Complex Ecological Networks

Mathilde Besson*
1,2
mathilde.besson@umontreal.ca

Eva Delmas*
1,2
eva.delmas@umontreal.ca

Timothée Poisot
1,2
timothee.poisot@umontreal.ca

Dominique Gravel
2,3
dominique.gravel@usherbrooke.ca

1 - Université de Montréal, Département de Sciences Biologiques
2 - Québec Centre for Biodiversity Sciences
3 - Université de Sherbrooke, Département de Biologie

* These authors contributed equally to the work

Abstract: Ecological networks provide a useful abstraction of ecological systems, representing them as graphs, composed of nodes (species) and edges (interactions). This formalism allows to use a whole 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 sheds new light on emerging properties of ecological systems. 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 to compare ecosystems and to relate species traits to community structure.

Keywords: Assembly, Coexistence, Communities, Graph theory, Network structure, Community dynamics, Species interactions, Stability

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 not.

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

Degree: The degree of a node is its number of links (*e.g.* interactions per species). At higher level, the degree distribution represents the cumulative distribution of links per node within the network or a subnet of the network.

Ecological interactions: Every type of contact between two species that alters the fitness of one or both species. Interactions can be directed or undirected, weighted or unweighted. They usually fall into one on these 5 main classes: competition, predation, parasitism, mutualism and commensalism.

Ecosystem functioning: Biotic and abiotic processes that sustain ecosystems, including flues of energy and nutrients between the components of ecological systems and the resulting stocks, *e.g.* biogeochemical cycles.

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

Network structure: General shape of a network emerging from the organization of the interactions between its components. It is commonly described in ecology using connectance, link distribution, topological indices (such as nestedness, modularity, centrality), 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 (and as a consequence, similar interactions).

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).

Introduction

Interactions between the components of any ecological systems are organized non-randomly. The species that form a community for example do not interact at random. The resulting organization of interactions between species drives some properties of the community such as stability, productivity, and the ability to resist extinctions, all of which eventually feedback on the organization of the system. The constant interplay between the organization of interactions and system dynamics constrains its structure. Studying the structure of ecological systems provides 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*, which is 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 interactions, energetic flues and more generally every kind of interactions. 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 labels (*e.g.* species identity). Specific information can be attached to edges, modifying the characteristics of the graph, *e.g.* the environmental dependence of an interaction. 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 (*Figure 1b*). The adjacency matrix A can be used to answer various ecological questions. Using it directly allows to follow direct interactions and the network structure, and using the inverse of A can be useful to obtain indirect interactions, and even more (Montoya *et al.* 2009).

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 as defined further.

Describing and understanding the structure of SIN is an active, and growing, field of ecological research. We provide here 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.

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, the overall network structure tends to remain unchanged (Kemp *et al.* 2017). Most ecological

networks have a very specific and similar *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 prey 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) showed that this relationship holds even across space; it is possible to estimate how many interactions a species will establish across its entire range. In other instances, networks may differ on some aspects of their structure, despite obeying to a shared underlying principle. For example, Fortuna *et al.* (2010) showed 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 large number of interactions are 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 (Poisot and Gravel 2014; Chagnon 2015), suggesting 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 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 subsets, which they called motifs (*Figure 1e*). Motifs can be more broadly defined as specific arrangements of interconnection between three (or more) nodes. The frequency at which they occur in a network can be computed and compared to randomized networks in order to reveal significant aspects of the structure. Three-species motifs represent the simplest building blocks of networks, and more importantly typical interaction modules found in communities. As such, they offer the possibility to integrate and test theories developed with simple modules in larger, more realistic networks (*e.g.* omnivory, McCann *et al.* 1998, Holt 1997). 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 (*Figure 1a,e*) (Bascompte and Melián 2005a; Camacho *et al.* 2007). Stouffer and Bascompte (2010) found that realistic motif 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 relates to evolutionary history. Phylogeny is a key determinant of ecological network structure, being related to species position and interactions

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into the community. Phylogenetically close species tend to 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, a phenomenon called *phylogenetic signal*. 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, depending in the species role (*e.g.* host or parasite, pollinator or plant) the link organization will be different, leading to an asymmetrical structure for pairwise interactions. 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) showed that phylogenetic structure of ecological networks explains almost entirely the formation and composition of modules and the connections between them. The species connecting modules together are indeed 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 is then influenced by the phylogenetic signal of interacting species and their traits compatibility. 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.

From structure to properties

The relationship between ecological network structure and stability is a long-lasting object of research in community ecology. 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 species lost. Despite their dissimilarities, these approaches are not totally independent (Donohue *et al.* 2013) 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 (Yodzis 1981).

As mentioned above, the degree distribution of ecological networks often follows a power-law distribution (Montoya and Solé 2002), indicating 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 buffers species variations and stabilizes the dynamics of the entire community (Bascompte *et al.* 2005b; Jacquet *et al.* 2016). Other aspects of community structure, such as the predator-prey body-mass ratio (Emmerson and Raffaelli 2004; Brose *et al.* 2006a) and network architecture (Montoya *et al.* 2006; Thébault and Fontaine 2010), determine the distribution and strength of

interactions and together drive the stability of ecological networks (Jacquet *et al.* 2016).

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

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

Eluding the consequences of biodiversity lost for ecosystem functioning is also an important field where the network approach has been useful. The hypothesis that an increase in species diversity results in an increased productivity dates back to 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 blur 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 groups 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 significant 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, essential

to ecosystem functioning. It seems then essential to integrate it in BEF studies.

Mechanisms underlying pairwise interactions

Ecological interactions between species should be viewed as the result of low level processes involving 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. 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 get in contact 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). 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 model interactions based on external information instead of documenting all of them (Morales-Castilla *et al.* 2015).

The realization of an interaction between individuals has, by definition, an effect on population 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 dynamic 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. 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.

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) revealed 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, 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) showed 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 variation in ecological network structure at large spatial scales may 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) and variation in some ecosystem functions (*e.g.* trophic regulation). Until recently, the prevailing idea was that at large spatial 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 species distribution models provide a useful approximation of their potential range shift (Pearson *et al.* 2002), there is mounting evidence 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 macro-ecological scales (Davis *et al.* 1998; Araújo and Luoto 2007; Heikkinen *et al.* 2007; Gotelli *et al.* 2010; Araújo *et al.* 2011).

It was proposed that the role of interactions in shaping species distribution could be approximated from knowledge of species co-occurrence (Araújo *et al.* 2011). This very active field of research has been recently pushed by the development of joint species distribution models (JSDM), which 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 estimating (J)SDM could shed

light on 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. The competitive exclusion principle states that the number of coexisting species should be equal or smaller than the number of resources. 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 (*i.e.* species coexistence). 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 for instance, the nested structure minimizes interspecific competition and increase the number of coexisting species (Bastolla *et al.* 2009; Sugihara and Ye 2009). Interactions structure also tend to impact species coexistence into communities, as highlighted by Bascompte *et al.* (2006), the fact that one species A depends strongly on another species B as resource for food or pollination, and the other species, B, only weakly depends on A, also called asymmetry of dependences, increases coexistence of species. As an other example, using food web structure Brose *et al.* (2006b) showed that the allometric scaling of metabolic rates of species improve community persistence. All these types of approach, whether they are based on motifs, species' role or allometric scaling, have highlighted the importance of network structure in species coexistence.

Ecologists have also questioned the way communities are formed and the hypothetical set of rules embedding their assembly. The network approach allows to explore in details the different processes influencing ecological communities assembly. Capitán *et al.* (2009), for instance, characterized the sequence of species arrival in a community 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. Verdú and Valiente-Banuet (2008), for instance, found that nested community provides generalists species which facilitate the presence of other species into the network. At the same time, Olesen *et al.* (2008) 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 object of debate.

The addition of ecological networks into models of diversity dynamics fostered the development

of theory of community assembly at both, fine and large spatial scales. Niche and neutral theories dominated most of community assembly research since the publication of Hubbell's book in 2001. A wide range of models have been used, most of them with very abstract and phenomenological representations of the niche. But only recently, with the addition of trophic constraints (Gravel *et al.* 2011) and other types of interactions (Cazelles *et al.* 2016) to MacArthur and Wilson's (1967) model of island biogeography, that all types of interactions were considered in the process of community assembly. The model was first extended by assuming that predator could only colonize communities with prey already present, and go extinct with their last prey. This modification was sufficient to explain the observation of a sequential construction of food webs after the defaunation treatment of the famous experiment by Simberloff and Wilson (1969, Petchey *et al.* 2008). The model was further use to illustrate a reciprocal feedback between colonization-extinction dynamics and local food web dynamics, where properties of the regional food web constrain the development of the local motif structure, and alternatively local dynamics influence the assembly process (Massol *et al.* 2017). This modeling approach allows a general representation of the niche in studies of assembly dynamics (Jacquet *et al.* 2017) and propose a unifying framework to explain the construction of local communities from a sample of the regional species pool.

Conclusion

Graph theory delivered important scientific discoveries, such as improved understanding of breakdown of electricity distribution systems or the propagation of infections in social networks. It is also a powerful tool to investigate key questions in ecology. Graph theory provides a remarkably simple way to characterize the complexity of ecological networks. Indices such as connectance, degree distribution or network topology serve as basic measurements to describe their structure. Such indices facilitate comparison between different systems and revealing commonalities and variations. 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 conditions 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.

Further Readings

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Figures

(a)

(b) Adjacency matrix

	A	B	C	D	E	F	G	H
A	0	0	0	0	0	0	0	0
B	1	0	0	0	0	0	0	0
C	1	0	0	0	0	0	0	0
D	1	0	0	0	0	0	0	0
E	1	0	0	0	0	0	0	0
F	0	0	0	0	1	0	0	0
G	0	0	0	0	1	0	0	0
H	0	0	1	1	0	0	0	0

(c) Connectance

22 Species ●

25 Interactions ➡

484 Potential interactions
(Species x Species)

$$\text{Connectance} = \frac{\text{Interactions}}{\text{Potential Interactions}}$$

$$= 0{,}05$$

Degree distribution

(d1)

(d2)

Interactions number

Number of species

Degree

(e) Motifs

Apparent competition   Resources competition
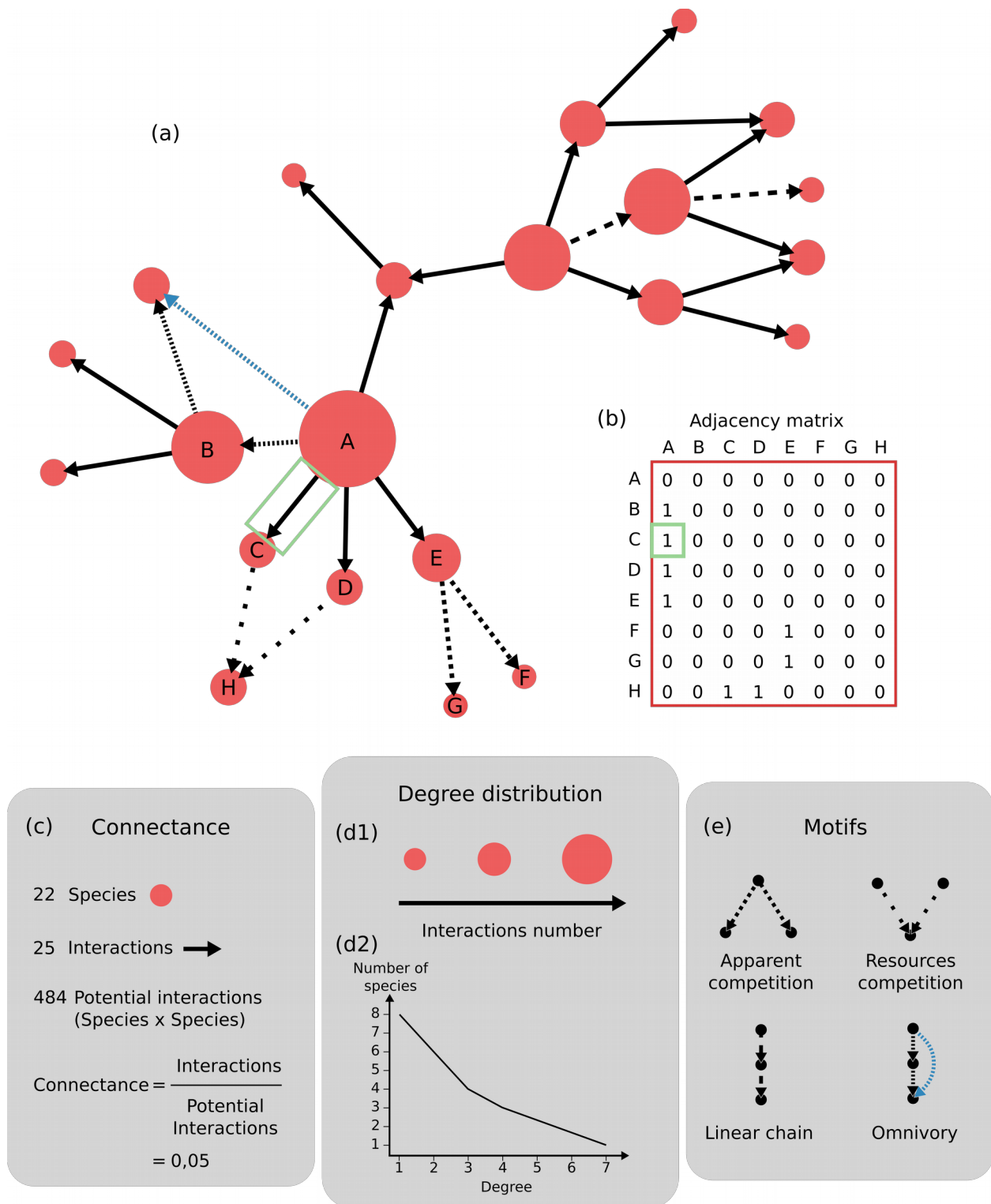
Linear chain   Omnivory

Figure: 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

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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 showed 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.
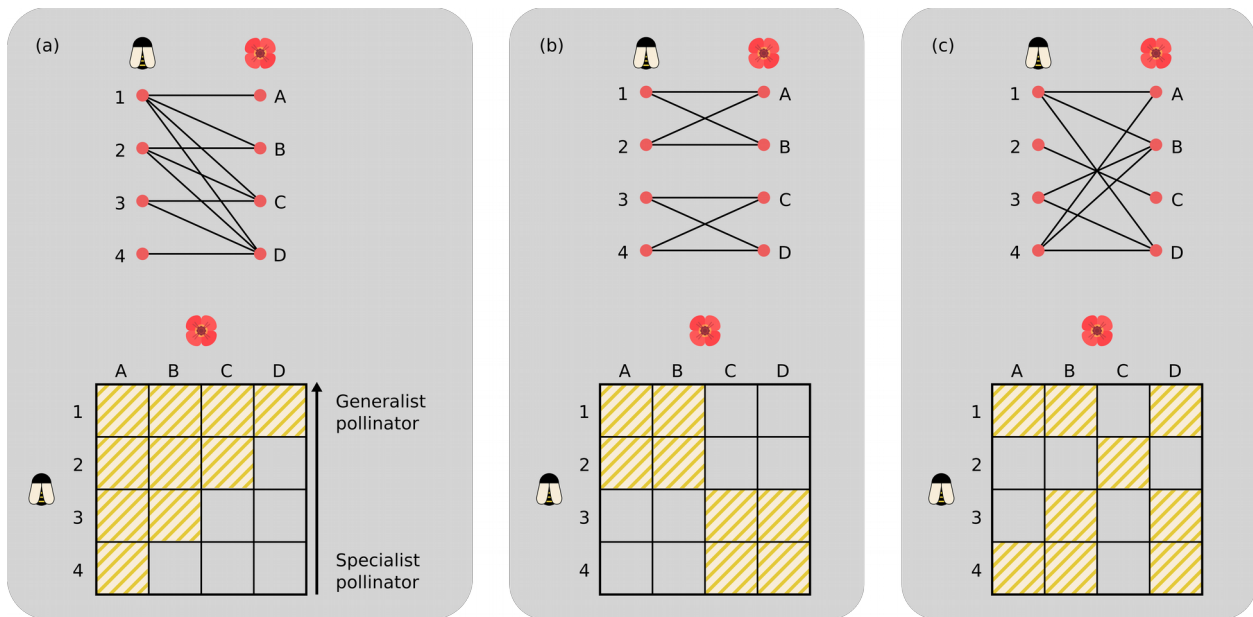
Figure 2: Network topology, example of a fictional plant-pollinator network. (a) shows a perfectly nested network, where specialists pollinators are visiting plants embedded into the diet of more generalist pollinators. (b) shows a perfectly modular network, where sub-groups of species interact more strongly with each over than with the rest of the network. (c) shows a random network. Two representations are 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.