Introduction

In ecological systems (*e.g.* communities), interactions between components (*e.g.* species) are organized in ways that are non-random, as interactions occurrence and properties are constrained by sets of rules (see section X). The organization of these interactions, in turn, drives or changes some properties of the community, such as its stability, productivity, or ability to resist extinctions, which eventually feedback on the system organisation. This constant interplay between interaction organisation and system functions results in signatures on the system structure (*e.g.* invariance in key features of the system structure, see section X). Detecting and analysing these signatures gives us informations on the system itself. Studying the structure of ecological systems is necessary to gain insights on the fundamental rules and processes that govern ecosystem formation, maintenance and functioning.

The way interactions are organized can be studied by investigating the structure of ecological networks. Created to analyze the structure of a studied system, the *graph theory* is a mathematical framework which seemed to be largely appropriate to answer ecological questions. Every system can be abstracted by a *graph*, a representation of the system components organization (*Figure 1a*). These components are called *nodes* and are linked together by *edges*. These combinations form the structure of the studied system. In an ecological system, nodes can be individuals, populations, communities or landscape patches and edges can represent trophic links, energetic flux, etc, every kind of interaction. Both nodes and edges can carry additional information such as weight (*e.g.* species abundance, intensity of the gene flow between two populations, etc.), location in space and time, edges direction and sign and nodes labels (*e.g.* species identity). Specific informations can be attached to edges, modifying the characteristics of the graph. Graphs can be *directed* (*i.e* interaction goes from A to B) or *undirected*, *weighted* (*i.e* different strength of interaction among the network) or *unweighted* (*Figures 1 and 2*). This information is summarized mathematically in the *adjacency matrix* (typically named A, see definition in glossary) (*Figure 1b*). The entire representation of the adjacency matrix offers an *unipartite* network representation, where the hierarchy between nodes and their position into the network is not always visible (*Figure 1*). On the contrary, a bipartite or k-partite network is a hierarchical representation of the network (*Figure 2*), where nodes are separated depending on their position or function into the network (*e.g* pollinator-plant as bipartite network). In this paper, for simplicity, time and space, we decided to focus on *Species Interaction Networks* (SIN). Ecological system such as landscape, genetic or nutrient network are not represented here, but they follow the same general rules and characteristics defined further.

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 the 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) (*Figure 1d*), whereby most species have a small number of interactions, and a small proportions 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 (*Figure 1c*), nestedness (the degree to which the diet of specialists and generalists overlaps – *Figure 2*) and modularity (the tendency of species to form densely aggregated clusters – *Figure 2*) 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 three-species subsets. Milo (2002) 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 or under representation of some of these three-species subset, which they called motifs (*Figure 1e*). Motifs can be more broadly defined as being particular shapes of intercon-

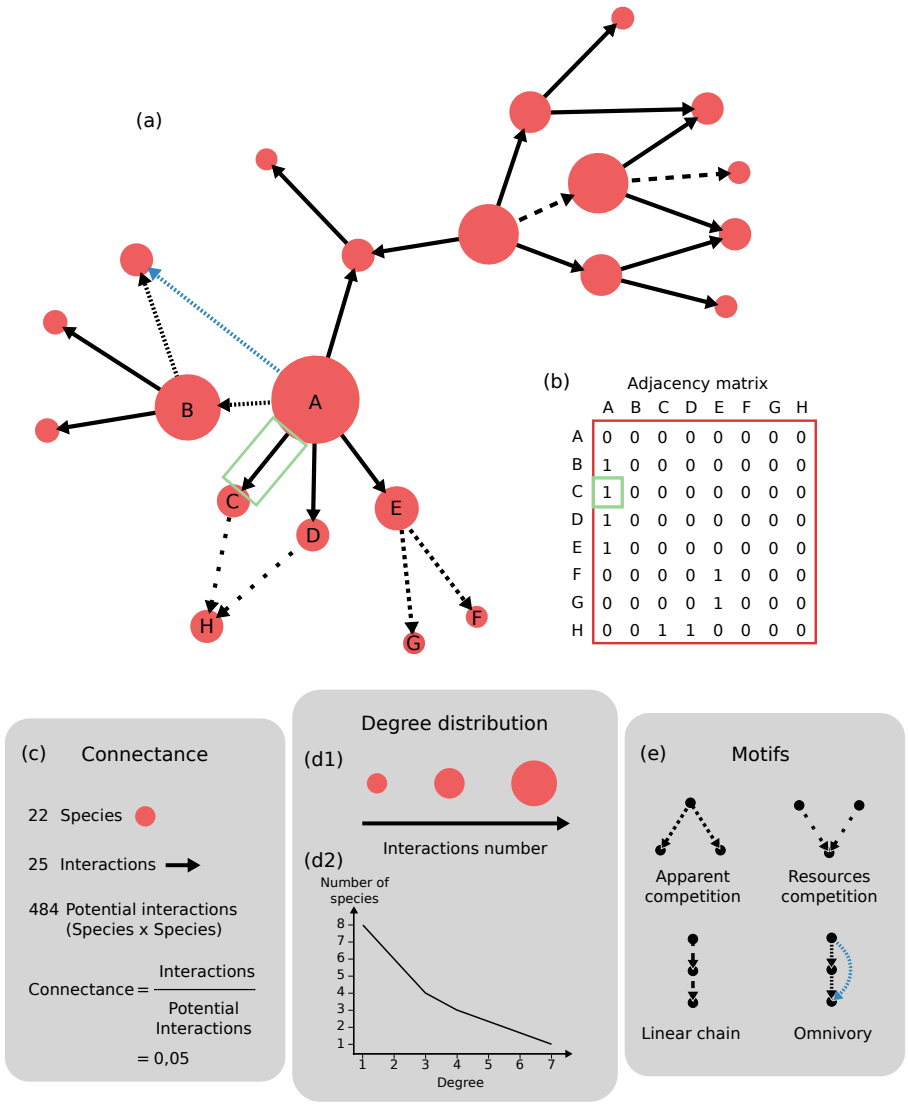

Figure 1: Graphical representation of a fictional ecological network (a), where species are represented by circles and their directed interactions by arrows. The representation is build from the adjacency matrix (b). In an unipartite representation as this one, each species is represented both as a column and a row. 1 indicates an interaction between two species (e.g. the green square in (b)), and 0 indicates the absence of interaction. This matrix allows to calculate network characteristics such as the connectance (c) and the degree distribution (d). (c) represents the level of connection into the network and is calculated as shown in the figure. (d) represents the distribution of interaction per species. The circles size is relative to the amount of interactions a species have (d1). This distribution is non-random and generally follows a power-law distribution (d2). The network can be split into subnets composed of 3 species, called motif (e). Among the 13 different possible motifs, we only represented the most commonly found in natural communities.

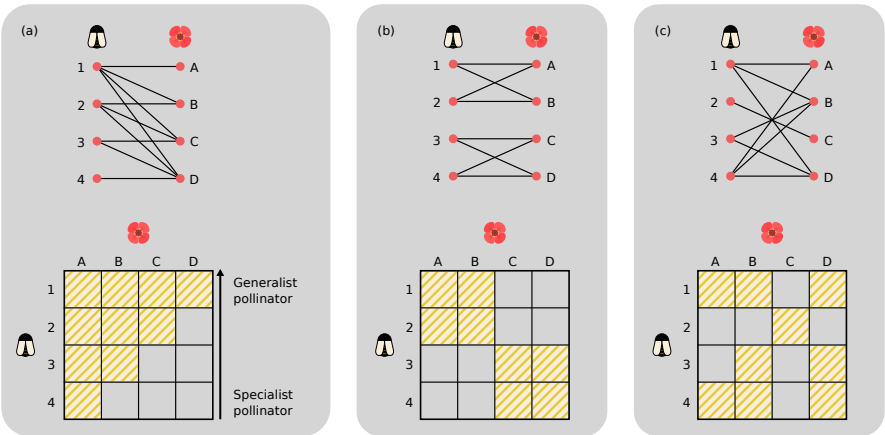

Figure 2: Network topology, example of a fictional plant-pollinator network. (a) shows a perfectly nested network, where specialists pollinators are visiting plants embedded into the diet of more generalist pollinators. (b) shows a perfectly modular network, where sub-groups of species interact more strongly with each over than with the rest of the network. (c) shows a random network. Two representations are possibles. Top: Bipartite representation using nodes and edges ; Bottom: Ordered interaction matrix. Here, we used striped yellow squares instead of 1 for presence of interaction and empty squares in absence of interaction.

nection between three or more nodes in networks at a frequency significantly higher than those found in randomized networks. Three-species motifs represent the simplest building blocks of networks, and more importantly the typical interaction found in communities. As such, they offer the possibility to integrate and test theories developed on simple modules (*e.g.* omnivory, McCann et al. (1998), Holt (1997)) in larger, more realistic networks. Food webs, for example, 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). Stouffer and Bascompte (2010) 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).

Another invariant network property lies in species phylogeny. Phylogeny is a key determinant of ecological network structure, allowing the understanding of species position and interactions into the community. Phylogenetically close species indeed inherit traits from their common ancestors (*e.g.* body size, habitat, defensive strategy, metabolic type, phenology), 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*]. However, every species role, such as host or parasite in antagonistic interaction, prey or predator in food web and plant or pollinator/seed disperser in mutualistic interaction, do not provide the same links structure. For instance, closely related host tend to share parasites, while closely related parasites, because of competition for resources, tend to have different hosts species [*ref*]. The conservatism of interactions is consequently unequal all over the network. Following the logic that closely related species interact with the same group of species, (**???**) shown that phylogenetic structure of ecological networks explains almost entirely the formation and composition of modules in the network, 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 [*ref*], and species that are modules connector are usually phylogenetically close. Cattin et al. (2004) also found, using a niche-hierarchic model, that diet is constrained by the phylogenetic origin of consumers. The nested structure of trophic networks, generated by the diet structuration, is then influenced by the phylogenetic signal of interacting species and the compatibility of their traits. In contrast, the nested structure of mutual-

istic networks would be a consequence of trait complementary between species [*ref*]. For now, mechanisms underlying the nestedness-phylogeny relationship remain to be further investigated. Moreover, because of species plasticity, phylogeny alone does not fully the structure and evolution of ecological networks.

From structure to properties

The relationship between ecological network structure and stability remains a main topic of discussion. First, (**???**) and Elton (1958) observed in natural ecosystems that diverse communities have a more stable dynamic than simple ones. Using a mathematical model based on random ecological networks, May (1972) undermined this hypothesis. Taking into account not only species diversity but also the connectance and the interaction strengths in the network, he found that, contrarily to the way of thinking at this time, diversity was destabilizing communities. This kick in the anthill was the beginning of a prolific complexity-stability debate, highly oriented on trophic networks (**???**; see Allesina and Tang, 2015). Two different approaches of the stability have emerged: one based on the general complexity-stability relationship and dynamics among species in communities and the second one based on the communities ability to resist biotic and abiotic changes. The both use different notions and definitions of stability, inducing different ways to study it (see **???**). Despite their dissimilarities, these approaches are not totally independent and have allowed highlighting that species diversity has no direct influence on communities stability. However, the structure of ecological network such as interactions distribution and strength seems to play a crucial role (**???**). The links distribution of ecological networks follows a power-law distribution [*ref*], meaning that few species are highly connected to the rest of the community and a large number of species are weakly connected to others. This organization combined with the myriad of weak interactions found across ecological networks, called the weak interaction effect [*ref*], buffers species variations and then stabilizes the entire community (Bascompte et al., 2005; Jacquet et al., 2016). Other parameters, such as the predator-prey body-mass ratio (Brose, Jonsson, et al., 2006; Emmerson and Raffaelli, 2004) or network architecture (**???**; Thébault and Fontaine, 2010), determine the distribution and strength of interactions and then contribute to the stability of ecological networks.

Perturbations in ecological communities, generally caused by landscape fragmentation, habitat loss, species loss or invasion, induce a decrease of species diversity. This loss of diversity is explained by extinctions of species due directly or indirectly to a first species loss (*i.e.* secondary extinctions or cascade of extinctions). These extinctions are used to measure the robustness of ecological communities and to explore what happen when a species is removed or changed in a network. The use of dynamic-based models led to highlight the fact that the probability of secondary extinctions increases with the community

size (**???**), and decreases with the network connectance (Dunne et al., 2002). Then, the focus on species removal have allowed to understand that the loss of an highly connected species, also called hub, induces a higher rate of secondary extinctions than the loss of a random, weakly connected species (Solé and Montoya, 2001). However, even if a species is weakly directly connected, if it represents a highway of energy-flow in the network (carbon, nitrogen or biomass), its loss will have similar impact in term of secondary extinctions than the loss of an hug (Allesina and Bodini, 2004). The network architecture also affects the community response to perturbations. For instance, thanks to their structural properties (hight nestedness and connectance, Jordano et al. (2003)), mutualistic networks persist longer than randomly structured networks (**???**; Memmott et al., 2004). On the other hand, presence of modules in the community structure limits propagation of perturbations across the rest of the network and then secondary extinctions (Stouffer and Bascompte, 2010).

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 biodiversity-ecosystem functioning (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). 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. Analyses performed on simulated food-webs with unchanged diversity have already 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 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.

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, 1938) – 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 straightforward, both in terms of directionality and intensity,

as there is different types of interactions and multiple factors influence their probability of occurrence 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):

$$\frac{1}{N_i}\frac{\mathrm{d}}{\mathrm{d}t}N_i = r_i \times \sum_j A_{ij}\alpha_{i,j}N_j$$

wherein the adjacency matrix A $(n * n)$, list the realized interactions in a given community composed of n species. $A_{ij} \neq 0$ when species i and j interact and 0 otherwise. α_{ij} quantifies the strength of the interaction. This equation model populations abundance N but 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 where 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 very small compared to that of abiotic conditions, and thought to only be important locally (Boulangeat et al., 2012; Pearson and Dawson, 2003). Empirical observations of species-environment relationship are then used to understand species physiological tolerance to environmental conditions and potentially predict their range under different scenarios of climate change (e.g. Araújo et al., 2006). While these climate envelope models provide a useful approximation of species potential distribution (Pearson et al., 2002), 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; Araújo et al., 2011; Davis et al., 1998; Gotelli et al., 2010; Heikkinen et al., 2007). 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 sheding light on the the fundamental processes underlying species distribution and thus making more accurate predictions (Cazelles et al., 2016). Additionally, Poisot et al. (2017) recently showed that biotic interactions respond to environmental conditions on their own, independently of species.

Ecological networks also offer an ideal framework to study the conditions for the maintenance of biodiversity in communities through species coexistence. Gause (1934) predicted that species that shared similar ecologies could not live together in the same area. This competitive exclusion principle states that the the strongest competitor will eventually come to dominate the other species and drive them to local extinction. This stands in contradiction with the existence of ecological communities containing species that overlap in some extent in their resources or consumers. Phytoplanktonic communities are a paradigmatic example of this paradox (Hutchinson, 1961), as they exhibit a high biodiversity while species are competing for a limited number of shared resources (e.g. light, nitrate). The use of consumer-resources models has allowed to highlight some mechanisms improving species coexistence (Chesson, 2000). These mechanisms are based on species traits that either decrease fitness differences (equalizing mechanisms) and/or increase niche differentiation between species (stabilizing mechanisms). The coupling of this type of model with the representation of ecological communities as their underlying network of interactions has brought new perspective on species coexistence, as it is allowing to integrate these mech-

anisms in large realistic communities. Using this methodological framework, Martinez et al. (2006) showed that the global non-random structure of the food webs improved community persistence. The distribution of motifs in food webs (Stouffer and Bascompte, 2010, see section "Invariants in ecological networks") as well as species' role within motifs (Stouffer et al., 2012) are related to community persistence. In mutualistic networks, the nested structure has been shown to minimize competition relatively to competition (Bastolla et al., 2009; Sugihara and Ye, 2009). In these networks, the asymmetry of dependences – the fact that when one species A depends strongly on another species B as resource for food or pollination, the other species (B) only weakly depends on A – also increase persistence (Bascompte et al., 2006). This type of approach also allowed to highlight the interplay between traits and structure. As an example, Brose, Williams, et al. (2006) showed that the allometric scaling of metabolic rates of species improve community persistence when the organization of the food webs is such that predator–prey body mass ratios are different from zero.

As for the species coexistence, ecologists have questioned the way communities are formed and the hypothetical set of rules embedding this assembly. Diamond (1975) have defined emblematic rules to understand community structure and assembly. In this continuity, network framework allows to explore in detail processes influencing ecological communities assembly. Capitán et al. (2009), for instance, have retraced the pathway, step by step, of the community assembly process through an assembly graph, based on the graph theory. For food webs especially, mechanistic models such as niche model (**Williams–Martinez2000**) and the cascade model (**Cohen1989**) originally constructed to understand networks structure, have actually be used to understand community assembly [*ref*] and the impact of invasion. Using also network framework, **Verdu-and-Valiente-Banuet(2008)** found that nested community provides generalists species which facilitate the presence of other species into the network. At the same time, thanks to an experimental network study, **Olesen-et-al2008** have observed that new arrival species tend to interact more easily with already well-connected or generalist species. These kind of results could let us think about the Drake's controversial idea Drake (1991) that species arrival history would be a *important* factor driving community assembly (Drake, 1991). Thanks to community network, Campbell et al. (2011) shown that history assembly process is and important factor for mutualistic networks. Community assembly have however, a myriad of different drivers, such as dispersion, interaction strength and phylogeny distance between species composing communities (Kraft et al., 2007; Leibold et al., 2017; Maherali and Klironomos, 2007; Montoya and Solé, 2003). Based on these drivers, two distinct types of models have been developed to predict community assembly dynamics (Gravel et al., 2006; Souza et al., 2016; Tilman, 2004). In one hand, niche-based theory models use coexistence theory and niche differentiation. In the other hand, neutral theory models are based on species dynamics (migration, extinction and speciation) under stochastic processes. Theses two types of model are actually complementary, offering processes explanation at the metacommunity level (niche theory)

and at the phylogenetic level (neutral theory) [*ref*]. Network framework in community assembly have brought the field one step further and makes links between other ecological fields, such as disassembly prediction (see **Bascompte-Stouffer2009**) or co-evolutionary processes (**Nuismer-et-al.2012**) much more easier.

Conclusion

As networks and graph theory allowed to understand breakdown into electricity system in United States [*ref*] or the structure and functioning of social network, it is also a powerful tool to investigate ecological questions. As long as the studying system contains interactions, links or connections, the graph theory provides a perfectly adapted simple framework to characterize complicated networks such as ecological networks. Indices such as connectance, degree distribution of network topology serve as basic measurements to describe systems. Using theses indices, this framework facilitates comparison between different ecological networks. And the relatively important number of network studies leads to a myriads of ways to sample, analyze and interpret them [see *Delmas_et_al._2017*].

Studying ecological networks have however a larger purpose than just their description and classification. Basic measurements are correlated to several environmental factors and network analysis appears to be helpful in different ecological fields. As we seen through this paper, it can be used to study dynamics of ecological systems and their responses to changes, according to their stability over time or the BEF relationships in the system. It also highlight the understanding of mechanisms underlying ecological properties such as community assembly, coexistence and species distribution. *Network studies were a key to reveal relationships between different properties of ecological network such as trait and structure.

Glossary

Adjacency matrix: square matrix representing species interactions. If two species i and j interact, the intersection of the matrix at i, j will be 1, and if no interaction.

Assembly rules: Ecological processes that lead to a specific species' composition of a community, *e.g.* competition, predator-prey interactions, arrival history, etc.

Bipartite / Unipartite network

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

Ecosystem functioning: Biotic and abiotic processes that regulate ecosystem, allowing energy and matter flux between trophic levels and between ecosystems, *e.g.* biogeochemical cycles.

Graph theory: Mathematical framework used to model the relationship between the objects of a network

Jacobian matrix

Network structure: General shape of a network. It is commonly measured using connectance, link distribution, general architecture (nestedness and modularity), etc.

Nodes/Links, Vertices/Edges: Following graph theory, species are represented as nodes (or vertices), and interactions between them are represented by links (or edges).

Phylogenetic signal: tendency of phylogenetically close species to have similar traits.

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