

Chapter 9

The rise, and possible fall, of network ecology

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Abstract Ecology, much like any other discipline, has its fashions and fads, and each brings its own buzzwords and jargon. “Network ecology” is an example of such a fashion, which has for a few decades imprinted heavily on ecological publications. However, the topics of network ecology are of course much older, as are most of its methods. This invites the question whether network ecology is on a good path to providing different viewpoints and new insights. I here try to outline a somewhat opinionated view of why there is a high risk that this avenue of research may prove to be a cul-de-sac, for two reasons. On the one hand, the word “network” has become an empty buzzword void of specific meaning. On the other, there are six problems that I deem to be “deal breakers” in research on interaction networks: unless they all are resolved, this approach cannot make meaningful contributions. They are: (1) sampling bias; (2) ecological meaning of recorded interactions; (3) data aggregation over individuals; (4) lack of quantitative expectation; and (5) ecologically meaningless indices. Together they lead to the biggest problem (6) confusion in what it all means ecologically. Until these issues are being tackled by improved field and computational research, there seem to be little progress possible in our understanding of assemblages of interacting species under the header of “network ecology”.

9.1 Introduction

When many scientists work on a more or less well-defined topic, it is called a “field” of that discipline. In ecology, the prefix “network” has been used, in the same spirit as “landscape” or “animal” or “movement” ecology to define one such field. We can usefully define “network ecology” as a subfield of community ecology, which focusses, largely or exclusively, on *endogenous* processes, i.e. those among its members, rather than on the environment

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(such *exogenous* effects would still be covered in community ecology).¹ And similar to these other examples, it is worth questioning whether the focus of this subfield has contributed to our understanding of ecological topics more widely. Has “landscape ecology” led to myopia with respect to smaller-scale processes? Do principles of “animal ecology” not apply similarly to plants? Are there questions unique to “movement ecology”, or only methods? Or, to paraphrase Monty Python: “What has network ecology ever done for us?”

In the end, we study the relationship of organisms to their environment and to each other in order to understand their abundance and distribution (merging the definitions of Haeckel 1866, p. 286, and Andrewartha 1954). Any specific field is to some extent only a means to that end. If network ecology lets us see why a species is here or not, or why one species is common and another is not, why one species has a higher population growth rate or lower mortality than another, great. If, however, it only shows patterns in some indices that do not link back to understanding the ultimate ecological questions, then what’s the ecological point?

The question for network ecology is even more relevant, as most topics have already a home in ecology: community ecology, macroecology and food web ecology. (We shy away from questioning the validity of these fields here.) Who interacts with whom is the subject of community ecology, as founded by the seminal books on the topic in 1975 and 1986 (Cody and Diamond 1975; Diamond and Case 1986), but has been followed ever since (Gee and Giller 1991; Lawton 2000; Carson and Schnitzer 2011; McPeck 2017). These books feature loop analyses, interaction matrices, connectance and even nestedness before network ecology was a thing. It is only fair to ask, then, what defines network ecology and whether such a field is progressing the field more than community ecology has done in the last 40 or so years.

The majority of current studies investigate interactions between two guilds, such as pollinators and the flowers they visit, described by a two-mode or bipartite network.² However, these can be layered (multiple locations, times) or stacked (tripartite networks). When doing so, they become more like a very selective section of a food web, focussing on what is measurable by a predefined method, or possibly a specific ecological hypothesis involving only this subset of species. When such networks are arranged along gradients (say of altitude or aridity), the exogenous drivers may well dominate community assembly, and community ecology in the wider sense may offer a more comprehensive set of theories and tools (see references cited above).

On the next few pages I want to focus on some known problems in network ecology, which researchers in this field are happy to ignore. I selected those I consider “deal breakers”, i.e. so grave that without a solution no progress can be made. Indeed, I would argue that

¹ This definition is consistent with the way McCann and Gellner (2020) re-interpret “Theoretical Ecology”, as well as a non-representative poll among participants of a workshop on networks in 2022.

² I write this based on my experience as maintainer of the R-package bipartite (Dormann et al. 2008), which computes a range of network indices, alongside null models and some visualisation, for *bipartite* networks, and may hence have a biased view on the field. What started as a service to the network ecological community has turned into some fruitful and a much larger set of fruitless collaborations. Many questions I received were caused by misunderstanding what a network index may mean, or how it relates to a specific question. Others were naive, assuming that analysing networks invariably will yield interesting answers.

without solutions virtually all previous and current research is void and immaterial, as we have no way of knowing whether it is correct or not. As a theoretical physicist may quip, citing Wolfgang Pauli, network ecology may be “not even wrong”. I will start, however, with a reflection of why ecological networks are different to networks in other disciplines, and that this difference matters for the successful application of a network approach.

9.2 Which paths did network ecology open for community ecology?

Claims that network ecology has yielded new insights abound (e.g. Guimarães Jr et al. 2011; Fortin et al. 2012; Bascompte and Jordano 2014; Delmas et al. 2019), but are they correct? That is, are network ecological breakthroughs actually related largely to interactions within a community?

Outside ecology, “network theory” has been applied to power grids, transport connections, metabolic interactions and brain networks, aiming at identifying vulnerable or particularly important parts (e.g. Crucitti et al. 2004; Wang et al. 2018; Guimerà and Amaral 2005; Bullmore and Sporns 2009; Guimerà et al. 2005). In all these cases, the networks exist to achieve a specific goal: provide a steady supply of electricity, connect cities, affect a specific enzyme reaction, or excite neurons belonging to the same task, respectively. It is much less clear, what the “network” in a pollinator-flower network is, what is flowing between nodes, and what actually constitutes the network.

The situation of ecological interaction networks is more similar to the other large group of network studies: social networks. What is the function of the actor-movie network (Peltomäki and Alava 2006) or the supervisory board member-company network (Harris and Helfat 2007)? While we may be able to identify a central actor or CEO, extract power-laws of degrees, in which way does that represent a scientific advance over a classical ordination?

If there are electricity, carbon, consumables flowing in a network, then a shortest path, for example, is a useful information for optimising energy use. In the case of (bipartite) pollination networks, such flux is only between plants connected by the same individual pollinator; pollen isn’t deposited, then picked up by another pollinator to be carried over to the next flower and so forth. Similarly, screen time of an actor in one movie does not “flow” to another movie, just because the cast is similar. The analogy occasionally invoked by network ecologists to power grids and brain networks is not obvious, if it exists at all.

If a power grid node is a “hub” then that means many power lines enter and get re-distributed. Any fault in that hub affects in an obvious way lower-order power nodes. What, then, is a hub in a pollination network (Olesen et al. 2007)? Will the network fail in whatever it does when a hub-species is lost? No, it will not. A hub pollinator is simply so generalised that it visits flowers that otherwise are predominantly visited by specialists, thereby “connecting” the network graph, but no ecological functions. An attractive flower may well provide resources to many visitors, but that does not mean it “connects” them in any ecologically obvious way.³ The analogy of a network is simply meaningless. (That

³ If anything, it would suggest that pollinators may be competing for this resource, which would stretch the meaning of “connect” beyond recognisability.

is not to say that there aren't keystone or foundation species, but those are not the ones identified by this network approach.)

So, in the following, we audit a few subjectively selected claims of “network-ecological insight”, by (a) investigating what is specifically “networky” about that insight, and (b) whether that insight is actually ecological and not merely describing an abstract analogy without representation in ecology (such as the “hub species”). No representative or even comprehensive review is aimed for, but merely an illustration of the point that most “network” texts are full comprised by traditional ecological, non-network research, and/or do not demonstrate that an “endogenous processes only”-approach would approximate well community ecology.

9.2.1 Claim: Network motifs reveal something new

Losapio et al. (2021) stated that “The over-representation of network motifs is positively linked to species diversity globally” (p. 1). The motifs they investigate, in interactions in alpine plant communities, are competition and facilitation among sets of three species. That is, plants may all three compete with each other, some with some but facilitate others, or, at the other end of motifs, all facilitate each other. Since some configuration do not lead to coexistence (e.g. intransitive hierarchies), they find some motifs more often than others.

True to our definition of “network ecology”, the scope and approach of this paper is entirely on endogenous interactions. However, there is no detectable element in this paper that warrants or benefits from relabelling competitive interactions as “network analyses”. No attempt is being made to explain what is being shared in such a network, or what theoretical expectation would be based in a network-specific theory. Also, no demonstration is given that motifs yield a better description or access to an ecological process than traditional competition/facilitation perspectives.

My point: nothing is gained by using the term “network” in this paper – apart from access to a high-ranking journal.

9.2.2 Claim: Networks more useful for conservation than a focus on species

Harvey et al. (2017) claim that “a shift in focus from species to interaction networks is necessary to achieve pressing conservation management and restoration ecology goals of conserving biodiversity, ecosystem processes and ultimately landscape-scale delivery of ecosystem services” (p. 371). They do not provide quantitative evaluations of studies or experiments as evidence in this commentary piece, rather a narrative based on own previous studies and hand-picked anecdotes.

Most interesting to my point are the arguments they find for arguing that networks are useful. In my reading, all such arguments are based on using “network” as synonym for “analysis of interactions”. For example, a study they cite prominently notes that loss of hosts are driving local extirpation of butterflies; no network quantification or theory involved. Of course, the largest driver of species extirpation is loss of habitat, i.e. a non-network cause. A “network approach” would thus definitely be too narrow. Indeed, it seems strange to

argue that a focus on endogenous processes (the network approach) is *more* comprehensive than a traditional community approach, which does include exogenous processes.

All of their arguments may be valid, but replacing a narrow “species-centric” approach by one that ignores exogenous drivers (implied by a “network approach”) will get conservation biology from the fire into the frying pan.

9.2.3 Claim: Networks reveal community processes across spatial scales

Galiana et al. (2022) report that for interaction networks of various types several characteristics scale as power law with spatial scale, but the number of interactions per species does not.

While this pattern is intriguing, it does not use any network theory to explain it. Post hoc explanations resort to moving from unspecific network jargon into the vague quagmire of complexity, evolutionary adaptations and “factors beyond species richness and number of links” (p. 5).

I read this paper as a description of network topologies without linking them back to processes at population or community level *beyond* that of classical coexistence theory (Grover 1997; McPeck 2022). Also, in their interpretation the authors recourse to exogenous drivers, leaving the network focus that they claim to be behind all patterns observed.

9.2.4 Positive effects of a network focus?

It has been argued that networks make ecologists think of the wider context and system (e.g. Kennerley et al. 2022). If so, this may be more indicative of a too narrow focus in ecological research than of the usefulness of a network angle. Of such a narrowness I find hints only in conservation ecology, where conservation targets are defined (arguably rightly so) by societal preference (furry and feathery; or rarity, but not functional importance); of course here a wider context would be desirable, if legally difficult to implement. Indeed, my selective and prejudiced reading in particular of recent ecological publications with network spin leads me to believe that the term is largely a selling point, without any benefit to current ecological understanding.

One special but in my view well-justified truly network-ecological study is that of Bisanzio et al. (2010). They model the robustness of a network to transfer of pathogens among host species by visiting vectors (following up an idea in Pimm and Lawton 1980). Here, it is clear what flows (the pathogen’s spores), why a generalist visitor acts as a hub (as it connects different sets of host species), and why modular networks would reduce spread of the infection (because there it reduces pathogen flow from one subset to another). This is such a special case (a very generalist pathogen that can be transported by all vectors) that it cannot serve as a blueprint for network processes more generally.

With our minds thus critically tuned, let us move on to the core points of this contribution: deal breakers for network ecology.

9.3 Deal-breakers in network ecology

Deal-breaker 1: How we sample networks

The median network study today is of bipartite networks, focussing on a set of species in either guild: hummingbirds and the flowers they visit in selected patches (Tinoco et al. 2017); birds feeding on tree fruits (Dehling et al. 2016); or dung beetles burrowing seeds contained in faeces (Frank et al. 2018).

The problem here is that all these networks represent only **partial and biased samples** of the relevant ecological process. Also bees visit the hummingbird flowers; also mammals feed on tree fruits; and seeds also germinate without being buried by dung beetles first.

If, however, the network does not describe the process in its entirety or at least majority, then what can it tell us about the process? Arguably, if hummingbirds also feed on insects and rotting fruits, what relevance does the identity of the flowers visited has for their ecology? If stingless bees (*Meliponini*) visit and pollinate the hummingbird flowers, what is the relevance of the hummingbird-flower network to the plants? And so it goes for any and all published interaction networks.

The problem is that if networks are neither complete nor representative of the processes in the community, if they do not describe the most relevant functions for their members (growth, death, reproduction, birth), then what can such a network reveal about nature? Certainly it cannot be used to predict effects of climate change on its members (Sonne et al. 2022), as the interactions represented are not capturing what is relevant for the species concerned.

The standard answer is that networks tell us about the specialisation of its members. Except it does not, if the members do something “on the side” not recorded in the network. One hummingbird may be more specialised than another with respect to a flower available to both, so what? It is not until we have unveiled the consequence of such specialisation anecdotes that we can claim to have contributed a scientific insight. Any living organism is subject to evolutionary pressures (if you pardon such sloppy phrasing), and every organism has preferences in some and less in other facets of its life. What community ecology has been looking for are generalisable principles of what makes communities a recognisable entity, how interactions mould the stability and performance of the community; in which way does it help to know the degree of specialisation of a species in a *partially sampled* set of interactions?

A first step towards resolving this problem is to simulate complex communities and investigate theoretically the effect of partial and biased sampling for getting the presumed function right. A second step, in the field, would be to attempt to design the sampling in such a way that the majority of interactions relevant for that process are indeed covered. Knowing, e.g., the fate of almost all seeds of a tree is inconceivably difficult, but it would tell us whether the network interactions with frugivores are of any relevance.

Deal-breaker 2: What an interaction network contains

A food web describes who eats whom. An interaction network describes who interacts with whom. But **what is that interaction?** And what does binary and weighted information represent?

Several studies have argued and shown that binary networks, in which an interaction is present or not, have little chance of representing the actual specialisation of the participants (Blüthgen et al. 2006; Nielsen and Bascompte 2007; Dormann et al. 2009; Blüthgen 2010). The reasoning is simple: an observed link could mean a single instance or a great many interactions. A species with, say, 4 links could thus be a generalist or an extreme specialist, depending on how many interactions are actually hidden behind a single link (10, 10, 10, 10 vs. 36, 1, 1, 1). It thus seems clear that binary networks are not useful for addressing specialisation-related question, but specialisation is all that networks can provide beyond what standard community ecological procedures already report (species richness, abundances). Most new networks are quantitative, but the majority of recent network reviews still analysed binary networks (e.g. Neff et al., 2021, Galiana et al., 2022, Henriksen et al., 2022, Saravia et al., 2022; but see Luna et al., 2022 (itself criticised by Brimacombe et al., 2022), Sonne et al., 2022).

But even if the network matrix contains quantitative information, what do they represent? A flower visit may lead to pollination and to nectar/pollen consumption, representing a “Schrödinger interaction”, simultaneously positive and negative. Some studies show that indeed such a correlation between number of visits and pollen deposited exist in bee pollination networks (Alarcón 2010; King et al. 2013). The balance of negative and positive effects is particularly important in fruit-frugivore or dung-beetle networks (or in lizard pollination: Correcher et al. 2023), where consumption may destroy seeds, but also improve germination/establishment of those surviving. Typical studies compare gut-passaged seed germination to whole-fruit germination (de Carvalho-Ricardo et al. 2014; Fricke et al. 2019; Rogers et al. 2021), which ignores the effect of seed destruction or deposition at unsuitable sites (but see, e.g., Urrea-Galeano et al. 2019).

A different case are antagonistic systems, such as host-parasite/parasitoid networks. For parasites the problem is the same as for pollinators – the effect of a parasitic interaction on the host is typically unclear –, while for host-parasitoid systems the host must die if the parasitoid develops. Here a quantitative network is actually very informative, as it effectively samples the parasitism rate (Morris et al. 2004, 2014; Gripenberg et al. 2019). Combined with coupled population dynamical models, the network may show whether its structure affects community dynamics and species abundances in line with what network indices may suggest. While the data have been collected, I am not aware of any connection of host-parasitoid network data with population models. Hence the jury is still out, whether any index used to describe the network is meaningful for understanding the resulting species abundances.

The way forward could follow the lead of host-parasitoid studies by quantifying the actual demographic consequences of an interaction. Once such effects are quantified, they can be fed into interaction network models, based for example on coupled differential equations (Drossel et al. 2001; Bastolla et al. 2009; Benadi et al. 2012).

Deal-breaker 3: How we aggregate data

Sampling interactions typically does not allow differentiating between individuals (Quintero et al. 2022). Thus, the number of interactions between plant A and visitor B may reflect the behaviour of one pollinator or frugivore, or the attractiveness of a single flower out of

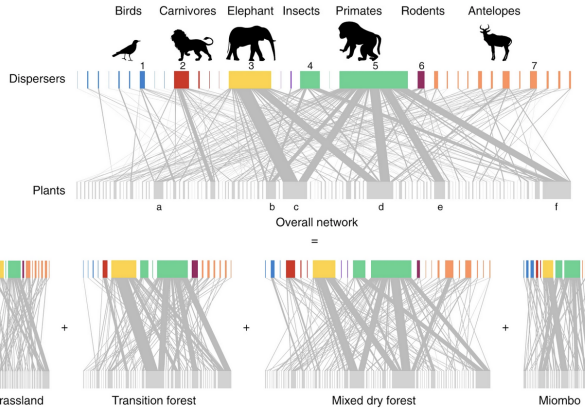


Fig. 9.1: Example of pooling across habitats. “Quantitative seed–dispersal network of the Gorongosa National Park, Mozambique. [...] The aggregated network was obtained by pooling all interactions across the four habitats, and summing their frequencies.” (Timóteo et al. 2018, p. 3). Nice graphs, but what do these lines actually mean ecologically, beyond the trivial ‘animals carry seeds’?

dozens in the patch. The well-known floral constancy of individual honey bees (Waser 1986; Cakmak and Wells 1994; Hayes and Grüter 2023) is a case in point: the behaviour of each bee is at odds with the generalistic behaviour of the species. Averaging across individuals suggests a very different pollen dilution than knowing about individual’s floral constancy. How representative are these data for the interaction studied, if the aggregate information across an unknown (or at least uncommunicated) number of individuals? Also, as data are collected over some time, networks are typically aggregated across hours to days, averaging out any variability that may have existed (Schwarz et al. 2020; CaraDonna et al. 2021). And, occasionally, the same happens in space, when several field sites are used to construct an interaction network (Dáttilo et al. 2019, see also Fig. 9.1).

Network structure is affected by aggregating individuals, samples, sites, but we do not know how (see Arroyo-Correa et al. 2023, for some early ideas). But if we do not know what **happens during aggregation**, we cannot know whether the result reflects interesting ecological patterns or aggregation artefacts.

A first step towards resolving the aggregation problem is to do a sensitivity analysis: aggregate a bit more and a bit less than the focal aggregation level and see how it affects the results. If they are more or less unaffected, then aggregation did not seem to introduce substantial artefacts. If the dataset is particularly rich, analyses at different aggregation levels may even be possible (Schwarz et al. 2020).

A next step would be, again, to explore this issue by simulation, ideally using individual-based simulations, which are then sampled by a virtual ecologists (Zurell et al. 2010) and analysed by different types of aggregation. In the field, attempts should be made to tell between individuals, in order to separate within-species from between-species specialisation.

Deal-breaker 4: What we can expect

Networks are typically described by indices, which quantify some pattern in the data. Many such indices exist, but for most of them **we have no quantitative expectation**. For example, what is a high (or low) value for “linkage density” in a plant-herbivore network?

The absolute value depends a lot on our sampling intensity, on the species richness of the involved guilds, and on their abundances. We can thus compare linkage density between two habitats or treatments, but the actual value is of no practical use. For any single network, however, we need a point of reference. That is where null models come in.

A null model simulates what a network would look like if a specific process was *absent*. In a regression, the null model is the intercept-only model, i.e. a model without predictors. That would also be the go-to approach for networks (Wells and O’Hara 2013), but regrettably such approaches currently cannot accommodate the non-independence of entries in the interaction matrix.

Parametric likelihood of an interaction matrix

There are two avenues towards a solution to this problem, each with its own set of unresolved issues. The first is an (unpublished) way to correctly compute the likelihood of observing an interaction matrix’ entries given a probability matrix of the same dimensions *and* fixing marginal totals. This is a bit different from assuming that the matrix is actually the outcome of a multinomial distribution with given per-cell probabilities (as used, e.g., by Vázquez et al. 2009; Benadi et al. 2022). It additionally observes the constraint that species interaction are not independent across rows and columns. One consequence is that once all observed interactions in a column or row are accounted for in the likelihood, this column/row probability must be relocated to the remaining cells per row/column, respectively.⁴ In practice, this “Bjorn”-likelihood is only little different from a multinomial likelihood. The sticky point remaining is: where to get the probabilities from in the first place?

Null models

The second avenue is interaction null models, of the same type used in co-occurrence and biogeographical analyses (Gotelli and Graves 1996; Gotelli 2000; Vázquez and Simberloff 2003; Dormann et al. 2009). For example, the Patefield-algorithm often used for quantitative network null models takes the observed abundances as given and assumes all species to interact randomly. Simulated interactions are thus proportional to species abundances, as deduced from the interaction matrix marginal totals.

Other assumptions can be, and have been, made. For example one could choose to keep the number of links in the network constant (Vázquez and Aizen 2003; Vázquez et al. 2007). There are, however, two fundamental problems with modifying the Patefield approach (see also Molina and Stone 2020). First, a null model is not just any simulation algorithm that yields a network. Rather, it has to have two necessary properties, which have been shown for no existing quantitative null model except the Patefield algorithm: (1) full configuration space: the null model algorithm has to be able to find all possible

⁴ A function implementing this algorithm by Björn Reineking is included in the R-package **tapnet**.

configurations of the network that exist; and (2) uniform sampling: when generating simulations, all these configurations must be generated with the same probability. These are extremely stringent conditions, and it is mathematically extremely difficult to prove that they are met (see Carstens 2015, for an example for a binary null model). If either of the conditions is violated, the simulations do not represent what is possible, and they do not represent what is possible fairly, i.e. they are biased.

This is no small matter, and it may be common. When I attempted to construct a null model that maintains marginal sums (like Patefield's) *and* the observed number of links, it all seemed to work nicely. On closer investigation, however, I realised that certain configurations were found by the algorithm much more readily than others, and some were never found. This faulty algorithm can still be examined as `bipartite::swap.web`, but using it would be simply wrong. The null model comparison performed with this null model were too aggressive: it found much stronger deviations between the null and the observations than is correct.

To repeat: using a null model only makes sense if this null model is able to sample the entire space of possible configurations uniformly. Proving this is mathematically difficult, and simulations are infeasible, as the configuration space is typically much too large. So, currently we must consider all non-Patefield algorithms as experimental and provisionally – and the results drawn from them, too.

Abundances: cause or effect of network structure?

Another fundamental problem with formulating an expectation, using null models, is to use the number of interactions we observe per species as its abundance. (I omit here the problem that activity confounds such abundance estimates. The abundance problem is bad enough already.) These “abundances” are potentially a consequence of the interactions in the network. If so, they cannot logically be used as independent estimates of abundance for the null model. This dilemma has been referred to as the “chicken and egg problem” (Fort et al. 2016): if the network structure affects the abundances, then the abundances cannot be used for the null model. While Fort et al. (2016) argue that the chicken-or-egg problem can be solved even with the data at hand, I remain unconvinced until formal simulations have demonstrated that to be the case.

It is unclear when external abundances are independent of network structure, and when the Patefield algorithm can thus still be used. Species in pollination networks typically are much less dependent on interactions for their abundance than host-parasitoid networks, so at that end of the dependence gradient the null model can probably still be useful. Using the Patefield algorithm for host-parasitoid networks “only” tells us whether the observed interactions are surprising given the observed abundances. But it cannot serve as a null model in the sense of “in the absence of specialisation”, as abundances are at least to some degree the result of network structure, too.

A different step towards resolving the chick-and-egg problem is to sample abundances in the field independently of the actual network. While that does not remove the circularity of the null model, it at least gives expectations that do not immediately emerge from the network data. A further step would be to collect data over time, so as to be able to represent the population dynamics of the different species involved. With a coupled population

dynamic model this system could than be analysed for network configurational effects on species abundances.

Deal-breaker 5: What it means

Network indices abound. Some are plain and general, such as connectance, others are involved and specific to a interaction type, such as the pollination dependence index. Some are based on binary network information, which is problematic for reasons mentioned earlier, others are very ad-hoc attempts to try and extract something meaningful from a network. Very few, if any, network indices have been shown to map to an ecological process or pattern. Only one or two indices have been subject to rigorous simulation or mathematical analysis to investigate their behaviour (Blüthgen et al. 2006; Poisot et al. 2012). As a consequence, the majority of them is affected severely by network dimensions, sampling intensity, degree of lumping species into morphotypes, misidentification and so forth (Nielsen and Bascompte 2007; Dormann et al. 2009; Gibson et al. 2011; Chacoff et al. 2012; Rivera-Hutinel et al. 2012; Fründ et al. 2016; Vizentin-Bugoni et al. 2016; de Aguiar et al. 2019; McLeod et al. 2021).

Many indices have been transferred from other fields of science, such as small world properties, motifs or degree distributions (Vázquez et al. 2005; Olesen et al. 2006; Jácome-Flores et al. 2020). Reading these papers provides **no justification for their purported usefulness in ecology**. What does it mean that a network is robust to extinctions, if the underlying procedures are unrelated to ecology (assuming static interactions as if they were an electricity grid)? What does it mean for the abundance of the species in a network that some motifs of interactions are more common or rare? How can a (truncated) power law of degrees explain abundances of species or traits? How can (lack of) nestedness explain which species dominates in a guild? There is a surprising number of high-ranking publications that I regard as void of ecology, as they are not embedded in an ecologically meaningful concept and which fail to logically relating some “network topological” index to community processes.

To clean this Augean stables of network indices, we must work harder to demonstrate that an index has an ecological meaning. Such demonstration will typically take the form of a simulation study, which as to show that (1) an index does what it claims, and (2) no other ecological cause can affect this index. That is hard! The well-intended and seemingly sound partitioning of β -diversity into nestedness and turnover of Baselga (2010, cited 2453 times) was soon shown to be incorrect and yielding nonsensical results (Almeida-Neto et al. 2012, cited 167 times). To me, this shows that we are not trained in rigorous index development and need to demand a higher standard for any old, new or transferred index applied to interaction networks (one of the points emerging in Brugere et al. 2018).

Deal-breaker 6: Confused minds

Networks can be seen as a third-order pattern (Dormann et al. 2017). The first order is the number of species (two numbers), the second their abundance (two vectors, i.e. $n+m$

units of information).⁵ If we can explain a pattern in nature with first-order information, why would we resort to the network matrix ($n \cdot m$ units of information)? Not only does it violate the parsimony principle, it also fosters unclear thinking (also see critique by Brimacombe et al. 2022).

Take, for example, connectance. It is strongly dependent on sampling intensity, and on the number of species observed, and hence connectance is typically a non-linear function of first-order property “number of species observed”. It does not represent further information about the network, because it is almost completely explained two levels further down. When we interpret connectance as “forbidden links” (Jordano et al. 2003), we invoke an unproven complicated explanation when a simple one does exactly the same job (Vázquez 2005). Note that this does not argue against the sound idea of implausible interactions, only that connectance cannot possibly be responsible; but lack of matching traits can be.

A striking example of **misconceptions behind networks** is a conceptual figure in Moreno-Mateos et al. (2020), which represents recovery of community properties during secondary forest succession. First, species numbers recover, then species abundances, and then with some temporal delay, “networks”. Such a delay implies that there is something that prevents the species to interact as before the disturbance. Why should that be the case? If a species is there, it will interact. Network indices are the direct consequence of interacting species, and species interact as part of their existence. There is no lag between recovery of abundances and “networks”. In fact, following the chicken-and-egg arguments, the networks *must* be similar to before the disturbance, otherwise the abundances would be different, too.

To me such mistakes point to a deeper confusion. Networks seem imbued with some near-magical properties that make them the target of much current research, without requiring the scientist to justify *why* a network-ecological approach was taken for a specific question. The added benefit of such an approach, which certainly exists in some cases, should be demonstrated by first failing to explain a pattern with first- and second-order properties of the network.

Furthermore, it is easy to claim some underlying coevolutionary or community ecological cause for a pattern, but very difficult to show (as deconstructed for modularity in Dormann et al. 2017). It is unfortunate that one can simply claim that this or that process underlies a pattern, without proper demonstration. It is, of course, not only network ecology that falls into this trap (see, for example, the many studies which claim that “species distribution models are useful” without ever citing a study that demonstrates, only studies that claim, such usefulness).

9.4 From networks to ecology

The near-trivial equation underlying ecology is $N = B - D + I - E$, describing the number of individuals in the population of a given species as the result of demographic (birth and

⁵ To complicate things a bit more, there is another level between 2 and 3, 2.5 if you like: Do we need to record all interactions together, or could we do species-level observations (e.g. in a cafeteria-experiment) and just place them next to each other? This would also require $n \cdot m$ units of information, but collected in isolation, rather than together. For the following arguments this distinction is not relevant.

death) and dispersal/migration (im- and emigration). Interaction networks, in their typical form, do not quantify the *I* and *E* component, in line with their focus on endogenous processes. If they do also not contribute to our understanding of *B* and *D*, then what is their point?

The ecologically interesting question is whether, say, specialism increases the number of offspring or reduces mortality; not whether a network has a specific topology. This is not the first time that network ecology has been argued to be disconnected from (community) ecology (Blüthgen 2010). Since then, little has happened with respect to the problems outlined above.

The road ahead will require overcoming substantial obstacles, if network ecology is to contribute to ecology, beyond buzzwords and enthusiasm: clear thinking, dedicated data collection for specific hypotheses, and demonstration of effects of network structure beyond mere claims of relevance.

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