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. We then 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. 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, indirect interactions, interaction frequency, interaction strength, modularity, multilayer networks, nestedness, network nodes, neutral processes, niche processes, sampling effects, species interactions, species roles

Resumen. Redes de interacciones ecológicas: qué sabemos, qué no sabemos, y por qué importa. Las especies que coexisten en las comunidades ecológicas interactúan de diferentes modos, formando 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, su 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 múltiples 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, identificando 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, frecuencia de interacción, fuerza de interacción, modularidad, redes multicaña, anidamiento, nodos de redes, patrones de redes, procesos neutrales, procesos de nicho, efectos de muestreo, interacciones interespecíficas, roles de las especies

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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-Jahiz’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: Food is the burning question in animal society, and the whole structure and activities of the community are dependent upon questions of food-supply (Elton 1927). The study of these “food webs” brought about many key insights in the conceptual development of 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 1991a, 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 made an effort 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. We then 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 native species are being replaced by exotic ones) (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, and which in addition 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 testing 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 (Fig 1a). More recently, ecologists have realized that the species-level resolution of nodes can obscure the intraspecific variability of interactions (Trojelsgaard and Olesen 2016), and 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 (Fig. 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 (Gonzalez 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).

Moreover, network 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 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
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 (Fig. 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 (Fig. 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 (Fig. 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 (Fig. 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 (Fig. 3d-e) offers
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 (Fig. 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 (Fig. 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 (Fig. 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). Furthermore, the above network patterns can occur simultaneously within 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 (Trejelsgaard 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, Trejelsgaard et al. 2015). Furthermore, 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
especies 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 (Fig. 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,
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 Valiente-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 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
et al. 2021, Kotula et al. 2021). Hence, unraveling the relative importance of species interaction drivers
could facilitate the prediction of interactions. Furthermore, 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 resulting from species attributes (crooked magnifier effect) and sampling methods (tendentious sampling effect; Fig. 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, Banaske-Richter et al. 2004, Vázquez and Aizen 2006, Nielsen and Bascompte 2007, Chacoff et al. 2012, Rivera-Hutin 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 in most network indices used to characterize network structure. Thus, we must interpret observed network patterns with caution, especially 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 (Martinez 1991, Polis 1991b, 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 (Martinez 1991, Polis 1991b), 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. 2011, 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 example, 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).
Similarly, 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 (DNA barcoding and metabarcoding) may also help improve
interaction sampling by focusing on groups whose interactions may otherwise prove difficult to

Fig. 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., Martinez 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
typically 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 acquire the lowest 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
methods that allow accounting for the sources of bias, such as 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 represent 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
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. For example, in a plant-frugivore bird meta-network, 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 hence 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 et al. 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 (herbivory, parasitism, and mutualism), in which networks including pollinators had greater fragility, a result attributed to network generalization (Pocock et al. 2012). Furthermore, 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).
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 (Heglund 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). Furthermore, 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). Similarly, 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). Similarly, 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 (see, 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 1991b), allowing us to understand the mechanisms of energy transfer to the whole community (Cohen et al. 2009). Similarly, 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, use 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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Figure 1. Illustration of 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 less 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. Ilustración de 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.
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 motivos. (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.
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 phylophic.org.
Figure 4. Illustration of the most commonly studied species interaction drivers. (a) Morphological trait matching and (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 y (b) superposición fenológica entre especies interactuantes. (c) Las 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 representa la abundancia de las especies y la frecuencia de las interacciones, respectivamente.
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. La 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 el 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 pero a la vez llevando a un fuerte submuestreo del otro grupo.