

The Structure of Ecological Networks Across Levels of Organization

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Abstract

Interactions connect the units of ecological systems, forming networks. Individual-based networks characterize variation in niches among individuals within populations. These individual-based networks merge with each other, forming species-based networks and food webs that describe the architecture of ecological communities. Networks at broader spatiotemporal scales portray the structure of ecological interactions across landscapes and over macroevolutionary time. Here, I review the patterns observed in ecological networks across multiple levels of biological organization. A fundamental challenge is to understand the amount of interdependence as we move from individual-based networks to species-based networks and beyond. Despite the uneven distribution of studies, regularities in network structure emerge across scales due to the fundamental architectural patterns shared by complex networks and the interplay between traits and numerical effects. I illustrate the integration of these organizational scales by exploring the consequences of the emergence of highly connected species for network structures across scales.

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1. INTRODUCTION

Ecological network:

a description of an ecological system as a set of nodes depicting units (e.g., individuals, resources, species, or higher taxa) connected by links depicting ecological interactions

Network structure:

distribution patterns of links across nodes in an ecological network

Ecological interactions affect key aspects of biodiversity across all levels of organization (Levin 1992, Margalef 1963). Individuals are the basic interacting units of ecological systems, and their interactions affect the demography (MacArthur & Levins 1967) and evolution of populations (Benkman 1999). These ecological interactions among individuals in turn connect populations of different species [Elton 2001 (1927)], affecting community stability (MacArthur 1955, May 1972) and organization (Cohen 1977, Estes & Palmisano 1974, Pascual & Dunne 2006), controlling the flow of energy in ecosystems (Odum 1960), and shaping trait evolution at the community level (Thompson 2005). At broader temporal and spatial scales, ecological interactions contribute to the rise and fall of clades throughout the history of life (Van Valkenburgh et al. 2004).

Pairwise interactions are seldom isolated but are instead connected to each other, forming ecological networks (**Figure 1**). Because interaction patterns affect and are affected by many evolutionary and ecological processes (Kaiser-Bunbury et al. 2017, Kondoh 2003, Loeuille 2010), interpreting network structural patterns is fundamental to ecology. There is no intrinsically correct scale for describing the structure of ecological networks (**Figure 1**). The appropriate spatial, temporal, and organizational scales depend on the question being addressed (Niquil et al. 2020). Independent of the spatial, temporal, and organizational scales, knowledge of network structure can inform our understanding of ecological systems in two ways. First, fingerprints of ecological and evolutionary processes are encoded in network structure. Thus, network structure provides insights into the role of these processes in shaping ecological assemblages (Gibert & Yeakel 2019, Loeuille & Loreau 2005, Ponisio et al. 2017, Vázquez et al. 2009, Williams & Martinez 2000). Second, network structure reveals pathways connecting units that do not directly interact with each other. Network structure thus allows the exploration of how indirect effects propagate across the system, affecting species abundances (Buck 2019, Wootton 1994, Yodzis 1988), extinction dynamics (Memmott et al. 2004, Solé & Montoya 2001, Vieira & Almeida-Neto 2015), the flow of energy and matter in ecosystems (Hannon 1973, Meysman & Bruers 2010), metacommunity

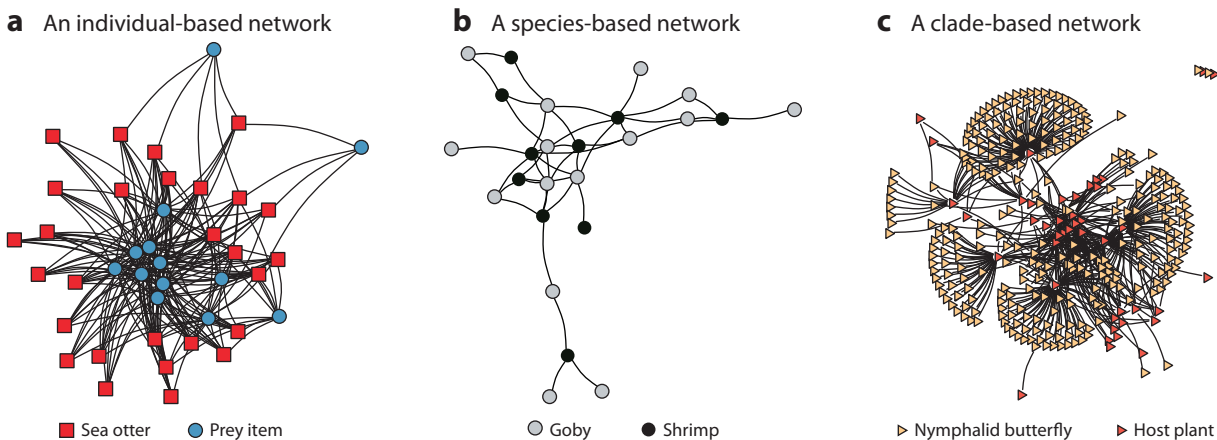


Figure 1

Examples of networks emerging at different levels of organization. In each network, the links depict ecological interactions, and the nodes depict the units of the system. The units of the system, however, vary with the level of organization. (a) An individual-based network describing interactions among sea otter individuals (red squares) and their prey items (blue circles) at a site in Monterey Bay, California (data from Tinker et al. 2012). (b) A species-based network describing interactions among gobies (gray circles) and shrimp (black circles) in Papua New Guinea (data from Thompson et al. 2013). (c) A clade-based network describing interactions between nymphalid butterfly genera (yellow triangles) and host plant orders (red triangles) across Earth (data from Braga et al. 2018).

dynamics (García-Callejas et al. 2019), immunogenetic diversity (Pilosof et al. 2014), and coevolution (Guimarães et al. 2017, Start et al. 2019). The network structure can thus unveil assembly processes and direct and indirect effects on the dynamics of ecological systems.

In this review, I explore empirical network patterns observed in ecological systems across different levels of organization and describe how these structural patterns provide insights into the processes shaping ecological systems. I focus on interactions involving individuals of different species and the patterns of niche overlap generated by these interactions (see the **Supplemental Material** for other kinds of ecological networks). First, I review the characterization of ecological network structures. Second, I explore how the network patterns observed within populations depend on the ways in which individuals use resources and interact with partners. Third, I illustrate how some basic patterns predicted by network theory emerge at the level of ecological communities in networks describing one interaction type (such as mutualistic networks), in food webs, and in networks of multiple interaction types. Specifically, I argue that highly connected species shape the structure of networks at the community level. Finally, I discuss the implications of network structures for our understanding of ecological and evolutionary processes operating across broader spatial and temporal scales.

2. STRUCTURAL ANALYSIS OF ECOLOGICAL NETWORKS

Ecological systems are depicted as networks or graphs in which nodes represent units, and links describe interactions between these units (**Figure 1**). Units can be individuals, species, or clades, depending on the level of organization under investigation. Links can describe a variety of ecological interactions between pairs of units. The astonishing diversity of natural histories underlying ecological interactions can be summarized by a few aggregated descriptors, such as interaction occurrences (in binary networks), interaction weights (in weighted networks), or multiple interaction types simultaneously (in multilayer networks) (see the **Supplemental Material** for different network representations).

Simplification and aggregation of biological information is at the core of ecological network analysis. An essential feature of ecological networks is their almost endless number of possible configurations. For example, networks available from the Web of Life (<http://www.web-of-life.es>) that describe interactions among fruiting plants and frugivorous species contain on average 31 plant and 21 vertebrate species ($n = 34$ networks). Given these numbers, there are almost 10^{196} possible binary network configurations, a number many times greater than the estimated number of electrons in the observable universe (Eddington 1939) (see the **Supplemental Material**). Thus, to characterize the structure of ecological networks, it is necessary to simplify and aggregate the heterogeneity in ecological systems using network metrics. Multiple metrics are available to characterize interaction patterns at the node, link, and network levels (Costa et al. 2007). The choice of metric depends on the patterns and questions being studied. In this review, I focus on metrics that characterize the macroscopic properties of networks (see the **Supplemental Material** for a visualization of network patterns).

Many metrics characterize the network structure by using sums or averages of node-level or link-level measurements, such as connectance, modularity, nestedness, and interaction diversity. However, across-node variation in interaction patterns partially reflects the processes influencing the structure and dynamics of the networks (Albert & Barabási 2002). This variation can be described by distributions of node-level metrics, such as the degree distribution (Jordano et al. 2003), distributions of interaction strengths (Bascompte et al. 2006), multiple forms of asymmetries (Rooney et al. 2006, Vázquez & Aizen 2004), motifs (Baiser et al. 2016), and graph spectra (Staniczenko et al. 2013).

Graph: a set of vertices and a set of edges in which pairs of vertices are connected by edges

Interaction weight: a value describing the interaction frequency, the interaction rate, or another measure of the quantitative importance of an ecological interaction

Weighted network: a network in which the links are associated with interaction weights

Multilayer network: a network with multiple layers describing different types of links, nodes, or spatiotemporal variation in the system

Connectance: the proportion of all possible links actually recorded in a network

Modularity: the level to which a network is arranged in semi-independent, cohesive groups of interacting nodes; also known as compartmentalization

Nestedness: the extent to which the partners of poorly connected nodes form a subset of partners of highly connected nodes

Interaction diversity: the degree to which interaction events are evenly distributed across different partners or pairwise interactions in a network

Degree distribution:

the distribution describing the probability of finding a given node with k links

Motifs: very small subnetworks recorded in a given network at a higher frequency than expected by a theoretical benchmark

Graph spectra:

distributions of the eigenvalues of the matrices associated with a graph

Jacobian matrix:

a matrix containing the first-order partial derivatives of a system of functions, e.g., a system of differential equations

Null models:

assembly models that generate theoretical predictions under the assumption that a particular process is not operating

Detailed information about the network structure, e.g., that obtained by meticulously describing all pairwise interactions, may uncover novel processes and provide inferences that are not apparent from single-value metrics (Stouffer 2010). However, increasing the network detail does not necessarily provide better insight into the ecology and evolution of the system. A detailed description of hundreds of pairwise interactions is logistically unfeasible. Just as importantly, the aim of pattern description from a theoretical perspective is not to provide a detailed assessment of an ecological system but rather to afford broader general insight. Multiple features of ecological systems can be explained using a coarse description of the network structure, as illustrated by the energy systems approach to ecosystems (Odum 1960). Additionally, some hypotheses provide predictions about network structure but not about the details of pairwise interactions. For example, theory predicts that modularity will increase the robustness of ecological systems to perturbations, and this prediction should be tested using the overall structure of the network (Gilarranz et al. 2017). A central question that must be answered in the study of ecological networks is, How much detail is needed to understand or predict the dynamics of entire ecological systems?

An example in which the level of detail used to describe the network structure is important involves the study of community persistence amid perturbations. The ecological dynamics of interacting populations can be modeled by a system of differential equations whose stability can be assessed using the eigenvalues of the Jacobian matrix (Novak et al. 2016), the elements of which are directly associated with interaction strengths (weighted links) connecting species. In this way, the Jacobian matrix provides a link between the network structure of a system and its ecological dynamics. Seminal works using random matrix theory on Jacobian matrices have explored the conditions that allow fixed stable points for species-rich communities (i.e., coexistence) by incorporating minimal structural attributes of ecological systems, e.g., species richness, connectance, and average interaction strength (May 1972). Network structure alters the conditions for stable coexistence (Allesina & Tang 2012, Gross et al. 2009), implying that network structure may affect how entire interacting assemblages respond to perturbations.

When studying network patterns, raw metric values provide information on the network structure. By combining different network metrics, we gain deeper insight into the complex ways in which network structure is affected by ecological and evolutionary processes (Gómez et al. 2010, Guimarães et al. 2007). Contrasting these patterns with theoretical benchmarks is useful for uncovering the role of simple processes in shaping ecological systems (Bascompte et al. 2003, Blüthgen et al. 2008, Vázquez & Aizen 2004). Theoretical benchmarks, obtained by means of analytical work and numerical simulations (e.g., null models), derive the expected patterns by incorporating minimal system features, processes, and sampling biases. Deviations from these theoretical benchmarks may suggest the importance of additional mechanisms affecting the structure of empirical networks. However, even when theoretical benchmarks reproduce an empirical pattern, this does not mean that the metric is uninformative. The only implication of such consistencies between theoretical benchmarks and empirical patterns is that the network structure can be reproduced by the simple factors built into the benchmarks and may not require additional explanations of its origin. The observed structure—even if reproduced by the theoretical benchmark—may deeply affect the dynamics of the studied system. For example, the small-world phenomenon, in which short indirect pathways often connect pairs of nodes in a network, is expected to emerge under simple assembly processes (Watts & Strogatz 1998). Despite being easily generated by simple assembly processes, the small-world phenomenon is among the most relevant consequences of network structure, favoring cascading effects in multiple systems (Watts & Strogatz 1998, Williams et al. 2002). In the following sections, I focus either on network patterns that are derived from the first principles or on network patterns that significantly diverge from theoretical benchmarks.

3. INDIVIDUAL-BASED NETWORKS: THE NICHE ORGANIZATION OF POPULATIONS

Ecological interactions affect individual fitness and, therefore, the demography and trait evolution of populations. Variation in ecological interactions among conspecific individuals is widespread, generating a distribution of traits and fitness outcomes within populations (Bolnick et al. 2003, Thompson 1988). The width and shape of these distributions differ among sites, affecting ecological dynamics and fueling local adaptation, population divergence, and the ongoing coevolution of species across space (Benkman 1999, Thompson 2005). Classical approaches to individual variation allow the description of the total population niche in terms of the relative contributions of variation in resource use within and among individuals (Bolnick et al. 2003). Analyses of individual-based networks (**Figure 1a**; **Supplemental Table 1**) reveal intricate patterns, such as modularity and nestedness (Araújo et al. 2008), that cannot be addressed by these classical approaches to individual variation.

The study of individual-based networks is in its infancy. To date, studies have focused on a small number of taxonomic groups (e.g., acanthopterygiid fishes, angiosperms, anurans, hymenopterans, and mammals) (**Figure 2**) and ecological interactions (e.g., predation, parasite-host interactions, and nectarivory/pollination) (**Supplemental Table 2**). Nevertheless, studies of individual-based networks have provided results on more than 160 species (**Figure 2**; **Supplemental Table 2**), showing how empirical patterns in individual-based networks often depart from the predictions of simple theoretical benchmarks.

Individual-based networks: networks in which at least some nodes depict individuals

Supplemental Material >

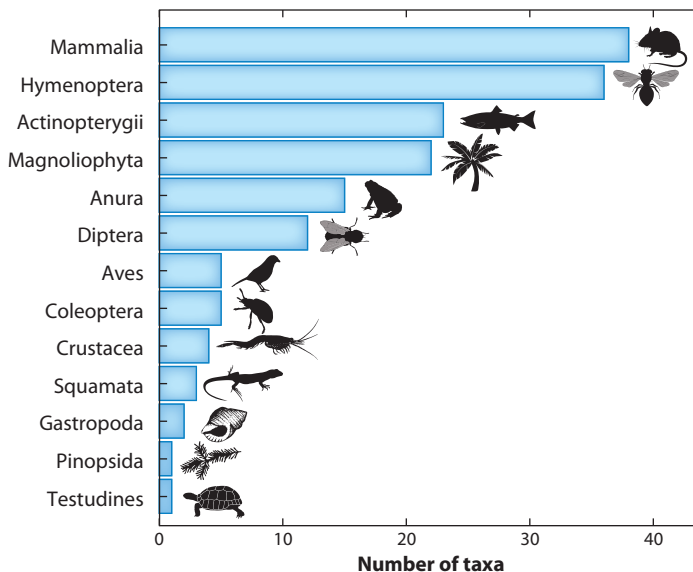


Figure 2

The number of taxa ($n = 167$) in different clades for which at least one individual-based network has been described, showing that our understanding of individual-based networks is biased toward some taxa (see the **Supplemental Material** for additional details). Organism images for Actinopterygii, Anura, Aves, Coleoptera, Pinopsida, and Testudines are PhyloPic images (<http://phylopic.org/>) under the Public Domain Dedication 1.0 license. The Testudines image was created by Andrew A. Farke, and the shell lines were added by Yan Wong. This image was used without any change (CC BY 3.0 Unported). Mathias M. Pires kindly provided the Crustacea and Gastropoda images.

In the simplest scenario, consisting of a homogeneous environment and no individual variation in traits or preferences, individual-individual networks (**Supplemental Table 1**) and those describing the overlap among individuals in their ecological interactions (niche overlap networks) (**Supplemental Table 1**) are expected to show a homogeneous structure, resulting in randomly or fully connected networks. Accordingly, individual-resource networks (**Figure 1a**; **Supplemental Table 1**) and individual-species networks (**Supplemental Table 1**) are expected to be structured by differences in the abundances of resources. Under these conditions, heterogeneity in interaction strength or in the number of individuals using a given resource varies with the relative frequency of resources. The patterns of interaction in individual-based networks depart from these theoretical benchmarks, revealing the role of variability in space, time, traits, and preferences in shaping ecological interactions (Araújo et al. 2008).

Space and time create templates for ecological interactions (Cantor et al. 2018) that favor departures from homogeneous and abundance-based network patterns. The spatial configuration of an environment may foster the rise of modules of interacting individuals (Fortuna et al. 2009, Tur et al. 2015). Similarly, temporal variation in the availability of partners affects the network structure on different timescales (Dáttilo et al. 2014b, Valverde et al. 2016). For example, networks describing interactions among individual insects and different plant species show temporal modularity, with different individuals sharing pollen resources at different times in the flowering season (Tur et al. 2015). Space and time may therefore promote spatiotemporal variation in the network structure by affecting the likelihood of potential interactions. Even so, the macroscopic properties of individual-based networks may show structural constancy. For example, networks of interactions among protective ant species and individual plants show daily turnover in ant species, while maintaining nestedness and average levels of reciprocal specialization (Dáttilo et al. 2014b).

Space and time set the scales in which individual-based networks occur, but the interaction patterns are further modified by variation in individual traits. For example, the numbers of individual honeybees (*Apis mellifera*, Apidae) visiting thistle (*Cirsium arvense*, Asteraceae) flowers increase with the number of flower heads and the height of the inflorescences on individual plants (Dupont et al. 2011). Network description of intraspecific variation in dietary niches uncovers subtle associations between traits and resource use that go beyond the number of resources used. For example, in a monomorphic population of three-spine sticklebacks (*Gasterosteus aculeatus*, Gasterosteidae), differences in trait combinations (e.g., body and snout shapes) were associated with dietary modules, i.e., groups of individuals feeding on similar prey (Araújo et al. 2008). Similarly, networks describing diet overlap among thick-billed murres (*Uria lomvia*, Alcidae) revealed sex-based dietary groups (Provencher et al. 2013). Network analyses can therefore reveal how patterns of interaction across individuals are associated with variation in individual traits.

The differing effects of individual trait variation on ecological interactions can be encoded as different network patterns. For example, the ontogenetic development of Spanish toothcarp (*Aphanius iberus*, Cyprinodontidae) leads to nested patterns of prey consumption in which older ontogenetic stages feed on a subset of the resources used by younger ontogenetic stages (Ramos-Jiliberto et al. 2011). In contrast, when analyzing prey electivity, successive ontogenetic stages form networks that combine nestedness with dietary modules, suggesting strong ontogenetic shifts in prey preferences (Ramos-Jiliberto et al. 2011). Thus, by extending niche descriptions beyond niche width and pairwise niche overlap, structural analyses of individual-based networks provide a quantitative assessment of how distinct traits affect intrapopulation variation of individual niches.

In several animal populations, individual variation in resource use is associated not with ontogeny, sex, or any obvious polymorphism but instead with individual dietary preferences (Bolnick et al. 2003). Models based on optimal diet theory provide a way of linking network structure to genetic-based preference ranks and intraspecific competition (Lemos-Costa et al. 2016). For

example, high levels of nestedness are expected if individuals show similar preferences but vary in their willingness to use additional resources (Lemos-Costa et al. 2016), as observed in the wasp *Sceliphron caementarium* (Sphecidae) when hunting spiders for offspring provisioning (Powell & Taylor 2017). Individual preferences are also modulated by population density and intraspecific competition, which can reshape dietary niches and, as a consequence, trophic networks. For example, at higher densities, sea otter individuals (*Enhydra lutris*, Mustelidae) specialize in distinct prey, leading to dietary modules, whereas at low density, individual animals have similar diets and no such modularity emerges (Tinker et al. 2012). However, dietary modules in sea otters are associated with the most consumed prey, whereas the binary description of resource use is nested, indicating the existence of different behavioral rules related to the consumption of primary and secondary resources (Tinker et al. 2012). From a broader perspective, these results exemplify how the combination of weighted and binary network metrics can reveal the intricate organization of individual niches (Araújo et al. 2008).

The association between trait variation and the intrapopulation niche structure characterized by individual-based networks may provide insights into diversification, adaptive evolution, and eco-evolutionary feedbacks. Network patterns may reveal how niches expand and separate during the diversification of a clade, as demonstrated by an association between a set of individual traits and dietary modules during the radiation of sharpfin sailfin silverside fish (Telmatherinidae) (Pfaender et al. 2010). Additionally, fitness measures increased with the centrality of plant individuals in individual-based networks involving floral visitors (Gómez & Perfectti 2012) and frugivores (Crestani et al. 2019), which may indicate that the structure of individual-based networks may be related to adaptive evolution. Accordingly, network patterns may have implications for average population fitness. For example, an analysis of networks describing how individuals of the plant *Erysimum medihispanicum* (Brassicaceae) share pollinator species across multiple populations revealed that the average population fitness varied with the network structure (Gómez et al. 2011). However, the mechanisms connecting population and individual fitness to the structure of individual-based networks remain unclear. By now, network approaches have revealed multiple novel patterns of variation within population niches shaped by space, time, and individual traits and preferences. A fundamental question that remains is the extent to which interspecific variation in ecological interactions affects the structure and dynamics of ecological communities (Bolnick et al. 2011; McPeck 2019; Melián et al. 2011, 2018).

4. NETWORKS AT THE COMMUNITY LEVEL: DISCONNECTED AND CONNECTED NETWORKS

Individual-based networks provide the building blocks for community-level networks (Dupont et al. 2011) (**Figure 3**). Examples of community-level networks include food webs and networks that describe one type of interaction among species, such as interactions among plants and seed dispersers or among parasites and hosts. Networks describing one type of interaction are often species-based networks (**Figure 1b**), in which almost every node depicts an individual species. In contrast, in food webs, nodes usually do not represent individual species (see the **Supplemental Material**). Recently, the network structures of an impressive variety of ecological interactions have been mapped (**Supplemental Table 3**). Our understanding of network structure diversity, however, is still biased toward food webs (Pascual & Dunne 2006) and particular types of mutualisms (Cagnolo 2018) (see the sidebar titled Mutualistic Networks). There are relatively few detailed studies on the structure of networks formed by commensalistic, facilitative, and competitive interactions (**Supplemental Table 3**).

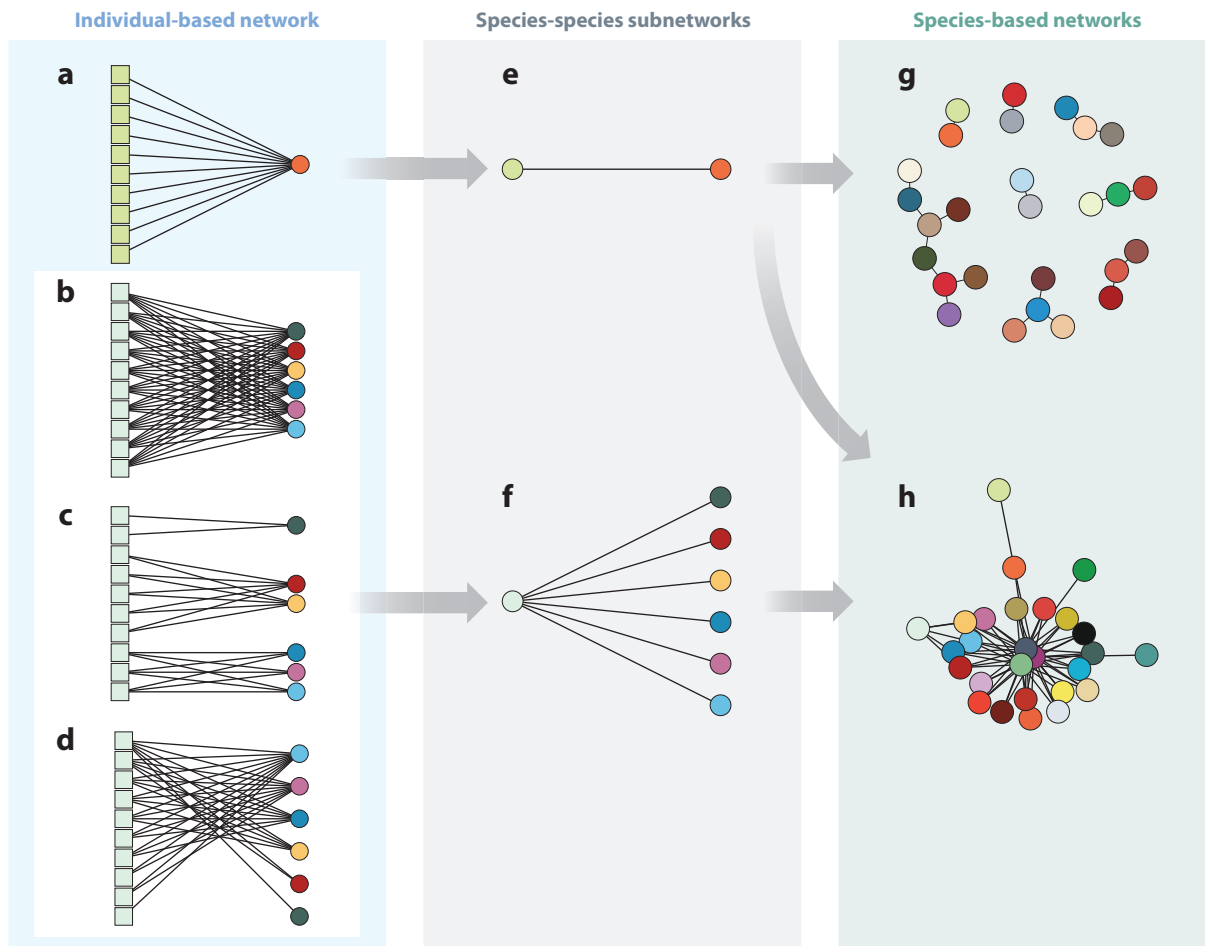


Figure 3

From individual-based networks to species-based networks. (*a–d*) Within populations, individuals (*squares*) can interact with a variable number of species (*circles*; different colors represent different species), leading to distinct individual-based networks. At the species level, these individual-based networks result in (*e, f*) species-species subnetworks. (*b–d*) Different individual-based networks can result in (*f*) the same species-species subnetwork. The species-species subnetworks combine with each other to form species-based networks. (*g*) Disconnected networks formed by multiple isolated groups of species can form only by combining (*e*) species-species subnetworks resulting from (*a*) populations of specialists, whereas multiple combinations of generalist and specialist populations lead to (*h*) connected networks.

MUTUALISTIC NETWORKS

Most of the so-called mutualistic networks include interactions that are not mutualistic. For instance, many pollination networks are actually networks of plants and floral visitors, including pollinators but also commensals and organisms with parasitic lifestyles, such as nectar robbers. Nevertheless, there can be no nectar robbers without plant-pollinator mutualisms. Hence, mutualistic networks can be viewed as networks that are built around a given type of mutualism, even if not all species or interactions in the network are mutualistic.

From the studies that have been done, we now know that variation in structure is common across species-based networks (e.g., Blüthgen et al. 2007). At the simplest levels, species-based networks vary in species richness, connectance, and bipartivity. Species-based networks also vary in more intricate aspects of their structure, such as nestedness and modularity. Variation in network structure is partially associated with environmental factors (Mendoza & Araújo 2019, Schleuning et al. 2012, Song & Saavedra 2020; but see Fontoura et al. 2020) and interaction rules (Allesina et al. 2008, Brose et al. 2019, Williams & Martinez 2000). By integrating three entities—(a) individual-based networks, (b) fundamentals of network science, and (c) basic attributes of natural history—we may obtain deeper insights into how networks at the community level are organized.

We are beginning to understand more precisely how individual variation is related to the structure of food webs (Gibert & DeLong 2017, Melián et al. 2011) and species-based networks (Tur et al. 2015). Two basic structural attributes of individual-based networks shape the structural patterns of species-based networks and food webs. First, the interaction patterns at the individual level determine the number of species interacting with a given species at the community level (**Figure 3a–f**). Second, how individuals from different species share resources and interaction partners defines the patterns of overlap among species at the community level. The number of interaction partners at the species level and the patterns of partner overlap among species are ultimately associated with the network patterns observed at the community level (**Figure 3g,b**). Therefore, the structural configurations observed across species-based networks partially emerge from the way in which different individual-based networks combine and interact with each other. These combinations of individual-based networks in turn may lead to novel ecological and evolutionary dynamics, reshaping the intraspecific variation in traits and preferences and, consequently, the structure of individual-based networks.

Ecological networks, like other complex networks, often have two basic structural configurations at the community level: (a) disconnected networks that are collections of small, isolated groups (components) of interacting species (**Figure 3g**) and (b) connected networks with a giant component (see the sidebar titled Connected Networks), in which most species are connected to each other through direct or indirect pathways (**Figure 3b**). Random graph theory predicts that disconnected networks and networks with a giant component represent two structural phases that are separated by a critical transition associated with changes in the distribution of interactions per species [the degree distribution (Newman et al. 2001)]. Specifically, disconnected networks (i.e., those in the subcritical phase) are associated with a small average number of interactions per species and with low variance in the number of interactions across species, whereas networks with a giant component (i.e., those in the supercritical phase) are associated with the presence of at least a few highly connected species (see the sidebar titled The Emergence of a Giant Component). Empirical species-based networks match these two different structural phases, and the transition between the two phases occurs near the critical point predicted for random bipartite networks with fixed degree distributions (**Figure 4**). Hence, the ecological and evolutionary factors that affect the mean number of interactions per species and the variance in the number of interactions across species may also lead to great changes in network organization at the community level.

Bipartivity: the degree to which interactions occur only between nodes from two different sets (e.g., plants and herbivores)

Giant component: a network shows a giant component if there are direct or indirect pathways of interactions connecting most nodes of the network

CONNECTED NETWORKS

Formally, a connected graph is a graph in which there is a direct or indirect pathway connecting every pair of nodes of the network. Here, I used a broader definition by also considering connected networks those networks characterized by a giant component, even if not all species are part of this component.

THE EMERGENCE OF A GIANT COMPONENT

In random networks, the critical point separating the structural phases (e.g., disconnected networks and networks with a giant component) is controlled by a connectivity parameter. This result applies to multiple forms of random networks. In Erdős-Rényi graphs, in which the probability of the occurrence of an interaction is constant and equal for all possible interactions, the giant component is expected to emerge if $\langle k \rangle > 1$, where $\langle k \rangle$ is the average degree. Erdős-Rényi graphs show binomial degree distributions, whereas ecological networks often show distinct forms of degree distributions. For random networks with arbitrary (fixed) degree distributions, the giant component is expected to emerge if $c_1 = \langle k^2 \rangle - 2\langle k \rangle > 0$, where $\langle k^2 \rangle$ is the average of the square of the degrees of the nodes in the network. For random networks with fixed degree distribution showing bipartivity, the emergence of a giant component occurs if $c_2 = \sum_{i=1}^{M_I} \sum_{j=1}^{M_J} ij(ij - i - j)p_i p_j > 0$, where M_I (M_J) is the largest degree recorded in set I (J), and p_i (p_j) is the relative frequency of nodes with a degree equal to i (j) (Newman et al. 2001). For the last two forms of random networks, the higher the variance in the degree distribution, the higher the connectivity parameter, and consequently, the network shows a giant component.

Among these factors, the natural history of ecological interactions at the individual level has a major impact on how species-based networks are organized at the community level (Guimarães et al. 2007, Poisot et al. 2013).

Disconnected networks are often observed for intimate interactions (Fontaine et al. 2011, Guimarães et al. 2007, Pires & Guimarães 2013). Intimate interactions are those between an organism that completes at least one life stage on a single host individual and that host (Ollerton 2006, Price 1980, Thompson 1994). Examples include antagonisms between flowerhead tephritids and Asteraceae plants (Prado & Lewinsohn 2004) and mutualisms between ants and myrmecophytes (Fonseca & Ganade 1996). In intimate interactions, each interaction event may have a major impact on individual fitness, and selection may lead to specialization at the individual and population level (Price 1980, Thompson 1994), thereby leading to individual-based networks in which all individuals interact with partners from the same small set of species (**Figure 3a,e**). If the interaction has a high impact on the individual fitness of both interacting partners, selection may foster reciprocal specialization (Fonseca & Ganade 1996, Thompson et al. 2013) or coevolutionary arms races (Pires & Guimarães 2013, Zu et al. 2020) at the population level. Either way, if this scenario holds for all species interacting in a particular way in a given community (e.g., all leaf-mining insects and their host plants), then selection may prevent the evolution of generalists in the system. As a consequence, the system would be characterized by a low mean number of interactions per species and low variance in the number of interactions across species, leading to a subcritical network with a disconnected structure (Guimarães et al. 2007) (**Figures 3g** and **4**).

Not all intimate interactions form disconnected networks, though. For example, many parasite-host networks form cohesive, connected networks (Poulin 2010, Vázquez et al. 2005). More research is needed to understand why some intimate interactions form disconnected networks, whereas others form connected networks. The answer may depend on the level of heterogeneity in traits that mediate interactions across species. If the traits mediating interactions in a given set of species are homogeneous, then the resulting network is expected to be connected (Pinheiro et al. 2019). In contrast, for intimate interactions that form disconnected networks, interaction patterns usually show a strong association with phylogenetic patterns (Fonseca & Ganade 1996, Lewinsohn et al. 2006), suggesting that similar traits are mediating interactions in groups of closely related species. In contrast, distantly related species have disparate traits and, as a consequence, a completely distinct set of interaction partners, forming disconnected networks.

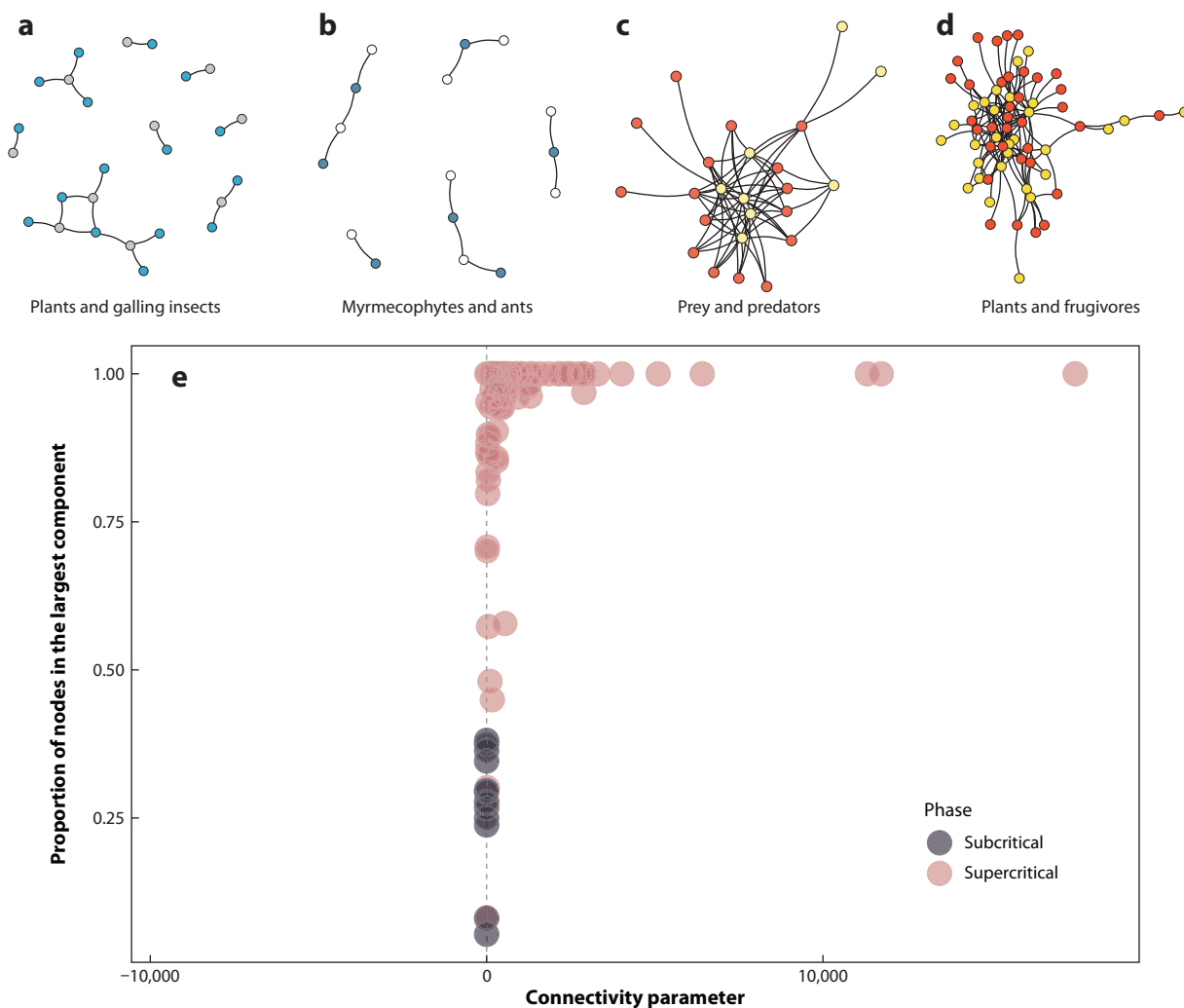


Figure 4

The two structural phases of species-based networks. Some ecological interactions form disconnected networks, such as (a) plants and galling insects (Tscharrntke et al. 2001) and (b) myrmecophytes and ants (Guimarães et al. 2007). In contrast, other ecological interactions form networks characterized by a giant component in which indirect or direct pathways connect most species, such as (c) prey and predators (Baskerville et al. 2011) and (d) plants and frugivores (Galetti & Pizo 1996) (**Supplemental Material**).

(e) Random graph theory predicts that disconnected networks and networks with a giant component represent phases separated by a critical transition point. This point is modulated by a connectivity parameter that depends on the distribution of the interactions per species (see text for further details). Colors indicate empirical species-based networks that are predicted to show a giant component (supercritical networks, *red circles*) or to be disconnected networks (subcritical, *black circles*). Note the sharp increase in the size of the largest component with the connectivity parameter. The data set includes 65 mutualistic networks and 27 antagonistic networks with species richness greater than 10 species. One outlier mutualistic network, with a connectivity parameter equal to 50568.34 and all species in a single component, was removed to improve the plot legibility. An online simulation that explores the emergence of giant components in random bipartite networks is available at <https://miudolab.shinyapps.io/giant-component-bipartite/>.

Supplemental Material >

Connected networks are always observed in species-based networks depicting interactions in which consumer individuals have multiple individual partners throughout their lives, as observed in plant-frugivore and predator-prey interactions. In these ecological interactions, the fitness consequences of each interaction event are likely to be small for consumers, leading to generalism at the individual level (**Figure 3b**; **Supplemental Material**). In some cases, individuals of a particular species rely on the resources or services provided by the network (e.g., fruits) and not on particular species. These highly connected species are termed supergeneralists (Jordano et al. 2003, Thompson 2005) and in fact have extremely specialized lifestyles that—despite having several interaction partners—depend on the network to survive (**Supplemental Material**). Supergeneralists are a recurrent element of species-based networks, and examples include obligate frugivores, hypercarnivores, obligate-cleaner fishes, and honey bees. Ecological opportunity, intraspecific variation in traits and preferences, high levels of intraspecific competition, and low levels of predation and interspecific competition (Araújo et al. 2011, Gibert & DeLong 2017, Melián et al. 2011, Pornon et al. 2017) may also foster the formation of individual-based networks with distinct combinations of specialist and generalist consumers within populations (**Figure 3c,d**). Highly connected resource species in turn may emerge as a consequence of multiple species specializing in an abundant resource (Xi et al. 2020). In all these scenarios, independent of the details of the underlying within-population niche structure, the resulting pattern at the species level would be a highly connected species (**Figure 3f**). Selection would favor the evolution of at least a few generalist species, leading to a larger mean number of interactions per species, a higher variance in the number of interactions across species, and supercritical networks with a connected structure at the community level (**Figures 3b** and **4**).

If there are even just a few generalist species, a connected network emerges (Martín-González et al. 2010), with multiple pathways connecting species. These pathways may have deep consequences for eco-evolutionary feedbacks and cascading effects. A disconnected network structure implies that the dynamical consequences of ecological interactions are limited to pairs or to small groups of interacting species (e.g., Guimarães et al. 2007). In contrast, a connected network structure implies that trophic cascades, trait-based cascades, and eco-evolutionary feedbacks can propagate across multiple species in the community. For example, indirect effects generated by the decline in sea otters in the Aleutian Archipelago propagated across trophic chains, resulting in a dietary shift in bald eagles (Anthony et al. 2008). In fact, most of the classic empirical examples of keystone species shaping ecological communities due to indirect effects show species with either (a) generalist diets or (b) generalism at the species level emerging due to intrapopulation variation in traits or preferences (Estes et al. 2003, Paine 1966). From a network perspective, at least some keystone species can be viewed as highly connected species that shift the community-level dynamics by promoting connectedness in ecological networks.

5. NETWORKS AT THE COMMUNITY LEVEL: THE STRUCTURE OF CONNECTED NETWORKS

In the previous section, I described how different forms of individual-based networks favor the occurrence of disconnected and connected networks at the community level. Specifically, I argued that highly connected species in ecological communities promote the emergence of connected networks. In this section, I will explore how the emergence of highly connected species impacts the structure of connected networks. Highly connected species represent one of the key features of food webs (Mora et al. 2018) and some species-based networks (Jordano et al. 2003). A general pattern observed in ecological networks is that just a few species are highly connected. The presence of a few highly connected species implies the existence of heterogeneous patterns of

interaction, such as wide variation in the number of interactions across species (Jordano et al. 2003, Solé & Montoya 2001), species centrality (Jordán et al. 2007), and interaction strength (Bascompte et al. 2006, McCann et al. 1998).

The primary factor associated with a heterogeneous network structure is variation in the abundance of different species. In the simplest scenario, where we assume a homogeneous environment and that individuals of all species are generalists, individuals interact randomly as there are no preferences (Krishna et al. 2008, Vázquez 2005). In this scenario, only a few species would end up with many interactions; most would end up with few interactions (Vázquez 2005) because, in ecological communities, most species are rare and only a few are abundant (Preston 1948). As a result of the heterogeneous patterns of species abundance, numerous potential interactions do not take place simply because individuals are unlikely to physically meet (Krishna et al. 2008). Similar heterogeneity can also be observed in the distribution of interaction strengths in mutualistic networks and food webs, i.e., most interaction strengths are weak (Bascompte et al. 2006, McCann et al. 1998, Neutel et al. 2002). These weak interaction strengths are also partially generated by differences in species abundances (Blüthgen et al. 2008). The effect of species abundance on network interaction patterns, however, is not unidirectional: Besides affecting heterogeneity in the number of interaction partners and interaction strengths, species abundances are also the demographic consequence of ecological interactions (May 1972, Xi et al. 2020). An open problem in the study of ecological network structures is how to detangle the potential feedback between interaction patterns and species abundances (Dormann et al. 2017, Fort et al. 2016).

Regardless of the direction of causality in the abundance-interaction relationship, these missing (Olesen et al. 2011a) and weak links are not merely the outcome of insufficient sampling efforts; instead, some links may be so rare that they have negligible impacts on ecological processes. Caution is needed, however, when assuming rare species and weak links have negligible impacts on ecological dynamics. For example, weak links may promote the stability of ecological systems against perturbation (McCann et al. 1998, Neutel et al. 2002, Ushio et al. 2018). Moreover, keystone species, which are, by definition, rare and highly influential species, provide a clear exception to the typical relationships between abundance and both the number of interaction partners and interaction strength (Power et al. 1996). Some weak links may represent important albeit infrequent interactions, such as the use of fallback resources by consumers (Marshall et al. 2009) or rare events of cross-habitat seed dispersal by frugivores (Carlo & Yang 2011, Donoso et al. 2020). Weak interaction strengths may also promote stronger opportunities for selection than strong interaction strengths in mutualisms (Benkman 2013).

Departures from expectations regarding the relationship between species abundances and network patterns illustrate the role of species traits in shaping patterns of interaction. In predator-prey interactions, the larger the predator, the larger the set of prey they usually consume, leading to heterogeneity in the number of interactions across species (Owen-Smith & Mills 2008) and in interaction strengths (Woodward et al. 2005). In ant-plant mutualisms, ants with effective recruitment monopolize plant-provided resources, whereas outcompeted ant species are limited to a few plant species (Dáttilo et al. 2014a). Heterogeneity in interaction strength may also be affected by the adaptive trophic behavior of consumers (Kondoh 2003, Valdovinos 2019). Traits (and preferences) may also decrease interaction heterogeneity in the network. For example, in mutualisms, cospecialization and preferences partially offset the effects of abundance, leading to higher levels of reciprocity in interaction strengths than expected based on the number of interaction events recorded per species (Blüthgen et al. 2008, Dehling et al. 2016, Sonne et al. 2020, Staniczenko et al. 2013). Thus, the level of heterogeneity in the different aspects of network structure is an outcome of the complex interplay between the effects of abundances, preferences, and traits.

NESTEDNESS IN MUTUALISMS AND ANTAGONISMS

Many mutualisms, like antagonisms, can be viewed as consumer-resource interactions (Holland et al. 2005). However, mutualisms differ from antagonisms in the fitness outcomes for interacting individuals. Levels of nestedness that are usually higher than those expected for simple random networks were first recorded in mutualistic networks describing seed dispersal and pollination by animals (Bascompte et al. 2003). The levels of nestedness observed in these mutualisms differ from those observed in food webs, suggesting that nestedness is a property of mutualisms (Bascompte et al. 2003). However, we currently know that nestedness is also commonly observed in species-based networks of different forms of antagonisms and that some forms of mutualisms show no evidence of nestedness (Fontaine et al. 2011). Indeed, a current challenge in the study of ecological networks is determining whether it is possible to separate antagonisms and mutualisms based on the network structure (Michalska-Smith & Allesina 2019, Song & Saavedra 2020).

The heterogeneous structure of connected networks implies the existence of structural asymmetries, such as the prevalence of pairwise interactions connecting poorly to highly connected species (Vázquez & Aizen 2004, Vázquez et al. 2005, Xi et al. 2020) and the asymmetries observed in interaction strengths within pairwise interactions (Bascompte et al. 2006). The variation in number of interactions per species, combined with interaction asymmetries and the presence of interactions among highly connected species, leads to nestedness (Bascompte et al. 2003, Verdú & Valiente-Banuet 2008). Because these three fundamental components of nestedness are fostered by differences in species abundances, nestedness is partially a consequence of species abundance distributions (Krishna et al. 2008). Some traits also foster nestedness by imposing forbidden links (Jordano et al. 2003, Olesen et al. 2011a, Santamaría & Rodríguez-Gironés 2007, Sinclair et al. 2003). Nestedness may be a simple consequence of skewed species abundance and trait distributions; as a result, it is observed in different types of ecological interactions (see the sidebar titled *Nestedness in Mutualisms and Antagonisms*).

Regardless of the process by which it is generated, a nested structure implies a profusion of pathways connecting species at the community level. From a mathematical perspective, nestedness and the presence of highly connected species imply high pathway proliferation, i.e., the number of pathways connecting two species increases exponentially with the length of the pathways (Borrett et al. 2007, Guimarães et al. 2017). Hence, the number of indirect pathways markedly exceeds the number of direct interactions in an ecological network. Due to their numerical dominance, indirect pathways may be fundamental for coevolution in large assemblages of interacting species (Guimarães et al. 2017); for energy, mass, and information flow in ecosystems (Borrett et al. 2007, Hannon 1973); and for the disparate consequences of the loss of apex consumers in natural communities (Estes et al. 2011).

In addition to creating multiple pathways connecting species, by sharing interaction partners with multiple species in nested networks, highly connected species reduce the distance in links between species pairs (Olesen et al. 2006). In general, short distances between nodes are one of the most fundamental expectations of network science, since only very special classes of networks, e.g., regular lattices, show large distances between pairs of nodes (Watts & Strogatz 1998). A number of additional factors also promote the presence of short pathways in networks at the community level. In food webs, short trophic chains between basal species and top consumers are partially explained by the fact that food-web trophic levels are not well defined (Wolkovich 2016). Additionally, a variety of constraints (Post 2002), such as inefficient energy transfer [Elton 2001 (1927)], demographic instability (Pimm & Lawton 1977), and changes in nutrient content and

Forbidden links:

pairwise interactions that cannot occur due to trait mismatching or spatiotemporal uncoupling

assimilation across trophic levels (Wilder et al. 2013), may prevent the emergence of long food chains. Hence, multiple ecological factors also contribute to the presence of multiple indirect pathways—many of them short—linking species in a connected network.

Short pathways indeed characterize pollination networks (Olesen et al. 2006), host-pathogen networks (Fodor 2011), food webs (Montoya & Solé 2002, Williams et al. 2002), and phytoplankton communities (Carey et al. 2017). Even in the presence of modules of interacting species (Pimm & Lawton 1980), which are expected to increase network pathway lengths, the presence of highly connected species shortens pathways by connecting species from different modules (Melián & Bascompte 2004, Olesen et al. 2007). For example, in food webs, modules can be generated by the presence of distinct energy channels, i.e., food chains that are maintained by one or a few basal species groups (Zhao et al. 2018). These energy channels may lead to spatial modules (Krause et al. 2003, Raffaelli & Hall 1992). However, these spatial modules are not isolated but are connected to each other by highly connected top consumers (Baskerville et al. 2011, Rooney et al. 2006).

Highly connected species may also connect modules generated by trait variation across potentially interacting species (Donatti et al. 2011, Schleuning et al. 2014). High trait variation across species may lead to the formation of modules due to specialization (Poisot et al. 2013), intervality (Guimerà et al. 2010, Stouffer et al. 2006), interspecific competition (Dalerum et al. 2016, Valverde et al. 2020), trade-offs in resource use (Pinheiro et al. 2019), and the combination of multiple ecological and evolutionary factors (Rezende et al. 2009). However, the impact of trait variation on species interactions is not straightforward, being dependent on the rules connecting traits of interacting species (Gibert & DeLong 2017, Gravel et al. 2016). If trait variation hinders the emergence of highly connected species, loosely connected networks should emerge in which some modules may present internal nested patterns due to differences in species abundance and forbidden links (Lewinsohn et al. 2006, Pinheiro et al. 2019, Vacher et al. 2008). If, however, some highly connected species are able to interact with partners with disparate traits, then different modules will be connected to each other through the pathways created by these highly connected species (Olesen et al. 2007, Schleuning et al. 2014). Therefore, the presence of highly connected species shapes the cohesiveness of ecological communities, markedly affecting different aspects of their network structure.

6. BEYOND FOOD WEBS AND SPECIES-BASED NETWORKS

Food webs and multiple types of species-based networks are connected to each other by shared species, leading to networks of multiple types of interaction (Hale et al. 2020, Kéfi et al. 2016, Olf et al. 2009, Pilosof et al. 2017, Yeakel et al. 2020). In this context, species interacting with multiple partners in distinct networks, such as plant species, may link otherwise isolated networks within a community (Dáttilo et al. 2016). Moreover, networks of one interaction type may create the backbone on which other ecological networks are built. For instance, some parasite-host interactions are, at least partially, built over the trophic links of food webs (Stella et al. 2018). Similarly, interactions among consumers and resources in a food web are the backbone on which multiple non-trophic interactions are built (García-Callejas et al. 2018), leading to the emergence of facilitative (Freilich et al. 2018) and competitive networks (Eurich et al. 2018). Networks of one interaction type are also coupled to each other by specific traits that simultaneously mediate different interaction types (Herrera 1986) or by genetic correlations among traits involved in different interactions (Berg 1960, Melián et al. 2018). In either case, traits under selection imposed by distinct interactions and/or integrated due to genetic correlations may allow indirect evolutionary effects to propagate not only across a given type of interaction (e.g., pollination by animals) but also across networks formed by distinct sets of interactions. The integration of ecological interactions and

Intervality:

in food webs, intervality implies that most resources can be ordered along a single axis such that consumers show high levels of dietary contiguity

complex genetic effects may foster unanticipated coevolutionary dynamics (Kauffman & Johnsen 1991). In the quest for understanding the evolutionary and ecological consequences of networks of multiple types of interactions, a fundamental step is to describe their structural patterns.

The few studies that have explored networks of multiple types of interactions suggest that heterogeneity also characterizes their structural patterns. In a network describing interactions between plants and their herbivores, pollinators, and seed dispersers, the ratio of mutualistic to antagonistic interactions varied widely across plants, with just a few plants showing very high mutualism to antagonism ratios (Melián et al. 2009). Similarly, in a network combining different types of mutualism, a small number of highly connected species had a strong impact on the structure, promoting nestedness and reducing modularity (Dáttilo et al. 2016). In contrast, analysis of a comprehensive network describing trophic, competitive, and facilitative interactions in a marine rocky intertidal habitat revealed that species were organized into groups and one interaction type prevailed in each group (Kéfi et al. 2016). We are just beginning to understand the structure of networks combining multiple types of interaction, but these examples suggest that highly connected species may, in at least some systems, promote the integration of disparate types of interaction. These linkages among species-based networks lead to different network structures with potential implications for ecological and evolutionary dynamics (Evans et al. 2013, Fontaine et al. 2011). For example, theoretical work suggests that the combination of antagonistic and mutualistic interactions promotes stability in ecological communities, challenging the long-standing notion that highly interactive, species-rich communities are intrinsically unstable (Hale et al. 2020, Mougi & Kondoh 2012, Qian & Akçay 2020). A fundamental challenge going forward will be to understand under which conditions the demographic and coevolutionary consequences of network structure will be restricted to a single species-based network versus having cascading effects on the network formed by multiple species-based networks.

Networks are connected not only to other networks within ecological communities but also across spatial scales (Albouy et al. 2019, Li et al. 2020, Timóteo et al. 2018). Interacting species often operate at very distinct spatial and temporal scales and, as a consequence, the spatial boundaries of species-based networks and food webs are rarely clear (Polis et al. 2004, Tylianakis & Morris 2017). Highly connected species that operate at broader spatiotemporal scales, such as top consumers, connect otherwise isolated habitats (Bartley et al. 2019, Dobson 2009, Vestbo et al. 2018), thus forming meta-networks (Tylianakis & Morris 2017). Across large spatial scales, the structure of ecological networks is the result of interaction patterns at the local level, variation in specialization across space, and spatial processes that determine species occurrence (Albouy et al. 2019; Baiser et al. 2019; Braga et al. 2019; Galiana et al. 2018; Gravel et al. 2011, 2018; Poisot et al. 2014; Tylianakis & Morris 2017). Spatial uncoupling of species distributions creates novel sets of forbidden links (Albouy et al. 2019), and as a consequence, networks at broader spatial scales may show very distinct structural patterns (Kissling & Schleuning 2015). For instance, at the local level, the intimate interactions between anemones and anemonefishes form disconnected networks. In contrast, at broader regional scales, these interactions form nested networks because some species have broad geographical distributions (Ollerton et al. 2007). Indeed, because nested patterns of distributions are common (Atmar & Patterson 1993), meta-networks may show nested interaction patterns. For example, the geographical co-occurrence of plants and nectarivorous and frugivorous bats contribute to nestedness within modules of interacting species in a multilayer network at the continental scale (Mello et al. 2019).

Ecological networks are also interconnected across temporal scales (Olesen et al. 2008, 2011b; Schwarz et al. 2020). At short temporal scales, the sequential description of an ecological network may provide information on the assembly and the turnover of pairwise interactions (Olesen et al. 2008, 2011b). In this context, some highly connected species are those species that interact with

multiple partners across time and create the constancy of macroscopic network patterns (Chacoff et al. 2018, Olesen et al. 2011b). At longer timescales, macroevolutionary associations between ecological interactions and traits can be revealed by the phylogenetic patterns of ecological networks (Emer et al. 2019, Segar et al. 2020).

Closely related species usually show similar numbers and patterns of interactions within and across species-based networks and food webs (Chamberlain et al. 2014, Eklöf et al. 2011, Gómez et al. 2010, Krasnov et al. 2012, Naisbit et al. 2012, Poulin et al. 2013, Rezende et al. 2007, Stouffer et al. 2012), suggesting macroevolutionary patterns of interaction. However, evolution and coevolution do not necessarily lead to phylogenetically structured interactions (Ibáñez et al. 2016, Nuismer & Harmon 2014). For instance, selection related to seed dispersal by animals may favor trait convergence mediated by highly connected species (Guimarães et al. 2011), erasing phylogenetic structure in traits and favoring the ecological fitting of novel partners (Vizentin-Bugoni et al. 2019, Thompson 2005). Thus, the association between phylogenies and network patterns can have many possible shapes.

By exploring the multiple possible associations between phylogenies and ecological interactions we can address how ecological interactions affect and are affected by macroevolutionary dynamics (Harmon et al. 2019, Zanata et al. 2017). In this sense, clade-based networks (**Figure 1c**) may provide insights into the organization of ecological interactions across long temporal scales. For example, in a comprehensive study of specialization across multiple taxa, closely related species were likely to be part of modules with similar hosts, defined at different taxonomic levels (Gómez et al. 2010), indicating that the modularity of species interactions emerges at different phylogenetic scales. As observed in species-based networks at a local level, the presence of highly connected species blurs the modular structure, and clades of generalist species often show weaker modular patterns than clades of specialists (Gómez et al. 2010).

By exploring distinct phylogenetic scales, one can investigate how interaction patterns shift when we move from species to entire clades. For example, at the local level, species-based networks of Lepidoptera larvae and their host plants are characterized by high levels of specialization and modularity (Pires & Guimarães 2013, Zu et al. 2020). In contrast, clade-based networks of Pieridae and Nymphalidae butterfly genera and their host plants (at the family and order levels, respectively) show that these networks are characterized by modules with internal nestedness (Braga et al. 2018). Nestedness, at this macroevolutionary scale, may be related to the use of ancestral hosts and to variability in host use across butterfly genera, whereas modularity may result from the colonization of new plant hosts by herbivore lineages (Braga et al. 2018). Thus, a highly connected clade may emerge from collections of species specialized in different resources in the same way that a highly connected population may emerge from collections of individuals specialized in different resources.

Despite the inherent difficulties involved in estimating ecological interactions in the past (Dunne et al. 2008), future work exploring the structure of clade-based networks may provide information on how ecological interactions affect the diversification of clades across large temporal scales. For example, the effects of ecological interactions on speciation and extinction rates can be described as networks in which clades are nodes and these effects are depicted as links (Silvestro et al. 2015). Network description may also provide insights into a number of macroevolutionary dynamics, such as the *de novo* evolution of highly connected lifestyles, for example, that of hypercarnivores (Van Valkenburgh et al. 2004); clade turnover in interacting assemblages (Drossel et al. 2001, Eriksson 2016); temporal variation in ecological disparity (Bush & Bambach 2011); and metabolic host reprogramming by viruses in eukaryotic lineages (Schulz et al. 2020).

7. CONCLUDING REMARKS: THE HIERARCHICAL ORGANIZATION OF ECOLOGICAL NETWORKS

After decades of research, we now have a better understanding of the structure of some types of ecological networks, such as food webs and some mutualistic, species-based networks. The picture is less clear for other types of species-based networks and networks at higher and lower levels of organization. Nevertheless, it is possible to identify potential regularities. Modularity, nestedness, and multiple forms of interaction asymmetry were observed in individual-based, species-based, and clade-based networks of different interaction types. Only by enlarging the set of empirical networks described at different levels of organization will we be able to create a map of how ecological networks are organized. Expanding network description across larger scales may also allow a better understanding of how interaction patterns, which are built over millions of years, are now being rapidly disrupted and reshaped by species extinctions and invasions promoted by human activity (Aizen et al. 2012, Bartley et al. 2019, Mendoza & Araújo 2019, Trøjelsgaard et al. 2019, Tyljanakis et al. 2007, Valido et al. 2019, Worm & Paine 2016). At a smaller scale, every individual plant, animal, or fungus hosts microbiotas, which form microbiome networks (Layeghifard et al. 2019, Vacher et al. 2016). Increasing evidence suggests that these microbiome networks may affect a number of features of their hosts and, consequently, host fitness (Gould et al. 2018, Layeghifard et al. 2019). By exploring microbiome networks and their underlying biochemical pathways, we may approach the integration of all biological networks and start to ask questions about how processes and patterns scale from the metabolic and genomic levels to ecological networks at the biosphere level (Melián et al. 2018).

A challenge that lies ahead will be to understand whether and how similar network structures emerge at different levels of organization. Fundamental architectural rules seem to hold for most networks (e.g., Mora et al. 2018), such as the rules governing phase transitions between disconnected networks and networks with a giant component (Newman et al. 2001) and the presence of multiple, short pathways connecting species (Guimarães et al. 2017). In addition to these fundamental rules, the interplay between numerical effects, traits, and preferences shape network structures at different ecological scales. Numerical effects, derived from the probability of encounters between potentially interacting individuals, species abundances, and geographical distributions, generate a template of potential interactions and fuel interaction heterogeneities and asymmetries in ecological networks. The set of potential interactions is further modified by the traits of individual organisms, species trait distributions, and trait distributions at the clade level, leading to intricate network patterns, such as modularity.

The emergence of similar network patterns at different ecological scales does not indicate that ecological networks are scale invariant. Studies exploring interaction patterns in the same system across multiple scales indicate that network patterns change with the scale of description (Tur et al. 2015). Therefore, to understand how similar and disparate network patterns are intertwined across scales, we need to explore the hierarchical organization of ecological interactions (Baiser et al. 2016, Melián et al. 2018, Poisot et al. 2014, Segar et al. 2020). For instance, distinct network patterns at an individual level lead to similar patterns at the species level (**Figure 3**). When scaling ecological interactions up, from individuals to species and beyond, we aggregate collections of interacting units of finer scales into interacting units at broader scales. As a consequence, sets of individuals specialized for different resources lead to highly connected populations at the local level (Bolnick et al. 2003), sets of populations specialized for different resources lead to highly connected species at large spatial and temporal scales (Thompson 2005), and sets of closely related species specialized for different resources lead to highly connected clades (Lerner et al. 2011). Since the presence of a few highly connected units is sufficient for connected networks to emerge,

I predict that ecological networks at higher levels of organization will usually show a connected structure. If this is the case, the pathways that characterize connected networks at higher levels of organization may indicate the existence of myriad indirect effects operating in different spatial, temporal, and organization scales. I suggest that a fundamental goal for the near future is to elucidate the role of these indirect effects in promoting the integration of interacting ecological assemblages of individuals, species, and clades.

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RELATED RESOURCES

An online simulation that generates bipartite random networks for the visualization of the phase transition that generates a giant component in complex networks is available at <https://miudolab.shinyapps.io/giant-component-bipartite/>



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