Complex Ecological Networks

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Ecological networks provide a useful abstraction of ecological systems, representing them as graphs, composed of nodes (species) and edges (interactions). This allows to use a whole new set of measures extended from graph theory, to study ecological systems. In this chapter, we review some of the most prominent findings and areas of research from the last decade. We start by reviewing how it was used to uncover invariance in the organization of ecological systems. Then we show the importance of structure when studying systems dynamics and how this coupled approach shed new light on ecosystems emerging properties. Through this chapter we want to highlight the important contribution of networks in clarifying ecosystem properties and functioning, but also the potential to develop new approaches for example for comparing ecosystem structure, relating species traits to community structure.

Keywords: Assemblage - Coexistence - Communities - Graph theory - Network structure - Population dynamics - Species interactions - Stability - -

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1   Glossary

Adjacency matrix: matrix representing species interactions. If two species i and j interact, the intersection of the matrix at i, j will be 1, and 0 if no interaction.

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

Ecological interactions: Every type of contact between two species that alters influencing the fitness of one or the two species. Interactions can be trophic, mutualistic or antagonistic, directed or undirected, weighted or unweighted.

Ecosystem functioning: Biotic and abiotic processes that regulate ecosystems, 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

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.

Unipartite / Bipartite network: The graphical representation of the entire adjacency matrix offers an *unipartite* network representation (see *Figure 1*), where the hierarchy between nodes and their position into the network is not always visible. On 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).

2   Nomenclature

N population size

r growth rate

A adjacency matrix

α interaction strength

3   Introduction

Interactions between components of ecological systems, such as species in a community, (*e.g.* species) are organized non-randomly and constrained by sets of rules. The organization of these interactions drives some properties of the community such as stability, productivity, and the ability to resist extinctions, all of which eventually feedback on the system organization. The constant interplay between the organization of interactions and system dynamics constrains its structure. 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 organization of interactions in a community is best represented as a network. *Graph theory* is a field of mathematics developed to analyze the structure of such systems. Every community can be abstracted by a *graph*, a representation of the system components and their arrangement(*Figure 1a*). These components are called *nodes* and are linked together by *edges*. 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, 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 in the *adjacency matrix* (typically named *A*, see definition in glossary) (*Figure 1b*). In this chapter, for simplicity, we

will focus mostly on *Species Interaction Networks* (SIN). Ecological systems such as landscape, genetic or nutrient networks are not represented here, but they can be studying using the same framework 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 community dynamics and 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 and spatial scales.

[Figure 1 about here.]

3.1   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) (*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) shown 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 becomes the opposite: networks with a

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large number of interactions are either nested (and not modular) or modular (and not nested). In the recent 91
years, it emerged that many aspects of network structure covary with connectance (Poisot and Gravel, 2014; 92
Chagnon, 2015), suggesting that simply knowing how many species there are, and how many interactions they 93
establish, is already very informative about the network structure. 94

[Figure 2 about here.] 95

Another remarkable generality of network structure is the distribution of particular interconnection between 96
three-species subsets. Milo (2002) found that networks (not just ecological but other types of networks such as 97
neuronal or electronical networks as well) can be characterized by the over or under representation of some of 98
these three-species subset, which they called motifs (*Figure 1e*). Motifs can be more broadly defined as specific 99
shapes of interconnection between three or more nodes in networks. The frequency at which they occur in a 100
network can be computed and compared to randomized networks in order to reveal significant aspects of 101
structure. Three-species motifs represent the simplest building blocks of networks, and more importantly 102
typical interaction modules found in communities. As such, they offer the possibility to integrate and test 103
theories developed on with simple models (*e.g.* omnivory, McCann *et al.* (1998), Holt (1997)) in larger, more 104
realistic networks. Food webs, for example, are characterized by an over representation of linear food chains 105
and omnivory and an under representation of apparent and exploitative competition (Bascompte and Melián, 106
2005; Camacho *et al.*, 2007). Stouffer and Bascompte (2010) found that this distribution promotes stability in 107
food webs, with over-represented motifs being more stable in isolation and correlated with higher stability in 108
large realistic communities, and conversely. Motifs can also be used to characterize species role in networks. 109
From the 13 different three-species motifs emerge 30 unique positions for species to occupy in these motifs, 110
representing how the species is embedded in its community. The different positions a species will occupy, and 111
the frequency with which it will occupy these different positions in networks are called species motif role 112
(Stouffer *et al.*, 2012). These roles have been shown to be evolutionary conserved in food webs (Stouffer *et al.*, 113
2012) and to have less variability in time than expected in host-parasitoids bipartite networks (Baker *et al.*, 114
2015). 115

Another invariant network property relates to evolutionary history. Phylogeny is a key determinant of ecological 116
network structure, being related to species position and interactions into the community. Phylogenetically 117
close species indeed inherit traits from their common ancestors (*e.g.* body size, habitat, defensive strategy, 118

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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 (Fontaine and Thébault, 2015). However, every species role –
e.g. host, parasite, pollinator, etc. – does not result in the same links organization. For instance, closely related
hosts tend to share parasites, while closely related parasites, because of competition for resources, tend to have
different hosts (Krasnov *et al.*, 2012). 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, Rezende *et*
al. (2009) shown that phylogenetic structure of ecological networks explains almost entirely the formation
and composition of modules and the connections between them. 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 (Krasnov *et al.*, 2012), 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 mutualistic networks would be a consequence of trait complementary
between species (Rezende *et al.*, 2007). For now, mechanisms underlying the nestedness-phylogeny relationship
remain to be further investigated. Moreover, because of species plasticity, phylogeny alone does not fully
explain the structure and evolution of ecological networks.

3.2   From structure to properties

The relationship between ecological network structure and stability is a long-lasting object of discussion.
MacArthur (1955) and Elton (1958) first proposed that diverse communities should have a more stable dynamic
than simple ones because disturbances are more easily spread through highly connected nodes. May (1972)
countered this hypothesis using a mathematical model based on random ecological networks and proposed
there should be a limit to ecosystem complexity. This counter-intuitive proposition sparkled live debates
still lasting today (McCann, 2000; see Allesina and Tang, 2015). Two different approaches to the problem
followed: one focused on dynamical stability and the other on the resistance of communities to changes in
the environment. Despite their dissimilarities, these approaches are not totally independent and revealed
that species diversity has no direct influence on community stability. However, the structure of ecological

network such as the distribution of interaction strength and network topology seems to play a crucial role [147] (Yodzis, 1981). As mentioned above, the degree distribution of ecological networks often follows a power-law [148] distribution (Montoya and Solé, 2002), indicating that few species are highly connected to the rest of the [149] community and a large number of species are weakly connected to others. This organization combined with [150] the myriad of weak interactions found across ecological networks buffers species variations and stabilizes [151] the entire community (Bascompte *et al.*, 2005; Jacquet *et al.*, 2016). Other aspects of community structure, [152] such as the predator-prey body-mass ratio (Emmerson and Raffaelli, 2004; Brose *et al.*, 2006a) and network [153] architecture (Montoya *et al.*, 2006; Thébault and Fontaine, 2010), determine the distribution and strength of [154] interactions and together drive the stability of ecological networks (Jacquet *et al.*, 2016). [155]

Perturbations in ecological communities such as landscape fragmentation, habitat loss, or species invasion, [156] are the primary drivers of species loss. Extinctions may happen directly, for instance if a particular habitat [157] is eliminated, or indirectly following a first species loss (a phenomenon referred as secondary extinction [158] or cascades). Such extinctions are used to measure the robustness of ecological communities. Simulation [159] experiments revealed that the likelihood of secondary extinctions increases with community size (Lundberg *et* [160] *al.*, 2008), decreases with network connectance (Dunne *et al.*, 2002) and primarily affects the most isolated [161] species in the network. The loss of an highly connected species, also called a hub, induces a higher rate of [162] secondary extinctions than the loss of a random and weakly connected species (Solé and Montoya, 2001). [163] Similarly, species responsible for important energy-flow in the network (carbon, nitrogen or biomass) can [164] trigger secondary extinctions (Allesina and Bodini, 2004). [165]

The network architecture also affects the community response to perturbations. In agreement with MacArthur's [166] intuition, it was found that species with low degree also more strongly propagate perturbations following [167] permanent changes in the environment because of their tight connections (Montoya *et al.*, 2009). Alternatively, [168] the most connected species (hubs) diffuse such perturbations through the network and even though they affect [169] more species, their average effect on other ones is much smaller. Overall network properties also affect the [170] response to perturbation. Thanks to their structural properties (high nestedness and connectance, Jordano *et* [171] *al.* (2003)), mutualistic networks persist longer than randomly structured networks (Memmott *et al.*, 2004 ; [172] Fortuna and Bascompte, 2006). On the other hand, presence of modules in the community structure limits [173] propagation of perturbations across the rest of the network and, as such, secondary extinctions (Stouffer and [174] Bascompte, 2010). [175]

Eluding the consequences of biodiversity lost for ecosystem functioning has been a central problem for ecologists over the last three decades. The hypothesis that an increase in species diversity results in an increased productivity dates back to Darwin (Darwin, 1859) and a formal theory for what is now called the biodiversity-ecosystem functioning (BEF) relationship was proposed in the mid 90s. In a trophic group (*i.e.* a group of species that all belong to the same trophic level, *e.g.* producers or herbivores), increasing diversity improves resource use efficiency and translates into larger productivity (Loreau, 2010) (*e.g.* nutrients for producers, or producers for herbivores). 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 (Harvey *et al.*, 2013), 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 developed for trophic group and for simple modules or sub-systems (Gravel *et al.*, 2016). 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 fixed species richness have shown that interactions, and more specifically their structure, have a significative influence on productivity (Thebault and Loreau, 2003; Thébault *et al.*, 2007; Poisot *et al.*, 2013). The structure of interactions is indeed a reflection of community properties, indispensable for the ecosystem functioning (see other sections). It seems then essential to integrate it in BEF relationship studies.

4   Mechanisms underlying pairwise interactions

Ecological interactions should be viewed as the result of lower level processes impacting pairs of individuals. A pollinator is able to effectively reach the nectar in a plant because their respective traits match, they have compatible phenologies, and 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 of two organisms in order for an interaction between them to exist.

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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) pointed out that interactions are happening between individuals, and as a consequence, it requires to consider not only how the traits are distributed at the individual scale, but also how different behaviors may allow organisms to overcome some of the forbidden interactions.

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) revealed that realistic food webs can be predicted with only knowledge of abundances. 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 their variability (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 has, by definition, an effect on populations dynamics. But it is also archetypical of complex system dynamics, where low level processes propagate up to higher level of organization and impact emerging properties of the community. 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 processes (Chesson and Kuang, 2008). That population 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 the entire set of interactions to understand population, community and ecosystem dynamics. But the effect of interactions on dynamics is not always straightforward to elude, both in terms of directionality and intensity, as there is different types of interactions and multiple factors influencing their occurrence and strength. Including interactions in population dynamics analyses is often done using models of the following general form:

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

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wherein the adjacency matrix A ($n * n$) lists the realized direct 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)).

5   DG: j'ai l'impression que l'histoire est incomplète. À quoi sert le modèle ?

Un point intéressant à révéler est que cette matrice peut être utilisée de nombreuses façons. Pour documenter les interactions directes et la structure du réseau (soit en utilisant A directemetn ou par un transformation binaire), en l'inversant pour obtenir les interactions indirectes, ou encore en calculant ses valeurs propres pour étudier sa stabilité et sa réactivité.

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.

5.1 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 on distribution is very small compared to that of abiotic conditions, and as such is important only locally (Pearson and Dawson, 2003; Boulangeat *et al.*, 2012). Empirical observations of species-environment relationship are used to approximate 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 (Davis *et al.*, 1998; Araújo and Luoto, 2007; Heikkinen *et al.*, 2007; Gotelli *et al.*, 2010; Araújo *et al.*, 2011).

It was proposed the role of interactions in shaping species distribution could be approximated from co-occurrence data (Araújo *et al.*, 2011). This approach is particularly popular to reconstruct microbial interaction networks (e.g. REF). More recently, joint species distribution models (JSDM) were developed to account simultaneously for the effect of the environment and co-distribution (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). Further work is therefore needed to move from correlative species distribution models (SDM) toward more theoretically sound models. 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, 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 resources ecologies could not live together in the same area. The competitive

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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 often considered to illustrate 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). Species coexistence mechanisms (Chesson, 2000) are based on species traits that either decrease fitness differences (equalizing mechanisms) and/or increase niche differentiation between species (stabilizing mechanisms).

The coexistence theory and the representation of ecological communities as networks of interactions has brought new perspective on species coexistence. Martinez *et al.* (2006) for instance showed that the global non-random structure of the food webs improve 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 minimizes competition relative 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 highlighted the interplay between traits and structure. As an example, Brose *et al.* (2006b) showed that the allometric scaling of metabolic rates of species improve community persistence and its overall diversity..

Ecologists have also questioned the way communities are formed and the hypothetical set of rules embedding this assembly. The network approach allows to explore in details the different processes influencing ecological communities assembly. Capitán *et al.* (2009), for instance, have characterized the sequence of community assembly with an assembly graph. It allows to follow step by step every possible path in community assembly from 0 to *x* species among several trophic levels, and to highlight underlying mechanisms. As mechanism, (Verdú 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 al.*, 2008) have observed that newly arriving species tend to interact more easily with already well-connected or generalist species. Such results could let us think about the Drake's controversial idea that species arrival history would be an *important* factor driving community assembly (Drake, 1991). This proposition was supported by network analyses, such as in Campbell *et al.* (2011) for mutualistic networks, but

still remains in debate.

The use of semi-mechanistic models of food web structures such as niche model (Williams and Martinez, 2000) and the cascade model (Cohen, 1989) to understand the impact of invasion on communities assembly, seems to have launched the investigation of community assemblage dynamics. The addition of diverse communities assembly drivers, such as dispersion, interaction strength and phylogeny distance between species composing communities (Montoya and Solé, 2003; Kraft *et al.*, 2007; Maherali and Klironomos, 2007; Leibold *et al.*, 2017) opened the way to new different types of models (Tilman, 2004; Gravel *et al.*, 2006; Souza *et al.*, 2016). 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). These models, coupled with a network framework, have brought the community assembly field one step further and make links between other ecological fields, such as disassembly prediction (see Bascompte and Stouffer, 2009) or co-evolutionary processes (Nuismer *et al.*, 2013) much more easier.

5.2   Conclusion

As networks and graph theory allowed to understand breakdown of the electricity distribution system in United States 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, graph theory provides a perfectly adapted simple framework to characterize complex systems such as ecological networks. Indices such as connectance, degree distribution or network topology serve as basic measurements to describe systems. Using theses indices, this framework facilitates comparison between different systems. Nowadays, 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 chapter, 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 highlights 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.

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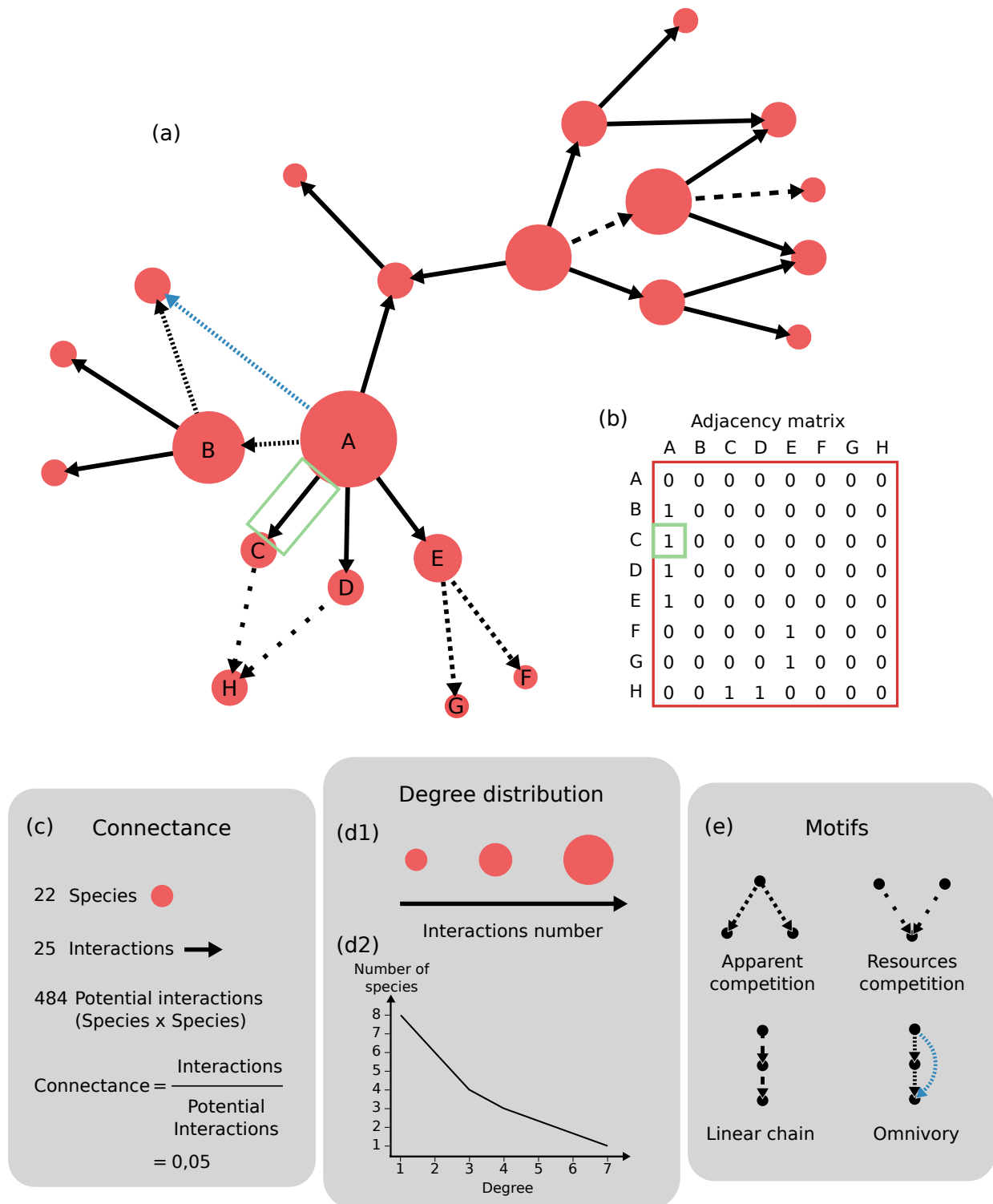
List of Figures

Figure -1 Graphical representation of an ecological network (a), where species are represented by circles and their directed interactions by arrows. The representation is formalized in 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 facilitates computation of 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.
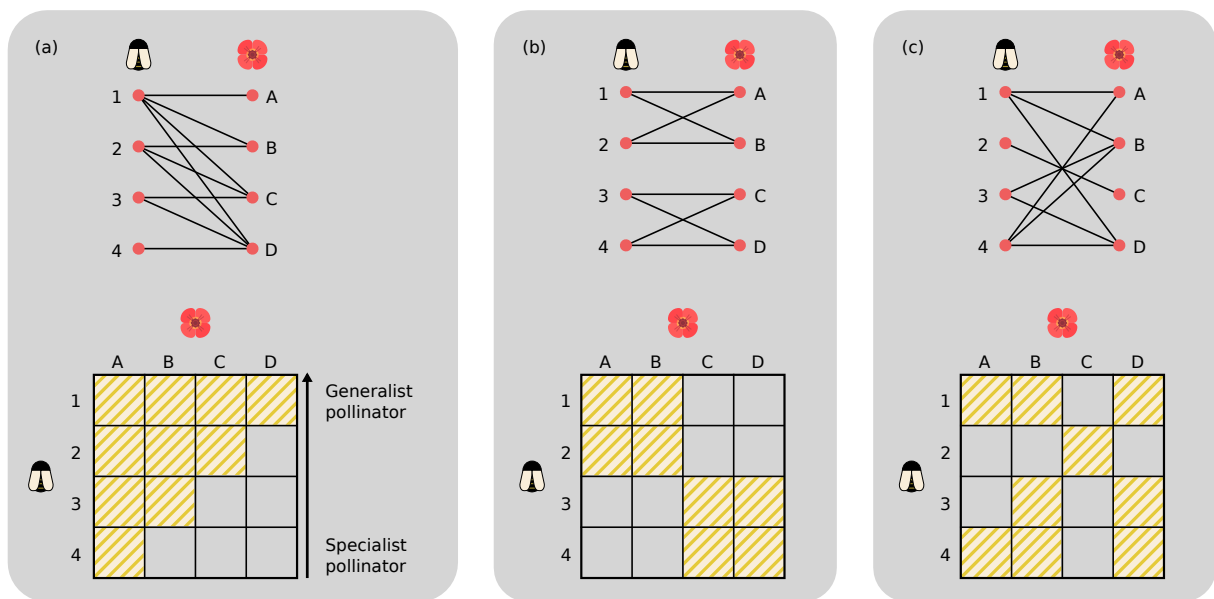
Figure 0 Network topology, example of a fictional plant-pollinator network. (a) shows a perfectly nested network, where specialists pollinators are visiting plants embedded into the diet of more generalist pollinators. (b) shows a perfectly modular network, where sub-groups of species interact more strongly with each over than with the rest of the network. (c) shows a random network. Two representations are possible. 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.