5 + 1 \times (1/2)^5 = 0.1875$, adding together the probabilities for 4 edges and for 5 pointing outward, and giving a probability that would not lead to rejecting the null hypothesis.

Connectance: the proportion of the positions where edges might occur that actually has an edge

Modularity: divisibility of a graph into highly connected subgraphs with few edges between them

Table 1 Typology of spatial graph comparisons

Basis of comparison	Graph characteristics	Methods
Graph structural properties		
	Same set of nodes all at the same locations	Compare nodes' degrees, node centrality, betweenness, etc.
	Same set of nodes but not at the same locations	Compare overlap of Voronoi areas of each node
	Set of nodes not identical	Compare samples of nodes
Graph functional properties		
Nodes with quantities (patch area): Area connected	Distance (Euclidean or resistance) between nodes	Compare node area connected based on distance thresholds
Edges with capacity: Degree of interaction between nodes	Amount of flow or energy or information between nodes	Compare weights of the edges between nodes, based on rate and directionality of flow or on genetic data
Nodes with quantities and edges with capacity	Source-sink relation of nodes	Compare properties of gravity models

In this example, we consider placing exactly the observed number of edges, 5, onto a set of 6 nodes. This is different from assigning an edge (yes or no) to each of 15 possible positions with a probability of 5/15. In the first case, each example created has the same number of edges. In the second case, the number of edges in a set of iterations will have a distribution. There is a finite probability that a graph thus created will have no edges at all [probability $(10/15)^{15} = 0.0023$] or that it will have edges in all 15 locations [probability $(5/15)^{15} \approx 10^{-7}$].

In this example, because the graph is small and simple, we can calculate probabilities directly, but in a real spatial graph, not only will the number of nodes and edges be large, but some edge positions may be forbidden by the physical arrangement of the units under study (e.g., physical barriers that completely prevent dispersal). For that reason, it is only possible to perform the probability calculations needed to evaluate null hypothesis, whether single or in a hierarchical series, using randomization or permutation techniques. In randomization methods, some of the characteristics remain fixed (e.g., the number of nodes and the number of edges), and others are allowed to vary (positions of the edges) in creating a reference set of graphs for comparison. Then, for some statistic of interest (e.g., the maximum node degree) the number of times the observed value is matched or exceeded in the reference set generated is used to evaluate the null hypothesis. In permutation tests, a similar process is followed, but usually the actual structure of the graph is kept constant throughout the development of the reference set, but the labels or weights associated with the nodes or edges are redistributed among the available objects. For example, in a bivariate spatial graph of diseased and healthy plants with the edges indicating Delaunay neighbors, the observed numbers of labels for diseased and healthy (N_D and N_H) can be redistributed 1,000 times and the proportion of healthy-to-healthy edges counted in each new graph. Redeploying the set numbers of the two labels among the graph's nodes is different from the process of creating new graphs of N_T nodes by labeling each node as diseased with probability N_D/N_T and as healthy with probability N_H/N_T ; in the permutation case, the numbers in each class are constant; in randomization, the probabilities are constant, but the actual numbers in each iteration vary.

Special Graphs with Spatial Applications

In a spatial context, there are some types of graphs that can be especially useful for studying specific properties of a system. Here we present a few of these special kinds of graphs.

Signed and directed graphs. The edges of a graph can have signs (+ or −), based on the relationship between the nodes, often indicated by a solid line for positive and a dashed line for negative; these are signed graphs. Edges can also have numerical weights, such as measures of similarity or dissimilarity (e.g., taxonomic distance between species). For asymmetric relationships, we can use graphs in which the edges have direction (a digraph). This distinction suggests one form of hierarchical analysis of digraphs, comparing the results with and without including the directions of the edges (see Fortuna et al. 2006).

Complete graph: all pairs of nodes are linked by an edge, and each node has the same maximum degree of $n-1$

Bipartite graph. A strictly bipartite graph has nodes in two subsets, with edges only between subsets, not within. Applications in ecology include depicting the relationship between pollinators (subset 1) and plants (subset 2) with edges joining each plant to its pollinators. A bipartite graph may also be applied to plants and their herbivores, or to other parts of food webs (Higashi et al. 1991). Plants, herbivores, and carnivores may form a tripartite graph of three levels, although omnivores may cause some blending of levels. In metabolic studies, strictly quadripartite graphs include examples with genes, enzymes, reactions, and metabolites being the four parts (Nikoloski et al. 2008).

Graph of graphs. A graph of graphs is a spatial graph where each node has its own associated graph representing some other structure (such as a food web). For example, Fortuna & Bascompte (2008) showed a graph of a metacommunity consisting of nodes, each of which contains a graph of multispecies interactions. Melián et al. (2005) compared two complete graphs of five nodes representing habitats, with edges' thickness depicting the number of shared trophic modules. The node representing each habitat has an associated tritrophic digraph showing a food chain with or without omnivory. As more spatial studies are completed, the number of examples of graphs of graphs will undoubtedly increase.

Special Graph Properties Useful to Test Ecological Hypotheses

There are several properties of graphs that can be used to test quite specific hypotheses about the structure of ecological systems. For example, the hypothesis that a very few species in a plant community have a disproportionate effect on the rest of the community could be tested by looking at the degrees of the nodes representing the species in a community graph (Dale 1977). In this section, we introduce a property that is of considerable importance in spatial aspects of community ecology.

Nestedness is usually an aspatial characteristic of a two-way data structure such as taxa and habitat islands, or hosts and parasites. Nestedness means that, for example, rare species tend to be found only at the richest sites, and species-poor sites tend to have only the most common species (**Figure 3**). In graph theory, nestedness is a nonspatial characteristic of a bipartite graph: Nodes of low degree are adjacent to high-degree nodes only, but high-degree nodes are joined to a full range from very low- to very high-degree nodes. Medan et al. (2007), working on the structure of mutualism, found that nestedness and the tendency of degree distributions to follow a truncated power law are closely linked. Examining the distributions of the degrees of the nodes of a graph is a common approach to characterizing some important properties of graphs and is frequently used to distinguish among possible models of graphs or networks, such as random versus scale-free graphs, as mentioned above.

As just described, nestedness has no spatial context, but given site compositions, each site can be assigned a nestedness score based on its concordance with all taxa and all sites. Those scores

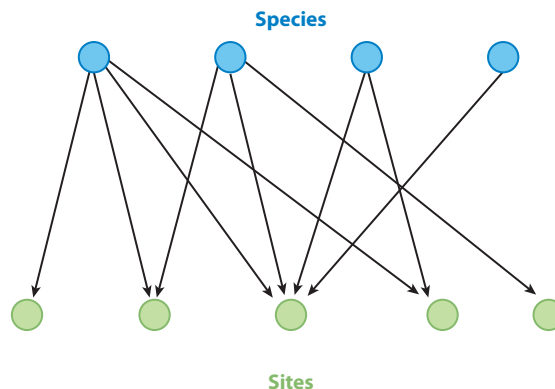


Figure 3

Bipartite nested digraph of species and sites. The edges show which species occur at each site.

are then a characteristic of the spatial structure. Because the nestedness graph is bipartite, one part (sites) can be a spatial graph with the other part (species) being nonspatial. Augmenting the initial bipartite graph, edges can be added within each part for different characteristics; for example, edges among species can depict phytosociological associations, taxonomic relatedness, or shared membership in functional groups. Inter-site edges can be based on the ease of dispersal or species complement similarity, or on the degree of relative nestedness of pairs of sites.

For a spatial graph with the nodes representing sites and the edges based on evaluations of the relationships among their species' complements, there are several possible criteria for edges to be included:

1. Compositional similarity between pairs of sites, using any of the following well-known indices of similarity (Legendre & Legendre 1998);
2. Similarity of species richness at the sites;
3. Similarity of the site nestedness scores;
4. A measure of mutual nestedness (relative nestedness of the two sites, compared to each other—not to all sites) of the species complements at the two sites;
5. Closest physical proximity or easiest dispersal between sites;
6. Greatest similarities of other site characteristics: area, range of habitat types, geological history, topographic profile, and so on.

These characteristics are mainly independent of each other and most combinations are possible.

Applying more than a single criterion for edges in nestedness graphs makes it possible to evaluate several hypotheses about the spatial distribution of species composition, including the comparison of the results of differential extinction and differential colonization. Spatial graphs in nestedness studies will be a useful addition to the application of spatial graphs in ecological and systematic studies, providing new insights into this phenomenon.

APPLICATIONS OF SPATIAL GRAPHS IN ECOLOGY AND EVOLUTION

Since their introduction more than a decade ago, several ecological and evolutionary studies have used spatial graphs to address specific issues. Here we present a few of these more recent research applications.

Ecological Applications

As in the study of food webs, where graph theory can evaluate the loss of nodes, thus simulating species extinction (Dunne et al. 2002), spatial graphs in habitat studies can quantify the effects of losing nodes or edges, mimicking the loss of habitat patches or of dispersal corridors (Urban & Keitt 2001). The application of graph theory in conservation ecology can be expanded to create a powerful synthesis by including spatial locations. The first ecological applications of spatial graphs approaches were in terrestrial systems (Keitt et al. 1997); they are now applied also in marine conservation (Treml et al. 2008).

Spatial graphs can be the conceptual basis for adding functional interrelations to physical connectedness and for adding physical structure to ecological function. The nodes' characteristics (e.g., habitat patches' size and shape) may be included in any analysis of a spatial graph, as may the characteristics of the edges (e.g., factors that enhance or impede dispersal; Urban et al. 2009). For example, the connectedness of three forest patches will be different for a ground beetle (low), for a bird (high), or for water (unidirectional). Studies of fragmentation affecting diversity often neglect spatial information and consider only properties of the individual patches. Directional graphs are needed to depict some ecological processes (Fagan 2002, Grant et al. 2007). For example, Fortuna et al. (2006) studied a spatial network of temporary ponds and the direction of amphibian movement during drought. The graph theoretical measures (degree distribution, correlation of directed and undirected degree, clustering coefficient) showed that the spatial structure is robust to drought, allowing movement from dry to flooded ponds, thus increasing the probability of reproduction in dry seasons. Similarly, in dendritic aquatic networks, directed graphs quantify the connectivity distance between specific node pairs (Fagan 2002, Grant et al. 2007, Schick & Lindley 2007) (**Figure 2c**). In these dendritic applications, directed graphs are most appropriate, and Côté et al. (2009) proposed a new *Dendritic Connectivity Index* to measure longitudinal (upstream-to-downstream) connectivity.

Clustering coefficient:

probability that any two neighbors of a given node are themselves joined by an edge

Animal Paths and Movement between Habitat Patches

The analysis of animal movement can focus either on the attractive or avoidance effects of each patch, or on the directionality and volume of movement between patches (Croft et al. 2008). Spatially explicit graph analyses of these two aspects can be examined separately or together using either gravity models or spatial graphs.

Gravity models. Transport models, of which gravity models are a class, look at the effects of distances, costs, and benefits of transportation corridors on the flow of goods. Gravity models assume that the strength of a link between two patches is proportional to the product of their weights divided by the square of the distance (Bossenbroek et al. 2001). Beaudry et al. (2008) used a gravity model to study the road mortality of freshwater turtles in moving between wetlands.

Landscape connectivity. In conservation studies for reserve network selection, one factor affecting movement between habitats through fragmented landscapes is connectivity (Chetkiewicz et al. 2006, Crooks & Sanjayan 2006, Gaston et al. 2008). Keitt et al. (1997) demonstrated that graph theory can characterize habitat connectivity for given animal dispersal abilities. They introduced landscape metrics, such as patch importance, which are computed for several Euclidean distance thresholds, corresponding to species' dispersal distances. Because of graph theory's power for visualizing and analyzing landscape connectivity, this approach has been applied frequently (O'Brien et al. 2006, Ricotta et al. 2000, Theobald 2006, Urban et al. 2009, Urban & Keitt 2001,

Dijkstra's algorithm:
finds the shortest path
between nodes

among many). Different connectivity algorithms (see sidebar, How to Join Nodes) have been used, mostly the minimum spanning tree (Urban & Keitt 2001) and Delaunay triangulation (Andersson & Bodin 2009, Bodin & Norberg 2007, Fall et al. 2007).

Least-cost paths. The permeability of the landscape matrix surrounding habitat patches is crucial to species movement, and so graph-theoretical approaches have incorporated landscape features by replacing Euclidean distance with an effective distance between patches (known as resistance or cost values; Chardon et al. 2003, O'Brien et al. 2006, Scotti et al. 2007, Spear et al. 2010, Urban et al. 2009) to determine the paths that offer the least resistance to movement. Estimates of resistance are based on expert opinion or on indirect measures of species occupancy of cover types. These estimates have much uncertainty, and the location of least-cost paths varies with the estimated relative cost values. Rayfield et al. (2010) produced a rigorous sensitivity analysis of this approach and found that the locations of least-cost paths were sensitive to the relative cost values assigned, as expected, and to the spatial configuration of the habitat patches. Least-cost paths have been incorporated into a formalized spatial theory by Fall et al. (2007). Habitat patch shape and size are explicitly accounted for by linking polygons (the graph nodes) boundary to boundary rather than centroid to centroid (**Figure 2b**). Applications of such spatial graphs include evaluating the design and effectiveness of natural reserves (Fall et al. 2007).

Corridors instead of line paths. Euclidean and least-cost edges identify single lines for movement between nodes, which may not reflect real animal movement in the landscape. Pinto & Keitt (2009) took Dijkstra's algorithm for finding the shortest path and modified it to find multiple paths with similar resistance costs to form corridors rather than a single line. Another approach is to evaluate all possible paths between any pair of nodes, as in electrical circuits (McRae & Beier 2007, McRae et al. 2008), so that more than the single easiest path is considered, with several parallel paths between two patches allowing greater flow. This leads to the concept of considering the sum of all possible paths between patches. Phillips et al. (2008) applied a network flow algorithm, based on directed graphs, to determine dispersal corridors of endemic plants, Cape Proteaceae, in South Africa.

Landscape connectivity measures. To measure landscape graph connectivity, area-based graph measures have been proposed to quantify the area connected at a given threshold distance (either Euclidean or least-cost): integral index of connectivity (Pascual-Hortal & Saura 2006), expected cluster size (O'Brien et al. 2006), *F* metric (Ferrari et al. 2007), and clumpiness coefficient (Estrada & Bodin 2008). Edge-based metrics have also been developed: subgraph statistics (Fortin 1994, Oden et al. 1993), least-cost path, route path diameter, dispersal likelihood, route redundancy, route vulnerability, and area connected (Pascual-Hortal & Saura 2006). Not all these measures have been evaluated sufficiently for a final assessment of their effectiveness to be provided here.

Evolutionary Applications of Spatial Graphs

In evolutionary studies, spatial graphs have been less frequently used. Bermudéz et al. (1999) used graph theory as a basis for the structural quantification and comparison of *Escherichia coli* transfer RNA. The graphs produced are not actually spatial graphs, because they are more schematic than dimensional, but they are certainly structural graphs.

Kelley & Ideker (2005) showed how the interpretation of genetic interaction data can be facilitated by information on protein-protein, protein-DNA, or metabolic networks to discover physical mechanisms for genetic effects. If physical mechanisms have spatial locations, such as on

or off membranes, the result could be spatial graphs, but currently this approach is nonspatial. Combining the spatial and the nonspatial graphs for molecular reactions could give rise to a graph of graphs. For example, different energetic reactions in a cell occur in different places—in the cytoplasm, on membranes, within organelles—and a graph could show spatial transport with the structural components as nodes of the graph and the molecular networks as reactions at each node. Evolutionary lineages could then be compared using the similarities among these graphs of graphs.

The application of circuit theory in ecology was described above, and in an evolutionary context, McRae & Beier (2007) used it to study gene flow in both mahogany trees and wolverines. They found that resistance distance (a measure incorporating multiple paths) gave much better predictions of gene flow at the continental scale than simple geographic distances or least-cost paths.

Landscape genetics. McFadden & Aydin (1996) used a hierarchical series of graphs based on threshold distances to analyze the small-scale genetic structure of a clonal soft coral on Tatoosh Island (Washington, U.S.A.). Join-counts of adjacent samples belonging to the same clone evaluated the autocorrelation structure of the population. Although there was significant within-clone autocorrelation at small distances (40 cm and less), there was no significant autocorrelation over larger distances (1 m to 40 m) among clones, suggesting that small-scale interclonal genetic structure has not developed in these populations due to isolation by distance.

To measure the connectivity of fisher (*Martes pennanti*) populations in Ontario, node centrality was correlated with the proportion of immigrants, suggesting that the central nodes were high quality habitat sources of emigrants to other sites (Garroway et al. 2008). Wang et al. (2008) combined genetic distance with landscape least-cost path analysis to determine the relationship of gene flow with landscape connectivity for a species of rat endemic to Taiwan.

Motifs in graphs are repeated subunits of the same structure. In food webs, some simple trophic modules emerge as unexpectedly common motifs and can be treated as the basic structural units of complex food webs (Bascompte & Stouffer 2009). Motifs are also common as modules in eukaryotic cells (Solé & Valverde 2006) and in bacteria (Wolf & Arkin 2003). In protein interaction networks, the study of their evolution using network motifs has yet to be proven as fruitful as it is interesting (Stouffer et al. 2007). The motif concept has been less often applied to spatial graphs, but the differences in common spatial motifs may be important, for example, if their structures enhance or impede flow-through. One clear example is that in digraphs of river systems, the confluence of two streams is an essential motif (Milo et al. 2002).

As in landscape ecology, there is great potential in spatial graphs for landscape genetics, in part based on multiple links between patches, for which there are at least three kinds of edges:

- A. Topological connectivity edges of a planar graph,
- B. Functional links of the shortest and least resistant corridors for dispersal, and
- C. Edges showing the highest levels of genetic similarity.

One question is then, What proportion of the genetic similarities in set C can be explained by the links of A and B? A first step in this kind of study would be to compare the spatial graphs with the three different sets of edges determined by the three different criteria. Randomization approaches will be helpful in assessing the relationships between the edges in the three categories.

Spatial epidemiology. Brooks et al. (2008) demonstrated how spatially explicit graphs with weighted edges can predict the spread of a disease (anther smut) through Fire Pink populations in Virginia. Similarly, Fortuna et al. (2009) applied graph theory to study disease spread and roosting patterns of the giant noctule bat in a park in Seville. The modularity and nestedness of the bipartite

Motif: repeating substructure of a graph or network

graph showed that both bats and trees occur as modules, with groups of bats sharing the same trees. Within each module, there is asymmetric use of the trees, producing a nested pattern, and this observed modularity may reduce the rate of disease spread through the population.

CONCLUDING REMARKS

There are very many phenomena in ecology, evolution, and systematics that can be depicted by a graph, but that is only the first step, and the full advantage of the approach is only realized when the graph theoretical properties of these structures are investigated. For spatial graphs in particular, the kinds of questions that can be answered include: What is the relationship between spatial habitat structure and gene flow? How does the connectivity of island archipelagos affect species survival? What is the role of intermittent streams in amphibian evolution? How does the pattern of migration routes affect the spread of disease? The application of spatial graph theory can be invaluable or even essential for answering such questions.

This brief overview of spatial graphs, and their application in ecology and evolution, stresses that there are many rich avenues of research to be explored, and much that is yet to be discovered, both in techniques and in applications.

In summary, the application of graph theory, in particular for spatial graphs, will prove to have exceptional value in future studies in ecology and evolution, as can be only outlined or hinted at in this review.

FUTURE ISSUES

1. There is a continuum from aspatial to spatial graphs as spatial information is implicitly or explicitly encoded in structure and the subsequent analyses performed. The sophisticated use of this continuum will reward more exploration.
2. Similarly, different edge weights and directionality can be used to test specific hypotheses about the interrelations between biological entities, based on undirected graphs, digraphs or bipartite graphs, and more detailed networks. A range of graph types will allow the evaluation of hierarchical hypotheses, providing insights otherwise not attainable.
3. In addition, quantification of several graph properties such as modularity, clustering, and nestedness can be used to determine and compare overall graph characteristics. This quantification should also prove useful in testing hypotheses by comparing observed graph characteristics with those of graphs resulting from models, and a hierarchical approach to this testing process should prove fruitful. Restricted randomization and permutation tests will be an important part of this exploration.

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An online log of corrections to *Annual Review of Ecology, Evolution, and Systematics* articles may be found at <http://ecolsys.annualreviews.org/errata.shtml>