

Expanding the paradigm of ecological network research

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Working paper

Introduction

Describing the structure of ecological communities requires to know not only the identity of species, but also their interactions. Because interactions drive ecological dynamics within communities (Berlow et al. 2009), their organization will confer certain ecological properties. The structure of interactions has been described by species interaction networks (Dunne 2006), that is, a mathematical and conceptual representation of both *species*, and the *interactions* they establish. This view generated a rich literature primarily focused on how certain mathematical properties of the network related to the robustness (Dunne et al. 2002), productivity (Duffy et al. 2007), or tolerance to extinction (Memmott et al. 2004) of the community it represents. Although this approach classically focused on food webs (Ings et al. 2009), it can be applied equally to all types of ecological interactions (Kéfi et al. 2012). By large, this literature assumes that, short of changes in local densities due to ecological dynamics, networks are *static* objects. If two species are known to interact at one location, it is assumed that they will interact whenever they co-occur (see *e.g.* Havens 1992). Recently, we established that networks are *dynamic* objects, that have structured variation in α , β , and γ diversity, due not only to the change of species composition at different localities, but also to the fact that the same species will interact in different ways over time or space. Of these sources of variation in networks, the change of species composition has been addressed by previous literature (Gravel et al. 2011, Dáttilo et al. 2013). However, because this literature mostly assumes that interactions happen consistently between species, it is ill-suited to address network variation as a whole, and needs be supplemented with new concepts and mechanisms.

In the current paradigm, interactions are established between species. Starting from empirical observations, expert knowledge, or literature surveys, one can collect a list of interactions for a given species pool. Several studies used this approach to extrapolate the structure of networks over space (Havens 1992, Baiser et al. 2012), by considering that the network at *any* location is composed of *all* of the potential interactions known for this species pool. This stands in stark contrast with recent results showing that (i) the identity of interacting species varies over space (Poisot et al. 2012), and (ii) the dissimilarity is not related to the dissimilarity in species composition. The current conceptualization of networks leaves us poorly equipped to understand the causes of this variation, and in this paper we propose a general research agenda to understand the mechanisms involved in the variability of species interactions. We propose that future research on interaction networks be guided by the following principles. First, at the regional scale, species interactions exist in a probabilistic state. Second, the probability that two species will interact can be determined as a function of traits and local abundances. Third, observations of interactions at local sites are the realizations of these regional probabilities. This approach is outlined in **Box 1**. Although this proposal is a major change in the conceptualization of network structure, we show in this paper that it is well supported by empirical and theoretical results alike, and will open the way to the development of predictive approaches integrating over a range of ecological mechanisms.

Recent studies on the sensitivity of network structure to environmental change provide some context for this approach. Menke et al. (2012) showed that the structure of a plant–frugivore network changed along a forest–farmland gradient. Specifically, at the edges between two habitats, species were on average less specialized, interacting more evenly with a larger number of partners, when compared to habitat cores. Even within different forest strata, differing by proximity to the canopy and visitation by birds, differences in network structure were observed (Schleuning et al. 2011). Eveleigh et al. (2007) demonstrated that outbreaks of the spruce budworm were associated to changes in the structure of its trophic network, both in terms of species observed, and their interactions. Poisot et al. (2011) used a microbial system of hosts and pathogens to study the impact of productivity gradients on the realization of infection events. When the species were moved from high to medium to low productivity, some interactions were lost, and some other were gained. These results suggest that the existence of an interaction is not only contingent on the presence of the two species involved, but may also require particular environmental conditions, and

perhaps presence of outside species.

We argue that there are three broadly-defined classes of mechanisms involved in determining the realizations of species interactions. First, individuals must be in high enough local relative abundances to meet (the “neutral” perspective of interactions). Second, there must be phenological matching between individuals, so that once encounter took place, the individuals will actually interact. Finally, the realization of an interaction is regulated by the surroundings of interacting organisms, and should be studied in the context of indirect interactions. We examine each of these mechanisms in turn, and show how they integrate to the proposed statistical framework outlined in **Box 1**. We propose that our understanding of the structure of interaction networks in a spatial context, and consequently our ability to predict this structure, will be increased our attention and methodologies are shifted from a species-centric perspective to a population-centric one.

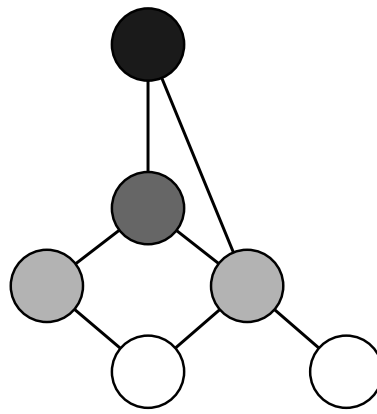
Population dynamics and neutral processes

Over the recent years, the idea of neutrality percolated into the analysis of the structure of ecological networks, most notably in bipartite networks (Blüthgen et al. 2006). For example, re-analysis of several host-parasite datasets showed that changes in local species abundances triggers variation in parasite specificity (Vazquez et al. 2005). Having minimal assumptions about the distribution of species abundance allows predicting the structure of trophic interactions (Canard et al. 2012). In this section, we review recent studies investigating the consequences of neutral dynamics on the structure of interaction networks, and show how variations in population size can lead to interaction turnover.

The basic processes

For an interaction to happen between individuals from two populations, these individuals must first meet, then interact. Assuming that two populations occupy the same locality, and are active at the same time of the day, then the likelihood of an interaction is roughly proportional to the product of their relative abundance. This means that individuals from two large populations are more likely to interact than individuals

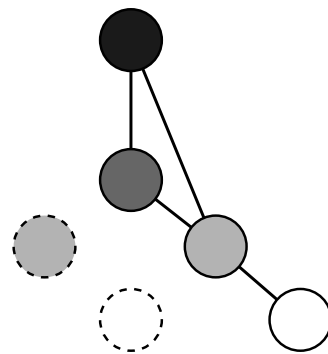
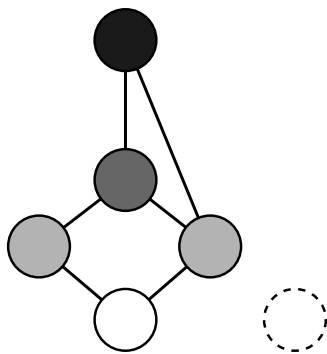
metaweb



Site 1

local species sorting

Site 2



local interaction sorting

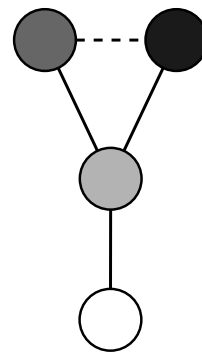
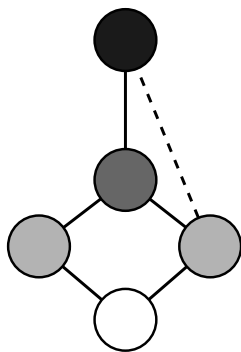


Figure 1: An illustration of the metaweb. In its simplest form, the metaweb is the list of all possible species and interactions between them for the system studied. The interactions could be based on observations or inferred from trait values and previous knowledge [Gravel2013_niche_allometric]. What is observed

from two small populations, simply because their individuals will meet more often. This approach can also be extended to the prediction of interaction strength (Blüthgen et al. 2006, Vázquez et al. 2007), *i.e.* how strong the consequences of the interaction will be. It predicts that locally abundant species should have more partners, and locally rare species should appear locally more specialized. In a purely neutral model (*i.e.* interactions happen entirely by chance, although abundance can be not neutral), the identity of species do not matter, and it becomes easy to understand how this can lead to a situation where, because species vary regionally in abundance, the structure of local networks will vary. Canard et al. (2012) proposed the term of “neutrally forbidden link” to refer to interactions that are feasible from a phenologic standpoint, but not realized because of population size distribution. The identity of these neutrally forbidden links will vary over time and space, either by stochastic changes in population sizes, or because population size respond deterministically to extrinsic drivers. A similar phenomenon was observed by Poisot et al. (2011). A soil community of bacteria (victims) and bacteriophages (enemies) was isolated from its natural environment, and all pairwise interactions were measured along a gradient of decreasing resource availability. The resulting lower abundance of the bacteria significantly decreased the encounter probability of the two species and thereby the network structure. This resulted in a strong link turnover, with some species being able to interact in the resource-rich environment, but not in the resource-poor ones.

Benefits for network analysis

It is important to understand how local variations in abundance, wether neutral or not, cascades to the structure of interaction networks. Simple statistical models can be used to quantify the effect of population sizes on local interaction occurrence or strength (see *e.g.* Krishna et al. 2008 and Box 1). These models can be further extrapolated to remove the contribution of neutrality to link strength, allowing us to work directly on the interactions as they are determined by traits. This allows comparing the variation of neutral and non-neutral components of network structure over space and time. To do so, it is important the future sampling of interaction networks (i) are replicated and (ii) include measurements of population sizes. An additional benefit is that these data will help refining neutral theory: Wootton (2005) made the point that deviations of empirical communities from neutral predictions were most often explained by species trophic interactions, which are notoriously absent from the original formulation of the theory.

Merging the two views will increase our explanatory power, and provide new ways to test neutral theory in interactive communities. This also offers a new opportunity, namely to complete the integration of network structure with population dynamics. To date, most studies focused on the consequence of one species having a particular position within a food web on the dynamics of its biomass or abundance (Brose et al. 2006, Berlow et al. 2009). Adopting this neutral perspective allows to go back, in that the abundance of a species will also dictate its position in the network: changes in abundance can lead to gained or lost interactions, and these changes in abundance are in part caused by existing interactions. For this reason, there is a potential to link species and interactions dynamics, and more importantly, to do so in a way which accounts for the feedback effects. From a practical point of view, this requires repeated sampling of a system through time, so that changes in relative abundances can be related to changes in interaction strength (Yeakel et al. 2012). Importantly, adopting this view will force to reconsider the causal relationship between resource dynamics and interaction strength; in a neutral context, both are interdependent, thus potentially complexifying our view of the feedbacks between them.

Traits matching in space and time

Once individuals meet, whether they will interact is determined by an array of behavioral, phenotypic, cultural aspects, that can conveniently be referred to as “trait-based processes”. Two populations can interact when their traits values allow it, *e.g.* viruses are able to overcome host resistance, predators can capture the preys, trees provide enough shading for shorter grasses to grow. Non-matching traits will effectively prevent the existence of an interaction, as demonstrated by Olesen et al. (2011). Under this perspective, the existence of interactions can be mapped onto trait values, and consequently interaction networks will vary along with variation in local trait distribution. In this section, we review how trait-based processes impact network structure and can create variation, and the perspective they open for an evolutionary approach.

The basic processes

There are evidences that at the species level, interaction partners are selected on the grounds of matching trait values. Random networks built on these rules exhibit realistic structural properties [Willi-

wams_simple_2000]. However, trait values vary from population to population within species, and so it is expected that the local interactions will be contingent upon trait distributions (Figure 2). The fact that the niche of species can appear large if it is the aggregation of narrow but differentiated individual or population niches is now well established (Bolnick et al. 2003, Devictor et al. 2010), and reinforced the need to understand intra-specific trait variation to describe the structure and dynamics of communities (Bolnick et al. 2011). This notion is yet, however, to percolate the literature on network structure, despite an immediate consequence: a species appearing generalist at the regional scale, can be specialized in each of the patches it occupies. There are several examples of intraspecific trait variation resulting in extreme interaction turnover. A particularly spectacular example is described by Ohba (2011): a giant waterbug is able to get hold of, and eventually consume, juveniles from a turtle species. Choh et al. (2012) demonstrated through behavioral assays that preys which evaded predation when young, were more likely to predate juvenile predators, than the “naive” individuals: the past interactions shaped behavioral traits that alter the network structure over time. These examples show that trait-based effects on networks can be observed even in the absence of genotypic variation (although we discuss this in the next section). In this perspective, the existence of an interaction is an emergent property of the trait distribution of local populations: variations in one or both of these distribution, regardless of the mechanism involved (development, selection, plasticity), is likely to alter the interaction. Importantly, when interaction-driving traits are under environmental forcing (for example, body size is expected to be lower in warm environments, Angilletta et al. (2004)), there can be covariation between environmental conditions and the occurrence of interactions. Woodward et al. (2012) demonstrate that changes in food-web structure happen at the same time as changes in body mass in experimental macrocosms. Integrating trait variation over spatial or temporal extents is now central if we are to understand network variation and response to environmental change.

Benefits for network analysis

Linking spatial and temporal trait variation with network variation will help identify the mechanistic basis of network dissimilarity. From a sampling point of view, having enough data require that when interaction are recorded, they are coupled with traits measurements. These measurements cannot merely be extracted from reference database, because as we exposed in the previous section, interactions are driven by *local*

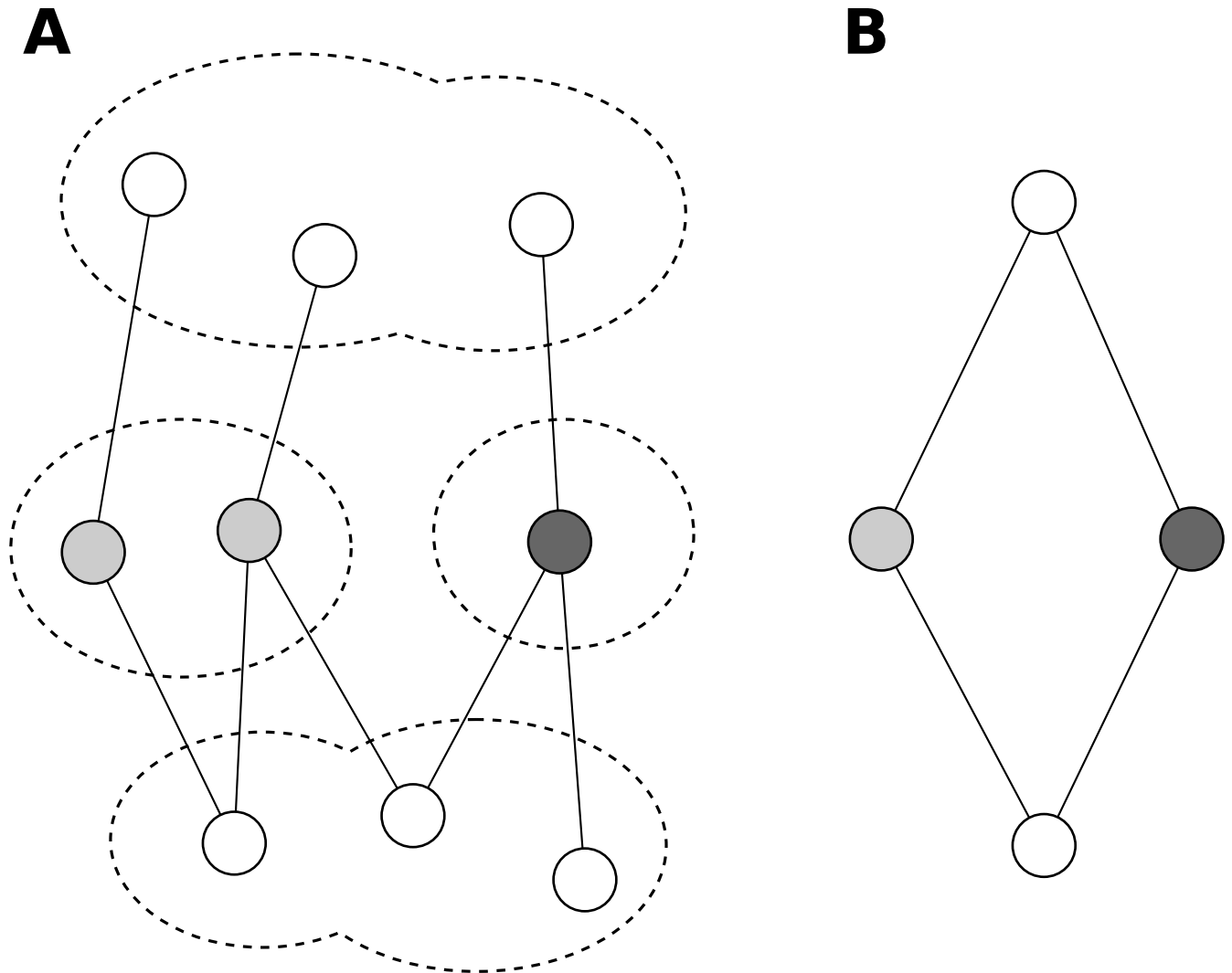


Figure 2: Panel **A** represents the interactions between different populations (circles) of four species, identified by the boundaries of their morphospaces (dashed lines). This network is mostly made of linear food chains, and has one generalist consumer. When aggregated at the species level however, as shown in **B**, it becomes a “diamond” food-web, with different dynamical consequences. Because the trait values of populations within a species differ, each individual population can interact differently than the species it belongs to..

trait values, and their matching across populations from different species. Within the statistical framework presented in Box 1, we can expect that (i) network variability at the *regional* scale will be dependent on the variation of population traits values, and (ii) variation between any series of networks will be dependant by the *covariance* between species traits. This approach, although requiring important quantities of data to test, could allow inferring an *a priori* estimate of network variation. This new generation of data will help relate the variation of network structure to variation of environmental conditions. Price (2003) shows how specific biomechanic response to water input in shrubs can have pleiotropic effects on traits involved in the interaction with insects. In this system, the difference in network structure can be explained because (i) traits values determine the existence of an interaction, and (ii) environmental features determine trait values. Accumulating empirical evidences will increase our ability to come-up with such mechanistic narratives. At a larger temporal scales, current distribution of traits also reflects past evolutionary history (Diniz-Filho and Bini 2008). This offers an opportunity to approach the evolutionary dynamics and variation of networks. Correlations between traits of different species, and between traits and fitness, drive coevolutionary dynamics (Gomulkiewicz et al. 2000, Nuismer et al. 2003). Both of these vary over space and time (Thompson 2005), which creates patchiness in the processes and outcomes of coevolution. Additionally, trait structure and traits correlations are disrupted by migration (Gandon et al. 2008, Burdon and Thrall 2009). Developing an understanding of how ecological and evolutionary trait dynamics affect network structure will provide a mechanistic basis to our interpretation of the historical signal found in contemporary network structures (Baskerville et al. 2011, Eklof et al. 2011).

Beyond direct interactions

In this section, we argue that although networks offer a direct access to direct interactions, there is potential in addressing indirect effects too. A direct interaction originates in the “physical” interaction of two species. For example, predation, or pollination, are instances of direct interactions. Indirect interactions, on the other hand, are established “at a distance”, either through cascading effect (herbivorous species compete with insect laying eggs on plants), or through physical mediation by the environment (bacterial exudates increase the bio-disponibility of iron for all bacterial species; plants with large foliage provide shade for

smaller species). As we discuss in this section, these indirect interactions (i) have relevance for the variation of interaction network structure, and (ii) can be studied using classical network theory formalism.

The basic processes

Several authors (Golubski and Abrams 2011) showed that biotic interactions themselves interact. Because the outcome of an interaction ultimately affects local abundances (on ecological times) and population trait structure (over evolutionary times), all interactions happening within a community will impact one another. Far from meaning that pairwise-centered approaches are bound to fail, this calls for a larger scale approach accounting for indirect effects. The occurrence or absence of a biotic interaction can either affect either the realization of other interactions (thus affecting the “interaction” component of network β -diversity), or the presence of other species, as we will illustrate below. There are several well-documented examples of the presence of an interaction allowing new interactions to happen (opportunistic pathogens have a greater success of infection on hosts which are already immunocompromised by previous infections Olivier (2012)), or conversely preventing them (a resident symbiont decreases the infection probability of a new pathogen (Heil and McKey 2003, Koch and Schmid-Hempel 2011)). In both cases, the driver of interaction turnover is the patchiness of species distribution, emphasizing why the two concepts ought to be integrated. Variation in interaction structure can happen through both cascading and environmental effects: Singer et al. (2004) show that caterpillars change the proportion of different plant species in their diet, favoring low quality items to load on chemical compounds which are toxic for their parasitoids. However, low quality food result in birds having a greater impact on caterpillar populations (Singer et al. 2012). It is noteworthy that in this example, the existence of an interaction will affect both the strength, and impact, of other interactions. In terms of their effects on network β -diversity, indirect effects are thus likely to act on components of dissimilarity. A common feature of the examples mentioned in this part is that pinpointing the exact mechanism through which species interaction interfere requires most often a good knowledge of the system’s natural history. In their current state, ecological networks most often account for a single type of interactions (although new datasets are starting to emerge, *e.g.* Mouritsen et al. 2011 and). Our ability to understand these complex phenomenon will be contingent on our ability to (i) integrate different types of interactions in ecological networks (@goudard_2008_non-trophic; Kéfi et

al. 2012), and (ii) to provide rich meta-data regarding the identity of each node in the network.

Benefits for network analysis

Accounting for the relationships between biotic interactions can be a powerful explanation for species co-occurrence. A recent experimental work by Sanders and van Veen (2012) showed that some predators species can only be maintained if another predator species is present, which regulates a competitively superior prey, hence allowing prey coexistence. These effects involving several species and several types of interactions across trophic levels are complex (and for this reason, have been deemed unpredictable in the past, Tack et al. 2011), and can only be understood by comparing communities in which different species are present/absent.

To better understand these effects, it is important that several networks with similar species compositions are sampled. Assuming that interactions are present is obviously not enough, and the data needed to characterize these mechanism need to include a precise measure of interaction strength between each species. It is true that such data are orders of magnitude more difficult to gather than literature surveys or expert knowledge, but they are the only way to go beyond the current paradigm of seeing networks as mostly a collection of pairwise interactions.

% DG: Isn't co-occurrence also important to other processes? It will contribute to the turnover of interactions under all three processes. It is only through this one though that it will affect the interaction strenght (beta link).

From a biogeographic standpoint, it require that we develop a theory based on interaction co-occurrence, in addition to the current knowledge encompassing only species co-occurrence. Araújo et al. (2011) and Allesina and Levine (2011) introduced the idea tha competitive interactions can leave a trace in species co-occurrence network. It is now time to apply this logic to other types of interactions. In part, this can be done through the re-analysis of already existing datasets, although the statistical foundation of such a work is still mostly unknown (Thuiller et al. 2013).

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effect of the environment on the beta)

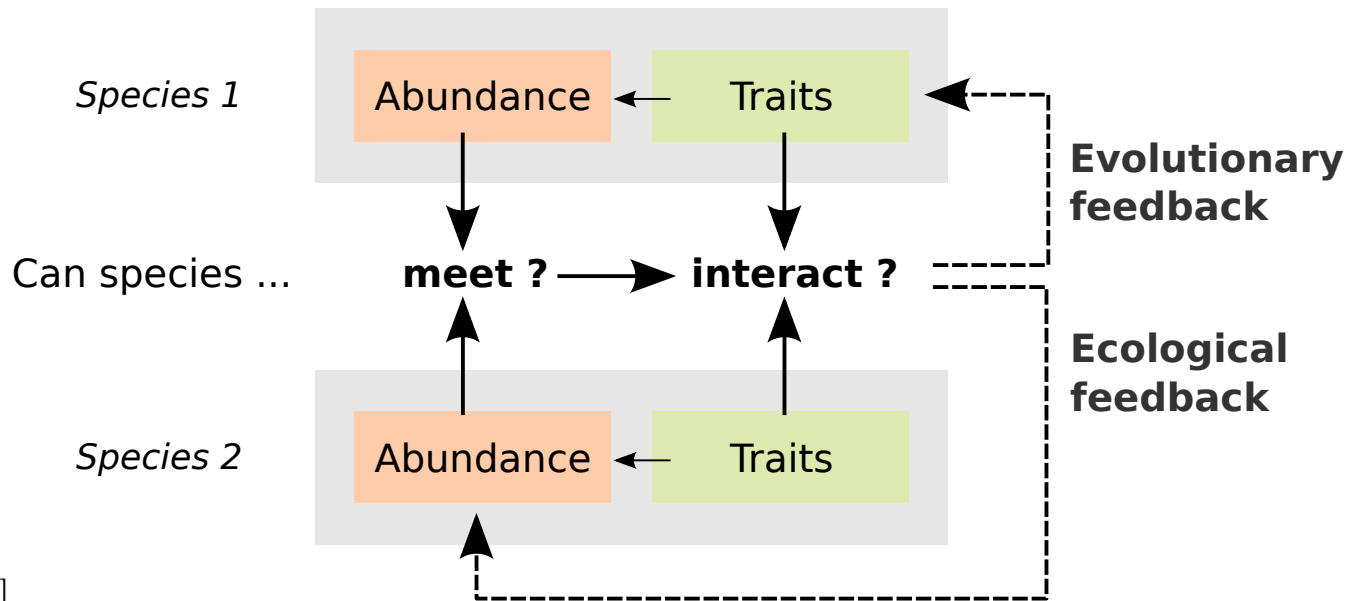
Conclusions

The notion of “species interaction networks” is an epistemological obstacle, as it shift our focus away from the level of organization at which most of the relevant processes happen — populations. As of now, it is difficult to understand how wrong we are (if at all), because data to properly separate the impact of different families of mechanisms on the variability of species interactions are scarce. Even when such data are available (*e.g.* Schleuning et al. 2011 , Menke et al. 2012, Schleuning et al. 2012), they were often not analyzed in this way, because the methodology is still mostly lacking. Some preliminary methods have been proposed. Blüthgen et al. (2008) claim that the impact of traits distribution on network structure can be inferred simply by removing the impact of neutrality (population densities), based on the idea that many rare links were instances of sampling artifacts. Their result is however of limited generality, because their simulation approach assumes no trait matching, and thus allows the maximal generality of each species. Under this framework, what is measured is sampling bias, but not trait (mis)matching. So as to understand the impact of neutrality and traits distributions, it is crucial that not only interactions, but also population densities (needed to define the neutral expectation) and local trait distribution (needed to quantify the niche processes), are sampled. In a recent contribution, we proposed to measure the turnover of interactions between communities (Poisot et al. 2012). The origins of this turnover will require more data to be fully appreciated, and the development of a new methodology partitioning the causes of variability in interactions. In the next sections, we synthesize the mechanisms mentioned in this paper, and conclude by stating the need to scale down the observation: from species to population, from occurrence to population density, and from trait values to local trait distribution.

A synthesis

Perhaps more importantly, all of these mechanisms will allow looking at the impact of environmental variation on the structure of networks. As illustrated in Fig. [fig:synth], because different environmental conditions will (i) affect local trait distributions and (ii) change population sizes, we expect a strong effect

of these changes on network structure. Looking at networks as a collection of interacting populations will allow testing the mechanisms through which environmental change affects network structure.



[tb]

[fig:synth]

Alesina et Eklof: number of traits and dimensions

Perspective: time to scale down

The common thread to all the processes reviewed here is that they act at the population level. Incidentally, they can be measured at the population level. So as to understand why there is turnover in the interactions in a metaweb, we need to gather more informations about the species. The value of relevant traits is an important information to have, and which traits are relevant can often be intuited from the natural history of the species. For example, proboscis length in pollination, jaw size in predation, attachment organs shape in ecto-parasitism, and so forth. Melián et al. (2011) showed that there is promise in studying interactions at the individual level, as it will bring in new knowledge about the eco-evolutionary dynamics. However, building a general theory of interactions biogeography will require a large number of accurately described metawebs, and expecting that each of them will be sampled to the individual level is not reasonable. Populations, although they aggregate individual-level mechanisms, can be reliably sampled over time and space (Stanko et al. 2002, Krasnov et al. 2004). We certainly do not call for the dismissal of species-level approaches, or of network inference based on databases of species traits. Rather than being used to

draw ecological or evolutionary conclusions, these should be used at a good approximation of the space of all possible interactions. Which of these interactions will be realized, hence taking part in ecosystem functioning and emerging community properties, is regulated locally by population-level processes.

The recent years saw a surge in the number of articles focused on describing the variation, structure, and dynamics of interactions networks over space. Most of these works were focused on food webs, but given the simple elements upon which they rely, it is likely that their conclusions will hold in other systems. Calcagno et al. (2011) demonstrated that meta-community dynamics allowed predicting the maximal length of trophic chains. Gravel et al. (2011) expanded the classical model of the *Theory of Island Biogeography* (MacArthur and Wilson 2001) to food webs, showing it predicted local connectance and richness of two large datasets accurately in any system which can be modeled as a series of connected islands. Pillai et al. (2011) showed that the regional structure of interactions can vary as a consequence of changes in competition for resources in local patches. While all these papers represent major advances, as they contribute to merge the fields of network analysis and biogeography (Cumming et al. 2010), they only address network-wide properties. Understanding the bases of variations between networks will be easier if we understand the sources of interaction variability (Poisot et al. 2012), and are able to predict it. The propositions made in this paper seek to make this understanding easier, through grounding it in well known mechanisms.

The next logical step is to build upon the knowledge of each of these mechanisms to refine our statistical approach of network structure. We see several important directions for future research in this field. First, it is important to decorticate the impact of large families of processes on network structure. We provide some insights about these approaches in *Box 1*. When traits and population sizes are known locally, approaches like variance partitioning can (i) measure the importance of trait-based and neutral processes, and (ii) remove these influences together, or in turn, and compare the resulting network structure. This is not possible by assuming that species interact in a consistent way across all locations. Second, ecologists working with networks should engage in a collective reflection about the relevant traits and informations needed to characterize a network. Homogenizing sampling procedures and meta-data will increase our ability to conduct meta-analyses, thus describing in much more depth the mechanisms involved in the variation of network structure.

Boxes

Box 1: A statistical framework for population level interactions

In this contribution, we propose that at the population level, the occurrence (and intensity) of ecological interactions relies on several factors, including relative local abundances, local trait distribution. It is important to tell apart these different factors, so as to better disentangle neutral and niche processes. In an ANOVA-like context, this amounts to see the occurrence of an interaction as a simple linear model of the general form

$$\mathbf{A}_{ij} \propto [\mathcal{N}(i, j) \times \mathcal{T}(i, j)] + \epsilon$$

wherein \mathcal{N} is a function giving the probability that species i and j interact *based on their relative abundances*, and \mathcal{T} is a function giving the probability that species i and j interact *based on their trait values*. The error term ϵ accounts for other effects, including environmental variability. Both of these functions can take any form needed. In several papers, $\mathcal{N}(i, j)$ was expressed as $\mathbf{n}_i \times \mathbf{n}_j$, where \mathbf{n} is a vector of relative abundances (@canard_neutral_2011; Vázquez et al. 2007). The expression of \mathcal{T} can in most cases be derived from mechanistic hypotheses about the observation. For example, Gravel et al. (2013) used the niche model of Williams and Martinez (2000) to draw interactions, with the simple rule that $\mathcal{T}(i, j) = 1$ if i can consume j based on allometric rules, and 0 otherwise. Following Rohr et al. (2010), the expression of \mathcal{T} can be based on latent variables rather than actual traits values. In a variance partitioning context, this apparently simple formulation will allow to understand, at the level of individual interactions, the relative importance of trait-based and density-dependent processes. Most importantly, it will allow to predict (i) how each of these components will vary over space, and (ii) how the structure of the network will be affected by *e.g.* changes in trait distributions or local abundances.

This model can further be extended in a spatial context, as

$$\mathbf{A}_{ijx} \propto [\mathcal{N}_x(i_x, j_x) \times \mathcal{T}_x(i_x, j_x)] + \epsilon_{ijx}$$

In which the x indice denotes sites, and i_x is the population of species i at site x . The structure of the error

term, *i.e.* its spatial or temporal auto-correlation, or covariance with either population sizes or trait values, can then be analyzed to further refine our predictions on species interaction variability. Most importantly, this model differs in that each site x is characterized by a set of functions $\mathcal{N}_x, \mathcal{T}_x$, that may not be the same for all sites considered. For example, the same predator can prefer different prey items in different locations, which will require to use a different shape for \mathcal{T} across the range of locations. In Gravel et al. (2013), we show that it is possible to derive robust approximation for the \mathcal{T} function even with incomplete set of data, which gives hopes that this framework can be applied even when all species informations are not known at all sites (which, for most realistic systems, will be an unrealistic requirement).

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