

INVITED VIEWS IN BASIC AND APPLIED ECOLOGY

**Why network analysis is often disconnected from community ecology:
A critique and an ecologist's guide**

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Received 19 September 2009; accepted 19 January 2010



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Abstract

Network analyses of mutualistic or antagonistic interactions between species are very popular, but their biological interpretations are often unclear and incautious. Here I propose to distinguish two possible implications of network patterns in conjunction with solutions to avoid misinterpretations. Interpretations can be either

- (1) *niche-based*, describing specialisation, trait (mis-)matching between species, niche breadth and niche overlap and their relationship to interspecific competition and species coexistence, or
- (2) *impact-based*, focusing on frequencies of interactions between species such as predation or infection rates and mutualistic services, aiming to quantify each species' relative contribution to an ecological effect.

For niche-based implications, it is crucial to acknowledge the sampling limitations of a network and thus control for the number of observations of each species. This is particularly important for those kinds of networks that summarise observed interactions in communities (e.g. bipartite host–parasitoid or plant–animal networks), rather than compile information from different sources or experiments (as in many food webs). Variation in total observation frequencies may alone explain network patterns that have often been interpreted as ‘specialisation asymmetries’ (nestedness, dependence asymmetries). I show analytically that ‘dependence asymmetries’ between two species (or two guilds) only reflect variation in their total observation frequencies. To depict true asymmetries in niche breadth, independent data are required for both species.

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Moreover, simulated co-extinction scenarios assume that each species ‘depends’ on its associated partners in the network (again niche-based), but species that appear most endangered are simply those with one or very few observations and are not necessarily specialised. Distinguishing niche-based and impact-based interpretations may help to bridge terminological and conceptual gaps between network pattern analyses and traditional community ecology.

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Zusammenfassung

Mutualistische oder antagonistische Beziehungen zwischen Arten einer Gemeinschaft werden derzeit häufig mit Hilfe von Netzwerkanalysen beschrieben. Da die biologische Deutung solcher Analysen oft missverständlich ist, wird in diesem Artikel vorgeschlagen, zwei Interpretationsarten zu unterscheiden:

- (1) *Ökologische Nische*, z.B. Spezialisierung, Nischenbreite und Überlappung, sowie Kompatibilität von Merkmalen zwischen Arten.
- (2) *Interaktionseffekte*, die von der relativen Häufigkeit der Wechselwirkungen abhängig sind, z.B. Prädations- und Infektionsraten oder mutualistische Funktionen.

Bei nischenbezogenen Deutungen von Netzwerken, die auf beobachteten Interaktionen basieren, muss jedoch berücksichtigt werden, dass die Gesamtzahl der Beobachtungen pro Art limitiert ist und sich zwischen Arten stark unterscheidet. Allein diese Variation kann viele Netzwerkmodelle erklären, beispielsweise “Nestedness”, was oft als asymmetrische Spezialisierung missverstanden wurde. Hier wird analytisch bewiesen, dass eine mutmaßliche “Spezialisierungs-Asymmetrie” zwischen zwei Arten allein auf deren unterschiedliche Beobachtungshäufigkeit zurückgeführt werden kann. Unabhängig erhobene Daten für beide Arten sind notwendig, um diesen Trugschluss zu vermeiden.

Das Aussterben von Arten durch Verlust des Assoziationspartners (Koextinktion) wurde in mehreren publizierten Studien modelliert. Solche Simulationen basieren auf der Annahme, dass jede Art von seinen beobachteten Assoziationspartnern abhängig ist (nischenbasierte Deutung). Hier kann jedoch gezeigt werden, dass vor allem solche Arten scheinbar gefährdet sind, die nur ein- oder wenige Male beobachtet wurden, also nicht notwendigerweise Spezialisten darstellen. Die explizite Unterscheidung zwischen nischen- und effektbasierter Interpretation könnte demnach eine hilfreiche konzeptionelle Brücke darstellen, um Netzwerkanalysen und klassische Gemeinschaftsökologie zusammenzuführen.

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Keywords: Ecological networks; Ecological niche; Nestedness; Mutualism; Sampling effects; Specialisation asymmetry; Species extinctions; Parasitism










Introduction

Analyses of ecological networks are highly fashionable, and have recently stimulated a revival of ‘descriptive’ observations of interactions in the context of natural communities. This may provide valuable insights that cannot be achieved when species are studied in isolation. In contrast to food webs, bipartite ecological networks comprise mutualistic or antagonistic interactions between two defined parties, e.g. plant and animal communities. Since the seminal work by Jordano (1987) and subsequent work (particularly Bascompte, Jordano, Melian, & Olesen, 2003; Olesen & Jordano, 2002), a large number of studies characterised the structure of bipartite networks (see reviews by Bascompte & Jordano, 2007; Ings et al., 2008; Vázquez, Blüthgen, Cagnolo, & Chacoff, 2009).

More generally, networks describe ‘nodes’ (or ‘vertices’), which are connected by ‘edges’ (or ‘links’, as it will be adopted for this paper) (Newman, 2003). Most ecological networks drawn so far comprise species as *nodes* and a particular kind of interaction between two species as *links*, e.g. feeding interactions, mutualistic associations or parasitism (Bascompte & Jordano, 2007). Network analysis is then typically concerned with describing the ‘degree distribution’ of the number of links (whether it reflects a scale-invariant power law function), small world properties or the density of links (‘connectance’). The distribution of the links is often described with regard to ‘nestedness’ (Box 1).

Do network tools and metrics help to understand community ecology? First, I will sketch some niche-based and impact-based questions raised in community ecology, before I highlight one general and two specific

Box 1. Ecological implications derived from network metrics.

					
		G	H	I	Σ
	A	8	3	1	12
	B	5	2	0	7
	C	2	0	0	2
	D	1	0	0	1
	E	1	0	0	1
	F	0	0	1	1
	Σ	17	5	2	24

A simple hypothetical example network comprises three plant and six flower visitor species and shows many typical features of real ecological networks such as the fact that several species are observed only once or few times. Cell entries (link weights) provide the interaction frequencies between two species, i.e. how many individual visitors were observed on a particular plant. Species are sorted by observation totals (Σ). For definitions of each metric and additional information, see [Bersier et al. \(2002\)](#), [Blüthgen et al. \(2006, 2008\)](#) and [Dormann et al. \(2009\)](#).

Descriptor of network topology**Ecological interpretation**

Connectance (C) is $C=9/18=0.5$, i.e. 9 of the 18 potential links are zeros.

Often interpreted as specialisation level of the network (high connectance=high generalisation), this metric is in fact a mixture of niche and sampling property. Note that most species are entered with very few observations, so that many zeros will be due to **limited sampling**. Sampling limitations usually increase in larger networks with more rarely observed species. Connectance only distinguishes whether links are present or absent (unweighted, binary links), hence information about interaction frequencies is lost.

Nestedness (N) is high: $N=69.7^\circ$.

Interaction strengths (b_{ij}) between species i and j ('dependencies') are **asymmetric**; b_{ij} gives the number of interactions between i and j as a proportion of the total observations for i , b_{ji} of the total for j , hence many $b_{ij} \neq b_{ji}$. The average interaction strength asymmetry is $AS_{ij} = 0.24$.

Both metrics are commonly interpreted as niche property: 'specialists interact with generalists' (asymmetric specialisation), e.g. suggesting that beetle species D is highly specialised and thus depends on flower species G ($b_{DG}=1/1=1.0$), but G not reciprocally on D ($b_{GD}=1/17=0.06$). However, note that most species such as D have only few total observations (here: 1) and thus inevitably few links with high 'dependence' values. Even if all species interacted randomly and were thus entirely unspecialised, the expected level of nestedness (unweighted links) and dependence asymmetries (weighted links) would be similar as in the example network. Rather than asymmetric specialisation (niche property), these metrics may simply reflect a **'frequency asymmetry'** (impact or sampling property). Before niche-based conclusions can be drawn, the limitation by observation totals needs to be carefully controlled.

The **degree distribution** follows a power law function. $P(k)=k^{-\gamma} (r^2=1.0)$

Some species have many links, while many species have few links. Except in highly specialised systems, the degree distribution is an inevitable consequence of the **distribution of total observations** per species (or the underlying species abundances), which is typically described by a log normal distribution. Like the indices above, it shows a mixture of niche and sampling properties.

Interaction diversity and evenness.

Some links are strong (i.e., high interaction frequencies), many others are weak (low frequencies), suggesting variation in **ecological impacts**. Low interaction evenness (E_2) depicts a high **variation in**

$$e^{H_2}=6.7$$

$$E_2=0.66$$

Complementary specialisation (H_2' and d_i').

$$H_2'=0.22$$

e.g.

$$d_A'=0.00$$

$$d_D'=0.00$$

$$d_F'=1.00$$

$$d_G'=0.12$$

$$d_I'=0.44$$

interaction frequencies between different species pairs. This may translate into relative contributions to ecological functions, particularly when the recorded interactions are representative for the community. The quantitative heterogeneity of links (E_2) reflects the ecological **connectivity** between the interacting parties. Given that links are weighted, E_2 may better reflect this connectivity than the connectance index using unweighted links. Moreover, the interaction diversity (e^{H_2}) may provide a measure of the **complexity** of the associations in the selected system. Comparisons of e^{H_2} across networks should consider whether they are based on comparable boundaries and decisions which species to include or exclude from analysis.

For the given number of observations per species, both indices (H_2' on the network-, d_i' on the species-level) describe the deviation from a completely neutral configuration of associations. Hence, these metrics remove the bias due to total observation frequencies on network patterns in order to describe a **niche property** that is independent from variation in observations between species. H_2' describes the **complementarity** (or **exclusiveness**) of interactions: when species are specialised on different association partners (high niche differentiation), d_i' of these species and consequently H_2' of the entire network increases. For the network shown above, H_2' is low and not significantly different from neutrality ($p=0.46$). Overall, species in this network are relatively conform, suggesting a high level of **niche overlap** or redundancy of interactions for the given limitation of observations.

H_2' is closely related to the weighted mean d_i' across all species (with each species weighted by its observation totals). For each species, d_i' is large for species that are found on otherwise rarely visited associates ($d_F'=1$ for species F) and small if predicted by neutrality (species D: $d_D'=0$). In contrast, species D and F are assigned a 'dependence' of $b_{DG}=b_{FI}=1.0$ (see above) irrespective of their particular association being likely or unlikely. Hence, d_i' represents an indicator of the exclusiveness of a species' niche that may be used to predict its **fragility** to co-extinction.

When a relatively rarely observed species (e.g. D) is truly specialised on a commonly visited partner, such asymmetric specialisations may go undetected in d_i' and H_2' , being indistinguishable from neutrality.

pitfalls in network interpretation, followed by suggestions how to overcome these problems.

Some basic questions in ecology

Among the most important topics tackled by community ecologists is the interplay between interspecific competition and the ecological niche (Begon, Townsend, & Harper, 2006). Competition is commonly linked to niche breadth (specialisation versus generalisation) and niche partitioning, and in cases of niche overlap, competition may drive shifts from fundamental to realised

niches. A narrow fundamental niche may also suggest a higher vulnerability of a species to disturbance, e.g. specialised consumers may suffer from declines of their food sources (Kleijn & Raemakers, 2008). Multiple other research areas in community ecology exist, but many can be boiled down to competition and niche. For instance, to reveal whether biodiversity is important for maintaining ecosystem functioning, knowledge about (functional) niche complementarity is crucial (Rosenfeld, 2002). If each species fulfils only a specialised function (narrow niche), the coexistence of several species with complementary functions is required to provide the full breadth of functions in a community. In turn, the insurance hypothesis assumes that different species are functionally

redundant (Hooper et al., 2005). Moreover, for a mechanistic and evolutionary understanding of interactions in communities, a closer examination of species or individual traits plays an important role. Such traits include adaptations such as attractive signals to mutualists or defences against antagonists.

Apart from niche-based questions, the ecological impact (or interaction strength) among species within a community and ecosystem is a typical focus of ecological studies (Wootton & Emmerson, 2005) including food web analyses (Berlow et al., 2004). Ecological impacts involve predation and parasitism rates, various kinds of mutualistic services or facilitation effects among many other kinds of multispecies interactions. These studies usually focus on the magnitude of effects, e.g. the extent of herbivory on plants, the contribution of different pollinators to reproduction, or mortality risks due to predation and parasitism. For assessing relative impacts of different species on a target organism, their relative interaction frequencies are often crucial (Vázquez, Morris, & Jordano, 2005) besides variation in species-specific or per-capita effect sizes. Although niche and impact can be related, the interpretation of ecological data benefits from a clear distinction between them, as we shall see.

Pitfalls in ecological interpretations of network patterns

Network patterns are often implicitly assumed to represent unbiased ecological niche properties, e.g. when drawing conclusions about specialisation or dependencies on certain association partners. However, when interactions are recorded in natural communities, only a small subset of the realised interactions is usually observed. This suggests that while some ‘zero’ entries in the network may truly mirror absent links, many ‘zeros’ rather reflect limited observations. The precision differs between species within a network and between networks. Therefore, comparisons of niche properties between different species should account for the fact that many, if not most of the species in a community are only rarely observed and thus provide only limited information compared to the common ones. In biodiversity studies, a meaningful comparison between habitat A and B calls for an appropriate control for the total number of observations (individuals) in each habitat (see Gotelli & Colwell, 2001) – in network studies, an interpretation that species A has a broader spectrum of associated partners than species B is often proposed without such control. Conclusions from network studies often ignore that the number of links, the magnitude of ‘interaction strengths’ and other network metrics strictly depend on the number of observations per species (Box 1). This represents a strong bias for assigning niche properties,

although not necessarily for impact-based interpretations to which I will come back in the final section.

The skewness in the number of observations per species (often reflecting an underlying log-normal abundance distribution), combined with a limited overall sampling intensity, may alone explain a high level of nestedness and ‘dependence’ asymmetries, power-law degree distributions and the variation in connectance and other commonly applied metrics (Blüthgen, Fründ, Vázquez, & Menzel, 2008; Dormann, Fründ, Blüthgen, & Gruber, 2009). The problem is particularly apparent in metrics that only account for the presence or absence of unweighted links (Banašek-Richter, Cattin, & Bersier, 2004; Dormann et al., 2009). For instance, when the connectance of two networks is compared, but one of them has been sampled less intensively than the other, it should not be surprising that they differ in this metric (Blüthgen et al., 2008; Goldwasser & Roughgarden, 1997).

A number of nearly universal trends were found in network analyses. For instance, when species with few ‘links’ (low ‘species degree’) are translated as ‘specialists’,

- (1) rare or rarely observed species appear more ‘specialised’ (Vázquez & Aizen, 2004),
- (2) larger, more species-rich interaction networks (Olesen & Jordano, 2002) or food webs (Rejmánek & Starý, 1979) have a lower connectance,
- (3) more ‘specialised’ species appear to preferentially associate with ‘generalised’ partners (Bascompte et al., 2003), and
- (4) ‘specialists’ appear to be more vulnerable to simulated losses of their associated hosts or partners (Dunne, Williams, & Martinez, 2002; Memmott, Waser, & Price, 2004).

However, all these trends may largely or even solely reflect a sampling bias for drawing conclusions about niche breadth: for rarely observed species, only few links *can* be recorded – an inevitable consequence of limited information. An analysis of 51 mutualistic networks that controlled for the number of observations of each species found contrasting results to the above ‘rules’: (1) the degree of specialisation of a species is independent of its frequency, and (2) the seemingly higher specialisation in larger networks disappears (Blüthgen, Menzel, Hovestadt, Fiala, & Blüthgen, 2007). For the other two conclusions (3–4), I will examine the pitfalls of observation limitation in more detail in the following two paragraphs.

Do specialisation asymmetries exist and promote community stability?

Several studies on mutualistic networks have claimed a high prevalence of specialisation asymmetries (e.g. Bascompte et al., 2003; Bascompte, Jordano, & Olesen, 2006; Guimarães, Rico-Gray, dos Reis, & Thompson, 2006;

Vázquez & Aizen, 2004) which were then also reported from non-mutualistic networks (e.g. Burns, 2007). Specialisation asymmetries have been proposed to generate a more stable association between mutualistic communities (Bascompte et al., 2006; Bastolla et al., 2009). It has been argued that for a specialised species A, it may be beneficial to specialise on a partner B that is a generalised mutualist (*asymmetry*). If instead B would be reciprocally specialised on A (*symmetry*), both may be more vulnerable to co-extinction after one of the partners becomes less reliable, e.g. due to a declining population (Ashworth, Aguilar, Galetto, & Aizen, 2004). However, it can also be argued that true specialisation asymmetries may lead to higher interspecific competition when the associations represent limited resources or services. On a generalised resource B, a specialised consumer A may then experience stronger

interspecific competition with other consumers than on a resource with a narrow consumer spectrum. Competition may be avoided by interacting with more exclusive partners (i.e. symmetric or reciprocal specialisation), since niche partitioning should decrease interspecific competition. Interestingly, recent findings of network modelling challenge this view (Bastolla et al., 2009), showing a decreased interspecific competition for the scenario with highest niche overlap (nested or fully connected networks). However, these authors did not incorporate the dynamics of competition for mutualism in their model, thus conflicting with niche theory where mutualistic benefits are viewed as a limited resource.

The question of whether specialisation is symmetric or asymmetric may hold important insights for ecology and conservation, but also for understanding co-evolutionary

Box 2. Proof that interaction strength asymmetries reflect the ratio of observation totals.

Let a_{ij} represent the observed interaction frequency between animal species i and plant species j . The total observation frequency of the animal species is referred as $A_i = \sum_j a_{ij}$, the total number of observations on the plant species $A_j = \sum_i a_{ij}$, with I and J being the total number of animals and plants, respectively. The interaction strength (Vázquez et al., 2007) or ‘dependence’ (Bascompte et al. 2006) of animal i on plant j can then be defined as

$$b_{ij} = \frac{a_{ij}}{A_i}.$$

In turn, the interaction strength j confers on i is defined as

$$b_{ji} = \frac{a_{ij}}{A_j}.$$

In cases where $b_{ij} \approx b_{ji}$, one would regard interaction strengths as being symmetric or reciprocal, otherwise they are termed asymmetric. Bascompte et al. (2006) defined their ‘dependence asymmetry’ as

$$AS_{ij} = \frac{|b_{ij} - b_{ji}|}{\max(b_{ij}, b_{ji})} \quad \text{for all realised links } (a_{ij} > 0).$$

To maintain information on the direction of the asymmetry, this approach can be modified as

$$AS'_{ij} = \frac{b_{ij} - b_{ji}}{b_{ij} + b_{ji}} \quad \text{for all realised links } (a_{ij} > 0).$$

Accordingly, AS'_{ij} varies between -1 and $+1$.

However, resetting this equation shows that AS'_{ij} is completely independent of the interactions between a species pair and solely depends on the ratio of their observation frequency totals:

$$AS'_{ij} = \frac{b_{ij} - b_{ji}}{b_{ij} + b_{ji}} = \frac{\frac{a_{ij}}{A_i} - \frac{a_{ij}}{A_j}}{\frac{a_{ij}}{A_i} + \frac{a_{ij}}{A_j}} = \frac{a_{ij} \left(\frac{1}{A_i} - \frac{1}{A_j} \right)}{a_{ij} \left(\frac{1}{A_i} + \frac{1}{A_j} \right)} = \frac{\left(\frac{A_j - A_i}{A_i \cdot A_j} \right)}{\left(\frac{A_j + A_i}{A_i \cdot A_j} \right)} = \frac{A_j - A_i}{A_i + A_j}.$$

This also holds for the original AS_{ij} which becomes

$$AS_{ij} = \frac{|A_j - A_i|}{\max(A_j, A_i)}.$$

For each species, the mean interaction strength of each species i across all J potential links is simply

$$\overline{b_{ij}} = \frac{1}{J} \cdot \sum_{j=1}^J b_{ij} = \frac{1}{J}, \quad \text{since} \quad \sum_{j=1}^J b_{ij} = 1.$$

For each species j across all I links, this becomes

$$\overline{b_{ji}} = \frac{1}{I} \cdot \sum_{i=1}^I b_{ji} = \frac{1}{I}, \quad \text{since} \quad \sum_{i=1}^I b_{ji} = 1.$$

Consequently, the mean AS'_{ij} (analogously AS_{ij}) across all interactions is approximately determined by the balance between the species richness of animals (I) and plants (J) as

$$AS'_{ij} \approx \frac{\overline{b_{ij}} - \overline{b_{ji}}}{\overline{b_{ij}} + \overline{b_{ji}}} = \frac{I - J}{I + J},$$

which corresponds to simulations of randomised networks (Blüthgen et al. 2007). This argument shows that external network parameters (observation totals, species richness) directly determine the interaction strength (or 'dependence') asymmetries, irrespective whether the two species interact frequently or not. Rather than specialisation asymmetries, AS'_{ij} describes asymmetries of species total frequencies.

trajectories (Thompson, 2005). Unfortunately, a single count of the interactions between two species from a single network cannot be used to estimate specialisation of *both* species independently. In fact, the 'dependence' asymmetry between species A and B, discussed as stabilizing property of mutualism (Bascompte et al., 2006), simply reflects the ratio of total observations of A versus B – a mathematical consequence of its definition (see Box 2 for proof). When species A is observed five times, species B ten times, their dependence asymmetry (AS'_{ij}) is 0.33, no matter how often they interact. Consequently, the average 'dependence' asymmetry for the whole network is simply given by the ratio of species numbers (Box 2). In other words, when there are three times as many pollinator species as plant species, the average pollinator 'dependence' on plants is twice as high as that of plants on pollinators, resulting in an average asymmetry of 0.5. This is acceptable and may be desired for impact-based hypotheses where relative frequencies are part of the interpretation (e.g. Vázquez, Blüthgen et al., 2009; Vázquez, Chacoff, & Cagnolo, 2009; Vázquez et al., 2007). Hence, the pattern describes an interaction frequency asymmetry of associated partners, or abundance asymmetry when based on abundance data that are independent of the network (Vázquez et al., 2007). However, the constraints by observation frequency are an artefact if one intends to assign specialisation and thus 'dependence'. Most networks include numerous species with a single or very few observations, and the interactions of these species account for the majority of high asymmetries reported by Bascompte et al. (2006). Note that completely randomised interactions even yield the *highest* degree of interaction strength asymmetries

(Blüthgen et al., 2008), although randomised associations are, by definition, the opposite of specialisation.

When the effect of variation in observation totals is removed (Blüthgen, Menzel, & Blüthgen, 2006), specialisation in most networks indeed appears more symmetric than expected by chance (Blüthgen et al., 2007, 2008). This does not imply that specialisation asymmetries do not exist. The null model of randomised interactions may contain true specialisation asymmetries, but these simply cannot be distinguished from frequency asymmetries when a single network is analysed. As a solution to disentangle specialisation and frequency asymmetry, one could use external information on specialisation for one of the two guilds (e.g. pollinators) from data sources other than the network itself, or from experimental evidence. Alternatively, one could perform a comparison across different networks with varying partner availabilities. For instance, when the abundance of resource species is changed between different experimental treatments, a comparison of the consumers' preferences may help to clarify whether they are more likely to utilise the most common resource species or the most generalised ones.

Can we predict co-extinctions based on network patterns?

Specialised consumers depend on their specific resources and are thus more vulnerable to population declines or even local extinction if such resources become less available or disappear entirely. A higher level of generalisation in a

community may thus function as a buffer against such co-extinctions and represent a stabilising mechanism. However, when specialisation is inferred from a network as the number of ‘links’, there are two substantial errors that inflate the impression of instability:

- (1) Rarely observed species have fewer links and thus seem more vulnerable irrespective of their real level of specialisation.
- (2) Assuming that a ‘zero’ link in a network is ‘forbidden’ and cannot be realised may underestimate the dynamics of interactions in a community.

The first problem represents a bias in the estimation of specialisation and can be circumvented by quantitative metrics with appropriate corrections for the number of observations (see ‘proposed guide’ below). Solving the second problem may require comparing the behaviour of the same species across different networks to examine the dynamics of interactions under variable conditions.

Several studies simulated extinction scenarios based on networks (Dunne et al., 2002; Memmott et al., 2004).

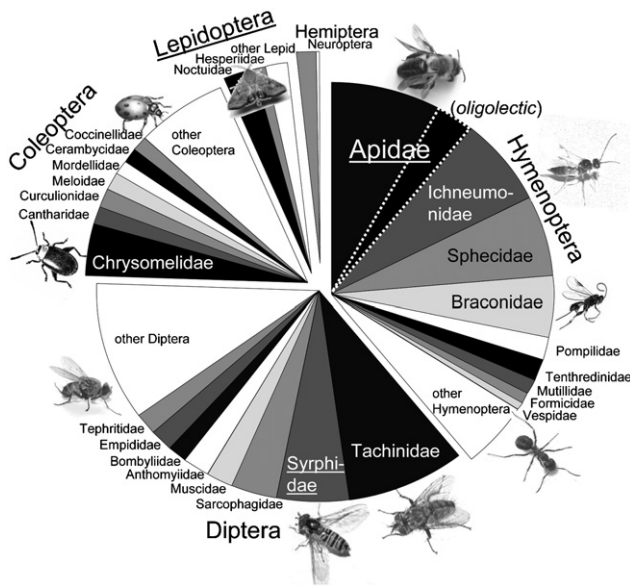


Fig. 1. So-called ‘specialised’ flower visitors assumed to depend on a single flowering plant species in co-extinction simulations. The diagram shows proportions of different insect taxa among the 382 identified visitors with a single link in Robertson’s (1928) dataset from Illinois, USA. Numbers of species are based on a database compiled by John Hilty, who incorporated taxonomic updates, but also provided additional biological information about the interactions recorded by Robertson and other ecologists (see <http://www.flowervisitors.info/>). Note that many of these taxa are parasitoids, predators and other guilds that may represent facultative consumers of floral resources and clearly do not ‘depend’ on single flower species. Three underlined taxa (bees, hoverflies and butterflies) are known to include some flower specialists (e.g. ‘oligolectic’ bees), but represent relatively small proportions.

Usually, species of one party (e.g. plants) are removed from a dataset to examine the putative impact to the other party (e.g. pollinators). This nicely illustrates the stability of networks, if the network pattern represents the niche breadth of each species and their constraints, i.e. ‘zeros’ mirror ‘forbidden’ links rather than insufficient sampling. However, this is clearly not the case for the datasets currently used. I will outline this problem for a network used to predict the consequences of climate change (Memmott, Craze, Waser, & Price, 2007), although it is a pervasive feature of such analyses in general. The simulation was based on an empirical binary flower-visitor ‘network’ recorded by Robertson (1928) in North America. The authors predicted that most animal species that may go extinct – due to a simulated phenological mismatch with flowers – are those recorded only on a single plant (link). A closer look at the taxonomic affinities of the single-link visitor species in Robertson’s data (Fig. 1) suggests that many of them are occasional flower visitors, which may only visit flowers opportunistically, but do not depend on a single flower species. Oligolectic bees represent one of the few taxa that are known to depend on one or few closely related plants, but they represent only ten (2.6%) of the single-link visitor species (Fig. 1). Moreover, only 17% of the total 1420 visitor species were recorded more than 5 times by Robertson. This sampling limitation is particularly severe for the single-link visitors, of which 95% had been observed only 1–5 times. As a result, the percentage of visitors that would go extinct might be overestimated in the simulations.

Analyses based on binary data (number of links) may not only overestimate specialisation, but also fail to distinguish the proportional distribution of different species. When an insect visits a single flower species most of the time, but occasionally other flowers, the number of links alone would underestimate its true ‘specialisation’. Binary network metrics may thus be inadequate to estimate the dependence of consumers on specific resources. Quantitative approaches use weighted links, e.g. by counting interaction frequencies. However, even the quantitative ‘dependence’ metric (Bascompte et al., 2006; Jordano, 1987) becomes inevitably 1.0 (maximum dependence) for those species with a single record, thus suffering from the same bias as the number of links when interpreted as niche breadth (Box 1).

A proposed guide to ecologists

When network patterns are translated into niche properties such as specialisation, trait matching, dependencies or secondary extinction risks, we need to test whether differences between species or between networks do not merely reflect differences in observation frequencies. Observation limitation is ubiquitous in community-wide ecological datasets and represents a familiar problem in biodiversity studies, e.g. when different habitats are compared (Gotelli &

Colwell, 2001). There are several non-exclusive ways to deal with this bias: (1) Rarefaction analysis holds appropriate tools to examine the effects of observation frequency. This can be performed on the network level to reveal overall trends (Banašek-Richter et al., 2004). Rarefaction on the species-level (Herrera, 2005) is needed to allow a fair comparison of species' niche breadths. (2) Null models can be applied based on the given number of observations per species or their abundance (Blüthgen et al., 2007; Dormann et al., 2009; Vázquez & Aizen, 2004; Vázquez, Chacoff et al., 2009; Vázquez et al., 2007). Alternative solutions, although only partly reducing the bias, may include (3) to intensify the sampling effort (Martinez, Hawkins, Dawah, & Feifarrek, 1999), (4) to exclude rarely observed species from the analysis, or (5) to use additional information sources as evidence which links may exist but have gone undetected in a network sample (e.g. Bosch, González, Rodrigo, & Navarro, 2009).

Quantitative network metrics that use interaction frequencies as link weight are more robust against variation in sampling effort and often more meaningful than metrics that only assign links as present or absent (Banašek-Richter et al., 2004; Bersier, Banasek-Richter, & Cattin, 2002; Blüthgen et al., 2008; Kay & Schemske, 2004; Vázquez, Chacoff et al., 2009). Focusing on the residual deviation of network patterns from a null model that accounts for observation frequencies alone, may help to explore niche-based specialisation (Blüthgen et al., 2007, 2008) and trait matching (Stang, Klinkhamer, Waser, Stang, & van der Meijden, 2009; Vázquez, Chacoff et al., 2009).

To describe niche properties of the network and of each species, only the information-theoretical metrics H_2' and d_i' (Box 1) are not systematically biased by the species' total observation frequencies. They can be used directly to compare different species within a network or make comparisons across networks despite variation in total frequencies. Their interpretation is arguably not as straightforward as e.g. counting the number of links, as they describe the degree of *complementary* specialisation (or exclusiveness of species interactions). This makes them partly insensitive to detect 'specialisation' on a niche that is shared with common species, because such a configuration would also be expected under neutrality (Box 1). Given that high complementarity or exclusiveness requires high specialisation, H_2' and d_i' can thus be viewed as a (conservative) measure of specialisation. Other measures of niche breadth and overlap are available (Krebs, 1999, see Blüthgen et al., 2006), and useful alternatives include quantifying the residuals from neutrality based on species abundances rather than interaction totals (Vázquez, Chacoff et al., 2009). However, species degree, nestedness and interaction strength or dependence are not independent from observation frequencies and should not be directly interpreted as niche properties (Box 1).

When impact-based interpretations are the scope of a study, e.g. describing variation in interaction frequencies

(e.g. Bersier et al., 2002; Tylianakis, Tscharnkte, & Lewis, 2007), a 'correction' for total number of observations may be inadequate. Relative abundances or interaction frequencies of species are often the most important part of their ecological effect, e.g. when the contribution of different pollinator species to the pollination success of a plant is examined (Vázquez et al., 2005). The heterogeneity of interaction frequencies among different species can then be described by quantitative interaction diversity metrics. Interaction diversity (such as e^{H_2}) and evenness (E_2) can be computed on the network level or for each species (termed 'generality' or 'vulnerability', Bersier et al., 2002). On the network level, e^{H_2} expresses a measure of the complexity of the interactions, E_2 the 'connectivity' between the two parties (Box 1). Comparisons between species or networks are most meaningful when the observed focal links are representative for the realised ones, and when the species' observation totals are not biased by the sampling protocol.

Finally, networks compiled from heterogenous areas or different seasons may contain numerous species pairs that cannot interact because of non-overlapping ranges, habitats and/or activity periods – resulting in erroneously high specialisation estimates. For instance, the observation catalogue compiled by Robertson (1928) covered a large area and contained many different natural and urban habitats and, hence, flowers that only occurred in habitats where some of the recorded pollinator species were absent and vice versa. Focusing on smaller units facilitates an ecological interpretation of a network, where the absence of a link may indicate a meaningful mismatch in species traits, which prevents its realisation (for example, the proboscis of a nectar feeding insect can be too short to access the nectar at the base of the flower tube; Stang et al., 2009), if it is not just due to limited sampling.

Network approaches hold useful tools to explore different ecological and evolutionary processes that may shape complex interaction patterns in local communities. However, this promising avenue requires a clear translation of network language to established concepts of community ecology, and an awareness of the pitfalls.

Acknowledgements

I am grateful to John Hilty (see legend of Fig. 1) for fruitful discussions on Robertson's data and their interpretability, and for making them available in his database. I further thank Diego Vázquez, Carsten Dormann, Martina Stang, Gita Benadi, Robert Junker, Florian Menzel and three anonymous reviewers for helpful comments on an earlier draft, Teja Tscharnkte for his kind invitation to submit this view, and Klaus Hövemeyer for improving its style. Our research is funded by the Deutsche Forschungsgemeinschaft, DFG (Biodiversity Exploratories, SFB 554 and BL 960/1-1).

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