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Mark R. T. Dale , Marie-Josée Fortin
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1 Ecological Processes and Network Systems

1.1 Introduction

This book is about ecological networks, and networks in ecology include almost anything that can be represented by a set of points joined in pairs by lines or “edges” (Newman 2010). By choosing the right network characteristics to investigate, network analysis allows us to develop concepts and to test hypotheses about ecological systems and processes that we could not express or investigate otherwise.

We will begin by suggesting how ecological questions and the quantitative analysis of the ecological networks are tied together. We cannot expect a simple one-to-one relationship between network structure or topological properties and network function and the related ecological processes, but we can provide some of the best matches. To illustrate the close connection between ecological questions and network analysis, Table 1.1 gives several examples of such questions and the network characteristics that might be used to help answer them.

We could cite many more examples of ecological questions for ecological systems for which the network approach seems like the best approach for finding answers, but the preceding list provides a good sample. It is obvious, too, that several network properties and measures appear frequently in the list, for example: degree, centrality, modularity (and clusters), and connectivity. These concepts and their measures will be described in detail in the chapters that follow. More characteristics and more in-depth analysis will be required to answer these queries for ecological networks, but the intention is to indicate where our analysis should start. Greater detail on the recommended quantitative analysis will be provided in the chapters that follow.

1.2 Network Analysis in Ecology

The phenomena and systems studied by ecologists span a huge range of spatial scales from molecules to ecosystems, but any objects we study have relationships with other objects in their system, thus creating the system’s structure. This structure can be treated as a network based on those relationships and then represented by a graph with the objects as the nodes (the points) and the relationships between them as the edges (the lines), as in Figure 1.9. Two important features of ecological networks are that (1) characteristics of the nodes and edges can be described qualitatively and quantitatively

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Table 1.1 Ecological questions for network analysis and key network properties to analyse them

The network terms may be unfamiliar, but they will be explained in later sections of the book (Chapters 2–5).

1. Can dispersal (field observation, genetic analysis) be predicted from the spatial structure (size, shape, interpatch distances) of habitat patches (vegetation type)?
   (Fall et al. 2007; Minor & Urban 2007; Urban et al. 2009)
   Node weights represent patch area, quality, or population density.
   Edge density and length or cost represent the difficulty of dispersal.

   What are the effects of dispersal and/or route topology on metapopulation persistence?
   (Shtileman & Stone 2015)
   Indegree (number of directed edges into the node) and outdegree (number of directed edges out from the node) indicate rates or ease of immigration and emigration.
   ➔ Figure 1.1
2. How can patterns of interindividual proximity or contact (frequency, order, relative timing) predict the spread of disease (transmission mode)?
   (Hamede et al. 2009; Marsh et al. 2011; Silk et al. 2017)
   Determine the temporal paths and distances to diseased or susceptible individuals.
   ➔ Figure 1.2
3. How do patterns of species interactions (positive or negative; weak or strong) change along environmental gradients?
   Are there consistent differences among positive versus negative interactions?
   (Pellissier et al. 2018)

   What are the association patterns among ecosystems?
   (Williams et al. 2014)
   Measure the similarities of the network structures between sites.
   Examine the node degree distribution and betweenness centrality as elements of association patterns.
   ➔ Figure 1.3
4. How can we best understand how interspecific interactions themselves interact (e.g. predation rate affects herbivore competition) and include these effects in the network?
   (Golubski & Abrams 2011)

   How important are multitaxa interactions in communities?
   (Connor et al. 2017; Layeghifard 2017)
   Modify network structure to allow edges to be secondary nodes.
   Create a correlation network for the community and determine the pattern of the strongest edges.
   ➔ Figure 1.4
5. What characteristics of trophic networks (compartmentalisation, number of levels, specialists, omnivores) are associated with system robustness and resilience?
   (Dunne et al. 2002)
   Measure connectivity, longest paths, and look for (low?) modularity.
   Are the trophic levels ambiguous or strict in a multilayer network structure?
   ➔ Figure 1.5
6. How does a multilayer temporal data structure affect the interactions of individuals and the analysis of those interactions?
   (Boccaletti et al. 2014; Kivelä et al. 2014)

   What factors can predict the spread of disease through a mobile population?
   (Craft et al. 2010; Godfrey 2013; Stella et al. 2018)
   Use distinctive edges to connect instances of the same individual in different times.

Table 1.1 (*cont.*)

Identify paths through spatial layers as time slices and the nodes as moving individuals; proximity (or contact) allows the formation of path elements within a layer.
➔ Figure 1.6

7. How are the different “layers” of interactions (plant-pollinator, pollinator-antagonist, plant-herbivore, etc.) integrated?
How to determine the key species or key interactions (frequencies, intensities) in such a complex multi-interaction network?
(De Domenico et al. 2015)
Study multilayer paths and subgraph structures. Investigate centrality measures of nodes as indicators of keystoneness
➔ Figure 1.7

8. How do phenological marker events (date of first leaf, first flower, . . .) observed at many sites (altitude, latitude, distances) over many years, flow through space and time, and how is the flow affected by changing climate?
(Schröder et al. 2014)
What processes mimic the spread of disease through a sessile population?
(Peyrard et al. 2006)
These require the study of network dynamics and flow, and the comparison of changing network characteristics.
Percolation is a network process determining the spreading of a state through adjacent nodes or through edges that share a node.
Percolation is a model of processes like disease or fire.
➔ Figure 1.8

9. How does metacommunity diversity depend on the arrangement of habitat patches?
(Chisholm et al. 2010)
Connectivity is a general measure of how difficult it is to break a network into pieces by removing nodes or edges; the more removals required indicates better connectivity.

10. How can we determine spatiotemporal hot-spots of disease in a population?
(Craft et al. 2010)
Multilayer cluster analysis examines networks of several spatially explicit layers, each representing a time slice, for clumps of disease that are close in space and in time.

11. How are species functional roles related to their pollination interactions?
(Coux et al. 2016)
Examine the nodes’ normalised degree (corrected for network size). Can nestedness indicate interaction asymmetry?

12. What are the similarities and key differences among the “versions” of an ecological network represented in a multilayer network?
(De Domenico et al. 2013; Kao & Porter 2017)
Examine multilayer clusters and multilayer centrality and compare the results with the same characteristics measured within layers.

13. How does the multilayer structure of a network affect robustness and resilience?
(Pilosof et al. 2017)
Focus on the interactions between layers as interlayer edges and compare with aggregated within layer characteristics.

14. What are the key species or key interactions in a multi-interaction (multilayer) network?
(De Domenico et al. 2015)
Measure multilayer centrality of nodes, also called versatility.
Compare with the within layer characteristics.

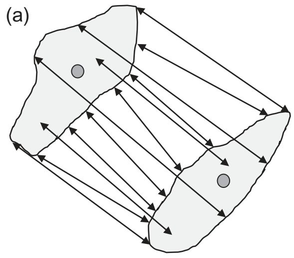

Figure 1.1 Dispersal between patches may follow (a) any one of several paths, not just the shortest or easiest (“least cost”), but (b) all of these can be summarised by a single path from centroid to centroid, a sum of all paths.

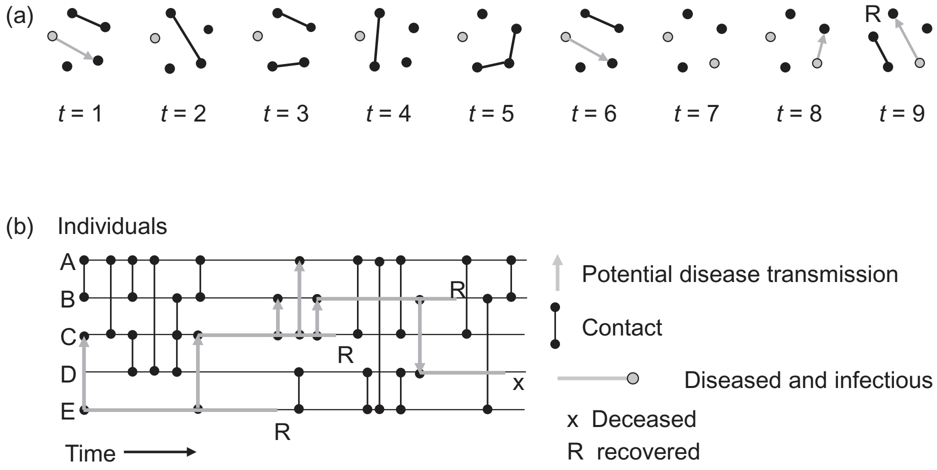

Figure 1.2 Temporal network of inter-individual contacts and disease transmission. Pairwise contacts recorded at time intervals: (a) explicit network format and (b) time-only graph format.

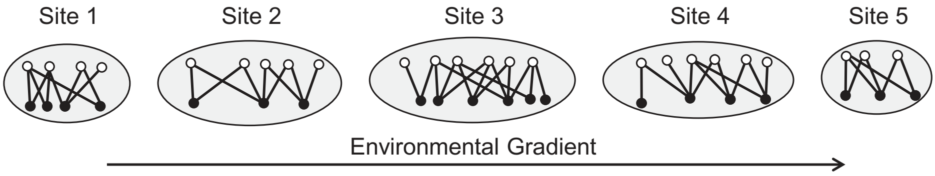

Figure 1.3 Locations as layers in a multilayer network. Pollination mutualisms in patches on an environmental gradient: bipartite graphs of plants (black dots) and pollinators (white dots) at five sites. Examine the structure for differences in degree (specialist vs. generalist), degree distributions, neighbour degree correlation, nestedness, and so on.

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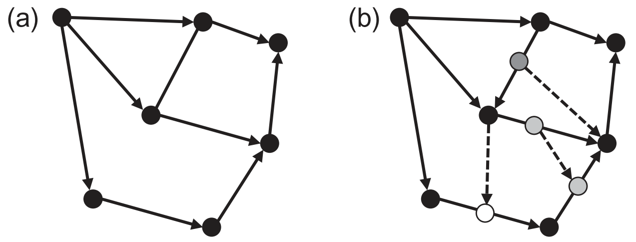

Figure 1.4 Interactions among interactions. Starting with 9 two-species directed interactions (edges) among 7 species (nodes) in (a), modifications can occur in which edges now act secondarily as nodes. The secondary interactions are shown by coloured edges. One modification is for a third node to affect another two-species interaction (black species node to blue interaction node). Another variant is for a two-species interaction to affect a third individual species (red interaction node to black species node). Last, one two-species interaction can affect another two-species interaction (green interaction node to green interaction node). (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

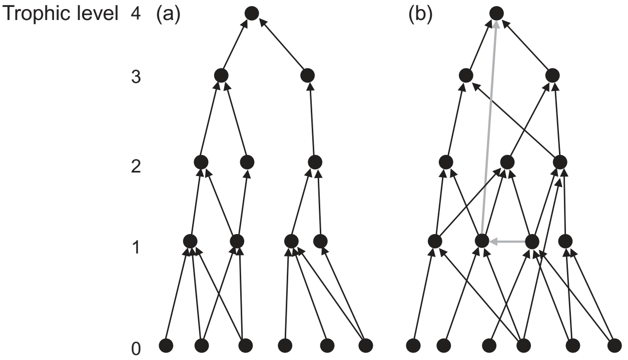

Figure 1.5 What trophic network characteristics are associated with robustness/resilience? (a) The first food web has a strict hierarchy: orderly, fewer links, modular. (b) The second is less orderly: exceptional links in grey, more links overall, not modular.

(Delmas et al. 2019) and (2) they and their characteristics tend to exhibit spatiotemporal dynamics. Therefore, many ecological questions or hypotheses related to network systems can be evaluated only through quantitative analysis (Dale & Fortin 2010; Dale 2017). Furthermore, the dynamics studied in network analysis can be divided between the dynamics ***of*** the network, changes in the structure or topology of the network itself, such as adding or deleting servers in the internet, and the dynamics ***on*** the network, involving changes in network characteristics within a stable structure, such as passing packets of information through the connections of the internet (Figure 1.10; Peterson et al. 2013).

Graphs (such as Figure 1.9) can be used to represent ecological networks. Graph theory treats networks formally as mathematical structures and an extensive body of

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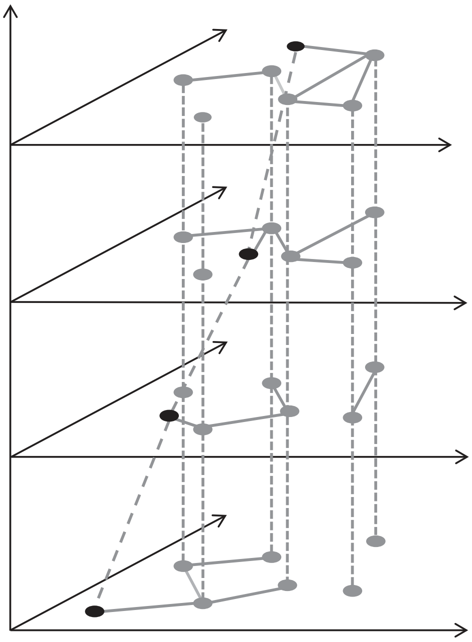

Figure 1.6 Multilayer network (possibly space and time). Layers show shared nodes and changing edges. Identity edges (dashed lines) join instances of the same node, even when it moves with respect to the others.

knowledge underlies the mathematics of network analysis (Harary 1969; Dehmer & Emmert-Strieb 2015). A broad range of applications of graph theory already exist in ecological research, as described in Dale (2017), but although this book on network analysis follows from that work, we will not assume the material as background knowledge. We will provide whatever graph theory is needed in context so that the presentation of the material on networks is complete. Like the graphs that represent them, networks can occur fully abstracted from the dimensional world of the original phenomena. On the other hand, graphs and networks may be embedded in one or several dimensions, such as time only, the spatial plane, or the four dimensions of spatiotemporal data. In addition to the useful aspects of graph theory, representing a network as a graph enhances our ability to visualise important aspects of the data, although that too can be challenging for very large networks (see Newman's 2010 for an example of the internet network of 2003). The future inevitably will see very large ecological networks, especially from spatiotemporal data sets, and we will have to follow the best approaches available to understand them, and effective visualisation should be a key element.

If graph theory is the main theoretical backbone of network analysis, statistical analysis is the analytical framework to quantify relationships between objects. The starting point for network analysis is complex and structured data, where complexity includes dependence, internal structuring, and heterogeneity over a range of scales (Barrat et al. 2008). Even with such a level of complexity, there is insight to be gained

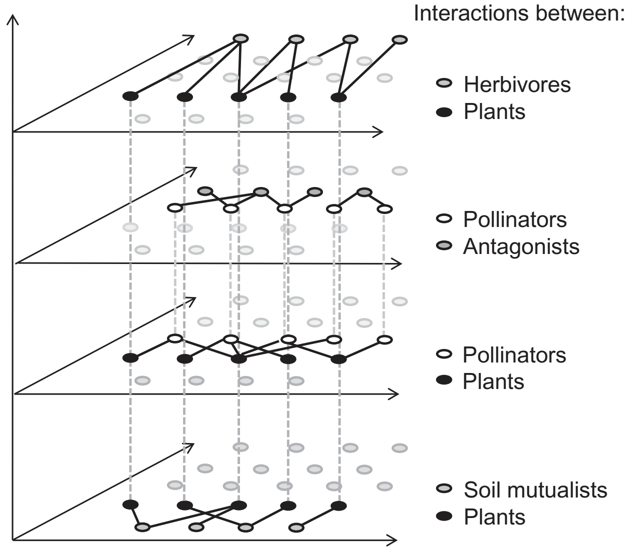

Figure 1.7 Multi-interaction network as layers. Layers show species nodes and edges for particular interactions: herbivory, pollinators and their antagonists, pollination mutualism, and soil-based mutualisms (e.g. mycorrhizae). Identity edges (dashed lines) join instances of the same node. (A black and white version of this figure will appear in some formats. For the colour version, please refer to the plate section.)

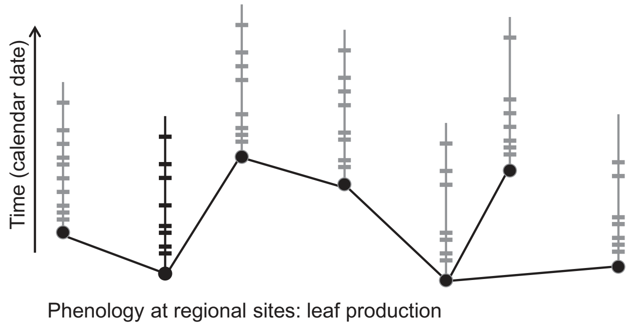

Figure 1.8 Phenology with permanent nodes and continuous time. Topological definition of permanent edges, minimum spanning tree (MST). One kind of event, leaf production indicated by bars (a single site indicated by black): examine for burstiness and synchrony of events, perhaps as function of absolute or relative locations (can be aspatial).

in evaluating network characteristics and their dynamics while comparing to those generated based on random dynamic graphs (Durrett 2007). Nowadays, given the availability of more complex data sets, novel approaches to statistical analysis and interpretation of networks are needed (Crane 2018). Such analytical developments can help to assess networks' emergent properties, their degree of self-organisation, and their potential to evolve through time given their resilience or redundancy.

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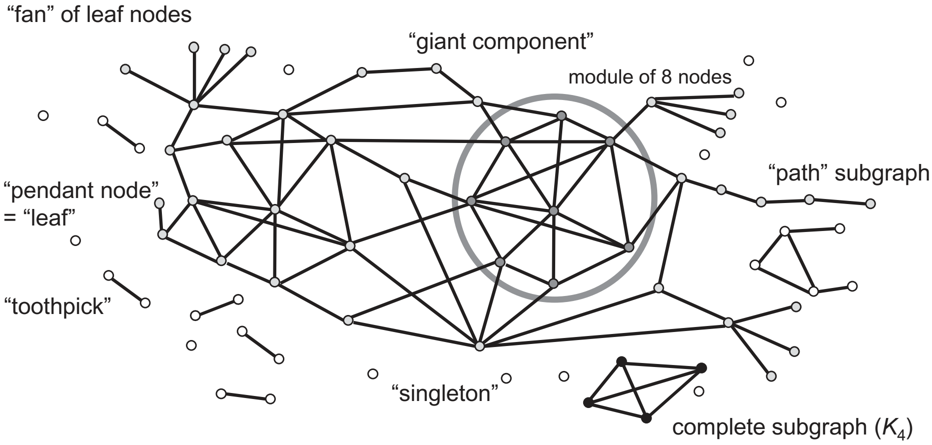

Figure 1.9 A graph of a network. Dots represent the basic units of the ecological system and are the nodes of the network graph. Lines represent relationships between units in the network and are the edges of the network graph. The various structural elements of the network graph are labelled.

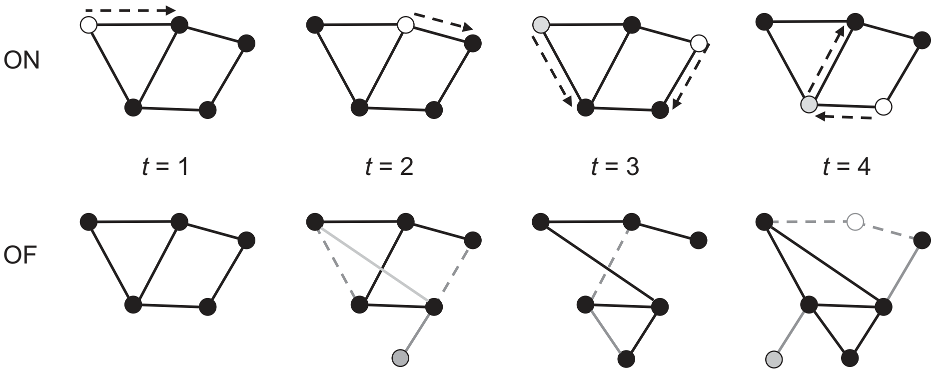

Figure 1.10 Dynamics ***on*** a network: Weights or labels may change but nodes and edges neither lost nor gained, e.g., node state passed on to neighbour (or not) as indicated. The topological structure of the network is maintained. Dynamics ***of*** a network: the configuration changes as nodes and edges are lost (white nodes and dashed grey edges) or gained (grey) through time.

The current popular view of network analysis is based mostly on social and information networks which tend to be sparse in their edge density and which may focus on hubs and centrality and power laws and small worlds (but see Newman 2010; Estrada 2012). Yet, most ecological networks (trophic networks, correlation networks, and phenology networks, among many) are different in their topological structure, edge density, and function. By choosing the right characteristics to investigate, network analysis allows us to develop concepts and to test hypotheses that we could not express otherwise. In this book, we highlight how many of the most important

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ecological questions can be answered only in the context of networks and network analysis. The questions, and the kinds of network analysis that apply, can be organised in several categories based on the dimensionality, what the edges represent, the interaction between structure and function, and the overall structuring of the network itself. After presenting a few examples, we will discuss several categories into which our examples may fall.

Current popular ideas that are based on social and information networks are correct about one feature shared by those examples and most ecological networks: they are both *complex*! The title of a well-cited book is *The Structure of Complex Networks*, (Estrada 2012). Ecology studies natural systems that are both complex and dynamic, consisting of organisms and their environment. The organisms interact with each other and there are reciprocal effects of the organisms on the environment and the environment on the organisms. The environment changes through space and time, and the organisms change and evolve, responding to the environment and the interactions they experience, giving rise to a complex adaptive system (Levin 1998). The spatiotemporal structure of an ecological network system and the key roles of the many interactions within it, together mean that many ecological questions cannot be answered or even formulated (!) without reference to the networks in which they all occur.

Later in the book (Chapter 2, Section 2.4), we will provide a discussion of the measurement of the complexity of the network itself, but the first complexity faced in network ecology is collecting and compiling the data on which the network is to be based. We will not provide a detailed guide to this part of the endeavour; it will vary greatly with purpose and system, but we need to acknowledge the importance and difficulties faced at this stage of a study. As just one example, consider the efforts of Timóteo et al. (2018) to investigate seed dispersal interactions in four habitats in Gorongosa National Park, Mozambique. They collected 1399 fecal samples from 98 animal species and found 12,159 undamaged seeds of 94 plant species from 29 dispersers. Each observed plant–disperser combination creates an edge between the two nodes representing them in the network, and edges occur only between the two groups, not within. That data provided 508 network edges; other observations gave 85 edges and camera traps provided 15 more. The network was treated as a multilayer structure, with each habitat being treated as a layer. The full network consists of 608 edges between 32 animal species and 101 plant species; the proportion of edge positions that are realised or the *connectance* is 608/3232, or about 20%. Each node and each edge have a quantitative value which is a numerical count or an interaction frequency of the seeds of a plant species associated with the activities of a particular seed disperser. The authors' own evaluation of the effectiveness of sampling was that the effort found 77% of the disperser species and 44% of the plant species. Primates were the most frequent dispersers and the study indicated the importance of the most versatile dispersers, those that were effective across habitats, the network layers. The network characteristic that was the most important in the study was found to be modularity: the existence of subsets of species that interact in and across different layers.

Incomplete data are inevitable in field studies, and there are some useful methods available to help understand the effects of the incompleteness (de Aguiar et al. 2019).

For example, Timóteo et al. (2018) used a non-parametric method for mark-and-recapture data to estimate the numbers of species missed (see Chao 1987). We will have more detailed comments on sampling and missing data in Chapter 5, Section 5.2 on constructing and reconstructing networks.

In addition to your own data, many data sets for network ecology are now archived and available online. For these, while the initial data collection has been accomplished, comparative or summary research requires compiling the data from more than one source or and ensuring that the comparisons are based on the same "currency" and have appropriate spatial and temporal scales. The archived data sets will also be subject to missing data, and the preceding comments about dealing with missing observations applies equally here.

1.3 Classification of Network Questions

There are many ways in which ecological networks and the questions that pertain to them can be classified. An obvious characteristic is how the network is embedded in dimensionality: time only, space only (two dimensions or three), space-and-time, not at all. Many ecological networks are about interactions between organisms, and so the interactions included can be the basis for categories of networks, as well as the relationship between network structure and the functioning of the system it represents. Similar to the criterion of dimensions, networks can also be classified by the criterion of their own structural framework, such as monolayer versus multilayer. These suggested criteria for classifying ecological networks and their associated questions are not exclusive, and so a single example may fall into several categories.

1.3.1 Criterion 1: Structure-and-Function

For many ecological networks, the truly important questions are those concerning the relationship between the structure and the function of the network (clearly these may also be about interactions or about relationships in the dimensions of space and time). How does network topology affect the dynamics of its system? How does the dynamics of and on a network affect its structure? These are the basic "structure–function" questions that can be expressed in many different ways and applied to many different systems: "pattern" versus "process," "topology" versus "dynamics," and so on. Another version of the same questions concerns what we can learn or deduce about network function from its structure, and what additional information is required. This is the inspiration for the use of various kinds of subgraphs (e.g. motifs and graphlets) to investigate the relationship between structure and function (e.g. Pržulj 2007; Sarajlić et al. 2016).

Familiar structure–function questions include: What structural characteristics indicate a keystone species in a food web (Lupatini et al. 2014)? What characteristics make established communities more resistant to invasion (Lurgi et al. 2014)? What trophic network characteristics contribute to robustness or resilience (Dunne et al.