

Introduction

In ecological communities, interactions between species are organized in ways that are non-random. The organisation of these interactions, in turn, drives or changes some properties of the community, such as its stability, productivity, or ability to resist extinctions. The way interactions are organized can be studied by investigating the structure of *Species Interaction Networks*. In this representations, species are “nodes”, and interactions are “edges”. Two species are linked by an edge if there is an interaction between them.

Describing and understanding the structure of species interaction networks is an active, and growing, field of ecological research. In this contribution, we will give an overview of some of the most prominent findings and areas of research from the last decade. Starting from a discussion of some invariant properties of the structure of species interaction networks, we will then discuss how this structure affects ecological properties. We will follow by a discussion of the ways ecological networks can be studied under familiar concepts from ecological theory, and finally how this approach scales up to larger temporal or spatial scales.

Invariants in ecological networks

One striking particularity of ecological networks is their consistency: even though they depict interactions between different organisms across all sorts of ecosystems, they all tend to look the same (Jordano et al., 2003). Remarkably, even when interactions among species themselves vary (see section **x**), the overall network structure tends to remain unchanged (Kemp et al., 2017). Most ecological networks have a very specific degree distribution (Williams, 2011), whereby most species have a small number of interactions, and a small proportion of species have a large number of interactions. In food webs, which represent interactions between preys and their predators, there is a well-described relationship between the number of species and the number of interactions: the number of interactions (L) increases proportionally to the number of species (S) raised to some exponent, or $L \propto S^k$. Martinez (1992) suggested that this exponent is approximately equal to 2, *i.e.* the number of interactions is proportional to the squared number of species. Brose et al. (2004) show that this general relationship holds even across space: it is possible to estimate how many interactions a species will establish across its entire range. In some other instances, networks may differ on some aspect of their structure, despite obeying to a shared underlying principle. For example, Fortuna et al. (2010) show that in networks with a low connectance, nestedness (the degree to which the diet of specialists and generalists overlaps) and modularity (the tendency of species to form densely aggregated clusters) are positively correlated. In networks with higher connectance, this became the opposite: networks with a large number of

interactions were either nested (and not modular) or modular (and not nested). In the recent years, it emerged that many aspects of network structure covary with connectance (Chagnon, 2015; Poisot and Gravel, 2014): this suggests that simply knowing how many species there are, and how many interactions they establish, is already very informative about the network structure.

Another remarkable generality of network structure is the distribution of particular shapes of interconnection between all three-species subsets. Milo (2002) indeed found that networks (not just ecological but other types of networks such as neuronal or electronical networks as well) can be characterized by the over-representation of some of these three-species subset, which they called motifs. Motifs can be more broadly defined as being particular shapes of interconnection between three or more nodes in networks at a frequency significantly higher than those found in randomized networks. Three-species motifs thus represent the simplest building blocks of networks, and more importantly the typical interaction found in communities. As such, they offer the possibility to integrate theories developed on simple modules (*e.g.* omnivory, (???), Holt (1997)) in larger, more realistic networks. For instance, food webs are characterized by an over-representation of linear food chains and omnivory and an under-representation of apparent and exploitative competition (Bascompte and Melián, 2005; Camacho et al., 2007). (???) found that this distribution promotes stability in food webs, with over-represented motifs being more stable in isolation and correlated with higher stability in large realistic communities, and conversely. Motifs can also be used to characterize species role in networks. From the 13 different three-species motifs emerge 30 unique positions for species to occupy in these motifs, representing how the species is embedded in its community. The different positions a species will occupy, and the frequency with which it will occupy these different positions in networks are called species motif role (Stouffer et al. (2012)). These roles have been shown to be evolutionary conserved in food webs (Stouffer et al. (2012)) and to have less variability in time than expected in host-parasitoids bipartite networks (Baker et al. (2015)).

Because communities structure and assembly are driven by species phylogeny, ecological network analysis is a powerful tool to understand phylogenetic structure and dynamics that lead to it. Closely related species inherit traits from common ancestors (*e.g.* body size, habitat, defensive strategy, metabolic type, phenology, etc.), increasing their propensity to interact with the same group of species or with similar species. This conservatism of interactions has been found to hold across different types of interactions such as antagonistic or mutualistic interactions (ref). Due to differential evolution rate of interacting species (*e.g.* parasites evolve more rapidly than their hosts), overlapping of fundamental niche or diet specificities (ref), conservatism of interactions is unequal all over the network, which influences the way networks evolve (ref). Following the same logic (closely related species interact with the same group of species), the network structure can explain almost entirely the phylogenetic structure of ecological networks. This is particularly true for the formation and composition of modules ((???)), and the connections between them (ref). For the same

reasons that conservatism of interactions is asymmetrical, the link between phylogenetic signal and module composition is different depending on the species role (e.g. host or parasite in antagonistic interactions) (ref). Cattin et al. (2004) also found, using a niche-hierarchic model, that diet is constrained by phylogenetic origin of consumers. The nested structure of trophic network, generated by the diet structuration, is then influenced by phylogenetic signal of interacting species and trait matching. In contrast, the nested structure of mutualistic networks would be a consequence of trait complementary between species (ref). For now, mechanisms underlying the nestedness-phylogeny relationship remain to be further investigated.

From structure to properties

The consequences of the erosion of biodiversity for ecosystem functioning has been for almost three decades a central problematic for ecologists. While the hypothesis that an increase in species diversity results in an increased productivity dates back to Darwin (Darwin, 1859), the emergence of experimental ecology and the shift from observation in natural systems to the quantification of ecology has made possible to develop a quite general theory for what is now called the BEF relationship. In a trophic group (i.e. a group of species that all belong to the same trophic level, e.g. producers or herbivores), the loss of diversity results in a loss of efficiency to capture the shared resource compartment (Loreau, 2010) (e.g. nutrients for producers, or producers for herbivores). This leading to a decrease in productivity or other index of functioning. Yet, when the trophic group under focus is coupled to other(s), the action of diversity on functioning is more variable (Duffy et al., 2007). Top-down and bottom-up controls are exemple of mechanisms that modifies the action of the diversity at one level on other(s). This makes the BEF relationship unpredictable in real-world communities, composed of several trophic groups that are virtually never differentiable – as intraguild predation and omnivory blurr the frontier between levels. The multiplicity of the factors influencing the BEF relationship calls for a more general framework that allows the integration of the theories developped for trophic group and for simple modules or sub-systems. By mapping transfer of biomass and energy and/or constraints on organism through the different compartments that compose a natural community ecological, networks – and food webs in particular – offer the possibility to perform this integration, reconciling at the same time ecosystem ecology and population ecology. Analyses performed on simulated food-webs with unchanged diversity have shown that interactions, and more specifically their structure, have a significative influence on functioning (Poisot et al., 2013; Thebault and Loreau, 2003; Thébault et al., 2007). The structure of interactions indeed translates the distribution of different types of properties important for ecosystem functioning, such as the presence of omnivory, the generality of species, the modularity of the food-web, etc.

The relationship between ecological network structure and stability has been and remains a central topic of discussion. Starting with the idea that increasing species diversity and connectance will increase stability of the observed communities, this relationship was rapidly contested. Based on random networks, May (1972) proposed that complexity is not bindingly related to community stability. From this day, the complexity-stability debate have been really prolific (see (???)), using real ecological communities with a non-random structure. To complicate, several measures have been used to evaluate the stability of ecological networks (*Pimm 2002*), such as the ability of communities to keep their species composition and species coexistence (i.e. persistence) and the rapidity of communities to reach a stable dynamic after a perturbation (i.e. resilience), rising the difficulty to have a clear idea of the relationship between network structure and stability. By now, it is known that there is no direct relationship between complexity of ecological networks and their stability (Jacquet et al. (2016)), but other components of the network structure have a stabilizing effect on communities. The power-law distribution of ecological network links has indeed a strong stabilizing effect on the network. The organization with few highly connected species and a large number of weakly connected ones contribute to temperate variations in populations dynamics and then stabilize the entire community. Moreover, when combined with a high frequency of weak interactions, this distribution results in a stable network ((???), Jacquet et al. (2016)). Also, because the predator-prey body-mass ratio determines the distribution of interaction strength, it has a stabilizing effect on a short trophic network ((???), Brose et al. (2006)).

The robustness of networks to species loss is an important concept to understand how ecological communities behave in front of species loss or replacement due to perturbation, such as landscape fragmentation, habitat loss or alien species arrival. Impact of species loss in the structure of ecological network is measured by the number of secondary extinctions (i.e. direct or indirect extinction of species due to a first species loss). Removing a random species in a network has no particular effect on the network robustness, whereas removing of a selected species has impressive consequences on the rest of the network ((???)). Depending on the interaction type, the network architecture will differ. Mutualistic networks (e.g. plant-pollinators networks) have a nested and highly connected structure (Bascompte and Jordano (2007)), while trophic networks are more modular (Thébault and Fontaine (2010)). This difference induce dissimilarities in network behavior in front of perturbation. On one hand, the large proportion of generalists and the redundancy of species function in mutualistic lead to a relative resistance to perturbations (ref). On the other hand, the modular structure found in trophic networks limits propagation of perturbations and secondary extinctions ((???)).

Linking interactions to ecological mechanisms

It is worth remembering that ecological interactions are the direct expression of ecological mechanisms. A pollinator is able to effectively reach the nectar in a plant because the traits of the two organisms match, because they have compatible phenologies, and because they occur in the same environment. A virus can infect its host because it is able to attach to the cell surface, effectively penetrate it, and hijack the cellular machinery to its benefit. Interactions that are not allowed because trait values do not match have been called “forbidden links” (Olesen et al., 2011). This prompted a search for “linkage rules” (Bartomeus, 2013) in ecological networks, *i.e.* the relationships that must exist between traits borne by two organisms in order for an interaction between them to exist. These can be identified from existing data on traits and interactions (Bartomeus et al., 2016), and then used to generate realistic ecological networks (Crea et al., 2015). González-Varo and Traveset (2016) point out that interactions are happening between individuals: this requires to consider how the traits are distributed at the individual scale, but also how different behaviors may allow organisms to overcome some of the forbidden links. Although traits are an important part of what makes interactions happen, they are only relevant insofar as the organisms are able to encounter one another. The importance of neutral dynamics (*i.e.* how abundances of different species can determine the probability that they can interact, based on how often they would bump into one another by chance) is, somewhat counter-intuitively, great. Canard et al. (2012) reveals that simulating food web dynamics by using only population abundances to predict interactions yields realistic food webs. In a host-parasite system, local abundances has also been identified as a key predictor of species interactions (Canard et al., 2014). Speaking more broadly, because interactions emerge from all of these ecological mechanisms, there is a need to develop a deeper understanding of them (Poisot et al., 2015). Beyond the fundamental advance that this represents, this would allow to predict interactions based on external information (Morales-Castilla et al., 2015).

The realization of an interaction between individuals from the same or different populations within a community also have ecological consequences as it modifies the dynamics of at least one of the interacting populations, and through it, the ecosystem emerging properties. If we consider for instance a population A, its dynamics is not the same when it multiplies in isolation – where it can grow exponentially if resources are unlimited (Malthus, 1798) or logistically otherwise (Verhulst, 1838) – or when it is embedded in a real-world community, composed of several species interacting with one another through different mechanisms (Chesson and Kuang, 2008). It can lose individuals to predation, have parasitism increase its death rate and at the same time see its establishment eased through facilitation. It then becomes necessary to account for interactions when studying the dynamic a population, community stability or ecosystem functioning. But the effect of interactions on populations dynamics is not always the straightforward, both in terms of directionality and intensity,

as it exists different types of interactions and multiple factors influence their probability and strength. Since the seminal work of May (1972), the analysis of these effects has been a prolific field of ecology, feeding in particular the famous “complexity-stability debate” (see Allesina and Tang (2015) for an overview). Including interactions in population dynamics analyses can be done by using model of the following general form (Poisot et al., 2015):

$$\frac{1}{N_i} \frac{d}{dt} N_i = r_i - \sum_j A_{ij} \alpha_{ij} N_j$$

wherein the adjacency matrix A ($n \times n$), list the realized interactions in a given community composed of n species. $A_{ij} = 1$ when species i and j interact and 0 otherwise. α_{ij} quantifies the strength of the interaction. We presented here an equation to model populations abundance N but it can easily be adapted to model biomass flows by replacing populations’ abundances by their biomasses B_i (see for instance Williams et al. (2007)).

Ecological networks are also spatially and temporally variable (Trøjelsgaard and Olesen, 2016). There are two drivers to this variability: changes in species composition, and changes in the way these species interact (Poisot et al., 2012). Changes in species alone are able to generate variation in network properties (Havens, 1992). Spatial variation in network structure can also reflect deep-time constraints; for example, Dalsgaard et al. (2013) reveal that historical climate change trends have a signature on the nestedness and modularity of pollination networks. Even when the same species are present, interactions between them can vary. Carstensen et al. (2014) and Trøjelsgaard et al. (2015) investigated this phenomenon in mutualistic networks. Interaction turnover results from variations in partner fidelity (some species pairs are extremely closely associated), but also from variations in the local environment in which the species interact. Interestingly, and as mentioned in section **x**, networks overwhelmingly tend to conserve their structure even when interactions within them change. Díaz-Castelazo et al. (2010) surveyed a pollination network over 10 years, and found important species turnover during this period. Nevertheless, the network retained its structure because species were replaced by their functional equivalent; a generalist pollinator often succeeded to another generalist pollinator. Conversely, species tend to retain their role in different communities: Baker et al. (2015) show that species keep occupying the same position in the network across space, regardless of the species they interact with at every location.

From the regional species pool to local structured communities

Describing the different local communities that occur at macroecological scales through their ecological networks represent an additional layer of information

compared to simple species lists. As such, ecological networks are a powerful tool to shed new light on the processes underlying species distribution (Cazelles et al., 2016). Until recently, the prevailing idea was that at large scales, the role of biotic interactions was minimized compared to that of abiotic conditions, and thought to only be important locally (???; Boulangeat et al., 2012). Empirical observations of species-environment relationship were thus used to understand species physiological tolerance to environmental conditions [ref] and potentially predict their range under different scenarios of climate change (e.g. ???). While these climate envelope models provide a useful approximation of species potential distribution (???), there is mounting evidences that biotic interactions – both positive and negative – play a critical role in shaping communities not only at local scales (Boulangeat et al., 2012), but also at macroecological scales (???, ???, ???; Araújo and Luoto, 2007; Davis et al., 1998). So far, the role of interactions in shaping species distribution is mainly estimated from co-occurrence data, used to build joint species distribution models (JSDM) (Pollock et al., 2014). But there are limitations to this approach. For instance, it does not allow to distinguish between co-occurrence caused by biotic interactions and correlated responses to unmeasured environmental variables (Pollock et al., 2014). Conversely, the lack of association between species is no evidence of absence of interaction (Cazelles et al., 2016). To move from empirical-based species distribution models (SDM) toward theory-driven SDM, further work is needed. In particular, developing methods allowing to include prior information about the underlying ecological network when building (J)SDM could help shedding light on the the fundamental processes underlying species distribution and thus making more accurate predictions (Cazelles et al., 2016). Additionally, (???) recently showed that biotic interactions respond to environmental conditions on their own, independantly of species.

Failing to account for biotic interactions when building species distribution models can thus lead to underestimating potential cascading effects such

- coexistence theory
- assembly dynamics

Conclusion

Glossary

Adjacency matrix definition

Allometric scaling

Assembly

Bioenergetics

Ecological interactions Every type of contact between two species that alters the abundance, biomass and/or behaviour of one or both species. Interactions can be trophic, mutualistic or antagonistic, directed or undirected, weighted or unweighted.

Ecosystem functioning

Graph theory

Nodes/Links, Edges/Vertices

Phylogenetic signal

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