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EDITORIAL

Describe, understand and predict: why do we need networks in ecology?

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Networks are collections of nodes that are connected to each other by links. Innumerable objects around us can be seen as networks, for example, the Internet (where nodes are computers and links are data connections between them), transportation systems (where nodes are train stations or airports and links are roads or connections between them), human and animal societies (where nodes are individuals and links are social interactions) and food webs (where nodes are species and links are feeding interactions). Although it goes back much further, the scientific study of networks has seen a resurgence since the late 1990s with the publication of seminal studies of the structure of the World Wide Web and other complex networks (Barabási & Albert 1999; Albert *et al.* 2000; Jeong *et al.* 2000).

Many of the network science tools developed since then have percolated through to ecology where networks have proven remarkably useful. Ecological networks can take on a variety of forms. For example, nodes can be individuals and the links contacts between those individuals (Melian *et al.* 2011), nodes can be species and the links the interactions (e.g. feeding, mutualistic, parasitic) between them (de Ruiter *et al.* 1995), or nodes can be ecological communities or ecosystems and the links fluxes between these localities (Proulx *et al.* 2005; Chadès *et al.* 2011). Without a doubt, it is the second case that has dominated the ecological literature (Berlow *et al.* 2004; Ings *et al.* 2009), in particular when studying the structure of ecological communities (de Ruiter *et al.* 1995; Neutel *et al.* 2002; Bascompte *et al.* 2003; Krause *et al.* 2003) and the dynamic or functional consequences of this structure (Thébault & Fontaine 2010; Stouffer & Bascompte 2011).

Ecological networks have so far attracted attention in the literature in mainly two ways: (i) providing sets of tools to visualize and describe ecological systems and (ii) contributing more fundamentally to the understanding of some of the longest standing and core questions in ecology (e.g. Why and how do so many species coexist?). As networks are becoming more popular, tools developed in network science keep increasing. At the same time, new types of ecological data are emerging, placing us at an opportune crossroad to reflect on when and how looking at ecological communities as networks leads to new and useful insights. In this Special Feature, the contributors present research at the frontier of what networks can do for ecologists, and outline an ambitious research agenda to integrate network approaches into the standard ecological toolkit. In this editorial, we use these studies as a platform from which to provide a broader overview of where we feel the field is headed.

The making of an ecological network

The study of ecological networks has benefited heavily from the development of tools, concepts and models developed outside of ecology, and in particular in network science (Newman 2010; Barabási 2016). For example, community detection approaches provide a way of partitioning a network into *communities*, i.e. 'groups of nodes that have a higher likelihood of connecting to each other than to nodes from other communities' (Barabási (2016); p. 322). These descriptive approaches have allowed us to observe and quantify the structure of ecological communities in ways that simply were not available previously. When applied to food web data, for example, they have suggested that food webs tend to be more compartmented than expected by chance (Krause *et al.* 2003) and that such compartmentalization could improve the resilience of ecological communities to perturbations (Thébault & Fontaine 2010; Stouffer & Bascompte 2011). Excitingly, the newest tools and approaches from network science (Mucha *et al.* 2010; Kivelä *et al.* 2014; Miele *et al.* 2014) are constantly being transferred to ecology (Kéfi *et al.* 2016) and are help to improve our fundamental understanding of the structure of ecological networks, the underlying ecological mechanisms and the functional consequences of these structures for the dynamics of ecological communities. More recently, these descriptive metrics have even been expanded to the study of multilayer ecological networks, allowing us to

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capture the structure of multiple types of interactions at once (Fontaine *et al.* 2011; Kéfi *et al.* 2016).

Descriptive or otherwise, anything we can infer from network data can only be as good as our understanding of the network itself; that is, our understanding of (i) which species are present (Jordano 2016b), (ii) the ways they interact (Nielsen & Bascompte 2007) and (iii) their local characteristics when observed (Poisot *et al.* 2015). While describing the identity of species that are present locally is comparatively simpler, documenting interactions proves far more challenging (Poisot *et al.* 2012; Gilarranz *et al.* 2015). This intuitively follows from the ecological reality that observing an interaction requires the observation of both species at the same time and place, and species co-occurrence is in itself a difficult phenomenon to accurately describe (Sanderson & Pimm 2015). Moreover, knowledge about the outcome, cost or benefit of the interaction itself often requires more than just a single observation at a given moment of time. Although the identification of trophic interactions may rely on observations alone (although several observations of a feeding event are needed to make sure that the prey is actually part of the diet of the predator), other interaction types typically require experiments (Berlow *et al.* 2004; Godoy *et al.* 2014; Kéfi *et al.* 2015).

As ecological data sets have been limited by our observation capacity (number of observers, time and cost involved, accessibility of the sites, etc.), ecologists have had to rely on indirect lines of evidence or diversify their toolkit (see Jordano (2016b) in this Special Feature). In the case of ecological networks, where the information needed to fully characterize them includes not only species identity and interaction details but also covariates like traits and/or species abundances, the observational approach alone is always going to be limited by logistic contingencies. To this end, Evans *et al.* (2016) (in this Special Feature) highlight how metabarcoding approaches can reveal ecological interactions at the ecosystem scale; this can significantly reduce the time needed to document ecological interactions, in addition to provide fine-grained information about interactions at the individual scale.

Another approach consists in inferring interactions, rather than observing them. Bartomeus *et al.* (2016) (in this Special Feature) demonstrate that existing records of interactions coupled with species traits allow the inference of other interactions when only traits are known. This is an important expansion upon previous work (Gravel *et al.* 2013), which now allows interactions to be quantified as probabilities rather than the presence/absence events. In parallel with the recent development of a toolkit for probabilistic networks (Poisot *et al.* 2016), there is an opportunity to compensate the uncertainty introduced using inference over sampling through the introduction of methods designed specifically to work on probabilistic data.

Phylogeny, as a proxy for evolutionary history, has also been recognized as one of the factors shaping species interactions. Indeed, phylogenetic signal has been detected in multiple types of species interaction networks (Eklöf *et al.* 2012; Rohr *et al.* 2014), and in network structure in particular. In this Special Feature, Peralta (2016) reviews the main findings and the methodological approaches for including phylogenetic information in ecological-network studies. A clearer picture of how evolutionary history shapes ecological networks could vastly improve our understanding of the drivers of ecological network structure and our ability to infer and predict interactions.

In summary, what ultimately makes an ecological network are the interactions, for the most part, and as Jordano (2016b) points out in this Special Feature, these remain notoriously difficult to document. Nevertheless, diversifying the tools we use to assemble networks offers some assurance that data collection, even at large scales, is in fact possible. Coupled with increasingly powerful predictive models and an expanding toolbox from network science, we anticipate that the next years of network ecology will see an even greater growth in the type of methods used to quantify network structure, re-analysis of existing data, and the emergence of new types of data (e.g. networks with multiple interaction types Kéfi *et al.* (2015) or rich network time series Olesen *et al.* (2011)).

Ecological networks: bandwagon, paradigm or useful tool?

It is not uncommon within the ecological network literature to encounter statements that argue that networks are an accurate representation of the complexity underpinning ecological communities. Some adherents of this idea have even gone so far as to suggest that the study of ecological networks represents a fundamental paradigm shift within ecology (Bascompte 2009). Such studies have promoted the use of networks in ecology as a powerful representation of ecological communities, which allows description and quantification their complexity (Bascompte 2009) and could contribute to finally unlocking key questions such as community assembly (Montoya & Sole 2003; Barberán *et al.* 2012), coexistence (Allesina & Levine 2011; Ulrich *et al.* 2014) and the concept of trophic niches (Dehling *et al.* 2016). Others have warned against the pitfalls of network analysis, and unclear and incautious interpretations that are not uncommon within the ecological-network literature (Blüthgen 2010).

Yet, those of us with ‘physics envy’ may be on the right path: networks can be far more than a set of tools to describe and visualize ecological communities (in fact, network visualization has very little to do with network *science* itself). Therefore, if ecologists are to be encouraged to embrace networks even more, we argue that it should be in a way that reframes descriptive questions and the never-ending quest for non-random ‘patterns’ into the testing of specific hypotheses, whether expressed at the scale of a single communities or at a global scale. Reflecting this tension, the most enticing of recent network studies have taken this road. For example, Emer *et al.* (2016) use network analysis to show that invasive species tend to conserve their functional role in native and alien assemblages. Likewise, Gilarranz *et al.* (2015) test the hypothesis that peripheral communities in a metacommunity have networks with a lower resilience. Although these are but two examples among many, they firmly illustrate how the full potential of networks is revealed when they are used not as a descriptive tool but as an investigative one.

The contributions by Trøjelsgaard & Olesen (2016) and Bartomeus *et al.* (2016) (both in this Special Feature) similarly strive to take this challenge head on. Specifically, they work from background knowledge, on the spatial and temporal dynamics of ecological communities and on the role of traits in determining interactions, respectively, to present networks as tools to help sort competing hypotheses. In general, we eagerly welcome this change and look forward to the trend continuing in the coming years. When the relative novelty of networks has worn off and we have developed the necessary hindsight to establish best practices about what to measure and how, using networks for understanding and prediction – and not description – should also become orders of magnitude easier.

That said, we argue that much more can be done at the crossroads between networks as an ecological paradigm and networks as a useful conceptual or quantitative tool to study ecological data. Indeed, just as metrics used to study presence–absence matrices (e.g. nestedness or beta diversity) or techniques like rarefaction from sampling theory have made enormous impacts in network ecology (Bascompte *et al.* 2003; Poisot *et al.* 2012; Jordano 2016b), there is a growing suite of network 'tools' that have barely made a dent elsewhere in ecology despite the potential payoff (but see Carstensen *et al.* 2012 or Carstensen *et al.* 2013 for applications of networks to biogeography). By better pinning network studies on the underlying ecological hypotheses and/or better explaining the versatility of the methodologies, we hope to see the reintegration of network tools into the rest of the field, and even if this means that networks as standalone paradigm will fall by the wayside.

What are the next steps?

Since networks are actively used outside ecology in fields that currently have challenging data sets, and where methodological development have been faster, ecology will probably continue to benefit from those tools, metrics and models developed in other fields. One of the exiting new developments in network science of the last few years is the study of multilayer networks (Boccaletti *et al.* 2014; Kivelä *et al.* 2014). A multilayer network consists in several networks (each being a layer) linked to each other (Boccaletti *et al.* 2014; Kivelä *et al.* 2014; Pilosof *et al.* 2015).

In ecology, such multilayer networks can represent different instances of a given community in time (each layer would then be a snapshot of the ecological network at a given moment in time), in space or a network where the layers represent different interaction types that link a given set of species (e.g. predation, facilitation, competition; Pilosof *et al.* 2015). As such multilayer data sets are also emerging recently in ecology (Melián *et al.* 2009; Olesen *et al.* 2011; Pocock *et al.* 2012; Kéfi *et al.* 2015, 2016; Pilosof *et al.* 2015; Sander *et al.* 2015), the application of these new tools to ecological data sets will provide a more detailed understanding of the spatio-temporal variability of ecological networks, their drivers and functional consequences but also of the multi-interaction architecture of natural communities (Kéfi *et al.* 2012).

Interestingly, and in what may be a departure from other fields of ecology, the study of ecological networks has produced a lot of methodological literature. Although far from entirely robust (because a lot of network measures remain untested; because the field does not have best practices established other than by tradition; and because the methodological development was often driven more by ecological thinking than by mathematical correctness), this means that ecologists have at their disposal a toolkit to explore most questions that can be asked with networks. This also means that the field is due to take a step back from methodological issues, and focus more on establishing networks as an investigative tool. In a way, we need to be prepared to accept some methodological ambiguity and chip away at larger conceptual issues.

One of the most exciting issue, which is largely unsolved, is to understand where the structure of ecological networks comes from. Although there are simple generative models, they tend to be phenomenological rather than mechanistic. This calls for a deeper understanding of the ecological, evolutionary and stochastic constraints that act on and shape, network structure. Because this will lead to an improved knowledge of the mechanisms that regulate the existence of ecological interactions, a return to a more small-scale, species-centric understanding of networks may help solve the issues of the difficulty to sample interactions (Jordano 2016b), give additional weight to statistical models of interactions (Bartomeus *et al.* 2016), and help predict changes in network structure over time and space (Trøjelsgaard & Olesen 2016). It will also, hopefully, keep the amount of hand-waving about 'complexity' to a much lower level than at the moment.

These are exciting times to practice network ecology, as we are slowly but surely moving out of the descriptive phase and into an era of understanding and prediction. As Jordano (2016a) recently pointed out, the study of networks essentially re-purposes the study of biodiversity by linking species together through their interactions. This contrasts to other analysis paradigms geared towards measuring community structure (e.g. Legendre & Legendre 2012) that tend to treat species as disconnected, discrete and independent entities. As networks provide an additional layer of information by making relationships between species *explicit*, approaches grounded in network science and graph theory ready to have the potential to transform the way we approach community ecology (Bascompte & Jordano 2007). By overcoming the incorrect assumption of treating species as disconnected entities, the central tenet of network ecology is that this level of observation – although less familiar than standard approaches to community ecology – is ultimately a more accurate reflection of the natural world.

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