# Ecological interaction networks. What we know, what we don't, and why it matters

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**Abstract.** Species coexisting in ecological communities interact in multiple ways to form complex networks. We review the growing literature on ecological interaction networks to address several key issues about this conceptual and methodological approach. We start by asking the most basic question: Why study networks and whether a network approach is (or is not) useful to understand the ecology of interacting species, the functioning and stability of the communities they belong to, and their response to global change drivers. We also discuss the multiple meanings of network nodes as individuals, populations and species, the different ways of quantifying node roles, the multiple meanings of links as presence/absence of interactions, per capita interaction strengths and species-level effects, and the available approaches to study networks with different types of interactions. Then, we review the structural patterns emerging in ecological interaction networks and the mechanisms driving network structure and function, identifying both what we already know and the knowledge gaps that we still need to fill in. We also discuss sampling effects and their influence in distorting observed network patterns. Finally, we review how different drivers of global environmental change influence the structure, dynamics and stability of ecological networks. With this review we hope to offer a balanced overview of what we have learned in the study of ecological interaction networks and point to several key avenues of research for the next decade.

[Keywords: global change, interaction strength, modularity, nestedness, network nodes, neutral processes, niche processes, sampling effects, species interactions, species roles]

**Resumen. Redes de interacciones ecológicas. Qué sabemos, qué no, y por qué importa.** Las especies que coexisten en las comunidades ecológicas interactúan de diferentes modos y forman redes complejas. Presentamos una revisión de la creciente literatura sobre redes de interacciones ecológicas para abordar varias cuestiones clave sobre este enfoque conceptual y metodológico. Comenzamos con la pregunta más básica: por qué estudiar redes y si un enfoque de redes es (o no es) útil para comprender la ecología de las especies que interactúan, el funcionamiento y la estabilidad de las comunidades a las que pertenecen y su respuesta a los impulsores del cambio global. También discutimos los múltiples significados de los nodos como individuos, poblaciones y especies, las diferentes formas de cuantificar los roles de los nodos, los numerosos significados de los enlaces como presencia/ausencia de interacciones, fuerza de interacción per cápita y efectos a nivel de especie, y los enfoques disponibles para estudiar redes que incluyen diferentes tipos de interacciones. Luego, ofrecemos una reseña de los patrones estructurales que emergen en las redes de interacciones ecológicas y de los mecanismos que determinan la estructura y el funcionamiento de las interacciones e identificamos lo que ya sabemos y los vacíos de conocimiento que todavía necesitamos llenar. También discutimos los efectos de muestreo y su influencia distorsionando los patrones observados en las redes. Finalmente, discutimos cómo los diferentes impulsores del cambio global influencian la estructura, la dinámica y la estabilidad de las redes ecológicas. Con esta revisión esperamos ofrecer una reseña equilibrada de lo que hemos aprendido en el estudio de las redes de interacciones ecológicas y señalamos varias prioridades de investigación para la próxima década.

[Palabras clave: cambio global, fuerza de interacción, modularidad, anidamiento, nodos de redes, procesos neutrales, procesos de nicho, efectos de muestreo, interacciones interespecíficas, roles de las especies]

## Introduction

Ecology is the science of interactions between organisms and their environment, which includes the physical environment and other organisms. Because environments consist of multiple components, ecological interactions form complex networks with characteristic structure and function. From al-Jâḥiẓ's (1323) idea that all animals eat and are eaten, to Alexander von Humboldt's 'net-like intricate fabric' (Wulf 2015), to Charles Darwin's (1859) analogy of the 'entangled bank' in The Origin of Species, to Charles Elton's (1927) 'elaborate and complex arrangements of the food-cycle', nature observers have long marveled at the intricacies of ecological interactions (Ings and Hawes 2018).

Early studies of ecological interaction networks emphasized trophic interactions:

ʹFood is the burning question in animal society, and the whole structure and activities of the community are dependent upon questions of food-supplyʹ (Elton 1927). The study of these 'food webs' brought about many key insights in ecology, including keystone species and their role in shaping the structure of species assemblages (Paine 1966), the influence of complexity in the stability of theoretical communities (May 1973) and the relationship between pattern and process in empirical food webs (Cohen 1977; Pimm et al. 1991). Some of these early ideas evolved with the availability of better, more resolved data for species and interactions (Martínez 1991; Polis 1991; Lafferty et al. 2008). More recently, incorporating non-trophic interactions, such as mutualism (Bascompte and Jordano 2014), has broadened our understanding of the complex nature of ecological interaction networks.

We review the growing literature on ecological interaction networks to address several key issues about this conceptual and methodological approach. We cover topics underemphasized in previous reviews (Bascompte and Jordano 2014; Dormann et al. 2017; Dáttilo and Rico-Gray 2018; Delmas et al. 2019; Guimarães Jr. 2020), which we believe represent important themes in the study of ecological networks. Furthermore, we tried to explain the ideas in a plain, simple way to provide a comprehensible general overview on ecological networks, especially for those new to the field.

We start by asking why to study ecological communities using a network approach. Then, we discuss the different meanings of network nodes and links. We also review the structural patterns of interaction networks, their spatio-temporal variability, the mechanisms driving network structure and function, and the influence of sampling effects in distorting observed network patterns. Next, we show how this conceptual and methodological approach can offer insights about the consequences of human-driven environmental change. We close by pointing to several key avenues of research for the next decade.

## WHY NETWORKS?

We can think of a number of reasons to adopt a network approach to the study of ecological interactions. At the same time, we acknowledge several caveats of a network approach to community ecology; as with any tool, if not used wisely it may distort our perception of ecological interactions.

### Why to study ecological interaction networks

A network approach allows summarizing the complex array of interactions in ecological communities (Elton 1927; Pimm 1982; Pimm et al. 1991), identifying interaction patterns (network structure). An interaction network thus provides an overview of the connections among species and the emergent structural properties of interactions at the community level. Cohen (1978) compared ecological networks ('webs') with city maps: "If an ecological community is like a city, a web is like a street map of the city: it shows where road traffic can and does go". Having this ecological street map may help us navigate through the intricacies of ecological interactions.

The interaction map represented by an interaction network also offers insights about the ecological processes driven by network structure, such as the flow of energy and biomass in ecosystems, reproductive and demographic processes such as pollination and seed dispersal, community stability in the face of perturbations, (co)extinctions and (co)evolution (Pimm 1982; Jordano 1987; Kearns et al. 1998; Pascual and Dunne 2005; Montoya et al. 2006; Thébault and Fontaine 2010; Bascompte and Jordano 2014). Considering interactions in the community context in which they occur may sometimes lead to surprising conclusions. For example, moving from a focus on small subsets of species to community-wide analyses of interaction networks has changed the way we envision plant-pollinator interactions, from an emphasis on specialization to a realization that many interactions are, in fact, generalized (Waser et al. 1996). Considering the community context also helps us grasp complex indirect interactions and feedback loops (Wootton 1994; Carvalheiro et al. 2014; Guimarães Jr. et al. 2017).

Flipping the coin, identifying network structural patterns leads to the question of what processes drive these patterns (Pimm 1982; Vázquez et al. 2009a; Dormann et al. 2017). Although teasing apart these different processes may represent a difficult task (Vázquez et al. 2009a; Dormann et al. 2017), as we discuss below (see Interaction network patterns and their drivers), ecologists have gone a long way identifying the relative contribution of different drivers of network

structure and the extent to which the observed patterns also reflect sampling effects.

Finally, a network approach can illuminate our understanding of how human-driven global environmental change affects not only species, but also their interactions (Montoya et al. 2006; Tylianakis et al. 2008; Ings et al. 2009; Burkle and Alarcón 2011; Valdovinos 2019). For example, the type of network structure and the order in which extinctions occur in a community may determine network robustness to the occurrence of secondary extinctions (species whose extinction follows the extinction of another species) caused by global change drivers such as habitat destruction or biological invasions (Dunne et al. 2002; Memmott et al. 2004; Fortuna and Bascompte 2006; Srinivasan et al. 2007; Vieira and Almeida-Neto 2015; Valdovinos et al. 2018; Pires et al. 2020).

*Why not to study ecological interaction networks*

Despite the above advantages of a network approach to the study of ecological interactions, we can also think of several arguments against this approach. First, the brush may be too coarse to paint the ecology of our study organisms, so that, when focusing on broad, community-level patterns and processes, we lose biological detail on focal species and their interactions. For example, from a conservation point of view, even if the network patterns don't change under certain habitat management conditions, it makes a huge difference whether species are native or exotic (or if exotics replaced natives) (Tylianakis et al. 2010).

Second, because we have so many network metrics available, we may feel tempted to use networks as wholesale pattern searching devices rather than as carefully selected tools for testing specific hypotheses. Many studies of ecological networks focus on multiple network attributes and indices, sometimes without clearly stated hypotheses behind these analyses. Such an approch may lead to spurious patterns resulting from multiple testing, especially in the absence of corrections for simultaneous testing of more than one hypothesis (Dormann et al. 2017).

Third, although we know that interactions vary widely in time and space and can rewire, many studies regard interactions as a fixed property of species (Poisot et al. 2015). Thus, we need to take a broader perspective to the

study of interaction networks, analyzing their dynamics through time and space. Fortunately, a growing number of studies considers the temporal and spatial dimensions of ecological interaction networks (Hagen et al. 2012; McMeans et al. 2015; Trøjelsgaard and Olesen 2016; Gravel et al. 2019; Schwarz et al. 2020; CaraDonna et al. 2021).

Fourth, and related to the previous point, the definition of the spatial and temporal scales of networks usually results from arbitrary decisions made by researchers. Such decisions may affect conclusions about network structure and function, and species roles (Trøjelsgaard and Olesen 2016; Dáttilo et al. 2019; Schwarz et al. 2020), as the ecological and evolutionary processes we seek to study take place at characteristic spatial and temporal scales (Ricklefs 2004; CaraDonna et al. 2021).

Fifth, some communities may seem arguably too small for a network approach to be informative, and a detailed analysis of specific interactions may represent a simpler and more informative approach. Yet, whether we use a network approach will depend on our questions and preferences, as we can't really set a minimum community size for a network approach; two species already constitute a network, although a tiny one. For some questions, studying small networks may be informative, and we can think of several influential studies that have focused on small networks. For instance, consider Hairston et al.'s (1960) paper on community structure, population control and competition, which focuses on population control within and among communities organized in three trophic levels (producers, herbivores and predators). Just a handful of species would suffice for this model to apply, and studies evaluating these ideas with such a small network may offer insights about the ecology of those communities (e.g., Shurin et al. 2002; Vidal and Murphy 2018).

Some of the above limitations apply not only to the study of interaction networks, but pervade the entire field of community ecology. Addressing these limitations and finding reasonable solutions to them thus seems crucially important for future progress in understanding the structure and dynamics of communities. In spite of the above caveats of using a network approach to the study of ecological interactions, and of other shortcomings that the reader may think of, we believe that, if used wisely, ecological

networks represent a powerful approach to the study of the structure, dynamics and functioning of ecological communities.

## Just a bunch of balls and sticks?

Ecological networks provide a graphical representation of co-occurring entities and their interactions (Newman 2003). Although the study of ecological networks has a long history, the precise meaning of the different components we draw in these cartoons of communities may be elusive.

### *The meaning of nodes*

Nodes in networks represent the convergence points of interactions. Historically, nodes represent species in ecological interaction networks (Figure 1a). More recently, ecologists have realized that the species-level resolution of nodes can obscure the intraspecific variability of interactions (Trøjelsgaard and Olesen 2016); considering such variability may help understand the causes and consequences of interactions. Thus, the level of biological organization represented by nodes will depend on our questions.

Representing individuals as network nodes (Figure 1b) recognizes that species interaction networks encompass the interactions observed from all sampled individuals in the community. Therefore, emergent properties of ecological networks might result from processes operating at the individual level since individuals within a population could be genetically and phenotypically heterogeneous and their selection of interaction partners may vary. The distribution of links among individuals may follow a predictable order where most individuals share similar resource preferences but some behave as opportunists, while others —such as good competitors— would still behave selectively consuming only preferred resources, which results in a nested distribution of interactions among individuals (Pires et al. 2011; Koch et al. 2018). However, individual-based networks can also be modular. For example, a study comparing species *vs.* individual networks of flower visitors revealed increased modularity at the individual level, driven mainly by phenology (Tur et al. 2014). Interestingly, modules consisted of taxonomically or functionally unrelated individuals, which shared the same pollen resources at different times of the season (Tur et al. 2015).

At a broader spatial scale, nodes can also represent local populations in metapopulations, in which individuals, propagules or gametes migrate among local populations, with potentially profound effects on population dynamics and genetic heterogeneity (González 1998; Hanski 1999). The spatial distribution of nodes represents a key aspect of population networks determining different connectivity patterns (Urban and Keitt 2001). For example, the spatial position of populations determines their vulnerability to perturbations, such as disease propagation (Zamborain-Mason et al. 2017; Gilarranz et al. 2017), a topic with renewed importance for human health at present (Calvetti et al. 2020).

Within species, networks nodes can represent both genotypes and phenotypes to test evolutionary hypotheses (Wilkins 2007). For example, networks of phenotype-genotype correlations may help unravel the association between genes and diseases (Han et al. 2015; Wu et al. 2020). Moreover, genotype-species
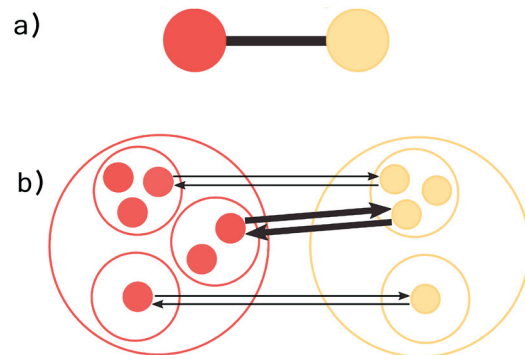


**Figure 1.** The most common meanings of nodes and links. a) A link between two nodes representing species. Nodes can also represent genotypes, phenotypes, and even interactions, although these are often found in the literature. b) Nodes can represent individuals (small circles) grouped in different populations (mid-sized circles) of different species (large circles) interacting with individuals of a second species; links represent bidirectional effects of interactions, with line width representing different magnitudes of effects.

**Figura 1.** Los significados más comunes de los nodos y los enlaces. a) Un enlace entre dos nodos que representan especies. Los nodos también pueden representar genotipos, fenotipos e incluso interacciones, aunque esto es menos frecuente en la literatura. b) Los nodos pueden representar individuos (círculos pequeños) agrupados en diferentes poblaciones (círculos medianos) de diferentes especies (círculos grandes) que interactúan con individuos de una segunda especie; los enlaces representan efectos bidireccionales de las interacciones, y el grosor de las líneas representa la magnitud de los efectos.

interaction networks indicate that plant genotypes determine the community structure of arthropod herbivores by constituting network modules, with consequences for their evolutionary dynamics (Lau et al. 2016; Keith et al. 2017). Nodes can also represent traits, for example, to define functional strategies to cope with environmental conditions (Messier et al. 2017; Flores-Moreno et al. 2019; He et al. 2020). Finally, even interactions can be represented as nodes in a multilayer network such as those where shared interactions between local networks are connected composing a regional metanetwork (Emer et al. 2018).

## *The meaning of links*

The multiple meanings of nodes discussed above opens a myriad of possibilities about the meaning of links or interactions in networks. The simplest link representation indicates whether two nodes interact or not (Newman 2003). This binary occurrence of interactions can be inferred from various sources including direct observation (Dáttilo et al. 2016), bibliographic compilation (e.g., Polis 1991), barcoding techniques applied to stomach contents (Evans et al. 2016), the temporal and spatial co-occurrence of nodes (i.e., whether two nodes coexist in the same place and at the same time [Bell et al. 2010]) and even morphological congruence (i.e., whether co-occurring nodes have matching morphological traits that may make theme likely to interact [Sebastián-González et al. 2017 ]).

Despite their simplicity and historical importance, binary links offer a limited picture of interactions, as interactions in nature vary substantially among species in their frequency and magnitude of effects (Figure1) (Paine 1980). There are many ways to weight interactions and the method selected may depend on the study system and the question under analysis. The most basic approach of weighting links consists in recording the number of interaction events (i.e., interaction frequency). Although interaction frequency can correlate with demographic effects and ecological function (Vázquez et al. 2005), the relationship may be nonlinear throughout the entire range of interaction frequency (Novak and Wootton 2008; Morris et al. 2010), requiring additional effort to estimate interaction strength.

Representing interaction strength through network links is difficult and time consuming, which has stimulated ecologists to develop a methodological toolkit to achieve this goal

(Laska and Wootton 1998; Berlow et al. 1999, 2004; Vázquez et al. 2012, 2015). The classic definition of interaction strength, based on population dynamics, involves representing how changes in the abundance of one species affect the population growth rate of another species (Wootton 1997; Wootton and Emmerson 2005; Vázquez et al. 2012, 2015). The quantitative translation of this conceptual definition requires quantifying per capita interaction strengths, which represent the direct effect of an individual of a species on an individual of another species (Laska and Wootton 1998). Accordingly, the per capita interaction strength represents the direct effect of an individual of one species on the entire population of a second species (May 1973), the total effects of the addition or removal of individuals on the abundance of another species (Yodzis 1988), or the effect of the removal of an entire population on the abundance of another species (Paine 1980). Although originally proposed for predator-prey interactions, these approaches can also apply to mutualistic interactions (Vázquez et al. 2012, 2015).

When dealing with plant-animal or other types of bipartite networks, we tend to envision interactions as unidirectional effects (e.g., animal-centered or plant-centered), but interactions may affect both sides and the reciprocal effects may be asymmetrical (Bascompte et al. 2006). Consequently, the optimal representation of network links should reflect the bi-directional nature of its effects (Figure 1b). Although quantifying reciprocal effects is straightforward in interactions involving deaths and births, such as host-parasitoid networks, for other interaction types (e.g., plant-pollinator) measuring demographic changes for all interaction partners could be difficult and time-consuming (Vázquez et al. 2012; González-Castro et al. 2015).

Species interactions can also be mediated by a third species. Indirect interactions pervade ecological communities and network approaches may help disentangle these complex indirect effects (Ohgushi 2005). In resource-consumer networks, such as predator-prey interactions, two types of indirect effects are prominent: resource competition, mediated by a common resource, and apparent competition, mediated by a common consumer (Holt 1977; Morris et al. 2004; Frank van Veen et al. 2006; McPeek 2019) (Figure 2a).
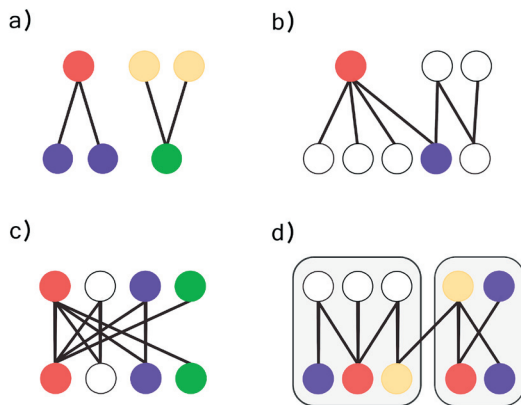
**Figure 2.** Structural roles of nodes in networks. a) Roles in two network motifs extracted from bipartite networks, each with three interacting species and representing apparent competition (left) and shared resources (right); circle color indicates four unique motif positions. b) Nodes can have a central role according to their degree (red) or by bridging distant nodes (purple). c) In a nested network, nodes can be part of the central core (red) or be peripheral (green) depending on their degree, but also can have an idiosyncratic role (purple) when their interactions depart from a perfect nested structure. d) In a modular network, nodes can be network hubs (yellow) when they connect different modules, module hubs (red), when they connect nodes within modules, and peripherals (purple) when they are loosely connected.

**Figura 2.** Roles estructurales de los nodos en las redes. a) Roles en dos *motifs* extraídos de redes bipartitas, cada uno con tres especies y representando competencia aparente (izquierda) y recursos compartidos (derecha); el color de los círculos indica cuatro posiciones diferentes de *motifs*. b) Los nodos pueden tener un rol central según su grado (el número de nodos con los que están conectados; rojo) o sirviendo de puentes entre nodos distantes (púrpura). c) En una red anidada, los nodos pueden ser parte del núcleo central (rojo) o ser periféricos (verde) dependiendo de su grado, pero también pueden tener un rol idiosincrático (púrpura) cuando sus interacciones se apartan de una estructura perfectamente anidada. d) En una red modular, los nodos pueden ser nodos centrales de la red (amarillo) cuando conectan nodos de diferentes módulos, nodos centrales modulares (rojo) cuando conectan nodos dentro de un módulo, o periféricos (púrpura) cuando están poco conectados.

Apparent competition plays an important role structuring multitrophic systems, promoting species coexistence and species diversity (Chesson 2018; McPeek 2019). More practically, apparent competition may indicate which wild species promote biological control in crops (Valladares and Salvo 1999; Carvalheiro et al. 2008; Alhmedi et al. 2011), even guiding management practices for species conservation (Ng'weno et al. 2019). For mutualisms, two nodes may also share a consumer, although the interpretation of this indirect interaction depends on the scale of node resolution. For instance, unipartite plant-plant individual networks connecting

individuals that share pollinators are good predictors of pollination effectiveness (Arroyo-Correa et al. 2021). At the species level, the potential for apparent competition via shared pollinators was related to the difference in the amount of resources offered and the phylogenetic distance between plant species (Carvalheiro et al. 2014).

### *Assessing the structural role of species*

Ecological networks exhibit a heterogeneous distribution of interactions (Montoya et al. 2006), which suggests that nodes vary widely in their structural importance. Although most network research has focused on network-level attributes, an increasing number of studies use network tools to characterize node roles, such as species with disproportionate effects on the community or keystone species (Paine 1966). Accordingly, the search for keystones in network studies succeeded at identifying species whose loss may generate important cascading effects (Berlow et al. 2004; Benedek et al. 2007; Martín González et al. 2010).

The number of interaction partners (degree) of a species represents the most basic measure of a topological role of nodes in networks (Figure 2b), depicting their participation regardless of the global network structure (Jordán et al. 2006). Despite its simplicity, degree offers information about the ecological niche of species (Cirtwill et al. 2018) and reveals key players for structural stability (Pocock et al. 2012). Species degree can be categorized according to the trophic level or guild involved, as the number of consumers (vulnerability or in-degree) or the number of resources a species has (generality or outflow degree) (Bersier et al. 2002). Interpreting species degree according to trophic levels may reveal different ecological and evolutionary aspects of networks. For example, changes in species vulnerability associated with anthropogenic disturbance revealed increased trophic niche overlap among predators, suggesting increased competition in disturbed habitats (Blanco-Torres et al. 2020).

The more complex measures of structural roles involve not just the 'local neighborhood' of species directly linked to the focal species, but also species topologically distant from the focal species. Several centrality measures provide information about indirect effects on other nodes (Estrada 2007; Jordán et al. 2007). Different centrality indices quantify species influence at different scales (Estrada 2007).

While degree centrality measures species influence at a 'local scale', betweenness centrality indicates the frequency in which a focal species 'bridges' other species not directly linked (Figure 2b) (Estrada 2007; Cirtwill et al. 2018). In turn, eigenvector centrality represents species importance at a 'global scale', assigning relative scores to all species in the network by assuming that links to highly connected species contribute more to connecting the focal species than links to less connected species (Estrada 2007). Although centrality indices depict partially overlapping information (Jordán et al. 2007), they constitute an important tool to identify keystone species for conservation practices (Martín González et al. 2010).

Networks can be decomposed into different sets of unique arrangements of n interacting nodes termed 'motifs' (Milo 2002). Studying motifs involves analyzing all possible combinations among a small subset of nodes, usually three, although they may include more (Figure 2a) (Lewinsohn and Cagnolo 2012; Simmons et al. 2019). Bipartite networks such as those between insect herbivores and their parasitoids include two possible three-species motifs, the most commonly studied of which consists of two herbivores sharing a common parasitoid (Figure 2a) (Holt and Bonsall 2017). Each motif, and the node positions within each motif, may have different consequences for network structural stability and energy/biomass transfer (Borrelli et al. 2015). Accordingly, each species may occupy different, nonrandom motif positions, and may be phylogenetically conserved, as certain taxa tend to occupy similar motif positions across different communities (Stouffer et al. 2012).

The global structural network attributes such as modularity and nestedness (Figure 3d-e) offer another possibility of defining node roles. In a nested network, highly connected nodes constitute the 'central core' of the network, playing a key role in maintaining network cohesion and stability under extinction scenarios (Memmott et al. 2004), while nodes deviating from perfect nestedness constitute 'idiosyncratic' nodes (Figure 2c) (Ulrich and Gotelli 2007). The comparison of the ecological attributes of species occupying different positions in nested networks may reveal clues about the determinants of specialization (Heino et al. 2009). In turn, in modular networks roles refer to the position of nodes in connecting other nodes within and between modules. Thus, nodes may

function as peripherals (when they have few links within and between modules), hubs (when they have many links within modules [module hubs] or between modules [network hubs]) and connectors (when they have links evenly distributed within and between modules) (Figure 2d) (Guimerà and Amaral 2005). Intriguingly, module species roles seem related to aspects of the functional and evolutionary position of species, as they tend to be conserved among the native and exotic ranges of plants and pollinators (Olesen et al. 2007; Emer et al. 2016) and among free-living animals and their parasites (Poulin et al. 2013).

As mentioned above, node roles represent different structural positions and, consequently, different ecological functions. One way to evaluate the ecological relevance of species occupying different positional roles in networks involves assessing the relationship between node roles and their functional traits. As species phenotypes determine who interacts with whom, network roles should indicate functional roles. For example, the trait uniqueness of species tends to be associated with the specialization of their interactions (Coux et al. 2016), which, in turn, is associated with species centrality (Mello et al. 2013). The extent to which the relationship between functional and network roles are stable across time and species is still an open question.

## Interaction network patterns and their drivers

### *The patterns and their variability*

Multiple studies have summarized the most common topological patterns of interactions in different network types (Ings et al. 2009; Vázquez et al. 2009a; Gu et al. 2015; Pringle and Hutchinson 2020). In general terms, both mutualistic and antagonistic interaction networks seem to encompass multiple weak interactions, with only a few strong interactions (Figure 3). Mutualistic and antagonistic networks also appear to have similar connectance, although highly diverse pollination networks tend to exhibit greater connectance than herbivory networks of similar diversity (Thébault and Fontaine 2010). In contrast, nestedness and modularity seem higher in mutualistic than in antagonistic networks (Bascompte et al. 2003; Thébault and Fontaine 2010). Moreover, the above network patterns can occur simultaneously within
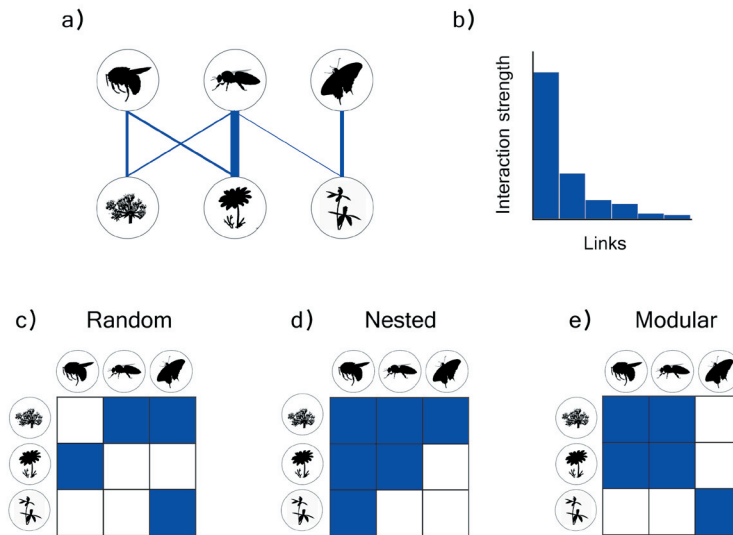
**Figure 3.** Illustration of some common network attributes discussed in the text. a) Bipartite quantitative plant-pollinator interaction network, where link width represents the magnitude of interactions. b) In general, interaction networks present only a few strong interactions with multiple weak interactions. c) Species interactions usually do not occur at random, but present clearly defined patterns (d, e). For instance, d) a nested pattern occurs when specialized species tend to interact with a subset of the interaction partners of more generalized species (Bascompte et al. 2003). e) Modularity (or compartmentalization) refers to the existence of clearly defined groups of species (modules or compartments) with many intragroup links and few intergroup links (Dicks et al. 2002; Olesen et al. 2007). Connectance is the proportion of potential links that are actually realized (Jordano 1987); for instance, network d has higher connectance than network c. Silhouettes extracted from phylopic.org.

**Figura 3.** Ilustración de algunos atributos comunes de redes discutidos en el texto. a) Red cuantitativa bipartita de interacciones planta-polinizador, en la que el grosor de las líneas representa la magnitud de las interacciones. b) En general, las redes de interacción presentan pocas interacciones fuertes y muchas débiles. c) Las interacciones suelen no ser aleatorias, sino que presentan patrones definidos (d, e). Por ejemplo, d) un patrón anidado ocurre cuando las especies especialistas tienden a interactuar con un subconjunto de los compañeros de interacción de especies generalistas (Bascompte et al. 2003). e) La modularidad (o compartimentalización) se refiere a la existencia de grupos de especies claramente definidos (módulos o compartimientos) con muchos enlaces dentro de los grupos y pocos enlaces entre grupos (Dicks et al. 2002; Olesen et al. 2007). La conectancia es la proporción de enlaces potenciales que realmente ocurren (Jordano 1987); por ejemplo, la red d tiene mayor conectancia que la red c. Las siluetas fueron extraídas de phylopic.org.

networks (Lewinsohn et al. 2006). Despite these broad generalizations, comparing network structure across different network types from different studies represents a challenge, because networks are built with different sampling techniques, efforts and scales across studies.

Most studies assessing species interaction patterns look at ecological network structure in a specific place and at a specific time, even though interactions are spatio-temporally dynamic. Pooling species interactions across space and time means that we still do not know how much of the observed network patterns come from the spatio-temporal accumulation of interactions (Trøjelsgaard and Olesen 2016). For example, modularity in food webs may emerge as a consequence of habitat boundaries (Pimm and Lawton 1980), as found in the Serengeti food web (Baskerville et al. 2011) and a bumble bee-flower network (Dupont et al. 2014). Unfortunately, most studies actively

select homogeneous plots for sampling, later pooling data for analysis, missing the opportunity to evaluate if habitat generalists connect different modules composed of habitat specialists.

The temporal and spatial turnover in species interactions can result from changes in species composition and/or changes in interaction partners (Poisot et al. 2012). For instance, in plant-pollinator interactions, the temporal and spatial turnover in species composition play a central role in driving interaction variability (Olesen et al. 2008; Petanidou et al. 2008; Trøjelsgaard et al. 2015). In addition, the availability of floral resources in a given day may also determine the diel dynamics of plant-pollinator interactions (Schwarz et al. 2021). Despite the high interannual variability in species composition and interactions, the structure of plant-pollinator, commensalistic and antagonistic networks seems to vary little across years (Olesen et al. 2008; Petanidou et al.

2008; Alarcón et al. 2008; Kaartinen and Roslin 2011; Dallas and Poisot 2018; Ramos-Robles et al. 2020). A potential explanation for this temporal stability of network structure posits that different species fulfill the same functional roles in interaction networks (Dallas and Poisot 2018), as recently demonstrated for seed-dispersal networks sampled across a spatial gradient in the Andes (Dehling et al. 2020).

Highly variable interactions in time and space tend to occur at low frequencies and at the periphery of the network, compared to frequent interactions located at the network core (Fang and Huang 2012; Chacoff et al. 2018; Resasco et al. 2021). Although some studies indicate centrality may reflect the evolutionary history of interacting species (Mello et al. 2013; Burin et al. 2021), others indicate that the structural position of species as core or peripheral seems quite dynamic, with most species that belong to the network core in some seasons and years moving to the periphery in other seasons or years (Miele et al. 2020). Therefore, the contribution of species interactions to network structure can vary temporally (Bramon Mora et al. 2020; CaraDonna and Waser 2020). Nevertheless, interaction variability caused by interaction rewiring (changes in who interacts with whom among a group of species [CaraDonna et al. 2017]) might depend on the interaction type. For instance, in non-intimate interactions such as those between plants and pollinators, rewiring dominates interaction dynamics over time (CaraDonna et al. 2017). In contrast, in more intimate interactions such as host-parasitoid interactions, species tend to interact with the same partner species over space and time, potentially due to stronger physiological and/or behavioral constraints (Elizalde et al. 2018). Species abundance also plays a prominent role in the spatial and temporal variability of interactions by influencing interaction frequencies (Chacoff et al. 2018; Peralta et al. 2020c). Furthermore, variability in species interaction frequency or strength might also be influenced by non-trophic and indirect interactions which contribute to community dynamics (Frost et al. 2016; Kawatsu et al. 2021), although these interaction types are less often studied. To fully understand the spatial and temporal dynamics of species interaction network structure and of its constituent pairwise interactions, we need to unravel the mechanisms that drive species interactions and network assembly rules.

### *The drivers*

Species interactions depend not only on the spatio-temporal distribution of species (i.e., co-occurrence), but also on niche and neutral processes that occur simultaneously (Figure 4). Niche theory posits that interaction probabilities are shaped by biological factors, such as morphology, phenology, behavior and evolutionary history (Jordano et al. 2003; Rezende et al. 2007; Vázquez et al. 2009a; Olesen et al. 2011; Morán-López et al. 2020). In addition, considering phylogeny may also help elucidate the influence of niche processes on species interactions, as they represent proxies for traits difficult to quantify and may act as indicators of trait similarity among closely related species (Webb et al. 2002; Rezende et al. 2007; Bersier and Kehrli 2008; Verdú and Valiente-Banuet 2011; Peralta 2016; Segar et al. 2020). Conversely, neutral theory posits that species are ecologically equivalent and hence their interactions emerge from random encounters among individuals (Vázquez 2005; Vázquez et al. 2007). Thus, species abundance plays a key role in determining species interactions and, consequently, abundance distributions constitute the drivers of interaction network structure (Blüthgen et al. 2008; Canard et al. 2014). Based on neutral theory, rare species are unlikely to encounter each other and interact, generating 'neutral forbidden links' (Canard et al. 2014), whereas the mismatch in niche space between species, such as morphological or phenological mismatch, results in 'niche forbidden links' (i.e., unrealized interactions due to species' incompatibility) (Jordano et al. 2003; Canard et al. 2012).

Current evidence suggests that both niche and neutral processes contribute to generating the structure of mutualistic and antagonistic networks (Vázquez et al. 2009a; Verdú and Va-liente-Banuet 2011; Chagnon et al. 2012). For instance, species abundance and phenology predicted network structure in plant-pollinator networks from the Monte Desert shrubland (Vázquez et al. 2009b), and abundance and phylogenies were key determinants of plant-herbivore and herbivore-parasitoid network structure from the Chaco Serrano District (Cagnolo et al. 2011). Although some drivers seem to dominate network assembly in some systems (Vizentin-Bugoni et al. 2014; Sebastián-González et al. 2017; Morente-López et al. 2018) and that their influence may depend on the network scale considered (Bezerra et al. 2009), the body of available evidence
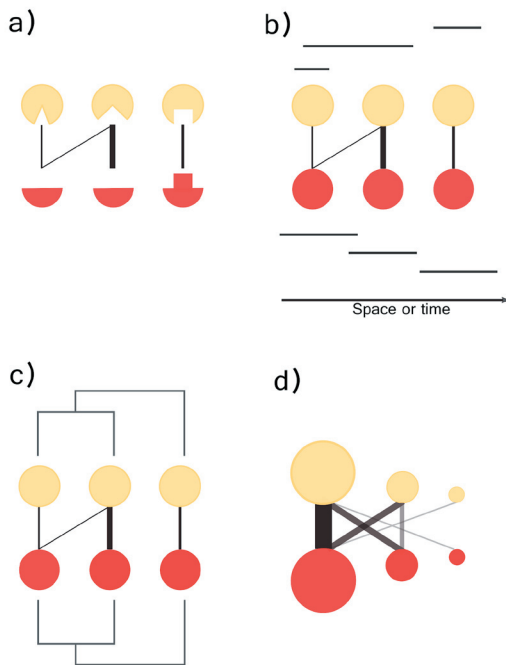
**Figure 4.** Illustration of the most commonly studied species interaction drivers. a) Morphological trait matching. b) Phenological overlap between interacting species. c) Species phylogenies, used as indicators of the evolutionary history between interacting species and of trait similarity among closely related species. d) Species abundances. Node size and link width represent species abundance and interaction frequency, respectively.

**Figura 4.** Ilustración de los determinantes de las interacciones estudiados frecuentemente. a) Correspondencia de caracteres. b) Superposición fenológica entre especies interactuantes. c) Filogenias de las especies, usadas como indicadores de la historia evolutiva entre las especies interactuantes y de la similitud de caracteres entre las especies altamente relacionadas. d) Abundancias de las especies. El tamaño de los nodos y el grosor de los enlaces representan la abundancia de las especies y la frecuencia de las interacciones, respectivamente.

supports the view that multiple neutral and niche processes contribute simultaneously to generate the structure and dynamics that we see in ecological communities (Vellend 2010, 2016). Nevertheless, untangling the relative contribution of niche and neutral processes for species interactions (Vázquez et al. 2009a; Sazatornil et al. 2016), and how this contribution varies across different communities, remains a challenge.

Researchers usually assume that niche and neutral processes affect all interactions equally. However, recent research indicates that the relative importance of niche and neutral processes may depend on species origin and specialization. Specifically, niche processes dominate interactions among native or specialist species of plants, frugivores and pollinators compared to interactions involving exotic or generalist species (Peralta et al. 2020c, 2020a; Coux et al. 2021). These studies may help explain why certain drivers, such as abundance, can influence interaction patterns more strongly than others, such as trait matching (García et al. 2014). In addition, the relative influence of niche and neutral processes can vary across space. For example, neutral processes seem to have a stronger influence in the ecotones between distinct biogeographical areas (Sazatornil et al. 2016), whereas niche processes seem to increase towards lower latitudes (Sonne et al. 2020).

Multiple methods to predict species interactions exist which rely on species interaction drivers. In fact, species traits, phenology, phylogeny and abundance are the most common drivers used to model and predict species interactions (Ives and Godfray 2006; Vázquez et al. 2009b; Pearse and Altermatt 2013; Olito and Fox 2015; Crea et al. 2016; Rohr et al. 2016; Brousseau et al. 2018; Benadi et al. 2021; Kotula et al. 2021). Hence, unraveling the relative importance of species interaction drivers could facilitate the prediction of interactions. Likewise, understanding how and why species interact can provide information about those ecosystem functions that rely on species interactions. For instance, morphological trait matching of flower visitors and plants can promote plant reproductive success (Garibaldi et al. 2015), in some cases by increasing the frequency of interactions among species (Peralta et al. 2020c). In addition, trait matching among interacting species and trait diversity relate to complementarity in partner use, which has been shown to promote ecosystem functions such as parasitism rates, seed dispersal and seed set (García et al. 2014; Peralta et al. 2014; Magrach et al. 2020). Therefore, understanding the drivers of species interactions could be useful not only to comprehend and predict species interaction dynamics, but also changes in ecosystem functions.

## Network structure. Real phenomenon or sampling artifact?

Sampling interactions in ecological communities represents a Herculean task, and despite such effort, it seems unlikely that

we ever achieve a complete representation of interactions in our study communities. This fundamental problem of sampling communities leads to the question of how much of the patterns we see in networks actually represent the real structure of the communities we seek to describe and understand, and to what extent these patterns represent sampling artifacts. Such artifacts may come from several sources, including insufficient sampling effort (lazy sampling effect), taxon resolution (blurred magnifier effect) and unequal detection probabilities of species and their interactions which may result from species attributes (crooked magnifier effect) and sampling methods (tendentious sampling effect) (Figure 5).

The lazy sampling effect refers to an incomplete representation of network structure resulting from low sampling effort. Several studies have assessed the extent to which sampling effort may influence observed patterns in interaction networks (Goldwasser and Roughgarden 1997; Banasek-Richter et al. 2004; Vázquez and Aizen 2006; Nielsen and Bascompte 2007; Chacoff et al. 2012; Rivera-Hutinel et al. 2012; Fründ et al. 2016; Jordano 2016; Vizentin-Bugoni et al. 2016; Falcão et al. 2016; Henriksen et al. 2019; Schwarz et al. 2020). These studies suggest that at least some network attributes change substantially with sampling effort (particularly, the number of species and —especially— interactions) and most network indices used to characterize
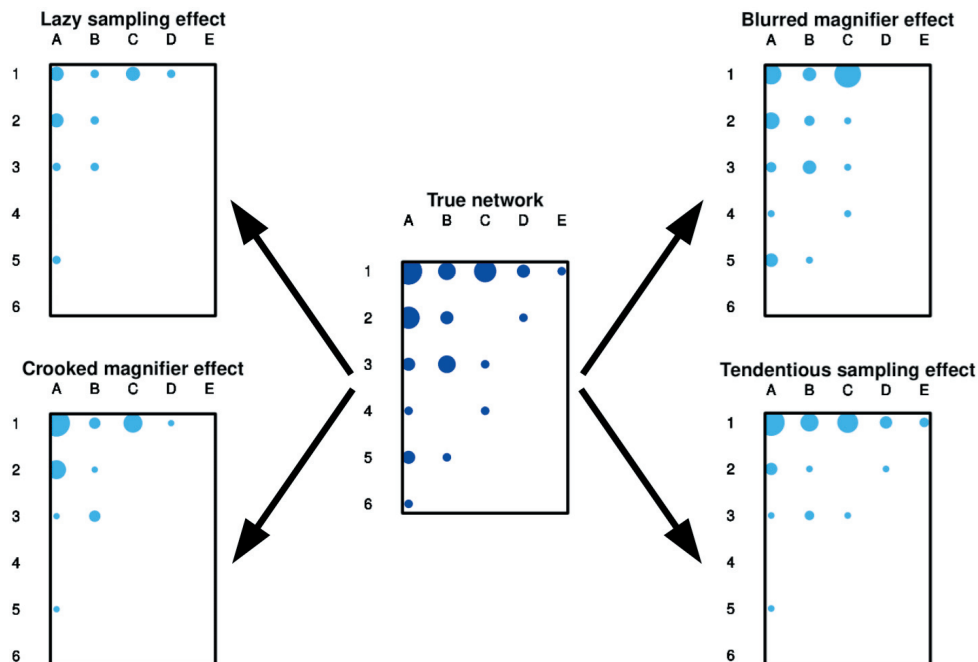


**Figure 5.** The influence of different kinds of sampling effects on network patterns. The central panel shows a hypothetical bipartite interaction matrix whose structure we want to describe through sampling. Different types of sampling effects can distort this structure. Undersampling (the lazy sampling effect) may homogeneously decrease the detection of interactions, causing researchers to miss the rarest interactions while preserving some of the overall network patterns such as nestedness. In contrast, low taxon resolution (the blurred magnifier effect) may lead to a sharp change in overall network structure. In turn, widespread heterogeneity in interaction detection probabilities, for example, determined by species relative abundances (the crooked magnifier effect) may lead to changes similar to those observed under the lazy sampling effect, exacerbated by the low detection probabilities of interactions involving rare species. Finally, focusing our sampling on a particular group (focal group bias, the tendentious sampling effect) may result in a reasonable sampling effort on the focal group, while leading to strong undersampling of the non-focal group.

**Figura 5.** Influencia de diferentes tipos de efectos de muestreo sobre los patrones de redes. El panel central representa una matriz de interacción bipartita hipotética cuya estructura queremos describir mediante muestreo. Diferentes tipos de efectos de muestreo pueden distorsionar esta estructura. Un bajo esfuerzo de muestreo (el efecto del muestreo perezoso) puede disminuir homogéneamente la detección de las interacciones, llevando a las/os investigadoras/es a perderse las interacciones más raras, pero, a la vez, preservando los patrones estructurales de la red como el anidamiento. En cambio, la baja resolución taxonómica (el efecto de la lupa sucia) puede llevar a un fuerte cambio en la estructura general de la red. A su vez, una gran heterogeneidad en las probabilidades de detección de las interacciones (por ejemplo, determinada por las abundancias de las especies [el efecto de la lupa torcida]) puede llevar a cambios similares a los observados bajo el efecto del muestreo perezoso, exacerbados por las bajas probabilidades de detección de las interacciones que involucran a las especies raras. Finalmente, enfocar nuestro muestreo en un grupo en particular (el sesgo del grupo focal, que lleva al efecto del muestreo tendencioso) puede resultar en un esfuerzo de muestreo razonable para el grupo focal, aunque, al mismo tiempo, llevando a un fuerte submuestreo del otro grupo.

network structure. Thus, we must interpret observed network patterns with caution, in particular when the number of species and links detected falls well below the expected number for the studied community, which seems likely for most networks based on analyses of sampling completeness and coverage (Schwarz et al. 2020).

In turn, the blurred magnifier effect evokes a situation in which low taxon resolution leads to a distorted representation of network structure. Low taxon resolution results from the aggregation of nodes whose taxonomic identity remains unresolved. Several studies have demonstrated that poor taxon resolution may strongly influence observed network patterns (Martínez 1991; Polis 1991; Hemprich-Bennett et al. 2021). For example, many of the early generalizations about food web structure (Pimm et al. 1991) changed after better resolved data became available (Martínez 1991; Polis 1991), whereas the use of molecular markers sometimes improves estimates of specialization compared to estimates based on morphology (Kaartinen et al. 2010).

The crooked magnifier effect refers to a situation in which different interactions have different detection probabilities for reasons beyond focal group bias, which may affect network structural attributes. A major source of such heterogeneous detection probabilities comes from the skewed species abundance distributions typical of most communities: interactions involving rare species may have lower detection probabilities than interactions involving abundant species (Vázquez and Aizen 2003; Blüthgen et al. 2008). Similarly, skewed temporal and spatial distributions may lead to interactions involving narrowly distributed species having a lower detection probability than those involving abundant species. Finally, phenotypes can also lead to heterogeneous interaction detection probabilities among species, as some traits such as body size, may make some species and their interactions more conspicuous than others (Vázquez et al. 2009a). Thus, species abundances, spatio-temporal distributions and traits influence interaction detection. The exclusion of interactions that are possible but hard to observe (missing links) can lead to a biased representation of the true interaction network structure.

Finally, the tendentious sampling effect refers to biased data resulting from interaction data collected by focusing on a particular trophic level or group, which may also introduce a bias in the interaction data (focal group bias; Sørensen et al. 2012; Jordano 2016; Dormann et al. 2017). True, focusing on one group may help increase the probability of detection of interactions in the focal group, but not in the non-focal groups. For example, many plant-pollinator interaction data come from visitation records from timed flower observations, which likely leads to more complete sampling for plants than for flower visitors. Likewise, many trophic data come from the analysis of gut contents, which may lead to greater sampling completeness for the animals subject to gut analyses than for their prey. Studies combining sampling methods that focus on different groups may offer insights into the extent to which focal group bias influences observed network patterns. For instance, a network built combining flower visitation data (plant-centered sampling) with pollen data collected from pollinator bodies (animal-centered sampling) led to increased network connectance and increased plant and animal connectivity compared to a network including only flower visitation data (Bosch et al. 2009). Likewise, estimating bee specialization from bee nest pollen provisions substantially increased the estimates of generalization of bee species recorded as specialists in flower visitation observations (Dorado et al. 2011). Molecular methods (e.g., DNA barcoding and metabarcoding) may also help improve interaction sampling by focusing on groups whose interactions may otherwise prove difficult to sample (Kaartinen et al. 2010; Jordano 2016; Evans and Kitson 2020).

Figure 5 illustrates how the above kinds of sampling effects may distort true network patterns. Undersampling (the lazy sampling effect) may homogeneously decrease the detection of interactions, leading to the loss of the rarest interactions, but preserving some of the overall network patterns such as nestedness (e.g., Nielsen and Bascompte 2007). In contrast, low taxon resolution (the blurred magnifier effect) may lead to a sharp change in overall network structure (e.g., Martínez 1991; Hemprich-Bennett et al. 2021); how precisely network structure will change as a consequence of low taxon resolution may be difficult to predict and will depend on particularly which taxa we decide to lump together. Meanwhile, widespread heterogeneity in interaction detection probabilities, for example determined by species relative abundances (the crooked magnifier effect) may lead to changes similar to those observed under the

lazy sampling effect, although exacerbated by the particularly low detection probabilities of interactions involving rare species (Blüthgen et al. 2008). Finally, focusing our sampling on a particular group (focal group bias, the tendentious sampling effect) may lead to reasonable sampling effort on the focal group, while leading to strong undersampling of the non-focal group, especially rare species (Jordano 2016; Dormann et al. 2017).

What can we do to minimize sampling artifacts? First, the obvious: sample as much as possible to achieve high sampling completeness. Second, use network metrics robust to sampling effort. Third, combine information from multiple, complementary sampling methods targeting different focal groups (e.g., flower visitation observations and pollen transport records; Bosch et al. 2009) and use molecular methods to achieve high taxon resolution (Evans and Kitson 2020). Fourth, standardize data in terms of scale, sampling method and sampling effort for comparisons among different systems (Gibson et al. 2011; Schwarz et al. 2020). Fifth, use null models as benchmarks against which to compare observed patterns (Gotelli and Graves 1996; Vázquez and Aizen 2003; Blüthgen et al. 2008; Dormann et al. 2017). Sixth, use simulated data and simulated noise to explore the sensitivity of network metrics (Dormann et al. 2009; Fründ et al. 2016). Seventh, use statistical methods that allow accounting for the sources of bias (e.g., species abundance or species richness) and separating their contributions as observation and process mechanisms (Weinstein and Graham 2017). Eighth, know the natural history of our study systems, which represents an irreplaceable source of intuition (Ricklefs 2012). Finally, accept that our conclusions about interaction network structure may change as we gather better data and improve the methods we use to sample and analyze them.

## Todo cambia. Ecological networks and global change

Human activities have accelerated the rate of change of natural environments through land use change, climate change and biological invasions, causing biodiversity decline through species extinctions and drastic changes in species abundances (Newbold et al. 2015; Wagner 2020). This variability in species composition influences network structure. We need to understand the interplay between human activities and the extinction of species and ecological interactions because of its implications for the loss of ecological functions and ecosystem services.

### *Land use change*

Land use change represents the main driver of biodiversity decline in terrestrial and freshwater ecosystems, with short and long-term consequences on natural and human-dominated ecosystems (Brondizio et al. 2019). Land use change implies diverse processes such as habitat fragmentation, habitat loss and habitat degradation (Foley et al. 2005; Hagen et al. 2012; Kremen and Merenlender 2018). However, because these processes usually occur simultaneously, as habitat fragmentation or transformation usually implies habitat loss, it may be hard to tease them apart (Fahrig et al. 2019).

Different species and interactions may differ in their susceptibility to habitat disturbance, and hence, their extinction risk. In a plant-frugivore bird meta-network, for example, interactions involving large-bodied frugivores and large-seeded plants tended to be lost with decreasing fragment size (Emer et al. 2018). Furthermore, generalist species tend to be more abundant (Fort et al. 2016) and might have a lower extinction risk than specialists in modified habitats (Figueroa et al. 2020; Schneiberg et al. 2020). Generalist species also connect different habitat types (Peralta et al. 2017), promoting spatial coupling of population dynamics (Rand et al. 2006; Frost et al. 2016; Hackett et al. 2019), with the potential to propagate disturbances across habitats and landscapes. In addition, invasive and exotic species tend to be more generalized than native species (García et al. 2014), homogenizing interaction networks (Fricke and Svenning 2020). In contrast, dietary specialist species tend to go locally extinct first under habitat disturbance, such as agricultural intensification or urbanization (Rader et al. 2014; Schneiberg et al. 2020; but see Vázquez and Simberloff 2002) and tend to contribute the most to functional diversity (Dehling et al. 2020), which means that habitat disturbance will tend to erode interaction complementarity and functioning (Tylianakis and Morris 2017).

Because of the intricate connectivity of ecosystems, the disappearance of some species from the community may lead to co-extinction cascades that propagate through

the network (Bascompte 2009; Brodie et al. 2014). Network robustness refers to the tolerance of ecological networks to secondary extinctions, thus providing some clues about the potential fragility of networks facing disturbance (Montoya et al. 2006), which may have structural and functional consequences for networks (Donoso et al. 2020). Previous studies have used robustness to assess how communities respond to different sequences of species loss (Dunne et al. 2002; Memmott et al. 2004), some of them including partner switching (Kaiser-Bunbury et al. 2010; Vieira and Almeida-Neto 2015), and applied to particular environmental perturbations such as habitat loss (Fortuna and Bascompte 2006). Studies on mutualistic and antagonistic networks have found that species extinction sequence may determine the rate of secondary extinctions: losing highly connected species first compared to a random sequence of species loss may lead to faster rates of secondary extinctions (Dunne et al. 2002; Memmott et al. 2004). In addition, the type of interaction may influence network robustness, as shown by an analysis of a 'network of networks' that included several interaction types (i.e., herbivory, parasitism and mutualism), in which networks including pollinators had greater fragility, a result attributed to network generalization (Pocock et al. 2012). Moreover, compared to randomized networks, the structural attributes of real world networks (high heterogeneity in species degree and nestedness) may make them more robust to habitat destruction, as indicated by a simulation study of metacommunity response to habitat destruction (Fortuna and Bascompte 2006). In turn, similarity in species composition among habitat fragments and delayed species and interaction extinctions due to recent habitat fragmentation may increase current network robustness to fragmentation (Evans et al. 2013; Santos et al. 2021).

## Biological invasions

The incorporation of new species in the community may lead to changes in network structure and contribute to network disassembly (Frost et al. 2019). Alien invasive species are usually introduced by humans outside of their natural distribution range, in areas where they establish, spread substantially and alter the community they invade (Blackburn et al. 2011; Heleno et al. 2013). Direct and indirect effects of invaders can cascade through the recipient communities,

resulting in the loss of species or interactions (Rodriguez-Cabal et al. 2013), sometimes also leading to drastic changes in the overall structure of the interaction network (Vázquez and Simberloff 2003; Aizen et al. 2008; Santos et al. 2012; Giannini et al. 2015; Valido et al. 2019; Vitali et al. 2021; but see Vilà et al. 2009; Montero-Castaño and Vilà 2017).

Several network attributes appear to enhance community resistance to invasion (Lurgi et al. 2014; Russo et al. 2014). In antagonistic networks, high connectance seems to confer resistance to invasions because invaders are more likely to encounter fewer available niches (Smith-Ramesh et al. 2017), even after controlling for species richness (Lurgi et al. 2014). In contrast to connectance, nestedness appears to decrease resistance to invasions (Hui et al. 2016), presumably because the arriving species tend to interact with generalist residents (Aizen et al. 2008), a mechanism of network buildup known as preferential attachment (Bascompte and Stouffer 2009).

Beyond network structure of the recipient communities, several traits might make species better invaders (Lurgi et al. 2014). Specifically, having more mutualistic partners (generality) and fewer interactions with enemies (vulnerability) may sometimes increase invader success (Keane and Crawley 2002). In mutualistic networks, when generalist invaders become highly abundant, they may take over some ecological roles of native species; for example, monopolizing interactions as super-generalized network hubs (Aizen et al. 2008; Albrecht et al. 2014).

## Climate change

Climate change represents a global threat for multiple levels of biological organization, from organisms to communities (Woodward et al. 2010). Because physiological rates are temperature-dependent, climate change should influence the performance of individuals and their interactions (Hegland et al. 2009; Huey et al. 2012; Vázquez et al. 2017), with the potential to cascade through the entire network (Memmott et al. 2007). For example, warming tends to increase animal mobility, which could imply higher prey capture and consumption rates, in turn affecting interaction strengths in trophic networks (Vasseur and McCann 2005).

Although a number of studies have considered the potential effects of climate

change on species richness, predicting effects on species interactions poses an additional problem because of interaction flexibility. Climate change could arguably have greater detrimental effects on animals than plants from pollination and seed dispersal networks due to narrower climatic niches of animals; in fact, simulations allowing interaction rewiring projected that plant extinctions are more likely to trigger animal coextinctions than vice versa (Schleuning et al. 2016). Moreover, because community structure partly reflects historical events (Ricklefs 2004), studying historical climatic changes may help understand current network structure and predict future changes. For instance, a study that assessed how past climate change influenced the current structure of a plant-pollinator network found that historical climate change is as important as contemporary climate in shaping modularity and nestedness (Dalsgaard et al. 2013).

Climate change may alter species phenologies (seasonal timings) and thus disrupt interactions. Much as a predator needs its prey available in its habitat, a bee needs that a flower opens when searching for it (Durant et al. 2007; Miller-Rushing et al. 2010; Kerby et al. 2012; Rafferty et al. 2015; Visser and Gienapp 2019). As both spatial and temporal coexistence drive network assembly, spatio-temporal mismatches caused by climate change may lead to network disassembly (Devoto et al. 2007; Memmott et al. 2007).

The above body of research suggests that global change drivers can exert strong influences on the structure of ecological interaction networks. At the same time, we clearly need more research to fully grasp the mechanisms behind those effects and to use that knowledge to devise management actions that may help curb the detrimental effects of global change on ecosystems.

## What next? Research priorities for the next decade

### *Predicting interactions in space and time*

We have made substantial progress in understanding the processes that drive network structure. This progress has been partly facilitated by the increased availability of data and the development of sophisticated statistical methods. Yet, we still fail to explain the full variation in network structure and, crucially, our ability to predict interactions in space and time seems quite modest

(Desjardins-Proulx et al. 2017; Costa et al. 2018; Benadi et al. 2021). For some species pairs which tend to engage in temporally and spatially persistent interactions we may have some greater confidence that they might interact (Chacoff et al. 2018; Miele et al. 2020; Resasco et al. 2021), but our ability to predict interactions at a broader scale still seems limited (Desjardins-Proulx et al. 2017; Costa et al. 2018; Benadi et al. 2021). Understanding the drivers of species interactions and its variability over space and time will help us improve our ability to predict network patterns and, hence, apply that knowledge to address management issues for applied problems (Tylianakis et al. 2010; Kaiser-Bunbury and Blüthgen 2015; Harvey et al. 2017; Kotula et al. 2021). Furthermore, the inclusion of space and time to our network studies will allow us to identify species with important roles, which may be keystones for community persistence (Cagnolo 2018).

### *Understanding the influence of variability in all its dimensions on species interactions*

So far, we have made only modest attempts to incorporate variability into our conceptual and methodological approaches to the study of ecological networks. Some interaction network studies have represented individuals as nodes as an attempt to include intraspecific variation in interactions, while others address intraspecific variation in phenotypic traits of the interacting partners. However, intraspecific variability influence on species interactions is still unresolved. Arguably, however, incorporating such variability will reduce the expected prevalence of forbidden interactions (González-Varo and Traveset 2016). In addition, an increasing number of studies considers interaction variability over time and space, although our understanding of the mechanisms behind such variation is still rudimentary (CaraDonna et al. 2021). Of course, obtaining community-level data that encompass intraspecific variation in traits and spatio-temporal distributions represents a major challenge that will require substantial funding and collaboration among research teams.

### *Understanding the ecological and evolutionary consequences of network structure*

Several studies have linked network structural properties such as species richness, connectance, nestedness and modularity on species persistence and community resilience

and stability (Okuyama and Holland 2008; Thébault and Fontaine 2010; Stouffer and Bascompte 2011; Grilli et al. 2016; Peralta et al. 2020b). Although these studies together suggest that network properties may influence stability in a predictable way, the relationships are typically weak and rest on critical assumptions which, if changed, sometimes lead to radically different conclusions. For example, incorporating the cost of mutualism into models of mutualistic interaction networks affects the strength of the network structure-stability relationship found in previous studies (Peralta et al. 2020b). Thus, ecological structures usually interpreted as favoring community stability may in fact come from historical processes unrelated to stability (Staniczenko et al. 2013; Maynard et al. 2018; Valverde et al. 2018).

We also need a better understanding of how network structure influences ecosystem processes and ecosystem functioning. A number of studies have explored the relationship between the structure of multitrophic systems and ecosystem functioning, finding some promising —albeit usually idiosyncratic— results, and often coming from simple food web systems with unclear relevance for more complex ecosystems (Thompson et al. 2012; Poisot et al. 2013; Soliveres et al. 2016; Wang and Brose 2018). Also, in studies of plant-seed disperser networks, estimating the seed dispersal function requires not only data on plant-frugivore interactions, but also on the seed dispersal distance and seed viability (González-Castro et al. 2015; Donoso et al. 2016; Acevedo-Quintero et al. 2020), the latter usually not available.

Finally, we need a better understanding of the influence of network structure on the (co)evolutionary dynamics of interacting species. Some recent studies suggest that some structural features of interaction networks may enhance coevolutionary processes, such as the symmetry in the reciprocal effects between pairs of interacting species (Lomáscolo et al. 2019) and the prevalence of indirect effects (Guimarães Jr. et al. 2017). Yet, inferring coevolution in nature represents a major challenge (Week and Nuismer 2019), and doing so for hundreds of pairs of interacting species will require substantial efforts in collecting data and refining the methods available to conduct such work.

*Broadening the catalog of interaction networks*

The number of studies documenting different types of networks has increased impressively over the last few decades; see for instance the Interaction Web Database (http://www.ecologia.ib.usp.br/iwdb/) and the Web of Life database (https://www.web-of-life.es/). At the same time, we need to broaden the scope of the catalog to make it more inclusive in terms of geography and interaction types. For example, 'global' studies of interaction networks include an heterogeneous representation of different world regions (Schleuning et al. 2012; Schwarz et al. 2020; Poisot et al. 2021); some ecosystem types, such as drylands, also seem typically underrepresented.

To assess the generality of network patterns we need a more representative sample of ecoregions across the globe. In some cases we also need to increase the representation of different functional groups. For instance, much of what we know about seed dispersal networks comes from studies of plant-bird interactions, whereas other interaction types, such as plant-bat or plant-mammal interactions, seem underrepresented (Mello et al. 2011). Similarly, our knowledge of the structure of plant-animal mutualistic networks usually comes from diurnal studies, and including data on nocturnal interactions may increase our understanding of the structure of interaction networks (Devoto et al. 2011). Likewise, in food web studies, we have historically ignored parasites, but studies that include them have shown that network structure changes significantly with such inclusion (Lafferty et al. 2006). Finally, the vast majority of our knowledge on ecological interaction networks comes from aboveground interactions, while we know relatively little about what happens below ground, and the little we know indicates that interaction networks can look quite different belowground (e.g., Toju et al. 2014, 2018), which suggests that we should increase our efforts to study this type of networks.

A broader catalog of ecological networks should ultimately include networks combining multiple interaction levels and layers (e.g., Melián et al. 2009; Pocock et al. 2012). For instance, early food web studies combined a variety of feeding modes (e.g., Polis 1991), allowing us to understand the mechanisms of energy transfer to the whole

community (Cohen et al. 2009). In a like manner, multilevel networks can help assess the reciprocal influence of non-contiguous trophic levels mediated by the intermediate level (Lewinsohn et al. 2005; Schemske et al. 2009). Recent studies attempt to combine different interaction types into a network (Pocock et al. 2012; Kéfi et al. 2016; Pilosof et al. 2017). The availability of new data and approaches, and DNA metabarcoding (Evans and Kitson 2020), might help achieve a more comprehensive picture of ecological networks across the globe.

### *Teasing apart sampling effects from true biological mechanisms*

To fully understand network patterns and their determinants we need to make further progress in teasing apart sampling effects from true biological mechanisms as determinants of network structure. Our ability to deal with such effects will require improved sampling and statistical methods to tease apart sampling from process. As we have argued, minimizing sampling artifacts will require increasing sampling effort as much as possible combining multiple, complementary sampling methods, using network metrics robust to sampling effects applied to standardized data in terms of scale, sampling method and sampling effort, often with the aid of null models, simulated data and sophisticated statistical methods,

while also improving our knowledge of the natural history of our study systems.

### *Quantifying interaction/effect strength*

We also need to improve the quantification of the two-way effects involved in the interactions we represent in networks in an ecologically and/or evolutionarily meaningful way. Although we have made some progress to clarify conceptually the meaning of the effects we want to represent in interaction networks and of the proxies we can use to conduct the needed measurements for the hundreds, or thousands, of pairwise interactions included in ecological interaction networks, we still need to refine these methods to make them more ecologically and evolutionarily meaningful.

## Conclusions

We hope to have offered a balanced overview of the state of knowledge (and of ignorance) on ecological interaction networks. Our review suggests that we have made substantial progress in describing, understanding and predicting the structure and dynamics of ecological interaction networks and in applying this knowledge to assess how ecological communities may respond to global environmental change. The outstanding issues we have identified will hopefully help to guide research efforts in the coming years.

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