

Introduction

- definition
- domains + questions
- other uses of networks
 - epidemiology
 - animal societies
 - landscape connectivity

Invariants in ecological networks

One striking particularity of ecological networks is their consistency: even though they depict interactions between different organisms across all sorts of ecosystems, they all tend to look the same (Jordano et al., 2003). Remarkably, even when interactions among species themselves vary (see section **x**), the overall network structure tends to remain unchanged (Kemp et al., 2017). Most ecological networks have a very specific degree distribution (Williams, 2011), whereby most species have a small number of interactions, and a small proportion of species have a large number of interactions. In food webs, which represent interactions between preys and their predators, there is a well-described relationship between the number of species and the number of interactions: the number of interactions (L) increases proportionally to the number of species (S) raised to some exponent, or $L \propto S^k$. Martinez (1992) suggested that this exponent is approximately equal to 2, *i.e.* the number of interactions is proportional to the squared number of species. Brose et al. (2004) show that this general relationship holds even across space: it is possible to estimate how many interactions a species will establish across its entire range. In some other instances, networks may differ on some aspect of their structure, despite obeying to a shared underlying principle. For example, Fortuna et al. (2010) show that in networks with a low connectance, nestedness (the degree to which the diet of specialists and generalists overlaps) and modularity (the tendency of species to form densely aggregated clusters) are positively correlated. In networks with higher connectance, this became the opposite: networks with a large number of interactions were either nested (and not modular) or modular (and not nested). In the recent years, it emerged that many aspects of network structure covary with connectance (Chagnon, 2015; Poisot and Gravel, 2014): this suggests that simply knowing how many species there are, and how many interactions they establish, is already very informative about the network structure.

Another remarkable generality of network structure is the distribution of particular shapes of interconnection between all three-species subsets. Milo (2002) indeed found that networks (not just ecological but other types of networks such as neuronal or electronical networks as well) can be characterized by the overrepresentation of some of these three-species subset, which they called motifs.

Motifs can be more broadly defined as being particular shapes of interconnection between three or more nodes in networks at a frequency significantly higher than those found in randomized networks. Three-species motifs thus represent the simplest building blocks of networks, and more importantly the typical interaction found in communities. As such, they offer the possibility to integrate theories developed on simple modules (*e.g.* omnivory, (???), Holt (1997)) in larger, more realistic networks. For instance, food webs are characterized by an over-representation of linear food chains and omnivory and an under-representation of apparent and exploitative competition (Bascompte and Melián, 2005; Camacho et al., 2007). (???) found that this distribution promotes stability in food webs, with over-represented motifs being more stable in isolation and correlated with higher stability in large realistic communities, and conversely. Motifs can also be used to characterize species role in networks. From the 13 different three-species motifs emerge 30 unique positions for species to occupy in these motifs, representing how the species is embedded in its community. The different positions a species will occupy, and the frequency with which it will occupy these different positions in networks are called species motif role (Stouffer et al. (2012)). These roles have been shown to be evolutionarily 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)).

- evo/phylogenetic structure **MB**
 - Eklöf et al. (2012) => network structure effect on evolutionary history

From structure to properties

- perturbations/extinctions **MB**

The consequences of the erosion of biodiversity for ecosystem functioning has been for almost three decades a central problematic for ecologists. While the hypothesis that an increase in species diversity results in an increased productivity dates back to Darwin (Darwin, 1859), the emergence of experimental ecology and the shift from observation in natural systems to the quantification of ecology has made possible to develop a quite general theory for what is now called the BEF relationship. In a trophic group (*i.e.* a group of species that all belong to the same trophic level, *e.g.* producers or herbivores), the loss of diversity results in a loss of efficiency to capture the shared resource compartment (Loreau, 2010) (*e.g.* nutrients for producers, or producers for herbivores). This leading to a decrease in productivity or other index of functioning. Yet, when the trophic group under focus is coupled to other(s), the action of diversity on functioning is more variable (Duffy et al., 2007). Top-down and bottom-up controls are examples of mechanisms that modify the action of the diversity at one level on other(s). This makes the BEF relationship unpredictable in real-world communities, composed of several trophic groups that are virtually never

differentiable – as intraguild predation and omnivory 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 group and for simple modules or sub-systems. By mapping transfer of biomass and energy and/or constraints on organism through the different compartments that compose a natural community ecological, networks – and food webs in particular – offer the possibility to perform this integration, reconciling at the same time ecosystem ecology and population ecology. Analyses performed on simulated food-webs with unchanged diversity have shown that interactions, and more specifically their structure, have a significative influence on functioning (Poisot et al., 2013; Thebault and Loreau, 2003; Thébault et al., 2007). The structure of interactions indeed translates the distribution of different types of properties important for ecosystem functioning, such as the presence of omnivory, the generality of species, the modularity of the food-web, etc.

- stability **MB**
– Jacquet et al. (2016)

Linking interactions to ecological mechanisms

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

system, local abundances has also been identified as a key predictor of species interactions (Canard et al., 2014). Speaking more broadly, because interactions emerge from all of these ecological mechanisms, there is a need to develop a deeper understanding of them (Poisot et al., 2015). Beyond the fundamental advance that this represents, this would allow to predict interactions based on external information (Morales-Castilla et al., 2015).

The realization of an interaction between individuals from the same or different populations within a community also have ecological consequences as it modifies the dynamics of at least one of the interacting populations, and through it, the ecosystem emerging properties. If we consider for instance a population A, its dynamics is not the same when it multiplies in isolation – where it can grow exponentially if resources are unlimited (Malthus, 1798) or logistically otherwise (Verhulst, 1838) – or when it is embedded in a real-world community, composed of several species interacting with one another through different mechanisms (Chesson and Kuang, 2008). It can lose individuals to predation, have parasitism increase its death rate and at the same time see its establishment eased through facilitation. It then becomes necessary to account for interactions when studying the dynamic a population, community stability or ecosystem functioning. But the effect of interactions on populations dynamics is not always the straightforward, both in terms of directionality and intensity, as it exists different types of interactions and multiple factors influence their probability and strength. Since the seminal work of May (1972), the analysis of these effects has been a prolific field of ecology, feeding in particular the famous “complexity-stability debate” (see Allesina and Tang (2015) for an overview). Including interactions in population dynamics analyses can be done by using model of the following general form (Poisot et al., 2015):

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

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. We presented here an equation to model populations abundance N but it can easily be adapted to model biomass flows by replacing populations’ abundances by their biomasses B_i (see for instance Williams et al. (2007)).

Ecological networks are also spatially and temporally variable (Trøjelsgaard and Olesen, 2016). There are two drivers to this variability: changes in species composition, and changes in the way these species interact (Poisot et al., 2012). Changes in species alone are able to generate variation in network properties (Havens, 1992). Spatial variation in network structure can also reflect deep-time constraints; for example, Dalsgaard et al. (2013) reveal that historical climate change trends have a signature on the nestedness and modularity of pollination networks. Even when the same species are present, interactions between them

can vary. Carstensen et al. (2014) and Trøjelsgaard et al. (2015) investigated this phenomenon in mutualistic networks. Interaction turnover results from variations in partner fidelity (some species pairs are extremely closely associated), but also from variations in the local environment in which the species interact. Interestingly, and as mentioned in section **x**, networks overwhelmingly tend to conserve their structure even when interactions within them change. Díaz-Castelazo et al. (2010) surveyed a pollination network over 10 years, and found important species turnover during this period. Nevertheless, the network retained its structure because species were replaced by their functional equivalent; a generalist pollinator often succeeded to another generalist pollinator. Conversely, species tend to retain their role in different communities: Baker et al. (2015) show that species keep occupying the same position in the network across space, regardless of the species they interact with at every location.

Section 4

- distributions and species interactions
 - Cazelles
 - Araujo
 - Lessard geographic species pool
- ???
- ???

Conclusion

References

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