Annual Review of Ecology, Evolution, and Systematics

Identifying Causes of Patterns in Ecological Networks: Opportunities and Limitations

Carsten F. Dormann,[1] Jochen Fründ,[1]
and H. Martin Schaefer[2]

[1]Biometry and Environmental System Analysis, University of Freiburg, 79104 Freiburg, Germany; email: carsten.dormann@biom.uni-freiburg.de, jochen.fruend@biom.uni-freiburg.de

[2]Fundacíon Jocotoco, Quito, Ecuador; email: martin.schaefer@biologie.uni-freiburg.de

Annu. Rev. Ecol. Evol. Syst. 2017. 48:559–84

First published as a Review in Advance on September 13, 2017

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

https://doi.org/10.1146/annurev-ecolsys-110316-022928

Keywords

coevolution, interaction network, null model, pollination network, sampling effect

Abstract

Ecological networks depict the interactions between species, mainly based on observations in the field. The information contained in such interaction matrices depends on the sampling design, and typically, compounds preferences (specialization) and abundances (activity). Null models are the primary vehicles to disentangle the effects of specialization from those of sampling and abundance, but they ignore the feedback of network structure on abundances. Hence, network structure, as exemplified here by modularity, is difficult to link to specific causes. Indeed, various processes lead to modularity and to specific interaction patterns more generally. Inferring (co)evolutionary dynamics is even more challenging, as competition and trait matching yield identical patterns of interactions. A satisfactory resolution of the underlying factors determining network structure will require substantial additional information, not only on independently assessed abundances, but also on traits, and ideally on fitness consequences as measured in experimental setups.

1. INTRODUCTION

The ecological reality of most species is, from a scientist's point of view, frustratingly complex, temporally variable, and full of interactions with other species, direct or indirect, of unknown intensity and importance. Ecological networks represent a slice through this complexity, listing observed interactions of a set of species. Food webs have been the most commonly studied type of ecological network (e.g., Pascual & Dunne 2006), but over the last 20 years, bipartite (two-group) networks have dominated the ecological literature (reviewed, e.g., in Bascompte & Jordano 2014). This is for a good reason: The quantitative sampling of interactions typically takes place with a focus on one group of species, such as plants or rodents, whose interactions with another set of species are recorded, such as pollinators or ectoparasites, respectively. Much effort is required to build up a complete, multitrophic interaction network, but we are likely to already learn from the bipartite samples, as long as these interactions are of importance for one or both groups of species.

However, a pattern we observe can be attributed to different processes (the eternal from pattern to process problem), and even the pattern itself may be distorted by the inevitable incompleteness of sampling. Thus, just consistently demonstrating the presence of a community-level pattern in species interactions must already be considered an achievement.

Building on hundreds of data sets (and even more publications), network ecology has matured to a state where some patterns can be taken for granted. We have entered a first stage of consolidation and, in this review, we explore the information contained in (bipartite) ecological networks, how much we can learn from them, and how we can proceed to tackle some unsolved, deep-rooted problems in this subdiscipline. The review starts by defining networks and how they are sampled, reflects on the importance of specialization, and then addresses the challenge of teasing apart the interdependent effects of abundance and network structure. We then explore potential evolutionary causes of network structure and close by exploring, as an example, the ecological questions around the separation of networks into modules. This network property has received some attention and is relatively intuitive, but the issues involved are similar for other network properties. Throughout this review, we try to keep an eye on which kind of data and measurements may eventually be required to unequivocally test hypotheses that are currently still tenuous.

2. SAMPLING INTERACTION NETWORKS

Network matrices summarize observations made in the field, in one way or another. As with any sampling, interaction networks also inevitably suffer from incomplete sampling or even sampling bias (reviewed in Jordano 2016). The focus of sampling may be the lower level (i.e., the species represented by rows), such as when recording all flower visitors to plants in a 2 × 2 m patch or when counting all parasites in a fish caught at sea. In these cases, we are relatively certain about the lower-level species (because we see or catch them even if they are not visited or parasitized), but undersampling may lead to missing species of the higher level (e.g., pollinators that have visited a patch nearby, but not ours). Obviously, the same applies to focal sampling of the higher level, e.g., gut content analysis of predators or herbivores or pollen analysis of wild bees' brood cells. The tenet is that interactions are sampled more completely for the focal level (Sørensen et al. 2011).

Both incomplete sampling and focal group bias have emerged as methodological concerns in recent studies (e.g., Nielsen & Bascompte 2007, Gibson et al. 2011, Sørensen et al. 2011, Rivera-Hutinel et al. 2012, Fründ et al. 2016, Vizentin-Bugoni et al. 2016). When looking at any network matrix, it is difficult to know how good the data are, how complete the sampling of each group is, and how many errors are in the data (e.g., species misidentification, typos, unresolved taxonomic groups, cryptic species). It would seem advisable to investigate the robustness of any reported network pattern with respect to a plausible range of such noise in the data [e.g., following the approach of Vesk et al. (2010)]. This has rarely been done, but the substantial noise added to observed networks by Dormann et al. (2009) had reassuringly little effect on the results. On the other hand, sampling incompleteness introduced substantial bias to almost all network indices in the simulations of Fründ et al. (2016). Using additional species information (e.g., independent abundance, floral traits) may help reconstruct the actual network (Bartomeus et al. 2016).

In the literature, null models have been used to represent sampling variation (Section 2.1). Given the observed marginal totals, how different could the network pattern actually be? For example, we may observe that a given network is nested. What would we expect without any network-level process? A null model could use only marginal totals to simulate a network and then compare its nestedness with our observations (Section 3 expounds in detail on why marginal totals should be interpreted with caution). Taking a real pollination network as an example (that of Junker et al. 2013), we may observe a nestedness of 4.32 [computed using NODF, where higher values indicate higher nestedness (see Almeida-Neto et al. 2008)]. Can this tell anything about the nestedness of this matrix? Null models provide us with a yardstick against which to measure absolute values for a network metric. In this specific case, null model simulations (based on marginal totals, using the Patefield algorithm) give a mean nestedness value of 14.06 (±0.714, 1 standard deviation). The observed value thus has a z-score of $(3.42 - 14.06)/0.714 = -14.91$, i.e., 15 standard errors lower than would be expected from the null model. It is thus extremely unlikely that the observed value is a happenstance of what we would expect given the marginal totals and indicates significant antinestedness. Ecologically, antinestedness may indicate competition-induced host utilization: Dominant species *A* monopolizes a specific plant species *a*, forcing a subdominant pollinator *B* to move onto other plant species *b*, *c*, etc. The result is a missing observation of *B* on *a* and hence a lower nestedness than in the null models. Note that some network indices are themselves already scaled relative to a null model [e.g., the expected value of a binary null model defines 0 for Bascompte et al.'s (2003) relative nestedness, whereas Blüthgen et al.'s (2006) H'_2 ranges between the theoretical minimum and maximum of a quantitative null model]. In addition to using null or similar models as a yardstick, quantitative rather than binary interaction data should be collected and used for analysis. Several studies have shown that indices calculated from binary networks have higher error rates than those for quantitative networks, and hence may yield misleading conclusions (e.g., Banašek-Richter et al. 2004).

Marginal totals: the column- and row-wise sums of an interaction matrix. For quantitative networks, these are often used as an approximation of a species' abundance

Nestedness: the observation that a matrix is filled primarily in the top-left part after sorting rows and columns by binary marginal totals. Perfect nesting means that, e.g., each predator with few links only interacts with prey that all predators with more links also interact with

2.1. Excursus on Null Models

Null models are numeric versions of counterfactual "What if not?" questions. More specifically, they attempt to describe the processes behind a pattern and explore whether switching off the one (or more) processes of interest can still reproduce the pattern. If so, the inference would be that this process is not necessary for the pattern (Gotelli & Graves 1996).

In experimental physics, we may attribute the conductivity of a solid to the existence of regularly spaced molecules of some kind. A null model would shuffle these molecules randomly and assess whether conductivity changes. If it does not, the null model demonstrates that the regular spacing is not required.

In network analyses, null models are invoked to explore whether network-level information is required to produce a certain pattern. For example, one can construct null models based only on first-order (network dimensions) or second-order properties (marginal totals). Also, a null model could be based on species traits, phylogeny, biogeographical distributions, or other suspected drivers of network structure. Although most network null models are currently based on marginal totals and, therefore, are inadequate for networks where structure strongly drives abundances (see Section 3), more sophisticated and appropriate null models are conceivable.

The challenges of null models are (at least) twofold. First, we want to formulate the null model so that it only excludes the process we want to test. That is not trivial; in fact, "a good deal of controversy surrounds the construction of any null model" (Gotelli & Graves 1996, p. 17).

Second, there is the challenge of correctly interpreting the results. In particular, if we can reproduce a network-level pattern P based on, say, marginal totals, this suggests that, for this pattern, we do not need to understand the exact network configuration. This does not mean that network configuration has no causal role to play; it just shows that P does not occur only through network configuration X. If we cannot reproduce pattern P with the null model, this does not imply that X is a necessary condition of P; it only means that this specific null model could not demonstrate how P may be generated without network-level information. The usefulness of null models is thus limited by our creativity in constructing them.

Rather than excluding processes by null models, one ideally likes to test for processes by comparing differently structured models based on their fit to data (Vázquez et al. 2009b). Null models are thus often a transient phase between the pure description of a pattern P and a set of more complete models that can be compared through standard statistical approaches (such as maximum likelihood or Bayesian model comparison). In the field of network ecology, such tests using statistical models are currently extremely rare and burdened with a large number of additional assumptions (Wells et al. 2014).

2.2. What Observed Network Structure Shows

Supplemental Material

The interaction matrix A is driven by two underlying sets of processes: those that affect the abundance of species and those that affect their ecological specialization sensu Armbruster (2017), including niche breadth and preferences. If all species in a network were equally abundant, then all patterns could be attributed to their (differences in) specialization. Similarly, if all species were perfect generalists, then all network patterns would emerge from differences in their abundance (see the **Supplemental Appendix** for an illustration). These processes are not ultimate: Both abundance and specialization may well be the product of network structure and its evolution (as we discuss in Section 4).

It is important to realize that the interaction matrix A harbors only limited information. Taking out abundance, all indices that one can compute to describe network properties must result from specialization of network members. This does not explain the causes of specialization, but in the context of this review, we need to stress that metrics such as degree distributions, connectance, modularity, or discriminant specialization are only describing different facets of specialization and its distribution among species (see the **Supplemental Appendix** for an illustration).

It would be a Herculean task to derive the exact interdependencies of network indices, both conceptually and mathematically, but it should be clear that the network pattern is (at least) two steps apart from the underlying mechanism:

specialization mechanism → realized interaction preferences → observed network pattern.

The implication is that, without additional information or assumptions, it is impossible to attribute a single cause to a network pattern: Whatever affects the realized interaction preferences will inevitably affect the observed network pattern, too. The interaction matrix A is like the two-dimensional screen on which we observe a multidimensional play (as in Plato's allegory of the cave).

Finally, studies reporting patterns in networks are likely to suffer from two further problems: multiple testing and publication bias. Because most studies explore many different network indices [possibly encouraged by software computing dozens of indices by default (see Dormann et al.

2009)], corrections for multiple testing need to be computed (e.g., Bonferroni adjustments). That has rarely been the case. Thus, type I errors will be inflated, and some of the reported patterns are likely to be spurious. In the same direction, studies that find no pattern are unlikely to be submitted or published (the file drawer problem). Thus, the published patterns are likely to be an overestimation of the true effect.

3. ABUNDANCE AND NETWORK STRUCTURE: THE CHICKEN-AND-EGG PROBLEM

The relationship between abundance of different species and network patterns is of central importance in many network studies. There are basically two important viewpoints here: (*a*) Abundance drives network patterns and species roles, both as a fundamental ecological mechanism and as a statistical problem. (*b*) Network patterns (and structure and interactions in general) are functionally important and drive species abundance. Few people would claim that only one of these directions is true: Abundance (or frequency or community composition) has an important influence on interaction patterns (Vázquez et al. 2009a). Likewise, the ultimate reason for studying networks in the first place may be that interactions matter for species abundance [or population size or species diversity (see Bascompte & Jordano 2014)]. Hence, if abundances affect network structure, and structure affects abundances, how can we solve this circular, chicken-and-egg problem?

Some studies emphasize the abundance-driven view, highlighting abundance distributions or species frequencies as drivers of observed interaction patterns (Vázquez et al. 2009a). This influence of frequency on network patterns may be considered as a nuisance that needs to be controlled to allow for the meaningful interpretation of interactions (Blüthgen et al. 2008). Other studies emphasize the structure-driven view, trying to relate observed network patterns to the effect on focal species or community dynamics and network stability. In this second approach, mathematical or computational models are often employed to infer the link to population and community processes. One should be aware that, although both of these approaches may yield useful insights, ignorance of the alternative causal direction may limit their interpretation. In what follows, we first provide an overview of each of the two views and then consider mechanisms of the feedback and drivers of its strength, how it has been approached, and what may constitute solutions to the circularity.

3.1. Abundance-Driven View: From Abundance to Network Structure

Thus far, this review has mostly looked at networks from the perspective of given abundances, highlighting the difference between first-, second-, and third-order information and raising awareness of methods such as null models that aim to isolate true network patterns (third order) from patterns that directly follow from community composition (first or second order). We have discussed the causes and consequences of network structure but mostly ignored that the consequences could feed back to the causes (abundances and traits) and become determinants of new networks. Supporting the abundance-driven view, network patterns are often strongly driven by species numbers and abundance distributions (e.g., Vázquez et al. 2007, Krishna et al. 2008). Many network indices (e.g., generality, species strength) strongly reflect first- or second-order information and so may mostly reflect variation in species richness and relative abundance, which might be driven by external factors (Blüthgen et al. 2008).

Abundance is also an important determinant of network patterns by driving interaction probabilities. First, abundant species may be more generalized because they interact with more species simply by chance (Poisot et al. 2015, Fort et al. 2016)—the so-called ecological sampling effect.

Second, abundant species are typically represented by more observations in a data set, making sampling limitation less severe compared to rare species (Blüthgen et al. 2008). As few observations lead to an overestimation of specialization and bias in almost all network indices (Fründ et al. 2016), many network patterns may be statistical artifacts correctable through null models (Blüthgen et al. 2008; Fründ et al. 2016, section 2). This observational sampling effect will be much stronger than the ecological sampling effect (Fründ et al. 2016), as the handful of recorded interaction events typical for many rare species in network data sets constrains the number of interaction partners more strongly than the hundreds or thousands of actual interaction events (e.g., flower visits) that take place in a real community even for rare species. These two types of sampling effects are hard to separate in practice but make an important difference in interpretation.

Although studies focusing on abundance emphasize the correction for sampling effects and ignore an influence of third-order processes on first- and second-order patterns, they still tend to acknowledge that abundance-driven network changes may have substantial ecological effects. This links them to the structure-driven view, where the effect of network structure is the starting point.

3.2. Structure-Driven View: From Network Structure to Abundance

Studies focusing on network structure emphasize the aim of predicting the consequences of observed network patterns. These studies tend to present raw metrics (such as the observed number of links), which represent an amalgam of first-, second- and third-order information. The strong assumption of the structure-driven view is that the network structure is taken as prescribed or fixed, i.e., determined either by external factors or by the disappearance of unstable networks. Thus, the influence of community composition (relative abundances) on who interacts with whom is not explicitly considered. In contrast to the abundance-driven view, which often focuses on relative abundances (as a cause), the structure-driven view may often be primarily interested in absolute abundance or species diversity (as a response), which we summarize under the term "community composition."

Mathematical models have played a key role in elucidating the role of network structure, because demonstrating the effects of interactions and network structure on the population sizes of entire communities is extremely challenging. A long tradition of theoretical models has linked network structure to species population dynamics. Early ecological network models (May 1973) have been refined for food webs, competition-based communities, and, more recently, for mutualistic networks (Bastolla et al. 2009, Thébault & Fontaine 2010, Benadi et al. 2013, Rohr et al. 2014). These theoretical studies have identified different network structures as increasing network stability and supporting high species richness. Such proposed stabilizing structural properties include nestedness, modularity, (low or high) complexity, and specialization (May 1973, Bastolla et al. 2009, Thébault & Fontaine 2010, Benadi et al. 2012, James et al. 2012; see also Section 5.1). Many of these theoretical studies bolster their conclusions with statistical analyses suggesting that stable structures are overrepresented in real networks (Bascompte et al. 2003, Thébault & Fontaine 2010, Rohr et al. 2014), following the logic of the structure-driven view that community composition follows from network structure, without any substantial external control through habitat, climate, or resources (but see Valdovinos et al. 2013).

Many empirical studies have measured observed network structures and referred to some of the above models when drawing conclusions about the consequences of what they have observed (Tylianakis et al. 2007, Dalsgaard et al. 2013). When these do not explicitly consider the different determinants and orders of information but rather describe observed differences in network metrics, they adhere mostly to the importance of structure. For example, plant invasions have been shown to decrease modularity and increase nestedness of pollination webs, with assumed consequences for function and stability (Albrecht et al. 2014). Functional consequences of network structure are often used to justify adding the network level to diversity analyses, but empirical evidence for such consequences is scant and hard to get. A step in this direction is represented by cage experiments that quantified the reproduction of all plants in a community and evaluated its response to pollinator diversity and flower–visitor network structure (Fontaine et al. 2006, Fründ et al. 2013).

In summary, there are many ways that observed community composition may result from network structure and vice versa. How do we solve this chicken-and-egg problem?

3.3. Excursus on Marginal Totals: A Proxy for the Drivers of Network Structure or for Its Effects?

Marginal totals are often seen as proxies for abundance and, through null models, are used to remove abundance effects on the observed pattern, yielding the pure network pattern (in the logic of the abundance-driven view). However, marginal totals may be the result of network structure and thus also be a useful proxy for network effects on future abundance. Controlling for marginal totals may thus be problematic under the structure-driven view.

Different interpretations of marginal totals can be illustrated by varying the influence of abundance and specialization on network patterns (**Figure 1**). When no preferences are used to compute the observed interactions (**Figure 1*a***), abundances completely drive the pattern, by definition. Marginal totals correspond very well with abundance, but a wide gradient in generality also emerges (due to the ecological or observational sampling effect). Marginal totals and relative abundance are similarly related to generality and can thus be used interchangeably.

When the interactions are more specialized, the observed pattern is determined by a combination of abundances and preferences (**Figure 1*b***). Marginal totals are less closely related to abundance (and generality). Whether and how many interactions of a certain species are recorded in the network depend on available partner species. Using marginal totals as a proxy of community composition would ignore some effects of the network.

When both abundance variation and sampling effects (**Figure 1*c***) are negligible, variation in marginal totals emerges only as a consequence of preferences, which might cause abundance heterogeneity in the future (e.g., plants receiving few visits will produce few seeds). In the simulation, we find a positive effect of generality on marginal totals (e.g., more generalized plants receive visits by more different pollinators and can thus achieve the highest marginal totals). However, the effect of generality tends to be weak, as how strongly partners interact with a focal species is more important than how many they are.

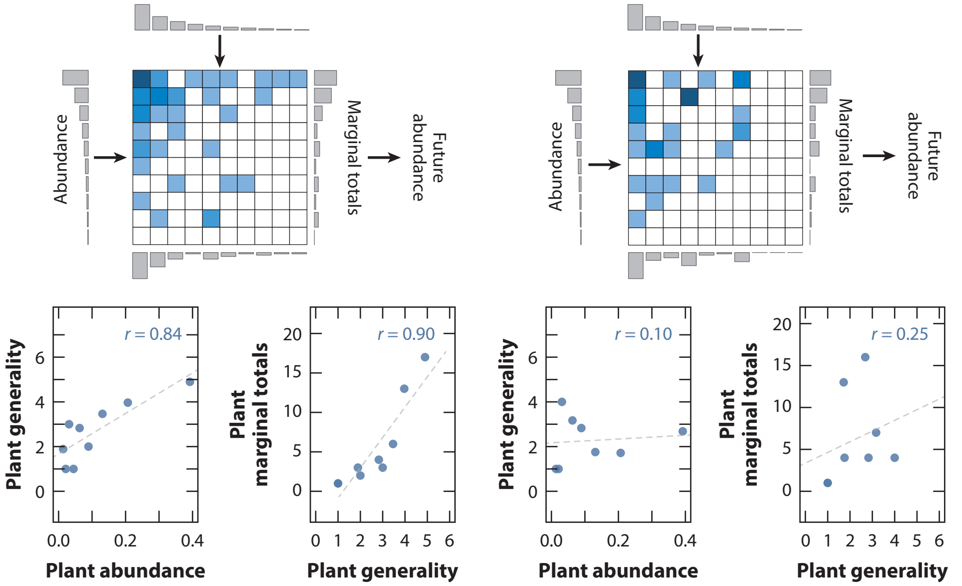
In conclusion, marginal totals can be interpreted for both abundance-driven and structure-driven views. They are good proxies for abundance if abundance effects are strong and preferences are weak, and they are an outcome of network structure if abundances are equal and interaction partners are highly selective. Beyond this, independent abundance data would be wise to consider.

3.4. Toward Merging the Two Views

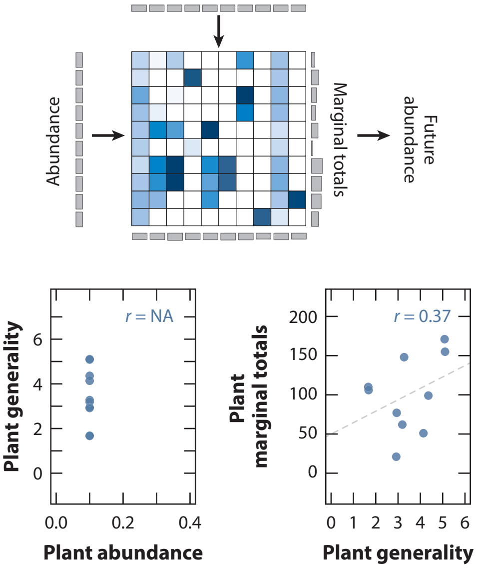
Fort et al. (2016) discussed the chicken-and-egg problem for the positive correlation between abundance and generalization, which could be explained from both viewpoints. In an analysis across multiple plant–pollinator webs, they find many rare generalists, but almost no abundant specialists. From this observation, they conclude that abundance is a sufficient condition for generality, whereas generality is only a necessary condition for abundance. Fort et al. (2016) further argued that this disproves a causality from generality to abundance and thus suggests a causal direction from abundance to generality (akin to the abundance-driven view), possibly through an ecological sampling effect. However, a causal direction from generality to abundance may also explain their correlation. If generalists can achieve higher abundance than specialists because they can exploit all available resources (the usual justification for the direction from generality to

a No preferences, uneven abundance, few observations (abundances rule)

b Strong preferences, uneven abundance, few observations (abundances and interactions rule)



c Strong preferences, even abundance, many observations (interactions rule)



abundance), other factors such as resource limitations or competition may still prevent high abundances of many generalist species.

In addition, the pattern reported may depend on the categorization method. Plotting the abundance–generalization relationship actually shows that the observational sampling effect makes it impossible to detect high generalization in species with very low abundance (see Fründ et al. 2016) (see Section 3.3). The pattern also depends on the choice of the specialization metric (Dormann 2011, Poisot et al. 2012). For example, Blüthgen et al. (2007) showed that the specialization index d' increases with abundance. In conclusion, Fort et al.'s (2016) approach cannot unequivocally decide which view is most appropriate.

Some criteria may help identify when a system is better described by the abundance- or structure-driven view: (*a*) When population size or activity patterns are strongly determined by the environment (e.g., nesting opportunities, extreme temperature), abundance rules. (*b*) When interactions are highly specialized and species fully depend on them, structure rules. Based on these criteria, a strong focus on abundance as a driver may, for example, be much more appropriate for generalized and flexible seed–disperser networks (Schleuning et al. 2011) than for highly specialized host–parasitoid networks (Morris et al. 2013). Deciding for one view and its given set of assumptions can help for analyses and can be valid for certain questions, but ultimately, the possible feedback should be acknowledged and tackled.

The gold standard for breaking the circularity would be to actually enforce a fixed community composition or network by manipulative experiments. However, such experiments are difficult because directly manipulating network structure is conceptually tricky [see attempts by Finke & Snyder (2008) and Russo & Shea (2016)], and fixing a community may only be possible for a short term (Petchey 2003). Also, the scale of experimental treatments (e.g., Lopezaraiza-Mikel et al. 2007) may often be quite small compared to the activity ranges of most animals. Nevertheless, lab or cage experiments (Fontaine et al. 2006), as well as removal experiments in the field (Brosi & Briggs 2013), can give valuable, causal insights into network processes. The massive changes in resource availability offered by mass-flowering crops may also be considered quasi-experiments, with demonstrated effects on pollinator populations (Riedinger et al. 2015). In the theoretical realm, dynamical network models could try to more closely account for the various effects of community composition on (observed) network structure put forward by the abundance-driven view (see, e.g., Wells & O'Hara 2013, Crea et al. 2015, and Bartomeus et al. 2016 for new developments in statistical network models, which may inform the integration into dynamical models).

The analysis of networks observed in the real world will not be fully replaceable by experiments or models. For conclusive analyses, a thorough understanding of the system beyond the observed

←

Figure 1

Simulated networks illustrate that interpretation of marginal totals depends on how relative abundances and preferences drive network patterns. The matrices depict the observed interactions, given external abundances (above and to the left of the matrix), as well as resulting observed marginal totals (below and to the right of the matrix). Scatter plots (*bottom*) focus specifically on the relationship between generality and abundance and show the effects of abundance on preferences (generality) and of preferences on marginal totals. (*a*) Variation in relative abundances determines network patterns, and both marginal totals and abundance are closely related to generality. (*b*) Network patterns are driven by both abundances and preferences, causing the relationship between generality and abundances (or marginal totals) to be weaker than in panel *a*. (*c*) Using the same preference matrix as in panel *b*, we minimize sampling effects by increasing the number of observations and exclude abundance effects by making abundances uniform. In this case, the relationship between generality and marginal totals can only be an effect of preferences and available interaction partners.

network is indispensable. We envision two approaches to go beyond the analysis of isolated interaction matrices: analyses accounting for the relationship between multiple matrices [e.g., how interactions of given species change over time, space, and with community context (Laliberté & Tylianakis 2010, Rasmussen et al. 2013, Poisot et al. 2015, Pilosof et al. 2017)] and analyses using additional information beyond interaction topology and frequency [e.g., traits, abundances, phylogenies, and selective pressures outside the observed network (Vázquez et al. 2009a, 2015; Elias et al. 2013; Schleuning et al. 2015)].

A promising approach to overcoming circularity problems and merging abundance- and structure-driven views is to explicitly consider the spatial or temporal scale of network processes [see the review by Tylianakis & Morris (2017) in this volume]. For example, patterns driven by flower choice or sampling effects may be seen at smaller scales than those reflecting population dynamics. Comparing patterns between different scales and developing hierarchical analyses [e.g., comparing regional to local networks (Spiesman & Gratton 2016)] may prove useful. The feedback from networks to, e.g., adult plant abundance and back to the network will only be visible after some time (Fründ et al. 2013, Schleuning et al. 2015) and may thus not matter in shorter-term studies that measure seed set or recruitment in relation to network structure and underlying plant abundance. Likewise, collecting time series of network snapshots may improve mechanistic understanding of network processes: Causality requires that the cause precede the effect, which might help sort out impossible causal links (see Rasmussen et al. 2013, in which indirect interactions are actually categorized with a similar argument).

A less fundamental (more practical) version of the chicken-or-egg problem is the relationship between abundance and marginal totals (Section 3.3). Marginal totals are often assumed to be equivalent to abundance (Dormann et al. 2009). Often they are the only available proxy for abundance of the higher trophic level in the network (Fort et al. 2016). However, true measured abundance sometimes predicts observed network structure much worse than marginal totals (Vizentin-Bugoni et al. 2014). As marginal totals are not independent of the network, the use of marginal totals as proxies of abundance has been criticized (Vizentin-Bugoni et al. 2014), but they may also be considered the more appropriate predictors of neutral effects because they are in the right unit of interaction propensity (Blüthgen et al. 2008). One problem is that marginal totals are a result of filtering by the network: Marginal totals are determined by sampling through partners, especially if these are specialized or few species. As a simple example, a specialist pollinator nesting at a site may not be found in the local network (marginal total of zero) if its resources are flowering elsewhere. Methods using marginal totals may thus be more appropriate for species-rich, generalized, and nondisturbed systems, where the assumption that the community uses all resources according to availability may be best met. Marginal totals may also roughly describe the effect of the network on a species (Vázquez et al. 2012) and thus be potentially useful for further estimating the functional consequences of the network. The ratio between actual abundance and interaction frequency gives a simple expectation for future changes in abundance. More explicitly acknowledging this marginal totals feedback may thus help resolve disputes between abundance-driven and structure-driven views. Network analyses and simulations could take marginal totals feedback into account; for example, indices such as d' allow the use of either marginal totals or external abundance, possibly yielding different interpretations. Separating these different interpretations may avoid circularity problems and improve our understanding of network patterns and processes.

Combining interaction network data with different types of additional data, such as abundances, fitness, traits, or phylogenies, might also help researchers better understand the causal mechanisms at play. In the following section, we take a closer look at elucidating such mechanisms and, in particular, the role that evolution plays in network structure.

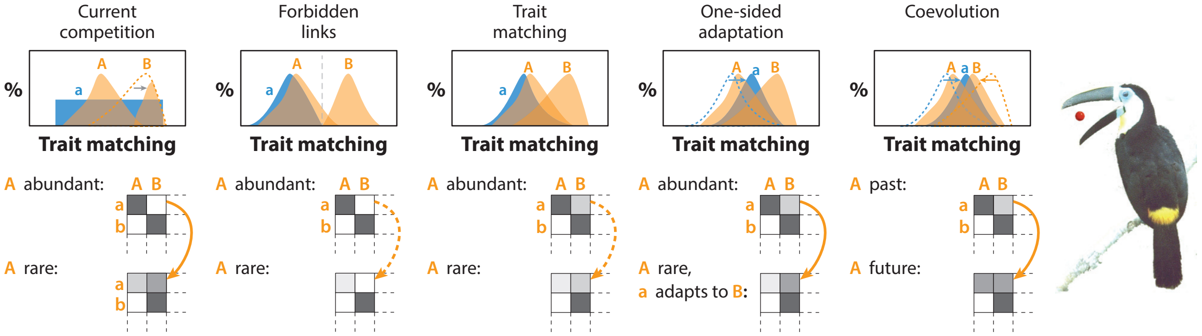


Figure 2

Processes and resulting changes in interaction patterns. Each column illustrates how a specific process affects the observed pattern in a quantitative adjacency matrix for two hypothetical higher-level species (A and B) and two lower-level species (a and b). In the leftmost panel, species A is dominant because its trait distribution overlaps more strongly with that of the resource a than that of species B. In the other panels, the match of traits between resource (*blue*) and consumer (*orange*) is depicted on the x-axis. Changes in trait matching are represented by dashed lines and arrows. Comparison of networks from sites with differently abundant species A, or from different points in evolution, can reveal the cause of the observed pattern. Scenarios for higher-level species A suggest ways to test for this specific process (e.g., comparing networks where A is abundant or rare). Photo courtesy of H.M. Schaefer.

4. WHAT DO ECOLOGICAL NETWORKS REVEAL ABOUT EVOLUTION?

Ecological networks describe patterns of current interactions among species. As such, it is difficult to infer patterns of evolution, which are historical processes (**Figure 2**). Nevertheless, there has been increasing interest among ecologists in the evolutionary past of species to identify the factors determining network structure (Peralta 2016). Phylogenetically conserved phenotypic traits can contribute to our understanding of ecological interactions. A shared evolutionary history can thus explain the tendency of closely related species to interact with similar partners (Thompson 2005; but see Elias et al. 2013). If past evolutionary events shape ecological networks, then we should expect a phylogenetic signal in current networks (e.g., Rezende et al. 2009). The underlying assumptions are that related species have similar traits and that trait matching between interacting species partially explains network structure (**Figure 2**). In seed dispersal networks, phylogeny partially explained the modular structure observed in both plants and animals (Donatti et al. 2011, Mello et al. 2011). Likewise, species that connect different modules are phylogenetically related in plants and animals (Schleuning et al. 2014, Nogales et al. 2015). Because species relatedness contributes to network cohesion, phylogenetically related species appear to have similar roles across different interaction networks (Stouffer et al. 2012, Poulin et al. 2013).

However, asking whether or not phylogeny plays a role in shaping network metrics is not in itself a very elucidating question because, even if answered affirmatively, it falls short of explaining the causal mechanism. Phylogeny may play a role because traits are conserved and do not change rapidly over time. In this scenario, the process of ecological fitting leads species to interact with partners whose traits match their own without this match being caused by a process of reciprocal coevolution (see Janzen 1985). The importance of ecological fitting as an alternative mechanism to coevolution cannot be overemphasized, as the former is simple and robust to changes in community composition but is often neglected in the literature. Alternatively, phylogeny may help explain network structure precisely because there has been adaptation, perhaps even reciprocal coevolution

Trait matching: observation that interacting species possess complementary traits (traits that provide a good fit)

Ecological fitting: species interact because they have preexisting, complementary traits that have not adapted to a particular interaction

Coevolution: reciprocal evolutionary change in at least two species to the selective pressures brought by the other species among interacting groups within the network. Thus, a phylogenetic signal alone does not allow us to infer the underlying mechanisms.

4.1. Trait Matching

The relative importance of traits for determining interaction probabilities can be analyzed by constructing several alternative models that contain multiple predictor variables and interaction probability as a dependent variable. Each predictor is represented in the same number of models. Then the statistical support for each predictor variable can be calculated by summing over all models (Schleuning et al. 2011, González-Castro et al. 2015; but see Galipaud et al. 2014). This approach can identify relevant traits (Eklöf et al. 2013) but quantifies neither trait matching between species nor how an interaction determines the evolution of traits.

Once functionally relevant traits are identified, we can ask how they shape the interactions with other species. Obviously, some fit is required in complementary traits, but it is often not resolved how well traits need to match, despite the fact that trait matching is seen as one mechanism causing nestedness by species interacting only with that subset of the community that has complementary traits (Coux et al. 2016, Dehling et al. 2016). Competition is an additional structuring mechanism that can stimulate specialization if that increases resource use (**Figure 2**). Due to the high temporal variability of resource use, competition effects can be almost impossible to detect.

Trait matching occurs in very distinct networks, from mutualistic pollination and seed dispersal networks to marine food webs and parasitoid–host interactions (Stang et al. 2009, Eklöf et al. 2013, Junker et al. 2013, Dehling et al. 2014). The degree of trait matching determines the strength of the interactions between flowering plants and hummingbirds (Maglianesi et al. 2014). Trait matching is easy to visualize if a single trait determines the interaction between two species. For example, the very long flower tubes of *Passiflora* species exclude most flower visitors, except those that pierce the flowers, and may have coevolved with bill length in the sword-billed hummingbird (*Ensifera ensifera*) (**Figure 3**). Typically, however, the situation is more complex because multiple traits and combinations thereof determine interactions.

Various approaches exist to measure trait matching. Most simply, interaction traits can be identified by a lower variance (or, more precisely, a lower coefficient of variation) in an intraspecific comparison relative to unrelated noninteraction traits. For example, variation in the length of the tail of frugivorous bird species is expected to be more pronounced than variation in its beak width. Such traits need to be selected carefully to avoid confusing selection for a network interaction with selection for something else. Moreover, the variance of a trait for a truly interacting species is expected to be lower than that for noninteracting species of the same community. For example, the tongues of visitors to a long-tubed flower will vary less than a random sample of flower visitors in the community. These approaches are useful but still limited because they analyze the traits of only one group of interacting species.

A key problem is quantifying the degree of trait matching. For example, Junker et al. (2013) calculated pairwise Euclidean distances among flower traits, weighted by interaction frequencies among flowers and pollinators, and compared the distances in floral traits visited by a single pollinator species to a null distribution of that community. The underlying reasoning is that relevant traits for shaping the interaction have lower variance than traits that do not influence the interaction (Junker et al. 2013). Dehling et al. (2016) overcame the problem of quantifying trait matching by projecting species into the phenotypic trait space of their interactions partners. These analyses are an important step towards quantifying the functional diversity of multiple traits across taxa or regions. Even though the approaches of both groups have the advantage of making few a priori assumptions on trait matching, neither Mantel tests nor null models provide strong

Figure 3

The sword-billed hummingbird is the only legitimate pollinator of very long-tubed flowers in Andean cloud forests such as *Passiflora mixta*. Photos courtesy of H.M. Schaefer.

evidence that trait matching actually determines the interactions, their frequencies and outcome (rather than another, unspecified but correlated trait).

4.2. Evolution

It is worth remembering that the data typically collected for performing network analyses are interaction rates, species identity, and quantifications of a suite of traits in the species assemblage of interacting groups. These data allow us to determine how traits influence interaction probabilities among species, but additional data are needed for quantifying the selective pressure relative to other selective pressures. Only the quantification of the selective pressures of an interaction, relative to other selective pressures, allows us to estimate how the interaction itself or the traits that determine the interaction will evolve. Clearly, such data are rarely collected in ecological network analyses.

One necessary layer of information would be an analysis of the reproductive output of at least one of the interacting groups as a result of the interaction, e.g., seed set after a pollinator visited a flower. Even though seed set could not be easily traced to the visits of individual pollinators in the absence of an experiment, variance in the degree of trait matching and in visitation rates of pollinators among individuals of the same species could be used to explain variance in reproductive output. Such analyses would represent an important advance in understanding the current selective pressures within the network. This would be a necessary first step to infer how the interaction, or the traits shaping it, evolves.

It is intuitive, and models have shown, that coevolution leads to trait matching among interacting species and convergence among unrelated species of one trophic group (Guimarães et al.

2011). Importantly, however, trait matching itself and also modules are not necessarily the result of adaptations to interacting partners, as they may occur without reciprocal adaptations if species preferentially interact with those partners whose preexisting traits are complementary to their own (**Figure 2**). Invasive species provide a good example of this process of ecological fitting if they share no evolutionary history with other species in the communities they invade and interact with. Thus, although trait matching is a necessary result of coevolution, it is not a proof of it, as it can be produced by an alternative mechanism.

4.3. Coevolution

Coevolution is defined as the process of reciprocal evolutionary change driven by natural selection among interacting species (Janzen 1980, Thompson 2005). However, collecting evidence of coevolution is not trivial. The question of whether coevolution shaped network structure is essentially concerned with a historical process (see also Tylianakis & Morris 2017), i.e., whether mutual adaptations have occurred over time. As such, it is not easily answered by sampling network structure and phylogeny at one point in time. Even repeated measurements of network structure over time may be insufficient for detecting adaptations because natural selection can be not only directional but also episodic or oscillatory (Grant & Grant 2002). Episodic evolution results in traits shifting occasionally, whereas traits shift back and forth in oscillatory selection. Such shifts may go unnoticed if observations are not done at sufficiently high temporal resolution.

Phylogenetic approaches (e.g., Rezende et al. 2007, Vázquez et al. 2009a, Verdú & Valiente-Banuet 2011) test for evolutionary signals in interactions after accounting for trait effects [which are themselves often phylogenetically correlated (Bascompte & Jordano 2014)]. Several studies found such phylogenetic signals (Rezende et al. 2007, Verdú & Valiente-Banuet 2011), pointing at different processes: (*a*) geographic relatedness (i.e., species originated in the same region and are hence interacting), (*b*) unobserved traits that are phylogenetically related (Vamosi et al. 2014), and (*c*) mutual adaptations (i.e., actual coevolution). To disentangle these not mutually exclusive hypotheses, a single network is not sufficient.

A surrogate for unobserved network structure in time is to sample networks and trait values across space if the suite of interacting partners differs predictably. For example, populations of the palm *Euterpe edulis* have evolved smaller seeds in sites where large seed dispersers went extinct over the last century compared to those sites where they were still present (Galetti et al. 2013). This study elucidates trait changes in response to the absence of previously common mutualists as a result of pervasive defaunation.

The concept of testing coevolution in space follows the well-established theory of the geographic mosaic of coevolution (Thompson 2005). There is geographic variation on how strongly the fitness of one species depends on the distribution of genotypes in another species. As a consequence, some populations may coevolve with an interacting species, whereas other populations do not (Thompson 2005). Populations are thus embedded into a geographical mosaic of local adaptation, with reciprocal selection among species occurring in some areas but not others.

A good example of geographic variation in coevolution is the triad between lodgepole pines (*Pinus contorta*), American red squirrels (*Tamiasciurus hudsonicus*), and red crossbills (*Loxia curvirostra*). Red squirrels are preemptive competitors and drive cone evolution in pines wherever they are present. When squirrels are absent, crossbills become more common and coevolve with pines in an evolutionary arms race (Benkman 1999). These findings illustrate the important point that the selective pressures of one species partly depend on those of other species and are not independent of each other. This situation is called diffuse coevolution, where the interactions with one species can alter the likelihood and strength of interactions with other species. Network analyses remind us that coevolution does not occur in isolation between a pair of species but among multiple interacting species (see also Section 5.1). This is an important aspect that network analyses could contribute to our current understanding of microevolution if data on fitness were included in the study design. Note that the same type of data would be useful for addressing the chicken-and-egg problem (network or abundance; see Section 3), which may rely on either an ecological or evolutionary mechanism.

Our tentative conclusion is that it is often difficult to identify a selective pressure, particularly because the necessary data are rarely collected in studies of ecological networks. This difficulty, rather than the short study periods of modern research, explains the rarity of convincing evidence of microevolutionary changes in ecological networks.

5. NETWORK STRUCTURE: THE CASE OF MODULES

In this section, we apply the lessons learned to a specific network structure, namely, modules. Among the numerous metrics that describe facets of network structure, those relating more directly to specialization are arguably more intuitive and relevant for our ecological understanding. In a way, all third-order patterns can be considered the product of specialization (see Section 2.2). As specialization increases across the species, networks may appear more like a collection of subcommunities (modules, compartments, or cliques). In this section, our focus is on modularity, largely because we feel that modules offer a more intuitive ecological interpretation (Why do these specific species interact more closely?) and can be better visualized than, e.g., indices for interaction evenness, network position, or robustness to species extinctions. Despite this specific focus, most of the key points could be made for many other structural properties of networks.

Networks are not fully connected graphs where every species interacts with every other. Instead, we can observe a certain clustering of links commonly termed a module (e.g., Guimerà & Amaral 2005). Formally, Newman's (2006) definition of modularity is the most widely accepted (Fortunato 2010). It demands that a module have a higher link density within the module than between modules. Formally, modularity of a network is defined as

$$Q = \frac{1}{2m} \sum_{i,j} (A_{ij} - P_{ij}) \delta(g_i, g_j), \qquad 1.$$

where P_{ij} is the null-model expectation (based on marginal totals) and δ is an indicator function with value 1 when species i and j are in the same module g (of which there are m) and 0 otherwise. There are variations on this formula; this one is apt for quantitative networks (i.e., with values other than 0 or 1 in the adjacency matrix) and extensions to bipartite networks (Barber 2007). Recently, Beckett (2015) convincingly demonstrated that, independent of the algorithm, binary and quantitative networks reveal different modules, drawing attention to the need for quantitative interaction data.

Today, there is no question that ecological networks are typically modularized. Despite the lack of compartments in the first review by Pimm & Lawton (1980), better algorithms and a focus on modules rather than strict compartments now discover modularization in virtually all ecological networks analyzed (e.g., Raffaelli & Hall 1992, Fonseca & Ganade 1996, Dicks et al. 2002, Krause et al. 2003, Allesina & Pascual 2009, Mello et al. 2011, Martín González et al. 2012, Dalsgaard et al. 2013, Thébault 2013, Schleuning et al. 2014, Sebastián-González et al. 2015). Particularly interesting are the biological reasons for modules that Pimm (1982) and later authors discuss

(**Table 1**). Various processes can lead to a modular organization of the observed network, but which process or processes are actually responsible for it is obscure (Vázquez et al. 2009a). What remains even more speculative, however, are the consequences of this modularization, which have been a matter of debate since early work by May (1972).

5.1. Causes of Modularity

Modularity is in itself rarely of interest. It will be correlated with the specialization of species in that network (Dormann & Strauß 2014), as well as with connectance (Mello et al. 2011) and sampling intensity (Rivera-Hutinel et al. 2012). However, the visualization of the modules (**Figure 4**) may be a very useful step for generating hypotheses about processes that affect the dynamics, and hence the structure, of the network under consideration. The identified modules are thus hypotheses of group-generating processes; incomplete sampling distorts the actual modules. As many different causes may lead to a modular pattern, we have to exclude the obvious but possibly less ecologically interesting ones first (**Table 1**).

Augustyn et al.'s (2016) study provided the strongest experimental evidence for a cause of modularity. Excluding competition in cage experiments, they found preferences in line with those observed for the full community of leafhoppers on Restionaceae plants, demonstrating that the observed modules emerge from species-specific preferences (suggesting one-sided adaptation; see **Figure 2**) rather than competition. Most other studies offer ad hoc explanations for the observed modules in varying degrees of speculation. For example, Dicks et al. (2002) detected modules in two pollination networks, but the characterization of the module as "flies visiting mainly *Ranunculus acris*" (p. 38) is not easily generalized to other systems.

The most commonly invoked cause of modules is coevolution, i.e., the mutual adaptation of interacting partners to each other. Coevolutionary compartments rarely comprise more than a few species, although in ant–tree networks, clear separation of ants by tree species has been observed (Fonseca & Ganade 1996). However, that may be easier to explain by a one-sided adaptation followed by radiation. Dupont & Olesen (2009) considered high connectance within modules as "possibly exerting strong reciprocal selection on mutualistic traits" (p. 351). Diffuse coevolution (see Section 4.3) among multiple species undoubtedly occurs but is often difficult to detect (Iwao & Rausher 1997). The best evidence for coevolution is to illustrate microevolutionary changes in the interaction traits of a set of species. The obvious problem is that changes in the traits of one species (say, a plant) would require adaptations of not one but several interacting species (say, pollinators) and, hence, a stable community in space and time. Additionally, the high connectance within the network suggests that other plants serve the pollinators equally well, preventing any need to adapt to trait changes in a single plant species. In the words of Lewinsohn et al. (2006), "In highly diversified interaction assemblages of varying specificity … evolutionary processes and dynamics yielding complex patterns can be extremely difficult to decipher" (p. 182) (see also **Figure 2**).

Phylogenetic (or taxonomic) patterns within modules are often interpreted as coevolutionary evidence (Fonseca & Ganade 1996, Lewinsohn et al. 2006). According to this view, modules have evolved, and species newly entering a network lead to a fusion of modules because they are not yet adapted (Olesen et al. 2007). None of these claims contradict one-sided rather than coevolutionary adaptation (**Figure 2**), and there are also some studies that show a convergence of different species to the same module (mammals versus birds versus fish versus rodents), suggesting trait-driven modules (Donatti et al. 2011). Furthermore, traits are often phylogenetically conserved, suggesting that traits rather than phylogeny are causes of modules. Phylogeny may thus be a proxy for unknown ecological processes.

Table 1 Possible nonexclusive causes of network modules and compartments

Reason	Explanation	Comment
Chance	Random variability in abundance or observations	The abundance of many animals is highly variable (e.g., between years), and sampling ecological communities will inevitably yield highly variable data (Petanidou et al. 2008, Dupont et al. 2009). Modules may emerge purely by chance.
Habitat separation	Networks are sampled across different habitats, which now form discernible subgroups in the network	This seems to be as much a sampling as a scale issue: As species are sampled more intensively (over longer time) or at larger spatial scales, species are found that connect different habitats (Pimm & Lawton 1980, Krause et al. 2003, Rezende et al. 2009). Sampling only, say, insects on plants across habitats (or, equivalently, ecosystem compartments, e.g., above- or belowground) may indeed reveal primarily habitat-driven modules.
Temporal dynamics	Activity patterns within a day or season	Plants may keep their flowers open longer when not visited by pollinators in the morning; such within-day niches of activity may show up as different modules if data from morning and afternoon were to be pooled (Fründ et al. 2011). Similarly, plants and animals have a seasonal rhythm (phenology) triggered by environmental conditions and evolved in response to competition or availability of forage. Pollination networks recorded at different times during the year, for example, may show up as phenology-driven modules (Parrish & Bazzaz 1979, Olesen et al. 2008, Martín González et al. 2012, Valverde et al. 2016). Frugivore networks depend on the fruit phenology of their forage trees (Kimura et al. 2001), potentially with a coevolutionary side (Thompson & Willson 1979).
Competition	Displacement of inferior competitor onto other interactors	Competition within the same trophic level can force the inferior species to interact with nonpreferred species. Excluding the dominant species should lead to shifts in observed preferences.
Trait matching	Required overlap of traits of interacting species	Biotic syndromes may represent overlapping resource niches without adaptations to a specific interaction (Williams & Martinez 2000), e.g., floral color (e.g., Dicks et al. 2002, Dupont & Olesen 2009, Ollerton et al. 2009, Martín González et al. 2012), gape width in frugivorous birds (Donatti et al. 2011), or body mass matching in predatory fish (Rezende et al. 2009). Sometimes we do not know the relevant traits and instead detect a phylogenetic pattern (Jordano 1987, Cagnolo et al. 2011, Krasnov et al. 2012, Stouffer et al. 2012).
One-sided adaptation	A (set of) species adapts to another	Taxonomic or phylogenetic closeness can be a good predictor of which species form a module (Cagnolo et al. 2011 and references therein; Stouffer et al. 2012), e.g., because radiation has taken place after a species adapted to a host or mutualist [e.g., leafhoppers to a host plant (see Augustyn et al. 2016)] without any (coevolutionary) changes in the interactor (i.e., the mammal or plant).
Coevolution	Evolution of a reciprocal interaction between two (or more) species	Coevolutionary adaptations favor a set of species and often exclude other species from interactions, e.g., *Cecropia* trees hosting *Azteca* ants (Fonseca & Ganade 1996) and the famous hawkmoth pollination cases (e.g., Sazatornil et al. 2016).

Invoking an explanation from rows lower down in the table should require dismissing potential causes from rows higher up.

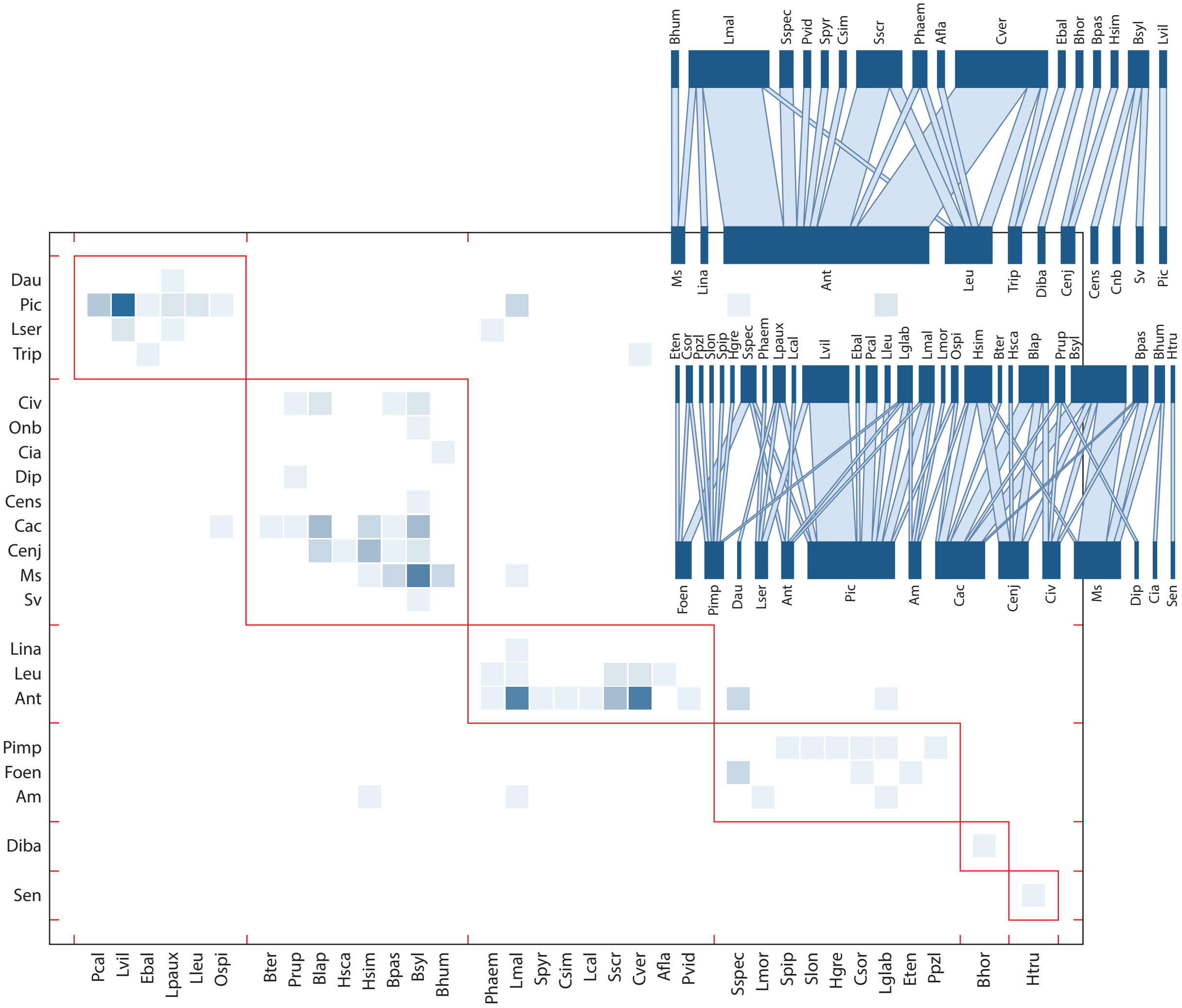


Figure 4

Modules (*red boxes*) of a pollination network pooled over June 22, 2006, and August 7, 2006. (*Insets*) Individual networks on the same pasture; the top inset is from June 22 and the bottom inset is from August 7. The modules are driven by plants visited only on one of the two sampling dates, such as Pic in the first module or Leu and Ant in the third (the two single-link modules are likely to be sampling artifacts with only one observation each). Data collected by Jochen Fründ.

For field ecologists, habitats are the most straightforward causes of modularity (Lewinsohn et al. 2006, Olesen et al. 2007), closely followed by phenology (Martín González et al. 2012). If networks were sampled across different habitats (or in different periods of phenology), they can easily show up as distinct modules (**Figure 4**).

In the absence of information about whether networks were sampled across habitats, macroecological analyses of modularity find correlations with mean annual temperature [positive (Dalsgaard et al. 2013) or negative (Schleuning et al. 2014)], temperature seasonality [a positive effect, suggesting phenological modules (Schleuning et al. 2014)], precipitation (Dalsgaard et al. 2013, Sebastián-González et al. 2015), insularity [island networks being more modular (Dalsgaard et al. 2013)], or human influence [an amalgam of population density, land cover change, and infrastructure, which correlates negatively with modularity in seed–disperser networks (Sebastián-González et al. 2015)]. These patterns may suggest certain interpretations but are currently speculative.

Overall, many different processes may lead to network modules. Without further information, none of them can credibly be invoked as single cause.

5.2. Consequences of Modularity

Historically, May (1972) reported that modules should have a positive effect on network stability, in line with his reasoning that more species will make networks less stable, and hence, separating them from each other will reduce the negative effect of diversity on stability. His argument was based on the coexistence condition for random interaction matrices with normally distributed interaction strength, $s(nC)^{1/2} < 1$, where s is the standard deviation of the normal distribution from which interaction strengths are drawn, n is the number of species, and C is the connectance of the matrix (see also Sinha 2005, Allesina & Tang 2012). May's interpretation was challenged by Pimm (1979), who considered the same condition but argued that, for a given connectance, modules destabilize networks and should thus be rare.

The current literature draws a more nuanced picture (**Table 2**), where the effect of compartments depends on which process is at play (Helbing 2013). Compartments will prevent a rapid spreading of diseases to other species (Krause et al. 2003, Ruiz-Moreno et al. 2006). On the other hand, positive effects, such as fertilization in only some habitats, will similarly be contained in the compartment. In line with this reasoning, simulations suggest that antagonistic networks are stabilized by modules (Garay-Narváez et al. 2014), whereas mutualistic networks become more

Table 2 **Possible consequences of network modularity**

Consequence	Explanation	Comment
Robustness	Disturbances are contained within the module.	As the majority of interactions are within modules (by definition), changes in the abundance of a species will primarily affect the other members of the module and not spread easily throughout the network [proposed, e.g., by Krause et al. (2003)]. There is no evidence to date. Extirpation of a species had no effect on modules or the network (Olesen et al. 2007).
Fragility	Hub species facilitate spread of diseases.	Interspecifically transmittable diseases will spread faster through modularized networks when hub species become affected [proposed, e.g., by Pimm & Lawton (1980) and demonstrated in models by Ruiz-Moreno et al. (2006) and Bisanzio et al. (2010)]. This is a consequence of the small-world property rather than modularity per se; modules make hubs more likely (e.g., Olesen et al. 2006). There is no evidence to date.
Higher species richness	Competition is reduced by separation of interactions.	As species sort themselves into different interaction modules, their reduction in experienced diffuse competition increases the possibility of coexistence (Bastolla et al. 2009). There is no evidence to date. Host similarity was not reduced within modules, suggesting no scope for reduced competition (Prado & Lewinsohn 2004).
Coevolution	Reduced number of partners facilitates coevolution.	"Strong reciprocal selection on mutualistic traits" (Dupont & Olesen 2009, p. 351) could make coevolution more likely than in a fully connected network. There is no evidence to date.

Evidence from field or lab studies is absent.

fragile (Thébault & Fontaine 2010). Observational or experimental corroboration is currently lacking.

Identifying patterns in ecological networks that are similar to, or different from, those in other systems (e.g., electric circuits, neural patterns, executive clubs, the World Wide Web) does not necessarily translate into ecological knowledge. Typical interaction patterns (motifs) are different in food webs than in other systems (e.g., energy grids); however, such analogies are ecologically meaningless until equivalent ecological processes can be identified. Modularity was found to be crucial for the evolution of cooperation in social systems (Gianetto & Heydari 2015), a mechanism much closer to ecological interactions. From the foregoing discussion, it should become clear that, despite many claims, few studies have contributed actual facts concerning the consequences of modularity.

This section builds on the available literature on network modules, and the approach could be analogously applied to other network metrics (which are beyond the scope of this review). In all likelihood, the conclusions will be very similar and are familiar to ecologists: Many different processes create similar network patterns, and the consequences for the system (e.g., abundances of species connected, or not, in this network) are largely speculative. Manipulative experiments with networks have only just begun, but with their help, ecologists may get a better grip on how structure arises, and what its effects are.

6. OUTLOOK: DIRECTIONS FOR NETWORK ANALYSIS

This paper has highlighted some of the challenges that network analysis faces: accounting for sampling effects, attributing processes through null models, and understanding the role of trait matching and adaptation. We have refrained from delving too much into technical details because the field is partly in rapid development: Data sources, data quality, analytical tools, and experiments may take this field to further heights. Below we outline four directions that future research efforts would be well invested.

FUTURE ISSUES

1. Future data will yield more highly resolved networks, e.g., due to DNA identification. Quantifying interactions at the level of the individual flower, pollinator, parasite, herbivore, or predator will enable us to better understand their behavior and choices and hence will also inform models that explore the consequences of such behavior. Temporally highly resolved assessments of use and the availability of resources, along with environmental conditions, will allow network analyses to reach beyond mere descriptions of who-interacts-with-whom and start elucidating the why behind it. The concept of multilayer networks (reviewed by Boccaletti et al. 2014) may help guide this new generation of network analyses.
2. Future network models will be process based, rather than null or statistical. Wells & O'Hara (2013) fit a statistical sampling model to (simulated) networks. An extension to include population dynamics will face the challenge that population dynamics for each species require many parameters for which additional data need to be collected (such as on growth rates, nest site limitations, population carrying capacities). It may require substantial efforts to fit network-level interaction models such as those of Bastolla et al. (2009) or Benadi et al. (2013) for dozens or hundreds of species to observational data.

3. Experiments will investigate physiological and morphological drivers of network structure. Manipulating the abundance of species (e.g., large-scale addition or removal) or the actual interaction (e.g., applying scent to repel a flower visitor, or training animals to use a novel resource) and then observing shifts in the preferences of other species is a sound strategy for getting closer to the causal mechanisms.
4. Future studies should combine network analyses with fitness data of interacting partners to elucidate the evolutionary processes underlying network structure. Experimental manipulations of interactions would allow an investigation of the direct population-level consequences. When traits are (genetically) variable, such consequences will lead to the rapid selection of the most adaptive trait and hence leave a measurable trace of fitness consequences.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

Discussions with Gita Benadi and Diego Vázquez greatly helped us develop our reasoning, and comments by Gita Benadi, Becky Morris, and Pedro Jordano improved the manuscript. J.F. acknowledges funding by the DFG (German Research Foundation) through grants FR 3364/2-1 and FR 3364/4-1.

LITERATURE CITED

Albrecht M, Padrón B, Bartomeus I, Traveset A. 2014. Consequences of plant invasions on compartmentalization and species' roles in plant–pollinator networks. *Proc. R. Soc. B* 281:20140773

Allesina S, Pascual M. 2009. Food web models: a plea for groups. *Ecol. Lett.* 12:652–62

Allesina S, Tang S. 2012. Stability criteria for complex ecosystems. *Nature* 483:205–8

Almeida-Neto M, Guimarães P, Guimarães PR Jr., Loyola RD, Ulrich W. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117:1227–39

Armbruster WS. 2017. The specialization continuum in pollination systems: diversity of concepts and implications for ecology, evolution and conservation. *Funct. Ecol.* 31:88–100

Augustyn WJ, Anderson B, Ellis AG. 2016. Experimental evidence for fundamental, and not realised, niche partitioning in a plant–herbivore community interaction network. *J. Anim. Ecol.* 85:994–1003

Banašek-Richter C, Cattin MF, Bersier LF. 2004. Sampling effects and the robustness of quantitative and qualitative food-web descriptors. *J. Theor. Biol.* 226:23–32

Barber M. 2007. Modularity and community detection in bipartite networks. *Phys. Rev. E* 76:066102

Bartomeus I, Gravel D, Tylianakis JM, Aizen MA, Dickie IA, Bernard-Verdier M. 2016. A common framework for identifying linkage rules across different types of interactions. *Funct. Ecol.* 30:1894–903

Bascompte J, Jordano P. 2014. *Mutualistic Networks*. Princeton, NJ: Princeton Univ. Press

Bascompte J, Jordano P, Melián CJ, Olesen JM. 2003. The nested assembly of plant–animal mutualistic networks. *PNAS* 100:9383–87

Bastolla U, Fortuna MA, Pascual-García A, Ferrera A, Luque B, Bascompte J. 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. *Nature* 458:1018–20

Beckett SJ. 2015. Improved community detection in weighted bipartite networks. *R. Soc. Open Sci.* 3:140536

Benadi G, Blüthgen N, Hovestadt T, Poethke HJ. 2012. Population dynamics of plant and pollinator communities: stability reconsidered. *Am. Nat.* 179:157–268

Benadi G, Blüthgen N, Hovestadt T, Poethke HJ. 2013. When can plant-pollinator interactions promote plant diversity? *Am. Nat.* 182:131–46

Benkman CW. 1999. The selection mosaic and diversifying coevolution between crossbills and lodgepole pine. *Am. Nat.* 153:S75–91

Bisanzio D, Bertolotti L, Tomassone L, Amore G, Ragagli C, et al. 2010. Modeling the spread of vector-borne diseases on bipartite networks. *PLOS ONE* 5:e13796

Blüthgen N, Fründ J, Vázquez DP, Menzel F. 2008. What do interaction network metrics tell us about specialization and biological traits? *Ecology* 89:3387–99

Blüthgen N, Menzel F, Blüthgen N. 2006. Measuring specialization in species interaction networks. *BMC Ecol.* 6:9

Blüthgen N, Menzel F, Hovestadt T, Fiala B, Blüthgen N. 2007. Specialization, constraints, and conflicting interests in mutualistic networks. *Curr. Biol.* 17:341–46

Boccaletti S, Bianconi G, Criado R, del Genio CI, Gómez-Gardeñes J, et al. 2014. The structure and dynamics of multilayer networks. *Phys. Rep.* 544:1–122

Brosi BJ, Briggs HM. 2013. Single pollinator species losses reduce floral fidelity and plant reproductive function. *PNAS* 110:13044–48

Cagnolo L, Salvo A, Valladares G. 2011. Network topology: patterns and mechanisms in plant-herbivore and host-parasitoid food webs. *J. Anim. Ecol.* 80:342–51

Coux C, Rader R, Bartomeus I, Tylianakis JM. 2016. Linking species functional roles to their network roles. *Ecol. Lett.* 19:762–70

Crea C, Ali RA, Rader R. 2015. A new model for ecological networks using species level traits. *Methods Ecol. Evol.* 7:232–41

Dalsgaard B, Trøjelsgaard K, Martín González AM, Nogués-Bravo D, Ollerton J, et al. 2013. Historical climate-change influences modularity and nestedness of pollination networks. *Ecography* 36:1331–40

Dehling DM, Jordano P, Schaefer HM, Böhning-Gaese K, Schleuning M. 2016. Morphology predicts species' functional roles and their degree of specialisation in plant–frugivore interactions. *Proc. R. Soc. B* 283:20152444

Dehling DM, Töpfer T, Schaefer HM, Jordano P, Böhning-Gaese K, Schleuning M. 2014. Functional relationships beyond species richness patterns: trait matching in plant–bird mutualisms across scales. *Glob. Ecol. Biogeogr.* 23:1085–93

Dicks LV, Corbet SA, Pywell RF. 2002. Compartmentalization in plant–insect flower visitor webs. *J. Anim. Ecol.* 71:32–43

Donatti CI, Guimarães PR, Galetti M, Pizo MA, Marquitti FMD, Dirzo R. 2011. Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. *Ecol. Lett.* 14:773–81

Dormann CF. 2011. How to be a specialist? Quantifying specialisation in pollination networks. *Netw. Biol.* 1:1–20

Dormann CF, Blüthgen N, Fründ J, Gruber B. 2009. Indices, graphs and null models: analyzing bipartite ecological networks. *Open Ecol. J.* 2:7–24

Dormann CF, Strauß R. 2014. A method for detecting modules in quantitative bipartite networks. *Methods Ecol. Evol.* 5:90–98

Dupont YL, Olesen JM. 2009. Ecological modules and roles of species in heathland plant: insect flower visitor networks. *J. Anim. Ecol.* 78:346–53

Dupont YL, Padrón B, Olesen JM, Petanidou T. 2009. Spatio-temporal variation in the structure of pollination networks. *Oikos* 118:1261–69

Eklöf A, Jacob U, Kopp J, Bosch J, Castro-Urgal R, et al. 2013. The dimensionality of ecological networks. *Ecol. Lett.* 16:577–83

Elias M, Fontaine C, van Veen FJF. 2013. Evolutionary history and ecological processes shape a local multilevel antagonistic network. *Curr. Biol.* 23:1355–59

Finke DL, Snyder WE. 2008. Niche partitioning increases resource exploitation by diverse communities. *Science* 2137:1999–2002

Fonseca C, Ganade G. 1996. Asymmetries, compartments and null interactions in an Amazonian ant-plant community. *J. Anim. Ecol.* 65:339–47

Fontaine C, Dajoz I, Meriguet J, Loreau M. 2006. Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. *PLOS Biol.* 4:e1

Fort H, Vázquez DP, Lan BL. 2016. Abundance and generalization in mutualistic networks: solving the chicken-and-egg dilemma. *Ecol. Lett.* 19:4–11

Fortunato S. 2010. Community detection in graphs. *Phys. Rep.* 486:75–174

Fründ J, Dormann CF, Holzschuh A, Tscharntke T. 2013. Bee diversity effects on pollination depend on functional complementarity and niche shifts. *Ecology* 94:2042–54

Fründ J, Dormann CF, Tscharntke T. 2011. Linné's floral clock is slow without pollinators—flower closure and plant-pollinator interaction webs. *Ecol. Lett.* 14:896–904

Fründ J, McCann KS, Williams NM. 2016. Sampling bias is a challenge for quantifying specialization and network structure: lessons from a quantitative niche model. *Oikos* 125:502–13

Galetti M, Guevara R, Côrtes MC, Fadini R, Von Matter S, et al. 2013. Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* 340:1086–90

Galipaud M, Gillingham MAF, David M, Dechaume-Moncharmont FX. 2014. Ecologists overestimate the importance of predictor variables in model averaging: a plea for cautious interpretations. *Methods Ecol. Evol.* 5:983–91

Garay-Narváez L, Flores JD, Arim M, Ramos-Jiliberto R. 2014. Food web modularity and biodiversity promote species persistence in polluted environments. *Oikos* 123:583–88

Gianetto DA, Heydari B. 2015. Network modularity is essential for evolution of cooperation under uncertainty. *Sci. Rep.* 5:9340

Gibson RH, Knott B, Eberlein T, Memmott J. 2011. Sampling method influences the structure of plant–pollinator networks. *Oikos* 120:822–31

González-Castro A, Yang S, Nogales M, Carlo TA. 2015. Relative importance of phenotypic trait matching and species' abundances in determining plant–avian seed dispersal interactions in a small insular community. *AoB Plants* 7:plv017

Gotelli NJ, Graves GR. 1996. *Null Models in Ecology*. Washington, DC: Smithsonian Inst.

Grant PR, Grant BR. 2002. Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 707:707–11

Guimarães PR Jr., Jordano P, Thompson JN. 2011. Evolution and coevolution in mutualistic networks. *Ecol. Lett.* 14:877–85

Guimerà R, Amaral LAN. 2005. Functional cartography of complex metabolic networks. *Nature* 433:895–900

Helbing D. 2013. Globally networked risks and how to respond. *Nature* 497:51–59

Iwao K, Rausher MD. 1997. Evolution of plant resistance to multiple herbivores: quantifying diffuse coevolution. *Am. Nat.* 149:316–35

James A, Pitchford JW, Plank MJ. 2012. Disentangling nestedness from models of ecological complexity. *Nature* 487:227–30

Janzen DH. 1980. When is it coevolution? *Evolution* 34:611–12

Janzen DH. 1985. On ecological fitting. *Oikos* 45:308–10

Jordano P. 1987. Patterns of mutualistic interactions in pollination and seed dispersal–connectance, dependence asymmetries, and coevolution. *Am. Nat.* 129:657–77

Jordano P. 2016. Sampling networks of ecological interactions. *Funct. Ecol.* 30:1883–93

Junker RR, Blüthgen N, Brehm T, Binkenstein J, Paulus J, et al. 2013. Specialization on traits as basis for the niche-breadth of flower visitors and as structuring mechanism of ecological networks. *Funct. Ecol.* 27:329–41

Kimura K, Yumoto T, Kikuzawa K. 2001. Fruiting phenology of fleshy-fruited plants and seasonal dynamics of frugivorous birds in four vegetation zones on Mt. Kinabalu, Borneo. *J. Trop. Ecol.* 17:833–58

Krasnov BR, Fortuna MA, Mouillot D, Khokhlova IS, Shenbrot GI, Poulin R. 2012. Phylogenetic signal in module composition and species connectivity in compartmentalized host-parasite networks. *Am. Nat.* 179:501–11

Krause AE, Frank KA, Mason DM, Ulanowicz RE, Taylor WW. 2003. Compartments revealed in food-web structure. *Nature* 426:282–85

Krishna A, Guimarães PR Jr., Jordano P, Bascompte J. 2008. A neutral-niche theory of nestedness in mutualistic networks. *Oikos* 117:1609–18

Laliberté E, Tylianakis JM. 2010. Deforestation homogenizes tropical parasitoid–host networks. *Ecology* 91:1740–47

Lewinsohn TM, Prado PI, Jordano P, Bascompte J, Olesen JM. 2006. Structure in plant–animal interaction assemblages. *Oikos* 113:174–84

Lopezaraiza-Mikel ME, Hayes RB, Whalley MR, Memmott J. 2007. The impact of an alien plant on a native plant–pollinator network: an experimental approach. *Ecol. Lett.* 10:539–50

Maglianesi MA, Blüthgen N, Böhning-Gaese K, Schleuning M. 2014. Morphological traits determine specialization and resource use in plant–hummingbird networks in the neotropics. *Ecology* 95:3325–34

Martín González AM, Allesina S, Rodrigo A, Bosch J. 2012. Drivers of compartmentalization in a Mediterranean pollination network. *Oikos* 121:2001–13

May RM. 1972. Will a large complex system be stable? *Nature* 238:413–14

May RM. 1973. *Stability and Complexity in Model Ecosystems*. Princeton, NJ: Princeton Univ. Press

Mello MAR, Marquitti FMD, Guimarães PR Jr., Kalko EKV, Jordano P, Martinez de Aguiar MA. 2011. The modularity of seed dispersal: differences in structure and robustness between bat– and bird–fruit networks. *Oecologia* 167:131–40

Morris RJ, Gripenberg S, Lewis OT, Roslin T. 2013. Antagonistic interaction networks are structured independently of latitude and host guild. *Ecol. Lett.* 27:340–49

Newman MEJ. 2006. Finding community structure in networks using the eigenvectors of matrices. *Phys. Rev. E* 74:036104

Nielsen A, Bascompte J. 2007. Ecological networks, nestedness and sampling effort. *J. Ecol.* 95:1134–41

Nogales M, Heleno R, Rumeu B, Traveset A, Vargas P, Olesen JM. 2015. Seed-dispersal networks on the Canaries and the Galápagos archipelagos: interaction modules as biogeographical entities. *Glob. Ecol. Biogeogr.* 7:912–22

Olesen JM, Bascompte J, Dupont YL, Jordano P. 2006. The smallest of all worlds: pollination networks. *J. Theor. Biol.* 240:270–76

Olesen JM, Bascompte J, Dupont YL, Jordano P. 2007. The modularity of pollination networks. *PNAS* 104:19891–96

Olesen JM, Bascompte J, Elberling H, Jordano P. 2008. Temporal dynamics in a pollination network. *Ecology* 89:1573–82

Ollerton J, Alarcón R, Waser NM, Price MV, Watts S, et al. 2009. A global test of the pollination syndrome hypothesis. *Ann. Bot.* 103:1471–80

Parrish JAD, Bazzaz FA. 1979. Difference in pollination niche relationships in early and late successional plant communities. *Ecology* 60:597–610

Pascual M, Dunne J, eds. 2006. *Ecological Networks: Linking Structure to Dynamics in Food Webs*. Oxford: Oxford Univ. Press

Peralta G. 2016. Merging evolutionary history into species interaction networks. *Funct. Ecol.* 30:1917–25

Petanidou T, Kallimanis AS, Tzanopoulos J, Sgardelis SP, Pantis JD. 2008. Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecol. Lett.* 11:564–75

Petchey OL. 2003. Integrating methods that investigate how complementarity influences ecosystem functioning. *Oikos* 101:323–30

Pilosof S, Porter MA, Pascual M, Kéfi S. 2017. The multilayer nature of ecological networks. *Nat. Ecol. Evol.* 1:0101

Pimm SL. 1979. The structure of food webs. *Theor. Popul. Biol.* 16:144–58

Pimm SL. 1982. *Food Webs*. Chicago: Chicago Univ. Press

Pimm SL, Lawton JH. 1980. Are food webs divided into compartments? *J. Anim. Ecol.* 49:879–98

Poisot T, Canard E, Mouillot D, Mouquet N, Gravel D, Jordan F. 2012. The dissimilarity of species interaction networks. *Ecol. Lett.* 15:1353–61

Poisot T, Stouffer DB, Gravel D. 2015. Beyond species: why ecological interactions vary through space and time. *Oikos* 124:243–51

Poulin R, Krasnov BR, Pilosof S, Thieltges DW. 2013. Phylogeny determines the role of helminth parasites in intertidal food webs. *J. Anim. Ecol.* 82:1265–75

Prado PI, Lewinsohn TM. 2004. Compartments in insect–plant associations and their consequences for community structure. *J. Anim. Ecol.* 73:1168–78

Raffaelli D, Hall SJ. 1992. Compartments and predation in an estuarine food web. *J. Anim. Ecol.* 61:551–60

Rasmussen C, Dupont YL, Mosbacher JB, Trøjelsgaard K, Olesen JM. 2013. Strong impact of temporal resolution on the structure of an ecological network. *PLOS ONE* 8:e81694

Rezende EL, Albert EM, Fortuna MA, Bascompte J. 2009. Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. *Ecol. Lett.* 12:779–88

Rezende EL, Lavebre JE, Guimarães PR Jr., Jordano P, Bascompte J. 2007. Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature* 448:925–28

Riedinger V, Mitesser O, Hovestadt T, Steffan-Dewenter I, Holzschuh A. 2015. Annual dynamics of wild bee densities: attractiveness and productivity effects of oilseed rape. *Ecology* 96:1351–60

Rivera-Hutinel A, Bustamante RO, Marín VH, Medel R. 2012. Effects of sampling completeness on the structure of plant–pollinator networks. *Ecology* 93:1593–603

Rohr RP, Saavedra S, Bascompte J. 2014. On the structural stability of mutualistic systems. *Science* 345:1253497

Ruiz-Moreno D, Pascual M, Riolo R. 2006. Exploring network space with genetic algorithms: modularity, resilience, and reactivity. In *Ecological Networks: Linking Structure to Dynamics in Food Webs*, ed. M Pascual, JA Dunne, pp. 187–201. Oxford: Oxford Univ. Press

Russo L, Shea K. 2016. Deliberately increased network connectance in a plant–pollinator community experiment. *J. Complex Netw.* 5:473–85

Sazatornil FD, Moré M, Benitez-Vieyra S, Cocucci AA, Kitching IJ, et al. 2016. Beyond neutral and forbidden links: morphological matches and the assembly of mutualistic hawkmoth–plant networks. *J. Anim. Ecol.* 85:1586–94

Schleuning M, Blüthgen N, Flörchinger M, Braun J, Schaefer HM, Böhning-Gaese K. 2011. Specialization and interaction strength in a tropical plant–frugivore network differ among forest strata. *Ecology* 92:26–36

Schleuning M, Fründ J, García D. 2015. Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait-based concepts to plant–animal interactions. *Ecography* 38:380–92

Schleuning M, Ingmann L, Strauß R, Fritz SA, Dalsgaard B, et al. 2014. Ecological, historical and evolutionary determinants of modularity in weighted seed-dispersal networks. *Ecol. Lett.* 17:454–63

Sebastián-González E, Dalsgaard B, Sandel B, Guimarães PR Jr. 2015. Macroecological trends in nestedness and modularity of seed-dispersal networks: Human impact matters. *Global* 24:293–303

Sinha S. 2005. Complexity versus stability in small-world networks. *Physica A* 346:147–53

Sørensen PB, Damgaard CF, Strandberg B, Dupont YL, Marianne B, et al. 2011. A method for under-sampled ecological network data analysis: plant-pollination as case study. *J. Pollinat. Ecol.* 6:129–39

Spiesman BJ, Gratton C. 2016. Flexible foraging shapes the topology of plant–pollinator interaction networks. *Ecology* 97:1431–41

Stang M, Klinkhamer PGL, Waser NM, Stang I, van der Meijden E. 2009. Size-specific interaction patterns and size matching in a plant–pollinator interaction web. *Ann. Bot.* 103:1459–69

Stouffer DB, Sales-Pardo M, Sirer MI, Bascompte J. 2012. Evolutionary conservation of species' roles in food webs. *Science* 335:1489–92

Thébault E. 2013. Identifying compartments in presence–absence matrices and bipartite networks: insights into modularity measures. *J. Biogeogr.* 40:759–68

Thébault E, Fontaine C. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science* 329:853–56

Thompson JN. 2005. *The Geographic Mosaic of Coevolution*. Chicago: Univ. Chicago Press

Thompson JN, Willson MF. 1979. Evolution of temperate fruit/bird interactions: phenological strategies. *Evolution* 33:973–82

Tylianakis JM, Morris RJ. 2017. Ecological networks across environmental gradients. *Annu. Rev. Ecol. Evol. Syst.* 48:25–48

Tylianakis JM, Tscharntke T, Lewis OT. 2007. Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature* 445:202–5

Valdovinos FS, Moisset de Espanés P, Flores JD, Ramos-Jiliberto R. 2013. Adaptive foraging allows the maintenance of biodiversity of pollination networks. *Oikos* 122:907–17

Valverde J, Gómez JM, Perfectti F. 2016. The temporal dimension in individual-based plant pollination networks. *Oikos* 125:468–79

Vamosi JC, Moray CM, Garcha NK, Chamberlain SA, Mooers AØ. 2014. Pollinators visit related plant species across 29 plant–pollinator networks. *Ecol. Evol.* 4:2303–15

Vázquez DP, Blüthgen N, Cagnolo L, Chacoff NP. 2009a. Uniting pattern and process in plant–animal mutualistic networks: a review. *Ann. Bot.* 103:1445–57

Vázquez DP, Chacoff N, Cagnolo L. 2009b. Evaluating multiple determinants of the structure of plant–animal mutualistic networks. *Ecology* 90:2039–46

Vázquez DP, Lomáscolo SB, Maldonado MB, Chacoff NP, Dorado J, et al. 2012. The strength of plant–pollinator interactions. *Ecology* 93:719–25

Vázquez DP, Melián CJ, Williams NM, Blüthgen N, Krasnov BR, Poulin R. 2007. Species abundance and asymmetric interaction strength in ecological networks. *Oikos* 116:1120–27

Vázquez DP, Ramos-Jiliberto R, Urbani P, Valdovinos FS. 2015. A conceptual framework for studying the strength of plant–animal mutualistic interactions. *Ecol. Lett.* 18:385–400

Verdú M, Valiente-Banuet A. 2011. The relative contribution of abundance and phylogeny to the structure of plant facilitation networks. *Oikos* 120:1351–56

Vesk PA, McCarthy MA, Moir ML. 2010. How many hosts? Modelling host breadth from field samples. *Methods Ecol. Evol.* 1:292–99

Vizentin-Bugoni J, Maruyama PK, Debastiani VJ, Duarte L da S, Dalsgaard B, Sazima M. 2016. Influences of sampling effort on detected patterns and structuring processes of a Neotropical plant–hummingbird network. *J. Anim. Ecol.* 85:262–72

Vizentin-Bugoni J, Maruyama PK, Sazima M. 2014. Processes entangling interactions in communities: Forbidden links are more important than abundance in a hummingbird–plant network. *Proc. R. Soc. B* 281:20132397

Wells K, Feldhaar H, O'Hara RB. 2014. Population fluctuations affect inference in ecological networks of multi-species interactions. *Oikos* 123:589–98

Wells K, O'Hara RB. 2013. Species interactions: estimating per-individual interaction strength and covariates before simplifying data into per-species ecological networks. *Methods Ecol. Evol.* 4:1–8

Williams RJ, Martinez ND. 2000. Simple rules yield complex foodwebs. *Nature* 404:180–83

Supplemental Material: Annu. Rev. Ecol. Evol. Syst. 2017. 48:559–84
https://doi.org/10.1146/annurev-ecolsys-110316-022928
Identifying Causes of Patterns in Ecological Networks: Opportunities and Limitations
Dormann, Fründ, and Schaefer

Opportunities and limitations for identifying the underlying causes of patterns in ecological networks

Carsten F. Dormann, Jochen Fründ, and H. Martin Schaefer

Annual Review in Ecology, Evolution, and Systematics 2017

July 12, 2017

A APPENDIX

A.1 Information in interaction networks

In many cases, analyses of interaction networks focus solely on the interaction matrix $\mathbf{A}$ (with elements A_{ij}), describing patterns through aggregated statistics (such as those defined by Bersier et al. 2002). Before we attempt to link any pattern back to a causal process, we shall briefly look at the layers of information offered by an interaction matrix.

The most basic information, of first order, is the number of species in each group, n_l (number of species in the lower level, e.g. plants, here defined to represent rows of the matrix) and n_h (higher level, e.g. herbivores, in columns). This are simply the dimensions of $\mathbf{A}$. From this we can compute the size of the network (i.e. the number of possible links: $n_l n_h$) and the asymmetry of the network $(\frac{n_h - n_l}{n_l + n_h})$. A value larger than 1 indicates more species in the higher level (more columns than rows). Web asymmetry merely describes how relatively more species are in the one than in the other group, but that already may suffice to fully predict some more sophisticated patterns (Blüthgen 2010).

One level up, or second order, are information provided by the *marginal totals*, i.e. the number of interactions observed for each species (see also Cazelles et al. 2015, who use the same concept and language). These marginal totals are two vectors, one for each group, each summing to the total number of interactions in the matrix, N. One may quibble whether N itself is the next level of information, but here we regard N as a value derived from marginal totals. We denote the vector of marginal totals for the lower level as $A_{i\bullet}$, with the dot indicating the indicator that is summed over (i.e. $A_{i\bullet} = \sum_{j=1}^{n_h} A_{ij}$, and equivalently $A_{\bullet j} = \sum_{i=1}^{n_l} A_{ij}$). Although often interpreted as describing the abundance of each species, marginal totals are really only the number of observed interactions per species, even it is was the same individual being recorded several times. Thus, the interpretation of marginal totals depends on the way data were sampled and on how species behave as much as on their abundance. Later on, we use species abundances to illustrate the role of marginal totals for network patterns, but in reality the exact values of marginal totals have different causes. When $\mathbf{A}$ contains only 0s and 1s, i.e. is binary or qualitative, the meaning of marginal totals has a specific meaning (and name): it represents a species' *degree*, i.e. the number of species it interacts with in the observed network.

Finally, we have the highest level of information, or third order, consisting of all elements of the interaction matrix itself, A_{ij}. Here each element has a specific value (often 0), and position in the matrix. All lower-level information can be computed from this third-order information. It is here that we actually see, for the first time, the network itself. First- and second-order information describe the network from the outside, but at this third level, the network matrix itself is the datum. One of the most simple network-level pieces of information is the proportion of observed links, i.e. $C = \left(\sum_i \sum_j A_{ij} I_{>0}\right) / (n_i n_j)$, where $I_{>0}$ is an indicator function taking the value 1, if $A_{ij} > 0$ and 0 otherwise. This measure is called *connectance.*

A.2 Specialisation and Abundance Effects on Networks

It is moot to explore the ecological underpinning of the many existing network descriptors, metrics and indices, particularly since some of them were taken from other fields and imbibed with ecological meaning in an ad-hoc fashion. The null model approach discussed above, which maintains marginal totals, allows us to formulate expectations for patterns emerging in the absence of specialisation. In other words, differences between the observed pattern and those of a constant-marginal-totals null model are *entirely* due to specialisation (see next paragraph for a simulation example). Similarly, we can keep specialisation constant and investigate effects of changing abundances (see the next but one paragraph). Interpreting, for example, the observed decreasing number of links per species (or species' degree) as a measure of specialisation at the network level would be misleading: in all networks, all species are perfectly generalised.

It's the Specialisation, Stupid! Effect of changing specialisation on network indices

We try to explore how different processes affect the realised interaction preferences (as captured by **A**), and how we can use additional assumptions (e.g. through null models) to trace a network pattern to its ultimate specialisation mechanism. As in illustration, **Figure 1** shows how some indices that are not immediately interpreted as specialisation indices respond to increasing specialisation uniformly across all species. Thus, nestedness, robustness to extinctions and asymmetry of interactions are also affected by the overall level of specialisation, even if their main interpretation focusses on the *balance* of specialisation, rather than specialisation itself.

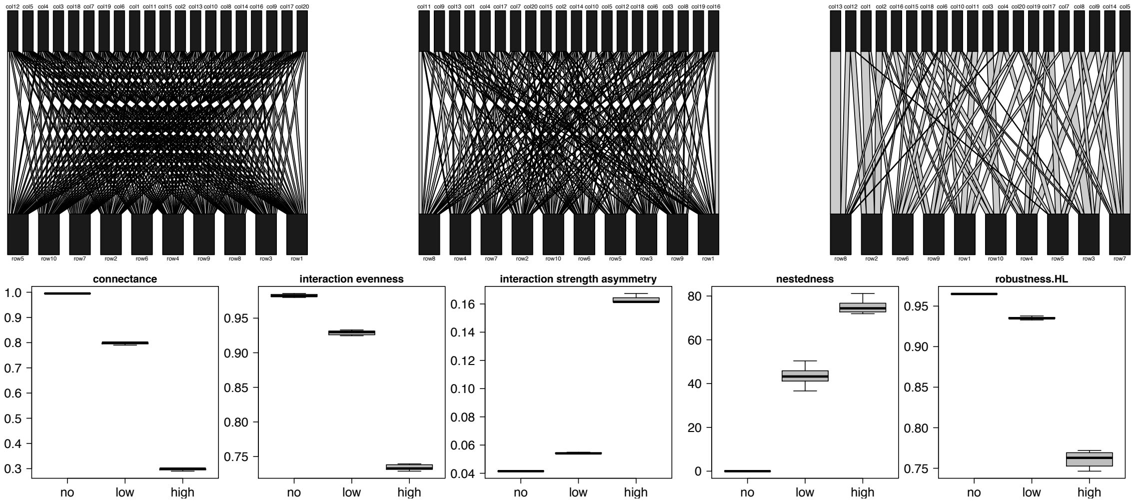


Figure 1: Effect of changing specialisation at the network level (keeping marginal totals constant and identical across species ot the same level). Although all species are equally specialised, network indices of interaction evenness or sensitivity to extinctions of lower-level species show strong responses.

It's the Abundance, Stupid! Effect of changing abundances on network indices

Next, we simulate the effect of changing the abundance distribution of the higher trophic level to illustrate that network matrix and derived indices may provide misleading information, naively interpreted. Holding everything else constant, we simulate networks with increasing skewness in how many individuals a species has. While the network graphs may not look very different, some network indices may respond strongly (**Figure 2**). Interpreting, for example, the decreasing number of links per species (or species' degree) as a measure of specialisation at the network level would be misleading: in all networks, all species are perfectly generalised.

A.3 Methods for Box Marginal Totals

Some more details for Simulations underlying a), b) and c) in **Box Marginal Totals**:

- Simulations are based on code from (Fründ et al. 2016), generating interaction probability matrices from log-normal abundances and a quantitative niche (trait-matching) model, and sampling from these matrices (with the network-based method)
- The quantitative niche model generates a preference matrix (standardized to sum to 1 per bee species: consumers selecting among resources), which is then multiplied with a matrix based on relative abundances (cross-product): this the overall interaction probability matrix, from which observed events are then sampled (50 obs in a and b, 1000 in c)

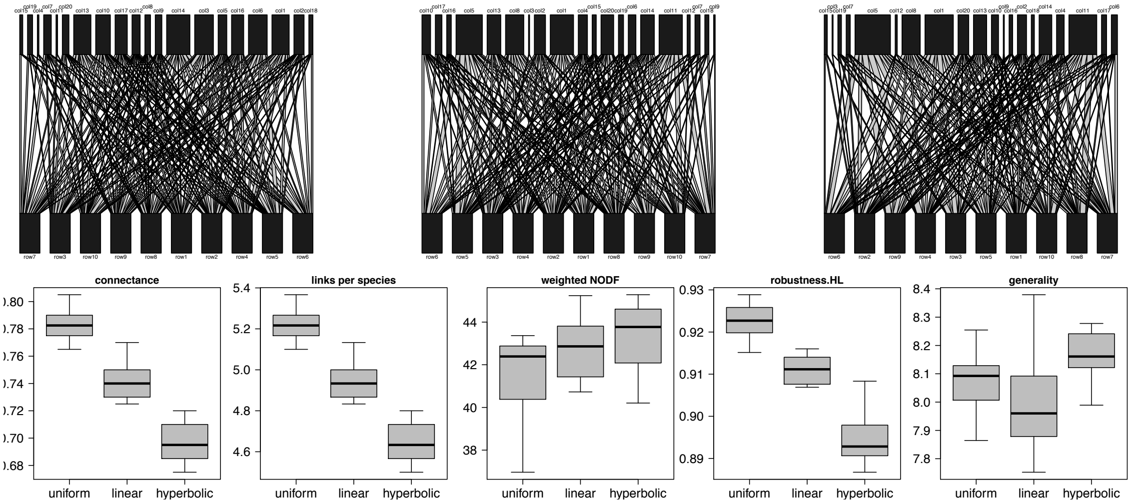


Figure 2: Effect of changing the abundance distribution of the higher level from uniform over a linear to a hyperbolic decrease (top row) on some network indices (10 replicate runs, 400 interactions, constant lower level, perfectly un-selective species). Marginals are drawn from a β-distribution with parameters $a = 1$ and $b = 1, 2, 8$, for the uniform, linear and hyperbolic case, respectively. The effect can best be seen in the box widths of the higher trophic level.

- Preference matrices are identical in b and c (and based on a mean specialisation parameter s=20, with among-bee-species variation of sd=10 added in difference to the original paper)

References of appendix

Bersier LF, Banašek-Richter C, Cattin MF. 2002. Quantitative descriptors of food-web matrices. *Ecology* 83:2394–2407

Blüthgen N. 2010. Why network analysis is often disconnected from community ecology: A critique and an ecologist's guide. *Basic and Applied Ecology* 11:185–195

Cazelles K, Araújo MB, Mouquet N, Gravel D. 2015. A theory for species co-occurrence in interaction networks. *Theoretical Ecology* 9:39–48

Fründ J, McCann KS, Williams NM. 2016. Sampling bias is a challenge for quantifying specialization and network structure: Lessons from a quantitative niche model. *Oikos* 125:502–13