

Chapter 28

Network Framework for Forest Ecology and Management



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Abstract Applications of network science to forest ecology and management are rapidly being adopted as important conceptualization and quantitative tools. This chapter highlights the potential of network analysis to help forest managers develop strategies that foster forest resilience in our changing environment. We describe how networks have been used to represent different types of associations within forest ecosystems by providing examples of species interaction networks, spatial and spatiotemporal networks, and social and social-ecological networks. We then review basic measures used to describe their topology and explain their relevance to different management situations. We conclude by presenting the challenges and potential opportunities for an effective integration of network analysis with forest ecology and management.

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28.1 Introduction

Understanding how human activities modify the structure and function of forest ecosystems is a central challenge for achieving sustainable forest management. To this end, in recent decades, forest scientists have started applying network theory to ecosystem management (Dale & Fortin, 2010, 2021; Fall et al., 2007; Hamilton et al., 2019; Martin & Eadie, 1999; Rayfield et al., 2011). Network theory provides a novel framework for designing effective strategies intended to maintain forest functions while conserving biodiversity (Aquilué et al., 2020; D'Aloia et al., 2019; Messier et al., 2019; Ruppert et al., 2016).

Forest ecosystems are composed of highly heterogeneous elements—organisms to forest stands—that interact through ecological processes over a wide range of temporal, spatial, and organizational scales (Filotas et al., 2014). Specifically, network theory can be used to model forest ecosystems as ensembles of connected elements (Aquilué et al., 2020; Mina et al., 2021; Ruppert et al., 2016). Examples include food webs linking species across several trophic levels (Eveleigh et al., 2007), nest webs linking species across microhabitat structures such as tree cavities (Martin et al., 2004), isolated forest fragments connected by wind or animal dispersed seeds (Aquilué et al., 2020), and social organizations engaged in a common management effort (Fischer & Jasny, 2017). Network analysis focuses on describing the topology of interactions linking elements together and can establish a relationship between this network topology and forest functions for management purposes (Ruppert et al., 2016). In particular, network analysis can be used to quantify the alteration of forest

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functions resulting from human-mediated and natural disturbances that directly or indirectly modify the ecological components of forest ecosystems, including their interactions and spatial setting (Aquilué et al., 2020).

A network is a simplified representation of a system based on connections—links—among its component elements—nodes. A food web, for example, is a network representing the trophic interactions among an ecosystem's constituent species (Pimm et al., 1991). Each element in a network is represented by a node, also called a vertex, which may be connected to other nodes by links, also called edges, representing potential or realized interactions between two elements. Nodes are defined by one or more attributes and their connections to other nodes. Links may be unidirectional or bidirectional and may be weighted to express the strength of an interaction. In a food web, for instance, nodes represent species, and links represent predator–prey interactions among species (Ings et al., 2009). A unidirectional link would represent a predator species feeding on a prey, whereas a bidirectional link could represent a mutual interaction or dependency between two species. Moreover, a node could be characterized by its species' abundance, and a link could be weighted to represent a predator's relative preference for a given prey.

Network science originates from graph theory, a fundamental topic in the field of discrete mathematics that can be traced to the work of Euler in the eighteenth century (Newman, 2003). Nowadays, the study of networks is pervasive across all fields of science, including molecular biology, neuroscience, linguistics, and epidemiology (Newman, 2003; Strogatz, 2001; Turnbull et al., 2018). The World Wide Web, social media networks, and global plane travel networks are only a few of many examples of networks present in our everyday life.

Network science continues to develop tools that characterize the topology of networks, a concept referring to the architecture of nodes and links. Moreover, it studies the possible relationships between a network topology and the ability of the corresponding system to function and adapt to disturbances. Generally, the strength of network science is the universality of tools available for studying disparate systems, varying widely in their nature and scale (Albert & Barabási, 2002). For example, the structure of a network can provide information about its vulnerability or adaptability to the loss or addition of nodes and links or the efficiency with which resources and information are propagated within the network (Fig. 28.1; Barabási & Albert, 1999; Watts & Strogatz, 1998). Will a food web collapse following the extinction of a given species? Is an epidemic more likely to spread within a population if a given demographic group is infected? Can consensus within a community divided over an environmental issue be improved by creating new communication channels? These and other important basic and applied science questions can be answered using the methods from network science.

The application of network theory to ecology and evolutionary biology has seen a remarkable development over the past 20 years (Dale & Fortin, 2010; Kool et al., 2013; Proulx et al., 2005). Well-studied ecological networks include protein and gene networks (Jeong et al., 2001; Vidal et al., 2011), pollination networks (Bascompte et al., 2003; Memmott et al., 2004), food webs (Dunne et al., 2002a), nest webs (Martin et al., 2004), and habitat conservation networks (Urban & Keitt, 2001).

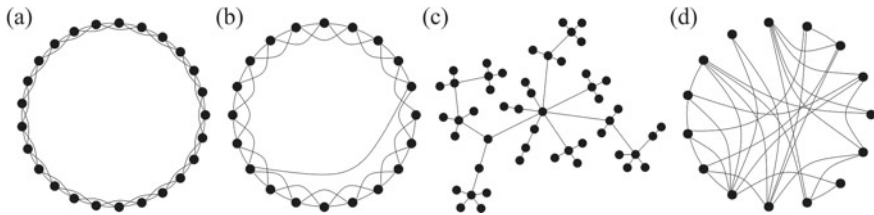


Fig. 28.1 Different topologies of undirected networks. **a** Regular network in which all nodes have the same number of connections; **b** a *small-world* network constructed by rewiring a few nodes of a regular network, thereby reducing its diameter and making each node easily accessible from any other nodes of the network (Watts & Strogatz, 1998); **c** a *scale-free* network created by adding connections to nodes with a probability that increases with their number of connections such that well-connected nodes become even more connected. Such networks are more vulnerable to disturbances that target hubs (Barabási & Albert, 1999). **d** Random networks in which the number of connections is randomly assigned to each node

Specific applications of network science to forest ecology and management are more recent, but this approach is rapidly gaining adoption as an important conceptualization and quantitative tool. For example, networks are used to understand how locally interacting entities drive forest ecosystem functions and inform management strategies that more directly integrate cross-scale interactions (Messier et al., 2019).

This chapter highlights the potential of network thinking to address key issues of cross-scale interactions in forest ecology and management. First, we describe how networks have been used to represent different types of associations within forest ecosystems by reviewing examples of species interaction networks, spatial and spatiotemporal networks, and social and social-ecological networks. We explain how nodes and links can be defined and synthesize the particular features that characterize each network type. Then, we review basic measures used to quantify the structure of networks and explain their relevance to different management situations. We conclude by presenting the challenges and potential opportunities for an effective integration of network analysis with forest ecology and management. The network framework may prove invaluable in helping forest managers to better anticipate and adapt to global change.

28.2 Representing Forests with Networks

As with any network, the identification of nodes and links varies with the questions of interest and with respect to how the system under study can be decomposed into sets of distinct and interacting components (Table 28.1). Here, we describe different network categories employed in forest ecology and management. These categories differ in the nature of nodes, including individual species, forest stands, and governance institutions. Consequently, the type and scale of interaction among nodes also vary between these categories.

Table 28.1 Different categories of networks employed in forest ecology and management. For each category, examples of nodes, links, and relevant references are provided

Network category	Nodes	Links	Examples
<i>Species interaction networks</i>			
Plant–herbivore or plant–frugivore	Tree or fruiting plant species and herbivore or frugivore species	Feeding interactions	<ul style="list-style-type: none"> • Variations in the level of specialization of plant–frugivore networks across a fragmented rainforest landscape (Chama et al., 2013) • Effect of species life-history traits on the structure of plant–leafminer networks in dry open woodlands (Cagnolo et al., 2011)
Pollination	Flower plant species and pollinating species	Pollination visits	<ul style="list-style-type: none"> • Variations in the structure of bumblebee pollination networks across an agricultural landscape of fragmented north–temperate mixed forests (Gómez-Martínez et al., 2020) • Temporal changes in the networks of pollen-carrying moth and pine species in a boreal forest (Devoto et al., 2011)

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Table 28.1 (continued)

Network category	Nodes	Links	Examples
Host–parasitoids	Host species and parasitoid species; sometimes including the lower (plant–herbivore) and/or higher (parasitoid–hyperparasitoid) trophic levels	Parasitoid attacks	<ul style="list-style-type: none"> Changes in the structure of plant–host–parasitoid networks in a rainforest following the introduction of an alien caterpillar as an agricultural biological agent (Henneman & Memmott, 2001) Changes in the structure of the balsam fir–host–parasitoid–hyperparasitoid network during a spruce budworm outbreak in a temperate forest (Eveleigh et al., 2007)
Nest webs	Cavity-bearing tree species and vertebrate cavity users: excavators and nonexcavators	Vertebrate–tree cavities interactions (excavation, breeding, roosting)	<ul style="list-style-type: none"> Robustness of nest webs to selective logging in a subtropical forest (Ruggera et al., 2016) Changes in nest webs structure during an outbreak of mountain pine beetle in a temperate forest (Cockle & Martin, 2015)
Fungal network	All tree genotypes within a sampling plot Plant and lichen species and their associated fungal species	A common fungal genotype shared between two different tree genotypes Symbiotic plant/lichen–fungi interactions	<ul style="list-style-type: none"> Change in the mycorrhizal networks formed between <i>Rhizophoron</i> and Douglas fir 25 years after selective logging (Van Dorp et al., 2020) Chagnon et al. (2012) used a network approach to demonstrate that a community of plants linked by arbuscular mycorrhizal fungi in a hemiboreal forest was highly nested and modular

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Table 28.1 (continued)

Network category	Nodes	Links	Examples
<i>Spatial graphs</i>			
Habitat-patch networks	Patches of habitat for a given wildlife species or group of species	Potential direct animal movement between habitat patches	<ul style="list-style-type: none"> • Trade-offs between timber harvesting and maintaining habitat connectivity for woodland caribou in a boreal forest (Ruppert et al., 2016) • Identification of key nodes and links for providing the connectivity of a network of protected forest areas fragmented by highways (Gurrutxaga et al., 2011)
Forest insect pests	Forest patches	Potential insect dispersal between forest patches	<ul style="list-style-type: none"> • de la Fuente et al. (2018) used a network-based model to predict the areas and speed of the natural spread of the pine wood nematode and suggested which forest stands should be harvested to stop the spread of the nematode by breaking the connectivity between the remaining forest stands • Wildemeersch et al. (2019) used a network-of-networks approach to simulate the outbreak dynamics of the geometrid moth in birch forests and the European spruce bark beetle

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Table 28.1 (continued)

Network category	Nodes	Links	Examples
Forest-stand networks	Forest patches	Potential seed dispersal between forest fragments	<ul style="list-style-type: none"> • Identification of key forest patches in which to focus conservation or restoration efforts to maintain a high functional response diversity across a fragmented agricultural landscape (Craven et al., 2016) • Trade-offs between different forest landscape management scenarios for maintaining the connectivity of a fragmented forest network subjected to potential disturbances, i.e., drought, pest outbreak, timber harvesting (Aquilué et al., 2020)
Spatiotemporal networks	Habitat patches at different moments in time	Potential animal movement between habitat patches at different moments that can be direct or indirect (through patches that were gained or lost)	<ul style="list-style-type: none"> • Martensen et al. (2017) proposed a new spatiotemporal connectivity algorithm that accounts for both spatial and temporal search windows to estimate how dynamic landscapes of forested patches can maintain animal movements • Huang et al. (2020) used the spatiotemporal connectivity algorithm to determine how future dynamic landscapes of forested patches combined with climate changes will maintain predators' range shifts while also accounting for their preys' range shifts under the same conditions

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Table 28.1 (continued)

Network category	Nodes	Links	Examples
<i>Social networks</i>			
Organizational networks	Actors or group of actors engaged in a common environmental or management issue	Associations between organizations, e.g., sharing information, working with each other	<ul style="list-style-type: none"> • Adaptation capacity of a network of organizations (local government agencies, nonprofit groups, federal agencies, universities, etc.) that share concerns about increasing wildfire risk (Fischer & Jasny, 2017) • Knoot and Rickenbach (2014) used a social network to examine the collaborative capacity of public- and private-sector foresters to help facilitate a landscape-scale multifunctional management of privately owned forests
<i>Social-ecological networks</i>			
Forest governance networks	Social nodes: organizations involved in the management of forests Ecological nodes: bounded forest lands managed by one or more organizations	Ecological links: ecological processes linking ecological nodes, e.g., seed dispersal, forest fire Social links: interorganizational interactions	<ul style="list-style-type: none"> • Likelihood of social organizations coordinating their management of wildfire risks on the basis of the spatial configuration of their risk interdependence (Hamilton et al., 2019) • Governance of small forests in an agricultural landscape among actors having varying forest uses and kinship relations (Bodin & Tengö, 2012)

28.2.1 Species Interaction Networks

In networks of species interactions, a single species sometimes provides a natural unit for denoting a node. This is the case, for example, in pollination networks (Devoto et al., 2011; Vázquez et al., 2009), host–parasitoid networks (Memmott et al., 1994), and nest webs (Martin & Eadie, 1999; Martin et al., 2004). However, other systems may highlight the need for different aggregation units, such as species playing a common function or a guild of species with a similar trophic position (Dunne et al., 2002a). Links between nodes denote potential or realized interspecific interactions that may or may not involve biomass transfer, including antagonistic (e.g., plant–herbivore and host–parasitoid networks), mutualistic (e.g., pollination networks), symbiotic (e.g., mycorrhizal network), and commensal associations (e.g., nest webs) (Delmas et al., 2019).

Networks of interspecific interactions may be unipartite, meaning that any two nodes may interact, or they may be ordered over multiple hierarchical levels where only nodes in different levels can interact (Fig. 28.2a; Delmas et al., 2019). In nest webs, which represent the relationships among tree species and cavity-nesting vertebrates, links connect tree species to one or more *nidic* levels (Martin & Eadie, 1999; Martin et al., 2004; Ruggera et al., 2016). These levels consist of cavities that originate either from tree decay or from animal excavators, and also include obligate cavity users, which cannot excavate a cavity and thus depend entirely on existing cavities for nesting (Cockle et al., 2019; Martin et al., 2004). Host–parasitoid networks may also encompass lower (plant–herbivore) and higher (parasitoid–hyperparasitoid) trophic levels (Eveleigh et al., 2007). On the other hand, some networks focus on representing the associations between two levels only, such as pollinator–plant (Devoto et al., 2011; Gómez-Martínez et al., 2020), plant–herbivore (Cagnolo et al., 2011), and plant–frugivore networks (Chama et al., 2013). Such networks, termed bipartite networks (Fig. 28.2b), can also be used to represent nest webs (Cockle & Martin, 2015; Ruggera et al., 2016) and host–parasitoid networks over narrower scales of interspecific organization (Tylianakis et al., 2007; Van Veen et al., 2008).

Ecological networks can also be used to represent mycorrhizal associations between plant roots and fungi, or relationships among algae, fungi, and sometimes bacteria within lichen (Southworth et al., 2005). Two different approaches may be

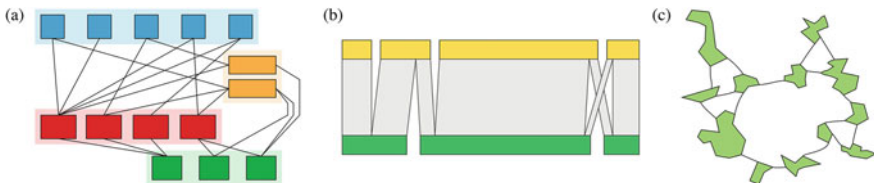


Fig. 28.2 Different categories of network in forest ecology. **a** Network extending over multiple hierarchical levels, e.g., food webs and nest webs; **b** a bipartite network where nodes are separated into two levels, e.g., pollinators (*yellow*) and plants (*green*); **c** an undirected spatial network where links denote potential least-cost movement between patches of habitat (*green polygons*)

adopted (Table 28.1). The first studies the bipartite network formed by the symbiotic interactions between the hosts (plant or algae species) and their associated (endophytic or endolichenic) fungi (Chagnon et al., 2012; Toju et al., 2015). The second adopts a phytocentric perspective where tree boles in a sampling plot correspond to nodes and links. This represents the pairwise connection of trees through the same fungal genet (Beiler et al., 2010, 2015; Simard, 2009; Van Dorp et al., 2020).

28.2.2 Spatial and Spatiotemporal Networks of Forest Ecosystems

In spatial and spatiotemporal networks, nodes are conceptualized as spatially localized units of contiguous area, such as forest stands that, when aggregated, compose forested landscapes (Table 28.1; Bunn et al., 2000; Fall et al., 2007; Pelletier et al., 2017; Urban & Keitt, 2001). We can distinguish between habitat-patch networks and forest-stand networks. The former stresses the relationship between habitat patches for wildlife connectivity—usually for the conservation of a specific species or group of species of concern (Gurrutxaga et al., 2011; James et al., 2005; Ruppert et al., 2016) or to predict the spread of undesirable species (de la Fuente et al., 2018; Ferrari et al., 2014; Wildemeersch et al., 2019)—whereas the latter focuses on the connectivity of tree communities (Aquilué et al., 2020; Craven et al., 2016; Saura et al., 2011). Nodes are defined either by the GPS locations of organisms, bird nests (Melles et al., 2012), and territories/home ranges or by delineated forested patches according to specific criteria, e.g., stand age, structure, and species composition (Aquilué et al., 2020). Nodes can be characterized by spatial, e.g., area, shape, edge/area ratio, and nonspatial attributes, e.g., species diversity, habitat quality.

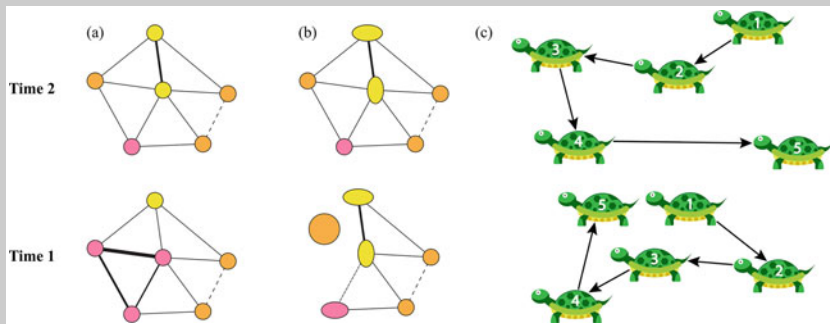
In spatial networks, links between nodes denote the movement of animals or plant seeds, either as a potential or a relative measure (Bunn et al., 2000; Fall et al., 2007; Urban & Keitt, 2001). Links can be determined according to species' dispersal abilities and behavioral responses to the intervening landscape that facilitates or impedes organism movement (i.e., functional connectivity; Rayfield et al., 2010). Thus, links can be represented by the Euclidean distances between patches or as a function of movement cost. In this case, the distance between patches is weighted by the additional difficulty for a given species to disperse through the given matrix cover types (James et al., 2005). Consequently, spatial networks provide a framework to evaluate the functional connectivity of a landscape for a particular species or tree community, transcending simpler structural connectivity assessments.

Unlike species interaction networks where links are mostly directed, thereby expressing relationships between consumers and their resource, spatial networks can have both directed and nondirected links and do not form a hierarchical structure (Fig. 28.2c). In habitat networks, links are nondirected because an animal's ability to move between two habitat patches can, theoretically, be assumed to be the same in

both directions (Ruppert et al., 2016). On the other hand, in forest-stand networks, a node contains a community of tree species that differ in their seed dispersal ability (Tamme et al., 2014). Thus, the flux of seeds dispersing from one stand to another is not equivalent in both directions, leading to directed links between nodes (Aquilué et al., 2020).

Box 28.1 Spatiotemporal networks

In spatiotemporal networks, habitat patches or forest stands are dynamic, where: **a** the weights of both nodes and links change through time but not the network topology, **b** as in **a** although the topology changes through time, and **c** the nodes and links are given by organisms' movements.



To determine the degree of functional connectivity of a habitat network and how it changes through time, one can quantify connectivity at specific times as a series of static snapshots. However, the degree of connectivity can be affected by the temporal dimension of the forest dynamics relative to the species' longevity (Zeigler & Fagan, 2014). For this reason, one cannot treat habitat networks at different times as independent static snapshots. To address the effects of such transient dynamics of habitat patches, Martensen et al. (2017) proposed a novel spatiotemporal connectivity algorithm to quantify the sequential spatial overlaps of habitat patches that are available to account for a temporal window matching species life history. Martensen et al. (2017) showed—by considering explicitly in their algorithm the spatiotemporal dimension of habitat patches and species dispersal abilities—that the transient use of habitat patches can favor a higher degree of connectivity compared with static spatial connectivity values.

Spatiotemporal networks express relationships within and between spatial networks at different times (Huang et al., 2020; Martensen et al., 2017). They add the temporal dimension to spatial networks by integrating the dynamic nature of forest stands and habitat patches (Box 28.1). They capture the fact that ecological processes and disturbances affect the persistence and attributes of spatial nodes. For

example, tree communities within forest stands and habitat patches undergo successional changes and are modified by natural disturbances (e.g., fire, insect outbreak, drought, and windthrow) and human activities (e.g., harvesting and land-use change). If network nodes change too quickly or are destroyed, organisms may not have time to reach other suitable nodes. Therefore, nodes and links that were present in a static spatial network could be absent in a spatiotemporal network. Moreover, this framework allows for the representation of indirect links between patches to indicate that an organism has moved through an intermediate stepping-stone patch that has been gained or lost during the two different time observations.

28.2.3 Social and Social-Ecological Networks

Nodes in social networks represent any social entity, from single individuals, e.g., a forest owner or user, to collectives of individuals, e.g., forest management organizations, forest-based communities, or groups of stakeholders sharing similar interests or belonging to the same governance sectors (Guerrero et al., 2020). Links between these social entities can correspond to both formal and informal relationships and represent (1) flows (e.g., information, resources, and money), (2) social relations (e.g., employee of, neighbor of) and interactions (e.g., work with, share information to), and (3) similarities (e.g., same location, same attitude) (Borgatti et al., 2009; Guerrero et al., 2020). Nodes may be characterized by demographic and social/cultural attributes (e.g., age and occupation), attitudes and behaviors toward a management or conservation issue, and features of the corresponding organization, e.g., size, mission, and governance level. Links can be weighted according to the strength of the relationship or frequency of the interaction (Guerrero et al., 2020).

Depending on the social system under study and the types of relationships considered, links in social networks can be directed, e.g., sharing information to, or undirected, e.g., same conservation goal as another entity, and form different hierarchical structures ranging from one to multiple levels of governance that include several jurisdictions and geographic areas (Fischer, 2018; Guerrero et al., 2020). Moreover, social networks are shaped by processes specific to human and social interactions, such as *homophily*, *intentionality*, and *reciprocity* (Fischer & Jasny, 2017; Guerrero et al., 2020; Knoop & Rickenbach, 2014). Homophily refers to the tendency to be connected to people having similar values and goals, whereas intentionality refers to the conscious choice to associate (or not) with someone else, and reciprocity is the tendency for mutual interactions.

Social-ecological systems can also be represented by networks (Folke, 2006; Kleindl et al., 2018) and aim to capture the interplay and possible feedbacks between human decisions and actions in managing an ecosystem and the structure and function of that ecosystem (Bodin, 2017; Bodin & Tengö, 2012; Fischer, 2018; Janssen et al., 2006). Generally, social-ecological networks are used in the context of governance challenges emerging from (1) a scale mismatch between the ecological and the social processes operating in the system, (2) competition for access, use, or management of

a shared ecological resource, and (3) sensitivity to the order with which management activities are realized, e.g., steps to take to reduce risk (Bodin et al., 2019; Hamilton et al., 2019). Therefore, social-ecological networks comprise both ecological and social nodes and focus on the interdependencies between these various kinds of nodes. For example, a social-ecological link could represent timber harvesting by a forest owner (social node) in their forest stand (ecological node). Ecological nodes usually consist of groups of plants or animals, or have a spatial dimension, such as specific forest patches. However, more aggregated biophysical forms, e.g., ecosystem services (Dee et al., 2017), may be a more appropriate node representation when social-ecological interactions are associated with specific ecological functions that are produced by multiple ecological entities (Bodin et al., 2019).

Social-ecological networks may develop via human activities that create interactions between ecological elements (Janssen et al., 2006). For example, firewood movement between localities is associated with the wide dispersal of emerald ash borer (*Agrilus planipennis*) across North American forests (Siegert et al., 2015), and the construction of forest roads has been associated with increased gray wolf (*Canis lupus*) movement across managed forest stands (Courbin et al., 2014). Social interactions may also emerge from ecological connections. For instance, when two organizations managing distinct forest lands decide to collaborate on a wildfire risk mitigation strategy following a forest fire that has burned across both lands (Hamilton et al., 2019). Sayles et al. (2019) distinguished between different kinds of social-ecological networks depending on how nodes and links are defined: (1) *multiplex networks* in which all nodes can be connected by social and ecological links; (2) *multilevel networks* in which social and ecological nodes are viewed as being on different layers and only one interaction between any two nodes is considered; and (3) *multidimensional networks* in which nodes are represented as in multilevel networks, but multiple interactions between nodes are possible (Fig. 28.3).

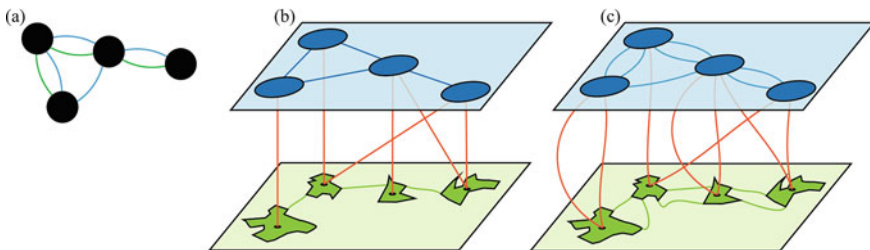


Fig. 28.3 Different frameworks to represent social-ecological networks, as suggested by Sayles et al. (2019). **a** Multiplex network where nodes (*black circles*) can be either social or ecological and connected by both social and ecological links; **b** and **c** multilevel networks with social (*blue circles*) and ecological (*green polygons*) nodes on different layers. Nodes are connected by intralayer links (*blue or green*) and/or interlayer links (*orange*). In **b**, only one link exists between pairs of nodes, and in **c** multiple interactions between nodes are possible, as in multiplex networks

28.3 Network Analysis

Multiple statistical measures can be extracted from networks to describe their architecture and determine the degree to which a system is connected, how interactions are distributed among nodes, and whether specific nodes occupy important positions. These measures are then used as indicators to better understand the system's function and its robustness or capacity to adapt to changing conditions and disturbances. Table 28.2 presents a few key fundamental network metrics; more in-depth discussions can be found in the literature on networks (Newman, 2003; Strogatz, 2001) and their application to community ecology (Bersier et al., 2002; Blüthgen et al., 2006; Delmas et al., 2019; Proulx et al., 2005), conservation biology (Dale & Fortin, 2010; D'Aloia et al., 2019; Galpern et al., 2011; Rayfield et al., 2011) and social (Bodin et al., 2006) and social-ecological systems (Janssen et al., 2006). Most measures described in Table 28.2 are general and apply to all types of networks, emphasizing the universality of many network metrics. However, a small number are specific to certain types of networks. For example, specialization is a measure used in bipartite networks, whereas connectivity is used in spatial networks. Network measures are termed qualitative when they apply to binary networks, i.e., networks with unweighted links that only report the presence or absence of interactions, or quantitative when they apply to weighted networks in which links represent the strength or frequency of interactions. Table 28.2 largely focuses on qualitative measures but includes some quantitative measures, e.g., specialization.

The most general measures used to describe a network are its *order*, meaning the number of nodes in the network, and its *size*, which is the number of links. These descriptors already provide an idea of the extent and possible complexity of the network. The average number of links per node measures the *density* of the network. In social webs, a high density is often associated with a better exchange of information among actors. This can facilitate the development of new ideas and also improve collective actions in natural resource governance (Bodin et al., 2006). Conversely, an extremely dense network of actors can homogenize information and impede the development of new knowledge. It can also be associated with a reduced diversity of management practices that could lead to lock-in and limit the capacity of actors and organizations to come up with novel strategies to adapt to changing conditions (Bodin et al., 2006; Janssen et al., 2006).


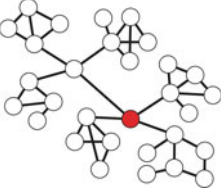
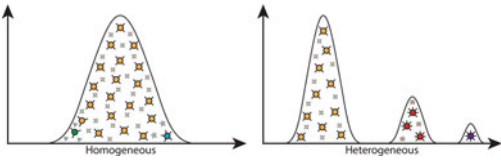

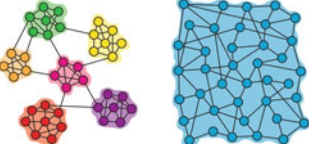
A measure similar to linkage density is *connectance*, the proportion of potential interactions that occur. Connectance is the term used to determine species interactions within ecological networks. It can be a good indicator of the sensitivity of ecological communities to disturbances resulting in the loss of species (Dunne et al., 2002b; Montoya et al., 2006). Connectance is also associated with community dynamics and may be used to understand variations in population density or infer potential indirect interactions (Van Veen et al., 2008). A spatial analog of connectance is functional *connectivity*, which applies to species-habitat and forest-stand networks. Functional connectivity is a species-specific measurement, as species perceive forest fragmentation differently depending on their movement ability. Multiple indices of connectivity exist, all with the general purpose of determining the availability

Table 28.2 Measures to quantify network structures and the corresponding illustrations. **a** Two networks having the same order, but the smaller-sized network (*right*) has a smaller linkage density and connectance but a longer diameter (depicted by the number of links separating the two blue nodes); **b** two spatial networks of the same order but one (*left*) has a larger size and a higher connectivity. **c** The yellow node has a lower degree than the red node. The vulnerability (*number of blue links*) of the red node is identical to its generality (*number of purple links*). **d** Pink nodes are generalists, whereas blue nodes are specialists. **e** The red node (*right*) has a low clustering coefficient, whereas the red node (*left*) has a high clustering coefficient; thus, it forms a clique with its neighbors. **f** The red node has the highest betweenness centrality in this network. **g** The degree distribution is homogeneous when all nodes have similar degrees (*left*) and is heterogeneous when degrees vary among nodes. **h** The bipartite network (*left*) has a nested structure contrary to that on the right. **i** A high modularity network (*left*) contains six modules, whereas the other network (*right*) lacks a modular structure. This table constitutes a nonexhaustive list of measures. Interested readers should consult references cited in the main text for a deeper exploration of network measures

<i>General Measures</i>	
Order Total number of nodes	
Size Total number of links	
Linkage density Average number of links per node	
Diameter Longest of the shortest paths between all pairs of nodes in the network	
Connectance Number of links over the total possible number of links	
Connectivity The degree to which spatial nodes are reachable through internode movement	
<i>Node-Level Measures</i>	
Degree Number of links for a specific node	
Specialization Diversity of partners for a given species	

(continued)

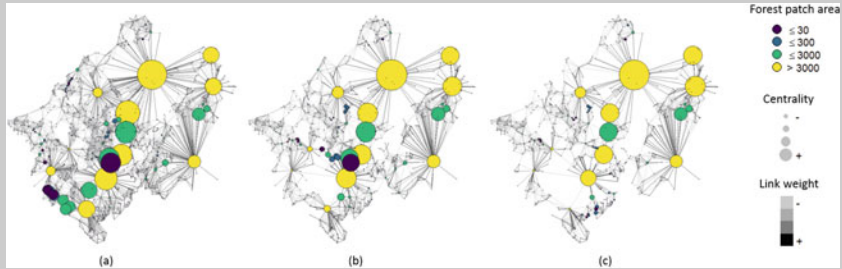
Table 28.2 (continued)

<p>Clustering coefficient Degree to which neighbors of a node are connected</p>	<p>(e)</p> 
<p>Betweenness centrality Number of times a node sits in a path between all pairs of nodes in the network</p>	<p>(f)</p> 
<p><i>Network-Level Measures</i></p>	
<p>Degree distribution Frequency distribution of degrees in the network</p>	<p>(g)</p> 
<p>Nestedness Degree to which specialist species interact with a subset of the group of species with which generalists interact</p>	<p>(h)</p> 
<p>Modularity How closely connected nodes are divided into modules</p>	<p>(i)</p> 

of habitat for a given species (Rayfield et al., 2011). Therefore, these indices are modulated not only by the number of patches and their connections but also by their area. For example, the probability of connectivity index is a quantitative measure that corresponds to the probability that two individuals randomly placed in habitat patches across the landscape can reach each other (Saura & Pascual-Hortal, 2007).

Functional connectivity measures are useful for conservation planning, such as designing reserve networks (D'Aloia et al. 2019; James et al., 2005; Saura & Pascual-Hortal, 2007) or evaluating changes in forest connectivity over time (Saura et al., 2011). They may also be used when planning harvesting operations. Ruppert et al. (2016) developed a heuristic procedure to schedule timber harvesting on the basis of a trade-off between wood volume and habitat connectivity for the woodland caribou (*Rangifer tarandus caribou*). Tittler et al. (2015) compared the habitat connectivity of various wildlife species across management strategies that differed in their distribution and aggregation of forest cuts. Functional connectivity is also considered a critical component of forest resilience (Box 28.2; Aquilué et al., 2020; Craven et al., 2016; Mina et al., 2021). High connectivity implies that source–sink dynamics may be possible in a fragmented forest landscape whereby disturbed forest patches can regenerate by receiving seeds from unaltered patches (Craven et al., 2016).

Box 28.2 Effect of Landscape Management and Disturbances on a Forest Patch Network



The variations in patch centrality in a spatial network of forest patches across increasing levels of timber harvesting; **a** no harvesting, harvesting at **b** 5%, and **c** 10% tree cover. Nodes are colored according to the size of their corresponding forest patch. The diameter of each node is proportional to its betweenness centrality. Links between patches are directed and weighted according to the tree species composition within each node as well as the seed dispersal capacity of each tree species

Spatial networks can guide landscape-scale forest management. Aquilué et al. (2020) used a network approach to model fragmented forest patches in a rural landscape in central Québec, southeastern Canada, and explore how connectivity among patches varied according to different management strategies—functional enrichment of current forest patches, plantations in newly created forest patches—and under different disturbance scenarios—timber harvesting, drought-induced mortality, and pest outbreak. Interested readers should read Chap. 31 for a discussion of the effect of functional enrichment on the resilience of fragmented landscapes.

The above figure illustrates how tree harvesting affects the betweenness centrality of forest patches. Indeed, cutting trees has the effect of removing

small patches and reducing the flux of seeds that can travel among patches, thereby affecting the entire functional connectivity of the landscape. As a result, the importance of each patch in maintaining connectivity is altered by disturbance. This figure also illustrates that small patches (*dark color*) can have a high centrality value (*large diameter*), emphasizing that the contribution of a forest patch to the connectivity of the landscape is not simply based on its surface area.

The *diameter* of a network is the maximum number of links between any two network nodes and thus measures the extent to which nodes are accessible to each other (Janssen et al., 2006). The small diameter of a habitat network can indicate its susceptibility to the rapid spread of an invasive plant (Minor et al., 2009). In organizational networks, a small diameter implies the existence of efficient channels to diffuse information (Bodin et al., 2006). Although a short diameter may be correlated with network density, this is not always the case. Linkage density does not account for how links are distributed among nodes. Therefore, it is possible to have a dense network characterized by a large diameter whenever nodes are distributed in a few well-connected clusters that are isolated from each other (Janssen et al., 2006). In social networks characterized by such a topology, shared information will tend to remain within clusters.

Network analysis allows for the identification of nodes that play a key role in structuring the system. The *degree* is a node-level measure that, in an undirected network, corresponds to the number of links that connect a node. In directed networks, the degree can be decomposed into in-degree and out-degree. In food webs, the former is an indication of the vulnerability of a species, i.e., the number of predators, whereas the latter relates to its generality, i.e., the number of resources (Delmas et al., 2019). In a bipartite network, such as pollination, frugivore, and host–parasitoid networks, a similar concept is that of *specialization*, which corresponds to the diversity of interacting partners of a species (Blüthgen et al., 2006; Chama et al., 2013; Gómez-Martínez et al., 2020). Gómez-Martínez et al. (2020) found that the level of specialization in bumblebee pollination networks decreased with the increased fragmentation of the surrounding forest landscape. Another related descriptor used in nest web studies is the *species importance index*. When measured for a tree species, this index corresponds to the proportion of bird species that use the particular tree species' cavities relative to the number of other tree species used by the same bird species. Identifying keystone tree species that cavity users and excavators routinely use is essential to define more specific conservation guidelines (Ruggera et al., 2016).

The degree of a node is, therefore, a measure of its influence on other nodes and is one of multiple measures assessing the *centrality* of a node. For instance, in studying the mycorrhizal networks of interior Douglas fir (*Pseudotsuga menziesii*), Beiler et al. (2015) found that large trees had a higher *degree centrality* in xeric

plots compared with mesic plots. This analysis suggests that the role of large trees—in facilitating the survival and productivity of newly established seedlings through shared mycorrhizal fungi—is more important under water-deficit conditions.

In social webs, the organization having the highest degree can play a determining role in coordinating a group of organizations with diverging opinions on the best risk mitigation strategy, e.g., forest fire, toward a consensus (Bodin et al., 2006; Hamilton et al., 2019). Yet, a node with a low degree can also exert a central importance within the network if, for example, its position connects clusters of nodes that would otherwise be isolated. Such nodes are said to have a high *betweenness centrality*. Actors or organizations that occupy these bridging positions in social webs are essential for developing trust among parties holding conflicting views. In species-habitat and forest-stand networks, determining patches of high betweenness centrality helps identify patches that are not necessarily large but that still have a high conservation value because they enable wildlife species to move across the landscape from one region of well-connected patches to another (Aquilué et al., 2020; Gurrutxaga et al., 2011). A spatial network is more vulnerable to the destruction of nodes having a high betweenness centrality because their loss can cause the fragmentation of the landscape into unconnected components (Box 28.2; Aquilué et al., 2020). This destruction could result, for example, from harvesting, pest infestation, or forest fire.

Different measurements can provide information about the possible asymmetric distribution of interactions within networks. The simplest approach is to derive the frequency distribution of degrees within a network, i.e., its *degree distribution*, which describes the level of degree heterogeneity. For example, scale-free networks (Fig. 28.1c) are characterized by a few highly connected nodes and a large number of poorly connected nodes. In one example, the degree distribution of the mycorrhizal networks of Douglas-fir trees followed a scale-free distribution (Beiler et al., 2010). The large mature trees in a plot had the most connections, suggesting that such networks are robust to the random loss of trees but fragile to the loss of large trees with consequences for the regeneration of the entire community of connected trees (Beiler et al., 2010).

In weighted networks, one can measure the interaction diversity—a Shannon diversity of links—to quantify how degrees are distributed among nodes. For example, Cockle and Martin (2015) found that the interaction diversity of a nest web increased during a mountain pine beetle outbreak because the greater availability of cavity trees allowed for a wider variety of excavators and new opportunities of interactions with secondary cavity nesters.

The *clustering coefficient* of a node measures the extent to which neighbors of that node are closely connected. In social webs, interconnected nodes with high clustering coefficients are said to form a *clique*. The formation of cliques, or clusters, results from the tendency of social partners to interact, a property of social interactions called *transitivity*. The presence of clusters may help maintain a heterogeneity of knowledge and experiences across the network. This may prove essential for innovation and adaptation to novel environmental conditions (Bodin et al., 2006).

Modularity measures the extent to which a network is divided into modules of well-connected nodes (also called compartments). Modularity is thus a concept similar to clustering. But while clustering applies to neighboring nodes, modularity is measured at the scale of the entire network (Delmas et al., 2019; Guimerà & Amaral, 2005). The modularity of a nest web, for example, can indicate whether a conservation strategy for a particular tree species will have a positive influence on an entire bird community of cavity excavators and nesters (if no modules are present) or whether strategies focusing on tree species in other modules are needed (Ruggera et al., 2016). For example, in analyzing the nest web of an Argentinian tropical forest, Ruggera et al. (2016) found that woodpeckers and nonexcavator birds formed distinct modules because the former interacts with both living and standing dead trees. In contrast, the nonexcavator birds use only decay-formed cavities in living trees. Consequently, they suggested that conservation efforts for cavity-nesting birds should focus on standing dead trees as much as on certain alive tree species. In species interaction networks and in spatial networks, a certain degree of modularity is beneficial to the system's stability or resilience because it impedes the negative cascading effects of species' extinction or prevents disturbances from rapidly propagating across the network of forest patches (Messier et al., 2019; Stouffer & Bascompte, 2011).

Nestedness is a characteristic of bipartite networks in which specialist species interact with a subset of the group of species with which generalists interact (Almeida-Neto et al., 2008; Delmas et al., 2019). Devoto et al. (2011) found strong nestedness in the moth pollination network of a boreal pine forest, which was associated with the dominance of a small core of generalist species that also interacted with the more specialized species. This asymmetric pattern made this hub of species, as well as the pollination service they provided, vulnerable to poor weather conditions.

Networks can also be analyzed by measuring the frequency with which different *motifs* appear in their architecture (Delmas et al., 2019). Motifs are smaller subsets of interacting nodes that are viewed as the building blocks of networks (Table 28.3; Milo et al., 2002). By simulating random networks that conserve some key properties of the observed network, e.g., order, size, and connectance, one can determine whether a particular motif occurs more frequently in the network than what would be expected by chance (Bodin & Tengö, 2012; Robins et al., 2007). In species interaction networks, motifs can be used to derive the different roles that individual species play in a network from their position in motifs (Stouffer et al., 2012). For example, Baker et al. (2015) found that despite variability in species composition in a host-parasitoid community with time and along a gradient of forest fragmentation, the role of species remained largely stable. In social webs, the analysis of motifs can be used to understand the relationships between structuring interactions and the ability of the system to adapt their management of natural resources. For instance, Fischer and Jasny (2017) found that homophily was a strong structuring pattern in the network formed by organizations concerned about increased wildfire risk. In this example, homophily may insulate organizations from being exposed to a diversity of ideas, thereby impeding their capacity to develop novel management strategies. In a social-ecological network that combined fire transmission (ecological links, see Table 28.1) and coordination of fire risk mitigation (social links), Hamilton et al. (2019) found

Table 28.3 Examples of possible motifs for different categories of network. Species interaction networks: **a** apparent competition of two consumers for a single resource; **b** a linear three-level food chain; and **c** omnivory in a three-level food chain. Social networks: **d** reciprocal interactions between three actors; **e** an actor acts as an intermediate between two actors that are otherwise disconnected; and **f** two disconnected actors report to a third that exerts a leadership role. Motifs of natural resource access in social-ecological networks (from Bodin & Tengö, 2012): **g** each actor manages their own resource independently even if their resources are ecologically linked, e.g., a spreading disturbance; **h** one actor depends on the other actor for access to the resource; **i** both actors compete for access to a single resource and are not engaged in any dialogue for co-management

Network category	Examples of possible motif
Species interaction networks	
Social networks	
Social-ecological networks	

that actors favored interactions with their immediate geographic neighbors, which constitutes an important challenge for the large-scale governance of wildfire risk.

28.4 Discussion

28.4.1 Challenges

The use of networks in forest ecology and management presents multiple challenges, the most important being the difficulty in identifying appropriate nodes and links. Creating species interaction networks requires intensive sampling to obtain high-resolution data. For instance, nest webs are constructed by identifying cavity-bearing trees and inferring excavator species by relying on the correlation between their body

size and the diameter of cavity entrances. Interaction between tree and bird species is then determined by routinely inspecting in the field cavities using a camera system to observe signs of breeding or roosting (eggs, feathers, nestlings, etc.), which is labor intensive (Cockle & Martin, 2015; Ouellet-Lapointe et al., 2012; Ruggera et al., 2016). Investigating mycorrhizal networks requires sampling needles and cambium tissue from study trees, as well as an intensive sampling of the forest floor to collect tuberculate mycorrhizae (Beiler et al., 2010). Moreover, the identification of pollinator–plant interactions requires field observations of flower visits (Gómez-Martínez et al., 2020; Memmott, 1999) or the capture of pollinator organisms to identify pollen on their body and quantification of the interaction by counting pollen grains (Devoto et al., 2011). Similarly, host–parasitoid interactions are determined by collecting host organisms in the field and then rearing parasitoids in the lab (Cagnolo et al., 2011; Van Veen et al., 2008). Accurate identification of species may rely on DNA barcoding, especially in species-rich systems where morphologically similar species abound (Smith et al., 2011). Obviously, reconstructing species interaction networks is sensitive to sampling efforts such that abundant species may receive more attention than rare ones (Cagnolo et al., 2011; Van Veen et al., 2008).

In spatial networks, nodes are identified from raster images, such as remote-sensing data, by aggregating adjacent cells that satisfy environmental criteria to be considered as forest or habitat patches, e.g., forest cover type and age, tree density (Bunn et al., 2000). Patches may be easily identified in landscapes presenting a dichotomous vegetation cover, such as fragmented forests in agricultural landscapes or urban settings. However, this task is more difficult in heterogeneous and continuous forest landscapes and for wildlife species whose habitat includes a diversity of cover types with varying preferences, e.g., the woodland caribou (*Rangifer tarandus caribou*; Galpern et al., 2011; O’Brien et al., 2006). In these cases, edge detection methods can be used to delineate patches from the matrix (Fortin, 1994). Moreover, field observations and expert opinions may be necessary to make certain assumptions regarding how organisms interact with their environment, such that cover types and patches can be ranked according to their quality or relative use by the species of interest (O’Brien et al., 2006; Pascual-Hortal & Saura, 2007; Saura & Pascual-Hortal, 2007).

Links in spatial networks are generally identified by least-cost paths between nodes. This approach assumes that organisms travel between nodes using the most risk-free and efficient route, which may not always be the case for organisms characterized by anisotropic or passive dispersal. Moreover, in networks where links denote the movement of wind-dispersed seeds or certain bird and insect species, least-cost paths can be estimated using Euclidean distances between patches. However, for most wildlife species, links will correspond to nonlinear paths that consider the environmental heterogeneity of the matrix and the biological traits that influence their dispersal ability (Fall et al., 2007). Therefore, the determination of least-cost paths can be sensitive to the values and resolution of the resistance surface (Etherington, 2016;

Rayfield et al., 2010), which, in turn, requires intensive parameterization efforts; thus, the results may be prone to bias (Etherington, 2016).

Defining and identifying nodes and links is also a pervasive challenge when translating social and social-ecological systems into networks. Not unlike ecological data, collecting social data to identify entities and their interconnections involves substantial investment and is prone to errors. For example, a common approach to identify nodes in social networks is snowball sampling, an approach based on multiple steps (Doreian & Woodard, 1992; Fischer & Jasny, 2017; Hamilton et al., 2019; Knoot & Rickenbach, 2014). In the first step, a subset of key actors (single individuals or organizations) is selected and interviewed to obtain the names of other actors with whom they interact. In the second step, these additional actors are then interviewed to obtain yet again other names. The process continues until no new actors are identified (Fischer & Jasny, 2017). Depending on the number of sampling waves or the depth of the interviews, this approach can be time-consuming and subject to selection bias, e.g., well-connected individuals being identified more easily, and bias in reporting (or not) certain conflicting relationships, e.g., between opposing individuals or organizations (Doreian & Woodard, 1992).

Additionally, the construction of social-ecological networks often requires a certain level of aggregation of the ecological or social units determined by the system and the question under study. For example, studying coordination between forest management organizations may require that ecological nodes be scaled up to represent forests within the jurisdictional boundaries over which these organizations interact, thereby losing the local environmental specificity and limiting the utility of the network approach for managers working at local scales (Hamilton et al., 2019; Sayles et al., 2019). Bodin et al. (2019) proposed that a starting point in conceptualizing nodes and links is defining the social-ecological interdependencies central to the investigated management issue. Focusing on these connections will facilitate identifying the most relevant nodes and choosing the appropriate level of aggregation. Likewise, creating a network necessarily requires bounding the system under study. This bounding imposes an artificial frontier with the implicit assumption that connections beyond its limit have negligible impacts on the system's structure and function (Sayles et al., 2019). Given that any network analyses are sensitive to the number of nodes and links, which are themselves the result of the bounding choice, Sayles et al. (2019) suggested that studying the effects of different bounding approaches is needed to advance the field of social-ecological networks.

Common natural resource governance challenges occur in a variety of ecosystems, contexts, and scales (Ostrom, 2009). One goal of social-ecological network research is to understand the causal pathways between network structures and how these challenges emerge or are solved (Bodin & Tengö, 2012; Groce et al., 2019; Guerrero et al., 2020; Janssen et al., 2006). However, because of the numerous methodological choices involved in translating a social-ecological system into a network, the resulting network analysis tends to be specific to the studied system, limiting the ability to compare studies (Bodin et al., 2019; Young et al., 2006). Recently, Bodin et al. (2019) emphasized the need to develop a set of research design guidelines, applicable across contexts and scales, to facilitate synthesis and gain insights

from diverse studies. These authors also suggested that advancing social-ecological network research requires a systematic classification of different basic causal relationships between simple patterns of network structure and environmental outcomes to help researchers make clearer assumptions about causality when more complex pathways are operating in their system (Bodin et al., 2019; Groce et al., 2019).

28.4.2 Benefits and Potential of the Network Approach in Forest Management

Managing for forest resilience has become imperative in a changing environment (Gauthier et al., 2015; Trumbore et al., 2015). Many symptoms of climate effects, invasive insects and diseases, and expanding land use are already evident within forest ecosystems (Hansen et al., 2013; Právělie, 2018). Moreover, due to global change, boundary conditions are shifting for many ecological processes, including disturbance regimes, species ranges, phenology, and carbon flux dynamics (Ramsfield et al., 2016; Seidl et al., 2017; Vose et al., 2019). Transition zones and locations where species exist at the limits of their current ecological tolerances, such as portions of the hemiboreal ecotone of eastern North America, may be particularly sensitive to these shifts (Thom et al., 2019). Management decisions that we make today must account for the uncertainty in future environmental threats, and they must anticipate uncertainty related to the rapidly changing economic and social context affecting demand for forest services and products. Network theory could help forest managers identify sensitivities and vulnerabilities linked with these changes and mitigate their effects accordingly, for instance through adaptive forest management (Gauthier et al., 2008; Millar et al., 2007). Moreover, the application of network theory could also likely be a key for monitoring biodiversity and projecting the future state of biodiversity in managed forests (Mina et al., 2021).

Recent applications of network theory have been proposed for evaluating and managing the resilience of large tracts of forests to global change stressors (Box 28.2; Aquilué et al., 2020, 2021; Mina et al., 2021). In these approaches, resilience is viewed as a multidimensional concept combining biodiversity and network topology measures likely to positively influence the capacity of spatial forest networks to cope with future disturbances (Messier et al., 2019). More precisely, resilience accounts for functional redundancy, the functional response diversity of forest metacommunities (Mori et al., 2013), their network connectivity, mean centrality, and modularity (Gonzalès & Parrott, 2012). Management strategies that modify one or more of these resilience-based properties can then be tested against scenarios of climate change and disturbance, e.g., drought, insect outbreak (Aquilué et al., 2020, 2021; Mina et al., 2021). For example, this approach can determine whether establishing plantations of functionally rare species or enriching forest stands to increase the variety of response traits, at locations that also improve forest network connectivity,

provide forest ecosystems the ability to resist or adapt to future environmental conditions. One can then use this approach to identify the management strategy that best conserves the forest landscape under a range of possible but uncertain disturbances.

Network theory is useful for managing ecological recovery from natural disturbances, especially in the context of climate change where many disturbances are expected to increase in occurrence, severity, and size (Práválie, 2018). For example, following large forest fires, seeds, fungal spores, and organisms often disperse from natural fire refugia (nodes in spatial forest networks) and then interact demographically as the landscapes recover through succession (Keeton & Franklin, 2004; Krawchuk et al., 2020). In landscapes where fire management is used to mitigate fire risk, network theory can assist in designing strategies, e.g., location and size of prescribed burns, that preserve habitat connectivity for wildlife species (Sitters & Di Stefano, 2020).

Spatiotemporal and spatial networks employed together with simulation models could help predict shifting conditions in forest ecosystems to adapt management practices accordingly. For example, Huang et al. (2020) used spatiotemporal networks together with species distribution models to determine how future climates will affect habitat availability for terrestrial mammals experiencing range shifts in North America. Future applications of networks are, therefore, expected to be used in conjunction with other models to better integrate changing environmental conditions and ecological processes occurring at different spatial or temporal scales. For example, Mina et al. (2021) coupled a spatial network approach with a spatially explicit simulation model of forest dynamics (LANDIS-II, Mladenoff, 2004) to determine how climate-induced changes in forest cover influence landscape connectivity. Wildemeersch et al. (2019) used a network-of-networks approach to simulate forest pest outbreaks. Their model included a landscape-scale network of forest patches as well as a stand-scale network within each patch. The small scale captured the local pest pressure, whereas the large scale captured the influence of landscape connectivity on the spreading behavior of the pest.

Networks are promising tools for multifunctional forest management because they effectively integrate the interactions between social and ecological elements. Spatial networks can help assess trade-offs between conflicting management goals. For example, they can be used to determine management strategies that account for ecological connectivity to satisfy conservation and economic targets (Ruppert et al., 2016) or optimize the provision of multiple ecosystem services (Vogdrup-Schmidt et al., 2019). Moreover, social-ecological networks can be used to identify linkages that would foster coordinated efforts in the management of natural disturbance risks (Hamilton et al., 2019), such as reducing fire risk hazards within the wildland–urban interface (Keeton et al., 2007; Vilà-Vilardell et al., 2020).

To summarize, this chapter has demonstrated the richness and flexibility of the network framework for forest management. Further applications of network theory to forest management will necessitate an adaptive approach, accounting for shifting

dynamics and interactions among nodes, be they ecological or social. Network analysis is a powerful tool for identifying sensitivities and vulnerabilities within networks. It may prove invaluable in helping forest managers to better anticipate and adapt to global change.

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