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A Critical Evaluation of Network Approaches for Studying Species Interactions

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Abstract

Ecological networks of species interactions are popular and provide powerful analytical tools for understanding variation in community structure and ecosystem functioning. However, network analyses and commonly used metrics such as nestedness and connectance have also attracted criticism. One major concern is that observed patterns are misinterpreted as niche properties such as specialization, whereas they may instead merely reflect variation in sampling, abundance, and/or diversity. As a result, studies potentially draw flawed conclusions about ecological function, stability, or coextinction risks. We highlight potential biases in analyzing and interpreting species-interaction networks and review the solutions available to overcome them, among which we particularly recommend the use of null models that account for species abundances. We show why considering variation across species and networks is important for understanding species interactions and their consequences. Network analyses can advance knowledge on the principles of species interactions but only when judiciously applied.

1. NETWORKS: WHO INTERACTS WITH WHOM, AND HOW OFTEN (OR NOT)?

Bipartite network: interactions or links between species in two clearly delineated (often trophic) levels

Network metric/index: mathematical descriptor quantifying a property of the network

Null model: randomization of the network under certain constraints; useful to distinguish pattern from chance in interactions

Functional consequence: ecological outcome of species interactions, often related to a specific ecosystem function (e.g., herbivory, parasitism, pollination, seed dispersal)

Link strength: relative frequency (number of interactions), intimacy, and/or importance of a link between species; used as the link weight

Observed interaction: a link between species that has been confirmed by direct observation in the study site

Inferred interaction: a link predicted from external data but not observed on site; often used in food-web studies

Analyses of networks of species interactions feature prominently in ecological research (Bascompte & Jordano 2013, Delmas et al. 2019, Ings & Hawes 2018, Vázquez et al. 2022). Network studies are being conducted across most subdisciplines of ecology, including (but not restricted to) community ecology (Spiesman & Gratton 2016, Staab et al. 2016), biodiversity–ecosystem functioning research (Fornoff et al. 2019, Fründ et al. 2013), biogeography (Trøjelsgaard et al. 2013, Windsor et al. 2023), restoration ecology (Kaiser-Bunbury et al. 2017, Pocock et al. 2012), invasion biology (Heleno et al. 2013, Olesen et al. 2002), applied ecology (Feit et al. 2021, Ramirez et al. 2022), and conservation biology (Harvey et al. 2017, Petsopoulos et al. 2021). To enable the quantification and comparison of species interactions, a large set of mathematical descriptors have been postulated (e.g., Bersier et al. 2002, Blüthgen et al. 2006, Jordano 1987). The advent of easy-to-use, open-source software—including the popular R packages bipartite (Dormann et al. 2009) and igraph (Csardi & Nepusz 2006), as well as the Pajek software (Batagelj & Mrvar 2004)—has further facilitated formal network analyses (Delmas et al. 2019). These advances have boosted the whole of ecology, spurred the creation of large datasets (Poisot et al. 2021), and stimulated the development of new theory (Krishna et al. 2008).

Detailed reviews on the application of ecological network analyses exist elsewhere (Bascompte & Jordano 2007, Delmas et al. 2019, Dormann et al. 2017, Vázquez et al. 2022, Windsor et al. 2023). Instead of reiterating them, we focus on pitfalls in network interpretations arising from effects of sampling, abundance, and diversity. Network analysis is still occasionally presented as a silver bullet in ecology, associated with high expectations for solving a huge set of questions. Against the backdrop of contagious network optimism, however, are a number of critiques, concerns, and caveats about network analyses and their ecological interpretation (Blüthgen 2010, Blüthgen et al. 2008, Brimacombe et al. 2022, Dormann et al. 2017, Fründ et al. 2016, Pringle & Hutchinson 2020, Vázquez 2005, Vázquez & Aizen 2003). We believe that progress in understanding the causes and consequences of species interactions is still hampered by conceptual shortcomings and biases, superficial or even spurious interpretations of network patterns, and an ignorance of the incompleteness of interaction data. After briefly introducing bipartite networks of species interactions and food webs, and describing how network metrics/indices are biased by incomplete sampling, species abundances, and diversity, we argue that the consequences of false interpretations of patterns are relevant and include flawed conclusions on ecological principles, ecosystem functioning, and stability. We then outline several methods, metrics, and null models that can compensate for these shortcomings. We suggest a framework based on abundance, diversity, specialization, and exclusiveness as separate dimensions of network complexity to facilitate a biological interpretation of networks and their functional consequences. In the end, we briefly allude to scale and aggregation of network data and to networks that do not consist of interactions between species.

2. SPECIES-INTERACTION NETWORKS VERSUS FOOD WEBS

A species-interaction network is composed of cooccurring species that are recorded to interact in a defined space at a specific time. Each network typically summarizes one predefined interaction type or ecosystem function, rarely mixtures of different ones (see the sidebar titled Bipartite Networks). The frequency of interactions (i.e., the link strength) is typically characterized by the observed number of interacting individuals per species or other quantitative measures of activities such as visitation rates or parasitism events. Empirical data on observed interactions in an ecosystem provide a great advantage over inferred interactions and help to weigh each link by its relative

BIPARTITE NETWORKS

Typical (bipartite) networks represent interactions between two functionally defined levels such as trophic interactions, mutualism, parasitism, commensalism, or symbiosis. Examples include plants and pollinators (Guy et al. 2021, Peralta et al. 2024), plants and seed dispersers (Muñoz et al. 2017), plants and herbivores (Robinson & Strauss 2020), and hosts and parasites or parasitoids (Staab et al. 2016). Others include plants with extrafloral nectaries and ants (Dáttilo et al. 2019), dung beetles and dung types (Frank et al. 2018), plants and mycorrhizal fungi (Toju et al. 2018), and cleaner fish and cleaned fish (Quimbayo et al. 2018), to name just a few.

frequency or its potential ecological relevance (i.e., total effect as the product of interaction frequency and per-interaction effect) (Vázquez et al. 2005). Generally, we suggest using weighted network metrics/indices (Blüthgen et al. 2008, Dormann et al. 2009, Lau et al. 2017) if the data contain meaningful link weights, as there are few reasons (if any) to use unweighted metrics.

Food-web graphs, however, are different, even though they are sometimes mingled with species-interaction networks. In a food web, interactions between species are usually inferred from literature data, assumptions regarding traits, or from their mere cooccurrence (Pringle & Hutchinson 2020). Strengths of interactions are sometimes estimated only based on body masses (e.g., big eats small), metabolic rates, or population densities (Cohen et al. 2009). Food webs have been critically discussed in the past for their lack of realism, coarse resolution, and incompleteness (Martinez et al. 1999, Paine 1988, Polis 1991, Pringle & Hutchinson 2020). Increasingly, however, food webs include observed interaction frequencies or other quantitative measures. Among several achievements, chemical and molecular analyses of gut contents or feces have started to enhance the precision of consumer interactions for omnivorous taxa or where interactions are hard to observe and quantify directly (Pringle & Hutchinson 2020, Wirta et al. 2014). DNA barcoding and meta-barcoding have also helped to generate data for network studies (Bell et al. 2017, Gripenberg et al. 2019, Harting et al. 2024) and improved our knowledge about interactions or their spatial and temporal resolution.

The shift in food webs from inferring links to observing links and the reliance on detection come with a significant cost that is also prevalent in species-interaction networks: Observed interactions and their frequencies are inevitably limited by the sampling effort and incompleteness of the data. Given the costs of sampling effort, it is surprising that few attempts have been made to compare observed links—particularly the unknown contribution of unobserved missing links—with predicted links known from other sites, from the literature, or from underlying models. For any kind of interaction network, it may be timely and valuable to compare both empirically observed and theoretically predicted links.

3. DETERMINANTS OF INTERACTION PATTERNS: FACTS, FICTIONS, AND SAMPLING

Species-interaction networks build upon the empirical observation of interactions. Like any observational data collection in ecology (e.g., Hulbert 1971), sampling of interactions is prone to biases. One major potential bias—but one that is often overlooked—is the taxonomic scope of a study, namely how representative the interaction data are for an ecological process. Studies often record or analyze only a fraction of interacting species, e.g., flower visits of hummingbirds but not concurrent visits of bees. For biodiversity surveys, it is well appreciated that complete detection of all species irrespective of a taxonomic focus, if even achievable, requires high sampling effort (Chao & Jost 2012, Gotelli & Colwell 2001). The same sampling limitation applies to interaction data;

Trait: measurable phenotypic property of a species; can be morphological, chemical, behavioral, etc.

Missing link: link that is absent in the observed network but possible; detection would require more sampling

Forbidden link: link that is absent in the observed network because it does not exist; i.e., a true 0

Network size: total number of species in the network, usually the sum of the species from both levels in bipartite networks

Specialist: a species that, irrespective of its abundance, interacts with relatively few species (or with an exclusive species) in the other level of a bipartite network

hence, any empirical network is incomplete (Chacoff et al. 2012, Chiu et al. 2023). The probability that two species interact in nature undoubtedly depends on their presence and abundance or activity. Moreover, the probability of detecting an interaction increases with the overall sampling effort of a study in the same way as the probability of detecting a species in a diversity assessment (Blüthgen et al. 2008, Chacoff et al. 2012, Gotelli & Colwell 2001). Sampling and abundance together determine the likelihood that an interaction is recorded in an empirical network, and how often (Peralta et al. 2024). Surprisingly, this fact is commonly ignored in network interpretations and needs to be considered carefully for comparisons both between networks and between the species within a network. Particularly from the viewpoint of zeros in the network (i.e., unobserved links), it is crucial to distinguish whether interactions are truly absent or just not observed due to sampling constraints and undersampling (Cirtwill et al. 2019, Olesen et al. 2011, Wirta et al. 2014). As illustrated by Jordano (2016), unobserved links may be either missing links, and may be detected with more sampling, or forbidden links due to linkage constraints, irrespective of sampling. Only forbidden links require a biological explanation, e.g., a defense mechanism, interspecific competition, phenotypic, or phenological mismatch, to understand why species do not interact (CaraDonna et al. 2021, Jordano 2016). The search for biological determinants behind a network, including the constraints that prevent certain interactions, therefore requires true patterns to be distinguished from biases due to variation in abundance, sampling, diversity, and choice of network indices.

3.1. Abundance and Sampling

The probability that two species interact is a function of their relative abundances (Vázquez et al. 2009), and the likelihood of detecting these interaction increases with the sampling effort taken by the investigator. Species abundance and sampling effort have fundamentally different meanings (Gotelli & Colwell 2001), but variations in these quantities have similar effects on network data: Low abundance and/or low sampling produce more incomplete networks. Independent abundance data are often missing and replaced by the total frequency of individuals recorded interacting, which prevents a clear distinction between abundance and sampling effects. Many mathematical descriptors of networks (network indices) (Lau et al. 2017) are biased by sampling method and effort (Ballantyne et al. 2015, Gibson et al. 2011, Rivera-Hutinel et al. 2012, Vizentin-Bugoni et al. 2016) and sensitive to the number of species and links (Brimacombe et al. 2022, Dormann et al. 2009, Fründ et al. 2016, Kuppler et al. 2017). This hampers direct comparisons across networks that differ in the number of species involved (network size), except when sampling and abundance are taken into account (Vanbergen et al. 2017).

For example, does a species with a single observation represent a specialist in the network? Ecologists would agree that one datum is an insufficient basis to answer this question. Yet, sampling incompleteness and rarity are surprisingly often ignored in the interpretation of networks. Rare species are thus frequently confused with specialists, and without additional information, whether these species are truly specialized or the putative specialization is an artifact of rarity cannot be easily inferred (Blüthgen 2010). In fact, upon scrutiny, most rare species turn out not to be specialized (Benadi et al. 2014, Dorado et al. 2011, MacLeod et al. 2016). Perceived rarity of links is also contingent on network size and sampling, as networks that involve more species typically contain fewer observations per potential link (Blüthgen et al. 2008). To prevent potential bias, the exclusion of rare (infrequently observed) species from network analyses has repeatedly been proposed (e.g., Bergamini et al. 2017, Robinson & Strauss 2020). However, rare species are the norm rather than the exception in communities and contribute to network architecture, consumer diets, ecological processes, and stability (Hutchinson et al. 2022, McCann et al. 1998). The risk of confusing low information density with specialization is greatest for rare species and diminishes only gradually with higher abundance and sampling (Blüthgen et al. 2008), so any abundance threshold for inclusion is arbitrary and potentially misleading. On the other end of the continuum, species can appear to be more generalized simply because they are abundant, and they are not necessarily abundant because they are generalized (Simmons et al. 2019). Therefore, instead of excluding rare species, we suggest that species abundance and/or sampling should be explicitly addressed in network analyses.

Even when sampling effort is high, many links between species are missed, particularly for rare species. Relative to the possible interactions based on exhaustive sampling, the number of locally observed interactions is still small (Poisot et al. 2017, Spiesman & Gratton 2016). This underscores the necessity of accounting for uneven sampling and differences in interaction frequencies, if networks are to be compared (Chacoff et al. 2012). Considering variation in sampling, abundance, and network size is particularly important when networks from different localities are analyzed across space and time or along environmental gradients (Pellissier et al. 2018, Tylianakis & Morris 2017), which is often the case in studies addressing questions of land use or macroecology (Windsor et al. 2023). Here, differences in sampling and mode of data collection can easily account for more variation in network structure than biological determinants (Doré et al. 2021). Similarly, within a given network, species cannot be compared without considering their relative abundances (Blüthgen et al. 2006). Otherwise, specialization may be confused with rarity, which has led to doubtful conclusions regarding extinction risks. For instance, the assumption that flower visitors with a single link are specialists that may go extinct if their preferred plant shifts its phenology (Memmott et al. 2007) has led to fundamentally flawed conclusions on climate change risks; many of these rare visitors even represented opportunistic rather than obligate consumers of floral resources (Blüthgen 2010).

3.2. Species Diversity

Apart from abundance, but not independent of it (Srivastava & Lawton 1998), a second critical determinant of any network pattern is the number of species involved. Network complexity is often defined in terms of the number or diversity of links. An increase in network complexity may reflect higher sampling effort, higher total abundance, and/or higher diversity (richness, evenness) of species, along with a greater number or diversity of links per species, termed generality (**Figure 1**). All these metrics are biased by sample coverage and abundance in a similar way to biodiversity metrics (Blüthgen et al. 2008, Chiu et al. 2023). Most network metrics (**Table 1**) scale with the number of species involved (**Figure 2**), except the complementary specialization metrics (network-level H_2' and species-level d'), which are conceptually independent of total abundance and diversity. Complexity and generality thus increase both with higher species diversity and with lower specialization (H_2'), while generality and specialization are orthogonal.

3.3. Weighted Metrics Are Preferable

Failing to account for abundance (e.g., Simmons et al. 2019) and sampling (e.g., Vizentin-Bugoni et al. 2016) per network and per species in a network affects both weighted (quantitative, i.e., where links are scaled by interaction frequencies) and, even more strongly, unweighted (binary) network metrics, which consider only the presence or absence of links (Dormann et al. 2009). The missing links (0 interactions) contrast with realized links (1 interaction) in unweighted metrics, whereas variation between rare and missing links is more subtle for weighted analyses (Pinheiro et al. 2022). Unweighted metrics are more, not less, sensitive to differences in sampling completeness and abundance (Banasek-Richter et al. 2004, Dormann et al. 2009, Fründ et al. 2016, Vizentin-Bugoni et al. 2016). Not surprisingly, comparisons across weighted versus unweighted networks (or networks that weight interactions differently) might reveal contrasting network

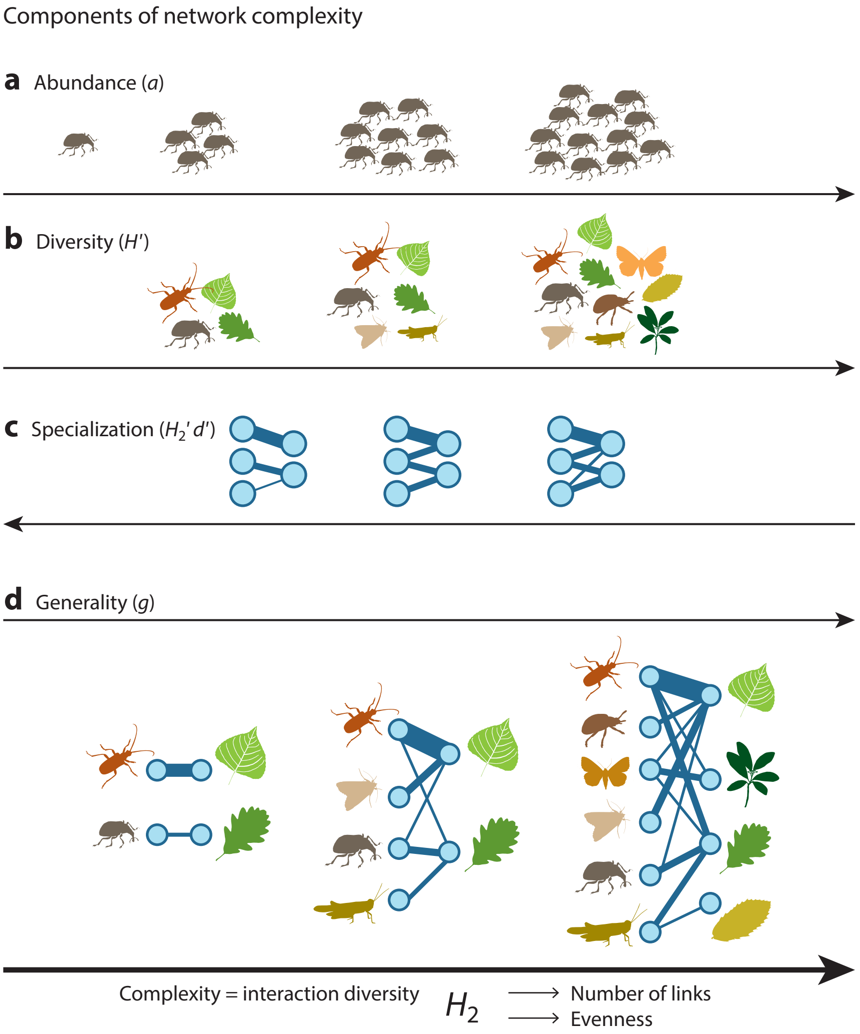


Figure 1

Conceptual representation of network complexity and its potential determinants. Higher network complexity, defined as the diversity of interactions, H_2, might result from an increase in total abundance (*a*), species diversity (*b*), and/or generalization of interactions [including lower network- or species-level specialization, H_2' and d' (*c*), respectively, or higher diversity of links per species, and thus (*d*) generality, *g*] (**Table 1**). Each of these determinants may pinpoint different underlying ecological mechanisms; e.g., resource densities may be responsible for total abundance, environmental heterogeneity for species diversity, and trait differentiation of prey or resource species for generality of consumers. Animal and leaf silhouettes taken from **https://www.phylopic.org** (CC0 1.0).

structures (Castro-Urgal et al. 2012, Dáttilo et al. 2014) but need to be examined always in the light of sampling effects.

3.4. Ecological Determinants of Network Patterns

To understand the underlying ecological causes of a pattern—rather than its mere existence—it is crucial to distinguish whether it is triggered by unequal sampling alone, by abundance, or

Table 1 Commonly used metrics for bipartite networks, with values for the plant–pollinator networks shown in Figure 3 [an observed network based on data from Olesen et al. 2002 and a Patefield null model with the same marginal totals as the observed network (Patefield 1981)]

Symbol	Metric	What it shows	Null model	Observed
S	Species number/network size	Total number of plant species ($S_1 = 10$) and pollinator species ($S_2 = 12$): $S = S_1 + S_2$	22 (fixed)	22
A	Interaction number	Total number of interactions observed	1,139 (fixed)	1,139
L	Link number	Total number of links in the network	93	30
C	Connectance	Proportion of observed links in relation to all potential links: $C = L/(S_1 \cdot S_2)$	0.78	0.25
e^{H_2}	Interaction diversity	Effective number of links (exponential Shannon index); describes the quantitative network complexity (analog of L)	49.4	19.9
E_2	Interaction evenness[a]	How evenly the complete matrix is filled, proportionally to a scenario in which all links have the same weight (quantitative analog of C): $E_2 = e^{H_2}/(S_1 \cdot S_2)$	0.41	0.17
$N_\mathrm{u}, N_\mathrm{w}$	Nestedness, unweighted/ weighted	The extent to which species with fewer links have a subset of links to species with more links (rather than exclusive links)	6.0°, 0.82	26.7°, 0.42
Q	Modularity, weighted[b]	The extent to which links are grouped into relatively exclusive clusters	0.06	0.50
$g_\mathrm{u}, g_\mathrm{w}$	Generality, unweighted/ weighted	Diversity of links per species (weighted: exponential Shannon index, like e^{H_2})	7.8 ± 2.0, 5.4 ± 1.3	2.5 ± 1.6, 1.7 ± 1.7
H_2'	Standardized network-level specialization	Complementary specialization, i.e., how exclusive the links of each species are; standardized to constraints by marginal totals	0.02	0.53
d'	Standardized species-level specialization	How exclusive each species is compared to the others; related to H_2'	0.03 ± 0.03	0.46 ± 0.12

The specialization–generalization continuum can be defined as the niche breadth and thus depicted by any metric of link diversity, i.e., L, e^{H_2} or g, or by $1 - C$ and $1 - E_2$ (Chiu et al. 2023), which are both standardized by the number of potential links (if all species interact). In contrast, the specialization metrics, d' and H_2', and modularity, Q, focus on the aspect of niche overlap and thus are used to compare each species to all others in the same network. Both d' and H_2' emphasize the exclusiveness of interactions (i.e., nonoverlap, niche partitioning) and are standardized by marginal totals. Most metrics (L, C, e^{H_2}, E_2, and g) represent sums or averages across all species, and L, e^{H_2}, and g scale with sampling, S, and A, but not d', H_2', E_2, and Q (**Figure 2**). Here, species-level metrics (g, d') are summarized as mean ± standard deviation of 12 pollinator species (i.e., higher level). For more detailed explanations and many more metrics, we refer to Blüthgen et al. (2008), Dormann et al. (2009), and Lau et al. (2017).

[a] Evenness is often defined for raw Shannon entropy (H_2), not effective diversity (e^{H_2}) (but see Jost 2010). This would result in the definition $E_2 = H_2/\log(S_1 \cdot S_2)$, which yields 0.81 in the null model versus 0.63 in the observed network.

[b] Method by Dormann & Strauss (2014), generally correlated with H_2'.

by diversity (Blüthgen 2010, Fründ et al. 2016, Jordano 2016, Vázquez et al. 2009). The ecological interpretations of abundance and diversity effects can differ. Abundance may be associated with energetic effects such as available resource densities, while diversity may mirror variation in resource or environmental heterogeneity and thus niche complementarity. Therefore, both represent partly independent and ecologically meaningful causes that help to interpret emergent network patterns. Abundance is a main determinant of many network patterns (Blüthgen et al. 2008, Vázquez & Aizen 2003, Vázquez et al. 2009), particularly when the reciprocal specialization of the network is not high (Simmons et al. 2019). This critical limitation of networks reinforces the need to control for abundance and diversity in network interpretations (Winfree et al. 2014) rather than to assume that certain factors play a role. Nevertheless, realized species interactions

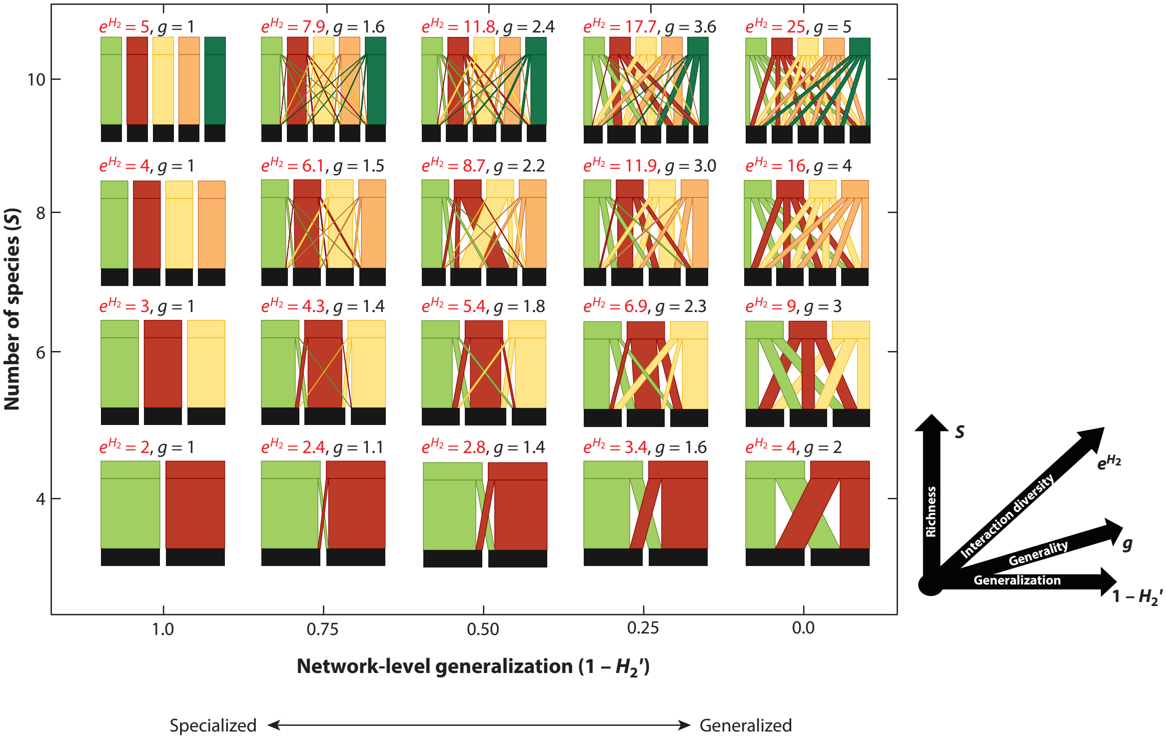


Figure 2

Dimensions of network specialization/generalization and complexity across 20 hypothetical networks (each with $n = 100$ interactions in total). The five networks per row have the same total number of species (network size S), but their link configuration varies from highest specialization ($H_2' = 1$, i.e., $1 - H_2' = 0$) to highest generalization ($1 - H_2' = 1$) along the x axis. H_2' is conceptually independent of S and thus orthogonal to the y axis. However, the diversity of links per network (interaction diversity H_2) and per species (generality g) increases with both increasing S and increasing $1 - H_2'$ and is not orthogonal to the x and y axes (*inset*). Both e^{H_2} and g are the effective diversities of links, calculated per network or per species, respectively, based on the Shannon diversity. Hence, their maxima are constrained by the total number of species, e.g., $e^{H_2} = 25$ and $g = 5$, if each of the five species has five links. These maxima are found for the scenario where all links are realized with the highest possible evenness (at $1 - H_2' = 1$).

are also promoted and constrained by multiple biological factors, including phenotypic traits and evolutionary history (Ehrlich & Raven 1964, Junker et al. 2013, Peralta 2016). Specialization mirrors characteristics of each species, i.e., traits. Including species trait measures in network analyses increases our understanding of the studied interactions and thus specialization patterns, especially for relatively specialized interactions that depend on morphological matching and mismatching, such as flower visitation by hummingbirds (Dalsgaard et al. 2021). Similar to biodiversity research, trait-based approaches have advanced our understanding of species interactions, and the underlying concepts and methods have been summarized elsewhere (Junker et al. 2013, Marjakangas et al. 2022, Schleuning et al. 2015).

It is now easy [for example, with the functions networklevel and specieslevel in the R package bipartite (Dormann et al. 2009)] to calculate dozens of network indices, some of which are depicted in **Figure 2** and **Table 1** (see Blüthgen et al. 2008, Lau et al. 2017). We believe that this opportunity is sometimes misused, and many indices that are not directly related to studies' hypotheses—or even are conceptually flawed—are calculated, possibly to fish for significant results. This is not only bad practice but also inflates type I error rates (false-positive results), an issue that is

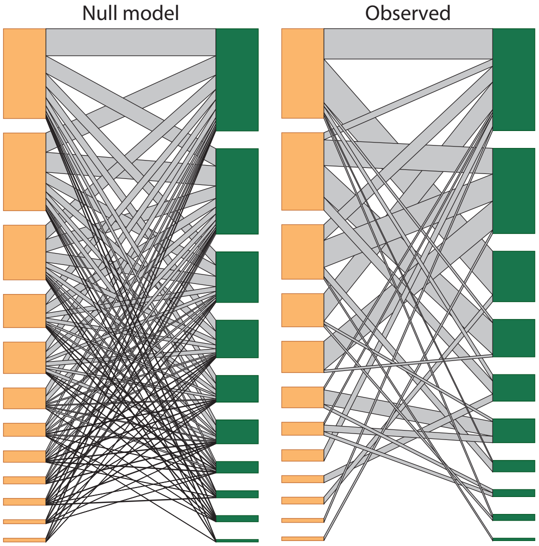


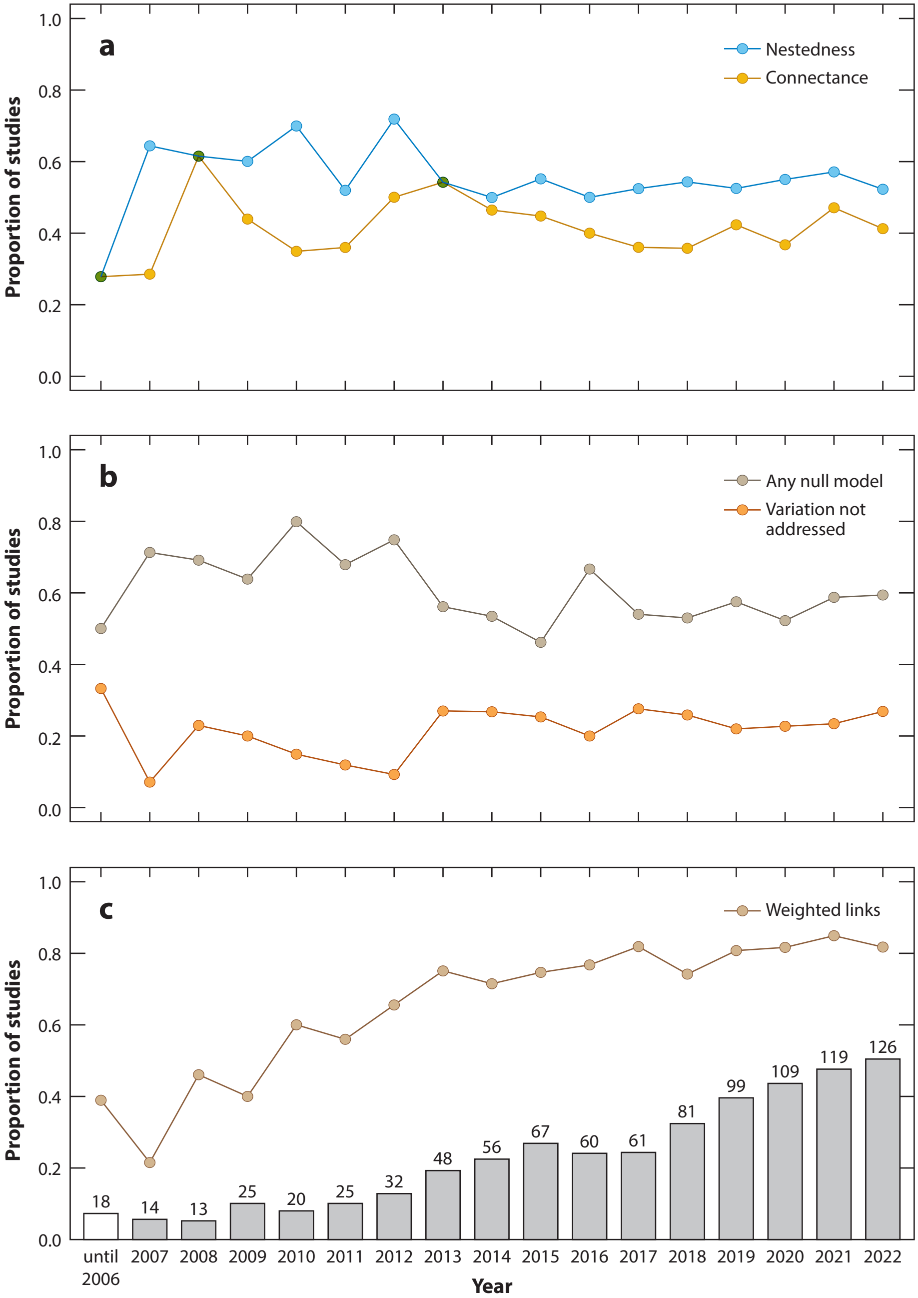
Figure 3

An observed network (*right*) and a null-model scenario (*left*). Values of commonly used metrics for these networks are shown in **Table 1**. The network is representative of empirical data, as it includes a few common and several rarely observed species and interactions (sorted by marginal totals). The null model uses the same combination of species and their abundances (fixed marginal totals, based on the Patefield null model). Consequently, specialization in the null model is lower than in the observed network [higher C, E_2, e^{H_2}, and g; lower d', H_2', and Q (**Table 1**)]. The example networks show interactions between 12 pollinator (*orange*) and 10 plant species (*green*) observed by Olesen et al. (2002).

fundamental to classical biostatistics and yet very rarely considered in network analyses (Simmons et al. 2018). Furthermore, many network indices are mathematically related and thus in practice correlated (Dormann et al. 2009). This is particularly expected for all unstandardized metrics that scale with sampling, abundance, and species diversity, as stated above. To cope with the correlation, multiple indices have sometimes been combined into a single variable via principal component analysis (Postic et al. 2020, Toju et al. 2018). In our opinion, this hinders the interpretation of the network structure and properties because different metrics have different implications (**Table 1**). To circumvent high type I error rates, we urge researchers to focus on selected indices that are most appropriate for testing their particular hypotheses. To achieve this, we suggest using a framework of a few selected network dimensions with complementary information (e.g., generality, network specialization, and complexity) and explicitly examining variation in total abundance and species diversity (**Figures 1–3**).

4. NESTEDNESS AND CONNECTANCE: PATTERNS OR ARTIFACTS?

Among the most widely reported descriptors of network topology are nestedness and connectance (**Figure 4*a***), which started as unweighted (binary) metrics and were later supplemented with weighted counterparts. Connectance (see the sidebar titled Connectance and Stability) is the proportion of the links observed relative to the total number of links possible in a network (Jordano 1987). Nestedness describes a specific configuration of the links, in which species with few links have only a subset of the links of species with more links (rather than having unique links) (Bascompte et al. 2003). In random networks, connectance and nestedness are correlated (Almeida-Neto et al. 2008, James et al. 2012), and their relationship differs between interaction types (Thébault & Fontaine 2010). Low connectance is often simply interpreted as high specialization (i.e., relatively few links are realized). Nestedness is often interpreted as specialization asymmetry, suggesting that specialists preferentially associate with more generalized partners (or resources) rather than with specialized partners—the opposite of reciprocal specialization.



(*Caption appears on following page*)

Figure 4 (*Figure appears on preceding page*)

Summary of analytical approaches in published empirical species-interaction network studies over time. (*a*) Nestedness and connectance continue to be frequently used network indices. (*b*) Consideration of null models (not distinguishing among null-model types) has been constant over time, as has the proportion of studies in which potential bias due to variation in abundance, sampling, and diversity has not been addressed at all. (*c*) Weighted links are now standard in the majority of networks. The number of assessed studies is indicated by the bars in panel *c* (with values above bars specifying the exact number; before 2007 there were only a few studies per year, which have been aggregated into a single category for better visualization). The figure is based on a systematic survey of the published empirical species-interaction network literature (see the **Supplemental Material**) and is not intended as a comprehensive map of the thematic or biogeographic representation of network research [which is available elsewhere (Poisot et al. 2021)].

Supplemental Material >

CONNECTANCE AND STABILITY

A debate has focused on whether connectance stabilizes or destabilizes communities, originating from May's (1973) pioneering work on destabilizing random networks and contrasting findings for different types of interactions (Allesina & Tang 2012, May 1973). In contrast to population equilibrium models, simulated extinction models show a higher robustness of more connected food webs, consistent with functional redundancy (Dunne et al. 2002). Hence, the mere number of links may affect network stability, particularly when simulations are performed on how species extinctions affect the number of coextinctions of species that depend on the missing species (Schleuning et al. 2016). However, the robustness of an empirical network to simulated extinction may also mirror the overall sampling intensity, abundance, and/or the number of species (Carpentier et al. 2021), since the number of links increases with sampling. Again, to understand the biological mechanisms behind this variation in stability, it is important to separate the effects of abundance, diversity, and specialization (see **Figure 1**).

However, both nestedness and connectance are strongly influenced by abundance and richness and thus a prominent example of a potential basis for flawed interpretation (Blüthgen 2010).

The simplest explanation for the observed nestedness is that it is an artifact of the species abundance distribution with few common and many rare species (Dáttilo et al. 2014) and/or the incompleteness of network data, combined with a certain degree of generalization or neutrality (Pinheiro et al. 2019). In fact, simulations of random interactions between sets of common and rare species produce a perfectly nested network, which has been shown by null-model simulations to be constrained by the total interaction frequencies per species (Blüthgen et al. 2008). Compared with such null-model patterns, virtually all empirical networks are significantly less nested [antinested sensu Poulin & Guégan (2000)], not more nested, than by chance alone (**Table 1**), calling into question the alleged stabilization of a nestedness pattern. Nestedness itself may be viewed as a random null model (Lewinsohn et al. 2006). Thus, it is surprising that nestedness in interaction networks was—and still is—incautiously interpreted as specialization asymmetry that is able to stabilize biodiversity (see the sidebar titled Nestedness and Stability), ignoring the fact that abundance or sampling alone suffice as an explanation (Krishna et al. 2008). The same problem is evident for the degree distribution, which describes the number of links per species (Vázquez 2005).

5. ADDRESSING VARIATION IN ABUNDANCE, SAMPLING, AND DIVERSITY

Real-world networks invariably differ in the number of species and links. Variation in the number of individuals and the diversity of species is an inherent property of communities and not, per

NESTEDNESS AND STABILITY

The paradigm that nestedness promotes diversity in mutualistic networks has not stood up to scrutiny (James et al. 2012, Staniczenko et al. 2013). The supposedly stabilizing role of nestedness relies on false assumptions in the underlying models: The influential theoretical analyses reporting a stabilizing role of nestedness compared to other configurations (e.g., Bascompte et al. 2003, Bastolla et al. 2009, Rohr et al. 2014, Thébault & Fontaine 2010) ignored the fact that there is interspecific competition for mutualists, as for other limited resources. Competition for mutualistic partners can be severe, e.g., competition among plants for pollinators (Mitchell et al. 2009) or among symbionts for hosts (Stanton et al. 2002). The stabilizing role of nestedness emphasizes an indirect selective advantage from specialization on a generalized partner: A consumer species that specializes on a resource shared by many other consumers should benefit from the partner's population stability. However, such a specialized consumer likely suffers from interspecific competition for limited resources, and the few network models that have considered limitation by resources or mutualistic services have rejected a stabilizing role for nestedness (Benadi et al. 2013, Staniczenko et al. 2013, Valdovinos et al. 2016).

se, a problem for the analysis, interpretation, and comparison of interaction networks. However, as outlined above, it is important to separate true differences in network structure from differences that could be a mere consequence of variation in sampling, abundance, or species diversity, which is still not consistently being addressed in empirical studies (**Figure 4*b***). The same is true for all comparative ecological studies (Gotelli & Colwell 2001, Hulbert 1971): When testing the influence of an environmental variable or an experimental treatment on, for example, species diversity, one has to disentangle whether the (statistical) effect of the treatment on species diversity is direct or mediated indirectly via a change in abundance. For network analyses, a toolbox to account for sampling effects and variation in abundance and species numbers among networks is available. Broadly, approaches to address differences among networks involve the inclusion of covariates, the accumulation or rarefaction of links, and in particular, comparison to appropriate null models.

5.1. Covariates

Considering appropriate covariates for sampling effort, abundance, or species diversity in the statistical analysis of network indices is straightforward and the easiest way to address variation across networks (sensu Burnham & Anderson 1998). In practice, including total abundance as a covariate distinctly increases the predictive power of models for network indices (Ceballos et al. 2016) or may render previously significant results nonsignificant (Heleno et al. 2013, Lázaro et al. 2016); the latter suggests that the inference is driven by abundance and not by any other hypothesized property (Morris et al. 2014). However, if the underlying positive relationship between total abundance or diversity and network metrics is biologically meaningful, its significance is masked and issues of collinearity may arise. Path models including a direct path of the respective covariate on the network index (Peralta et al. 2020, Schwarz et al. 2020) are thus better suited for maintaining cross-correlations when assessing potential biases. To account for differences in sampling, using sampling intensity as weights has also been proposed (Schleuning et al. 2012), but this provides no direct indication of the relationship between the covariate and the tested network index. Instead of covariates in the same model, some studies analyzed residuals of network indices after regressions with potential confounding factors (e.g., Olesen et al. 2002, Osorio et al. 2015), which is at best controversial (Freckleton 2002), as it can lead to biased parameter estimates. We thus recommend using the confounding variable directly in a path model or as a covariate in a multiple regression model.

5.2. Accumulation and Rarefaction

Species richness estimation: mathematical procedure to determine the expected (asymptotic) number of species under infinite sampling

Links in a network accumulate with sampling, making it possible to compare different networks via link accumulation and asymptotic extrapolation of expected link number (Chacoff et al. 2012). This follows the same logic as the use of species-accumulation curves and sample-based or individual-based species richness estimation when comparing community data differing in number of samples and individuals (Chao & Jost 2012, Gotelli & Colwell 2001). By using link accumulation and estimation of expected links, the sampling completeness (i.e., observed links divided by estimated links) of networks can be determined and compared. This metric itself can be used as a covariate controlling for potential sampling effects (Baronio et al. 2021). If individual networks in a study differ markedly in sampling completeness, this is a clear indication that network indices cannot be directly compared, as an influence of sampling cannot be ruled out. Because the number of species in a network reaches an asymptote much earlier than the number of interactions (Chacoff et al. 2012, Dáttilo et al. 2019), classical species-accumulation curves alone are not sufficient to compare networks or to judge how complete a network is.

Conceptually similar to link accumulation is rarefaction. Instead of extrapolation, rarefaction subsamples networks to a directly comparable number of species or interactions (Fornoff et al. 2019, Vanbergen et al. 2014), but unlike extrapolation, it maintains the structure of unobserved links in the network. Often, rarefaction uses the network with the fewest links or species to determine the size of the subsampled networks. Indices calculated on rarefied networks are directly comparable, and this method reduces the bias due to variation in sampling, abundance, or species diversity (Olito & Fox 2015) but may still include bias due to variation in sampling coverage (Chao & Jost 2012, Chiu et al. 2023). We caution against using extrapolation (adding unobserved links) in an attempt to correct standardized network indices and dissimilarity metrics (e.g., H_2', d') (**Table 1**) or metrics that describe the link configuration (e.g., modularity) to the same level of sample coverage. Extrapolation of links forces species within a network to become more similar to each other, potentially ignoring the fact that lower probabilities for specific links (or forbidden links) are an important part of the specialization pattern. In this respect, rarefaction of existing interactions is better suited and less biased than extrapolation. For unstandardized metrics (e.g., e^{H_2}, g) (**Table 1**) and functional or phylogenetic diversities (Chiu et al. 2023), extrapolation may be appropriate, however.

5.3. Null Models: Different Types of Randomness

Null models (**Figure 3**) are generally useful for distinguishing signal from chance (Gotelli & Graves 1996). Notably, many patterns in empirical networks can be reproduced in null models by the skewed abundance distribution of species and links (Blüthgen et al. 2008, Vázquez et al. 2007, Wells et al. 2014). This is the case not only for generalized interactions, where a certain degree of randomness is expected, but also for specialized interactions such as between hosts and parasites (Canard et al. 2014). When correctly employed, null models are probably the optimal standard method for addressing differences across interaction networks (**Figure 4*b***). In a null model of an observed network, the interactions are redistributed, while preserving specific characteristics of the network such as the number of species or number of links. Thus, null models represent neutral interaction patterns, allowing one to benchmark whether the characteristics of an observed network are due to biological properties of the interacting species or due to chance (Blüthgen et al. 2008, Gotelli & Graves 1996). The distribution of values for a metric drawn from null-model iterations is compared with the observed metric (see **Figure 3**, **Table 1**, and

OBSERVED METRICS VERSUS NULL MODELS

How can we compare observed network metrics and null models? Most commonly, each network is individually compared against its null model. In addition, null-model trends can be compared in parallel to observed metrics (Gotelli & Graves 1996), e.g., by plotting how network metrics change over gradients against the average levels obtained by null models. It is also possible to standardize observed metrics against null models in one metric by Δ-transformation or using *z*-scores. Both quantify the extent to which an observation differs from an average random pattern (Dalsgaard et al. 2017). In Δ-transformation, the mean index value obtained from the null model is simply subtracted from the observed value, such that $\Delta = X_{\text{null}} - X_{\text{obs}}$ (Schleuning et al. 2012, Vizentin-Bugoni et al. 2016). For *z*-scores, Δ is divided by the standard deviation of the null-model values; i.e., $z = \Delta / SD_{\text{null}}$ (Ulrich et al. 2009). In particular, *z*-scores can be used to directly compare metrics across networks. However, Δ and *z* may not always be independent of species number: Δ can increase and SD_{null} can decrease with species number (Song et al. 2017). Thus, networks with a very large variation in size should be compared only with care, e.g., via normalization by dividing the observed value by the maximum value under the null model (Song et al. 2017).

the sidebar titled Observed Metrics Versus Null Models), and if they poorly overlap (typically less than 5% on both tails of the distribution), this is taken as evidence for a nonrandom pattern. Different kinds of null models, however, constrain parameters of a network differently and have very different implications (Molina & Stone 2020). We highlight only four possibilities here: (*a*) For binary networks, which were standard in the early years of network analyses (**Figure 4*c***), there are null models that simply redistribute or shuffle the number of links recorded. Reshuffling can also be applied to quantitative networks. Hence, these null models preserve the total number of links per network but not the number of links per species. Obviously, this does not take abundance limitation into account, and a species with a single observation may receive many links in the null models. Only a few null models effectively account for sampling and abundance. An important requirement for null models is that all theoretically possible numerical configurations of a network are covered and have the same probability (Carstens 2015, Molina & Stone 2020). These strict properties are met for (*b*) the Patefield null model (Patefield 1981) (generated using the r2dtable function in the R package bipartite), which we recommend to test whether variation in any network metric can be explained by sampling, abundance, or diversity alone. Originally designed for statistics replacing chi-square tests, the Patefield algorithm uses the fixed marginal totals of the species-interaction matrix to preserve the relative abundance of each species and consequently also the diversity of species. (*c*) A null model proposed by Vázquez et al. (2009) is conceptionally similar but uses interaction probabilities calculated from a multinomial distribution rather than fixed marginals (mgen in bipartite) and is computationally demanding; how to correctly compute probabilities is also not fully resolved (Dormann 2023). (*d*) Some null-model types additionally fix the total number of links and thus preserve a more network-typical specialization level, e.g., low connectance (vaznull and swap.web in bipartite). Assumptions in these null models are more constrained than in the Patefield and Vázquez et al. null models and may, in addition to violating the property of all configurations having the same probability, deviate more strongly from the observed network than expected by chance (Dormann 2023). The specific choice of null model is crucial, as comparisons to different null models can have fundamentally different outcomes (e.g., Joppa et al. 2010, Kratochwil et al. 2009). To conclude, for network metrics that are sensitive to abundance, sampling, and diversity, we strongly suggest comparisons between the observed network and Patefield null models (**Figure 3**; **Table 1**).

Note that integer-based null models such as Patefield and rarefaction/extrapolation methods may be inappropriate when the data are in the form of decimal numbers rather than integers, which is the case for proportional values such as interaction rates (number of individuals divided by observation time). Any multiplications of such decimal values to obtain integers prevents the calculation of meaningful significance levels for such null models (Leonhardt et al. 2011). However, data for visitation rates or other derived link measures are often based on raw counts; therefore, null models and rarefaction may be applicable for the underlying raw count data, which are generally more suitable for describing networks than rates. A further important assumption for using null models in networks as statistical evidence for a nonrandom configuration is that interactions are independent replicates. For instance, workers from one insect colony might aggregate on an individual plant (nonindependently), but multiple counts of individual insects from the same colony then strongly inflate any metric of specialization and contrast to a null model that spreads individuals from a single colony over many plants. Ant–plant networks and other related interactions involving colonial organisms thus need to carefully consider what biological entity represents independent interactions (Blüthgen et al. 2007).

6. DO SCALE AND AGGREGATION MATTER?

In many studies, interactions are pooled over space and time for each network unit, but the scale of the data aggregation varies substantially. The spatial and temporal scale of a network is crucial for its interpretation (Morales & Vázquez 2008). For mobile organisms, a meaningful minimum spatial scale may be important for sampling interactions and for experimental approaches (Blüthgen & Staab 2021, Dáttilo et al. 2019, Guy et al. 2021). Species interactions vary more across space than does the presence of the interacting species alone (Poisot et al. 2017). In turn, when networks are small scale—assuming that all mobile individuals of all species can potentially interact in a space—interpretations based on traits, preferences, and specialization are more straightforward than for spatially aggregated data that potentially include otherwise-segregated species pools from different habitats or environmental conditions, making it impossible to distinguish forbidden from missing links (Jordano 2016).

Similarly, temporal aggregation of interactions can combine species in a network that are naturally segregated by life stage, time of day, or seasonal phenology (CaraDonna et al. 2021, Schwarz et al. 2020). Spatial or temporal variation can be tested and examined, ideally by explicitly comparing spatiotemporally distinct (sub)networks rather than analyzing a single aggregated network. Although smaller subnetworks may aggravate the problem of incompleteness, a focus on simultaneous interactions facilitates direct interpretations of traits, competition, and specialization. For example, many species are temporally specialized [even within the hours of a day (Schwarz et al. 2021)] but may appear as generalists in aggregated networks (CaraDonna & Waser 2020). Short-term flexibility of species reveals variation in species roles and network properties, and aggregation may mask biologically meaningful patterns that would otherwise be apparent. In turn, species may appear specialized in one year but be associated with many other species in another, which would be missed in aggregated networks (Petanidou et al. 2008). Such annual variation may, to some extent, mirror the stochasticity of interactions (Chacoff et al. 2018). Very few studies have comprehensively sampled the same sites in a standardized way, consecutively, over longer time spans, and insights from such time series are very valuable (e.g., CaraDonna & Waser 2020, Chacoff et al. 2018, MacLeod et al. 2016).

In addition to aggregation across space and time, network properties depend on the taxonomic resolution of the nodes. Aggregation of species into higher-level taxonomies such as genera or families results in less-specialized networks (Renaud et al. 2020). While this outcome is trivial, as interacting nodes and thus their interactions are being summed, meaningful comparison across individual networks with different taxonomic resolution necessitates consideration of the extent to which taxonomic aggregations bias the results. This fundamental problem of taxonomic resolution has been debated intensively for food webs (Martinez 1993, Pringle & Hutchinson 2020) but applies to any interaction type. On the other end of taxonomic resolution, evidence has started to accumulate that species interactions are influenced by intraspecific variation (Barbour et al. 2016, Cao et al. 2018); for example, certain plant genotypes are more susceptible to herbivores, which is a further argument against aggregating networks across large scales.

7. FROM PATTERN TO MECHANISM AND FUNCTION

Much of the interest in interaction networks comes from three directions: (*a*) understanding why certain species interact or not, e.g., which traits (Marjakangas et al. 2022) or cues promote or prevent interactions; (*b*) understanding the functional consequences, e.g., whether a more generalized network contributes to a higher functional performance or community stability (Fründ et al. 2013); and (*c*) whether and how interactions change along environmental gradients (Tylianakis & Morris 2017). Hence, the networks are fundamental in understanding the transition from causes to consequences of species interactions. Additionally, feedback loops from consequences to networks and even back to traits may also be interesting to study from a dynamic or (co)evolutionary point of view. Our argument for disentangling abundance and diversity from network patterns (**Figure 2**; **Table 1**) to understand complexity, specialization, and the role of traits also holds for attempts to understand how network topology affects function (community/traits → network → function). For instance, if the transition from community to network is driven mainly by abundance, it seems likely that the contribution of communities via networks to ecosystem function is based on abundance, too. While network metrics are sometimes used as surrogates for ecosystem functions, this assumption has rarely been empirically supported (Theodorou et al. 2017). In general, for causal relationships between network and function beyond mere correlations, understanding the underlying importance of variation in abundance and diversity is key.

To draw conclusions about the paths from network to function, it is important to know the ecological consequences of the recorded interactions. For example, most so-called seed-dispersal networks are actually observations of frugivory that only rarely assess the functional outcome (i.e., seed death versus dispersal and germination) (Simmons et al. 2018). Likewise, most supposed pollination networks are mere observations of flower visits. Functional plant–pollinator networks based on pollen transport differ from flower–visitor networks (Bosch et al. 2009), often being more specialized than comparative networks based on visits, as only a subset of visitors actually transport pollen (e.g., Ballantyne et al. 2015, Zhao et al. 2019). To reveal species' functional roles, dedicated experiments are needed. For example, Fründ et al. (2013) artificially combined species in cages, while others manipulated the presence or abundance of species in the field (Barbosa et al. 2017, Timóteo et al. 2016). The same is true for the effect of environmental variables on interaction networks and their functional consequences: While the vast majority of empirical studies have been observational and often agnostic to biotic and abiotic context, large-scale experiments have shown, for example, that network structure can vary strongly depending on the presence of species extrinsic to the network (Guy et al. 2021).

8. OTHER TYPES OF NETWORKS

Our review focuses on bipartite networks with two levels, in which nodes consist of species (e.g., plants and herbivores). Thus, these networks contain a single type of interaction. The real world is, of course, much more complex, which is now increasingly treated in network analyses, for example,

MULTILAYER, MULTIPARTITE, AND META-NETWORKS

Almost all species simultaneously interact with a multitude of other species across trophic levels. Such multiple interaction networks can be combined to form multilayer networks that may span several trophic levels (Pilosof et al. 2017) or multipartite networks (Timóteo et al. 2023), in which interactions are linked via a joint trophic level (e.g., plant–herbivore–parasitoid, with herbivores being the link). While not explicitly scrutinized by us, multilayer and multipartite networks are inherently composed of bipartite interactions, and consequently, they are as sensitive to variation in sampling, abundance, and diversity as bipartite networks. Similar limitations apply to meta-networks, a further emerging type of interaction network (Librán-Embid et al. 2021). Meta-networks usually consist of a collection of subnetworks, similar to meta-communities, which represent a collection of smaller communities. Thus, meta-networks often describe the turnover or persistence of interactions rather than network structure (e.g., specialization) per se.

in multilayer, multipartite, and meta-networks (see the sidebar titled Multilayer, Multipartite, and Meta-Networks). We caution against simple interpretations of networks that represent unknown mixtures of different types of interactions or no interactions at all. For example, cooccurrence networks are highly problematic for many reasons (Blanchet et al. 2020). While cooccurrence is a necessary prerequisite for any interaction to take place, whether species truly interact depends on multiple biotic and abiotic factors that cannot usually be deduced from species' mere presence (Goberna & Verdú 2022). Furthermore, cooccurrence networks lack basic properties of interaction networks such as interaction type (e.g., antagonistic versus mutualistic) and interaction strength.

There are more networks that do not represent interactions but for which network analyses and metrics may be useful to illustrate and characterize associations. Usually, these networks are similarly prone to the same shortcomings regarding sampling and abundance (or diversity) outlined here and require similar treatment to overcome them. Examples include the distribution of species across different microhabitats (Wehner et al. 2016), the differentiation of chemical profiles across species (Leonhardt et al. 2011), resource use of omnivorous consumers (Rosumek et al. 2018), individual-based networks (Smith-Ramírez et al. 2014), and social networks (Bierbach et al. 2014).

9. OUTLOOK

Did we learn anything new from network studies in the last decade? And are we at the point that we understand the mechanisms behind who interacts with whom? Can we predict population and community changes, extinctions, or functional consequences from the study of networks? These goals may be seen as very ambitious, and network analyses alone may not suffice. However, there are good studies that have identified causes of interactions along environmental gradients (Benadi et al. 2014, Fornoff et al. 2019, Vanbergen et al. 2014) or that improve our understanding of ecosystem functioning, particularly by using experimental approaches (Guy et al. 2021, Fründ et al. 2013, Kaiser-Bunbury et al. 2017). Networks continue to be popular in ecological research, with an increasing use of weighted metrics (**Figure 4*c***), and analyses of linkage rules, functional traits, or stability consequences play important roles. Although we have emphasized caveats in this review, we stress that if correctly applied, network analyses can make a meaningful contribution to knowledge of the biological principles and functional consequences of species interactions. Feasible consequences of specialization patterns include species' dependence on specific partners, functional stability, and sensitivity to coextinction. However, if rarity and specialization are confounded

Individual-based network: nodes in a bipartite network represent individuals of the same species, e.g., visitors to flowers of single plant individuals

Social network: nodes represent individuals (or groups of individuals) of the same species (unipartite network); often applied in behavioral studies or confused, erratic conclusions may be drawn about species' extinctions due to climate change or biotic changes. A significant number of empirical analyses so far have blurred the functional distinctions between sampling, abundance, diversity, and specialization, which must be isolated to understand the underlying mechanisms of variation in species interactions. Rarefaction and extrapolation methods have become a good standard in biodiversity analyses. For networks, similar awareness and care are needed. Rarefaction and null models, appropriate weighted metrics, or tests that explicitly examine abundance and diversity are key to deriving a more realistic and substantial understanding of the causes and consequences of network patterns, which is crucial for predictions based on specialization, stability, and the functional consequences of species interactions.

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AUTHOR CONTRIBUTIONS

N.B. and M.S. contributed equally to the preparation of this manuscript.

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