

## 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):

$$\frac{dN_i}{dt} = N_i(r_i * \sum_j A_{ij}\alpha_{i,j}N_j) \text{ where } \alpha_{i,j}$$

where 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.  $\alpha_{ij}$  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

- Jordano P, Bascompte J, Olesen JM. Invariant properties in coevolutionary networks of plant–animal interactions. *Ecology Letters* 2003;6:69–81. doi:10.1046/j.1461-0248.2003.00403.x.
- Kemp JE, Evans DM, Augustyn WJ, Ellis AG. Invariant antagonistic network structure despite high spatial and temporal turnover of interactions. *Ecography* 2017;n/a–a. doi:10.1111/ecog.02150.
- Williams RJ. Biology, Methodology or Chance? The Degree Distributions of Bipartite Ecological Networks. *PLoS One* 2011;6:e17645. doi:10.1371/journal.pone.0017645.
- Martinez ND. Constant Connectance in Community Food Webs. *The American Naturalist* 1992;139:1208–18.
- Brose U, Ostling A, Harrison K, Martinez ND. Unified spatial scaling of species and their trophic interactions. *Nature* 2004;428:167–71.

doi:10.1038/nature02297.

Fortuna MA, Stouffer DB, Olesen JM, Jordano P, Mouillot D, Krasnov BR, et al. Nestedness versus modularity in ecological networks: two sides of the same coin? *Journal of Animal Ecology* 2010;79:811–7. doi:10.1111/j.1365-2656.2010.01688.x.

Chagnon P-L. Characterizing topology of ecological networks along gradients: the limits of metrics' standardization. *Ecological Complexity* 2015;22:36–9.

Poisot T, Gravel D. When is an ecological network complex? Connectance drives degree distribution and emerging network properties. *PeerJ* 2014;2:e251. doi:10.7717/peerj.251.

Milo R. Network Motifs: Simple Building Blocks of Complex Networks. *Science* 2002;298:824–7. doi:10.1126/science.298.5594.824.

Holt RD. Community modules. AC Gange, VK Brown (Eds), *Multitrophic Interactions in Terrestrial Ecosystems*, 6th Symposium of the British Ecological Society, Blackwell Science 1997:333–50.

Camacho J, Stouffer D, Amaral L. Quantitative analysis of the local structure of food webs. *Journal of Theoretical Biology* 2007;246:260–8. doi:10.1016/j.jtbi.2006.12.036.

Bascompte J, Melián CJ. Simple trophic modules for complex food webs. *Ecology* 2005;86:2868–73. doi:10.1890/05-0101.

Stouffer DB, Sales-Pardo M, Sirer MI, Bascompte J. Evolutionary Conservation of Species' Roles in Food Webs. *Science* 2012;335:1489–92. doi:10.1126/science.1216556.

Baker NJ, Kaartinen R, Roslin T, Stouffer DB. Species' roles in food webs show fidelity across a highly variable oak forest. *Ecography* 2015;38:130–9. doi:10.1111/ecog.00913.

Eklöf A, Helmus MR, Moore M, Allesina S. Relevance of evolutionary history for food web structure. *Proceedings of the Royal Society of London B: Biological Sciences* 2012;279:1588–96. doi:10.1098/rspb.2011.2149.

Darwin C. *On the Origin of Species by Means of Natural Selection, or Preservation of Favoured Races in the Struggle for Life*. John Murray, London; 1859.

Loreau M. Linking biodiversity and ecosystems: towards a unifying ecological theory. *Philosophical Transactions of the Royal Society B: Biological Sciences* 2010;365:49–60. doi:10.1098/rstb.2009.0155.

Duffy JE, Cardinale BJ, France KE, McIntyre PB, Thébault E, Loreau M. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 2007;10:522–38. doi:10.1111/j.1461-0248.2007.01037.x.

Thebault E, Loreau M. Food-web constraints on biodiversity-ecosystem functioning relationships. *Proceedings of the National Academy of Sciences*

2003;100:14949–54. doi:10.1073/pnas.2434847100.

Thébault E, Huber V, Loreau M. Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure. *Oikos* 2007;116:163–73. doi:10.1111/j.2006.0030-1299.15007.x.

Poisot T, Mouquet N, Gravel D. Trophic complementarity drives the biodiversity-ecosystem functioning relationship in food webs. *Ecol Lett* 2013;16:853–61. doi:10.1111/ele.12118.

Jacquet C, Moritz C, Morissette L, Legagneux P, Massol F, Archambault P, et al. No complexity–stability relationship in empirical ecosystems. *Nature Communications* 2016;7:12573. doi:10.1038/ncomms12573.

Olesen JM, Bascompte J, Dupont YL, Elberling H, Rasmussen C, Jordano P. Missing and forbidden links in mutualistic networks. *Proceedings of the Royal Society of London B: Biological Sciences* 2011;278:725–32.

Bartomeus I. Understanding linkage rules in plant-pollinator networks by using hierarchical models that incorporate pollinator detectability and plant traits. *PloS One* 2013;8:e69200.

Bartomeus I, Gravel D, Tylianakis JM, Aizen MA, Dickie IA, Bernard-Verdier M. A common framework for identifying linkage rules across different types of interactions. *Functional Ecology* 2016;30:1894–903.

Crea C, Ali RA, Rader R. A new model for ecological networks using species-level traits. *Methods in Ecology and Evolution* 2015.

González-Varo JP, Traveset A. The Labile Limits of Forbidden Interactions. *Trends in Ecology & Evolution* 2016;31:700–10. doi:10.1016/j.tree.2016.06.009.

Canard E, Mouquet N, Marescot L, Gaston KJ, Gravel D, Mouillot D. Emergence of Structural Patterns in Neutral Trophic Networks. *PLOS ONE* 2012;7:e38295. doi:10.1371/journal.pone.0038295.

Canard EF, Mouquet N, Mouillot D, Stanko M, Miklisova D, Gravel D. Empirical evaluation of neutral interactions in host-parasite networks. *Am Nat* 2014;183:468–79. doi:10.1086/675363.

Poisot T, Stouffer DB, Gravel D. Beyond species: why ecological interaction networks vary through space and time. *Oikos* 2015;124:243–51. doi:10.1111/oik.01719.

Morales-Castilla I, Matias MG, Gravel D, Araújo MB. Inferring biotic interactions from proxies. *Trends in Ecology & Evolution* 2015;30:347–56. doi:10.1016/j.tree.2015.03.014.

Malthus TR. *An Essay on the Principle of Population, as it Affects the Future Improvement of Society: With Remarks on the Speculations of Mr. Godwin, Mr. Condorcet, and Other Writers.* 1798.

Verhulst P. Notice sur la loi que la population poursuit dans son accroissement.

- In.: Correspondance mathématique et physique, A. Quételet (Brussels); 1838, pp. 10: 113–21.
- Chesson P, Kuang JJ. The interaction between predation and competition. *Nature* 2008;456:235–8. doi:10.1038/nature07248.
- May RM. Will a Large Complex System be Stable? *Nature* 1972;238:413–4. doi:10.1038/238413a0.
- Allesina S, Tang S. The stability–complexity relationship at age 40: a random matrix perspective. *Popul Ecol* 2015;57:63–75. doi:10.1007/s10144-014-0471-0.
- Williams RJ, Brose U, Martinez ND. Homage to Yodzis and Innes 1992: scaling up feeding-based population dynamics to complex ecological networks. In.: *From energetics to ecosystems: the dynamics and structure of ecological systems*, Springer; 2007, pp. 37–51.
- Trøjelsgaard K, Olesen JM. Ecological networks in motion: micro- and macroscopic variability across scales. *Funct Ecol* 2016;30:1926–35. doi:10.1111/1365-2435.12710.
- Poisot T, Canard E, Mouillot D, Mouquet N, Gravel D. The dissimilarity of species interaction networks. *Ecol Lett* 2012;15:1353–61. doi:10.1111/ele.12002.
- Havens K. Scale and structure in natural food webs. *Science* 1992;257:1107–9. doi:10.1126/science.257.5073.1107.
- Dalsgaard B, Trøjelsgaard K, Martín González AM, Nogués-Bravo D, Ollerton J, Petanidou T, et al. Historical climate-change influences modularity and nestedness of pollination networks. *Ecography* 2013;36:1331–40. doi:10.1111/j.1600-0587.2013.00201.x.
- Carstensen DW, Sabatino M, Trøjelsgaard K, Morellato LPC. Beta Diversity of Plant-Pollinator Networks and the Spatial Turnover of Pairwise Interactions. *PLoS ONE* 2014;9:e112903. doi:10.1371/journal.pone.0112903.
- Trøjelsgaard K, Jordano P, Carstensen DW, Olesen JM. Geographical variation in mutualistic networks: similarity, turnover and partner fidelity. *Proceedings of the Royal Society B: Biological Sciences* 2015;282:20142925–5. doi:10.1098/rspb.2014.2925.
- Díaz-Castelazo C, Guimarães PR, Jordano P, Thompson JN, Marquis RJ, Rico-Gray V. Changes of a mutualistic network over time: reanalysis over a 10-year period. *Ecology* 2010;91:793–801.