Expanding the paradigm of ecological network research

T. Poisot, D.B. Stouffer & D. Gravel

Working paper

Abstract – key points (i) need for predictions about the dynamics (ii) the current way of thinking about networks is poorly adapted because essentially static (iii) review of the mechanisms of variation and how to instrumentalize them for predictions (iv) moving towards a probabilistic definition of networks

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, it has been 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 exists 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.
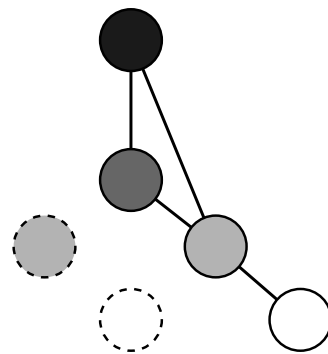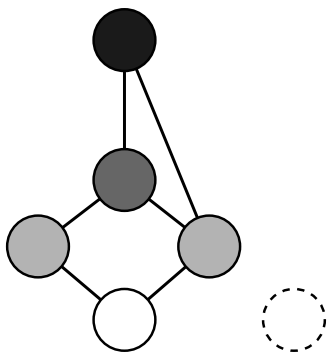
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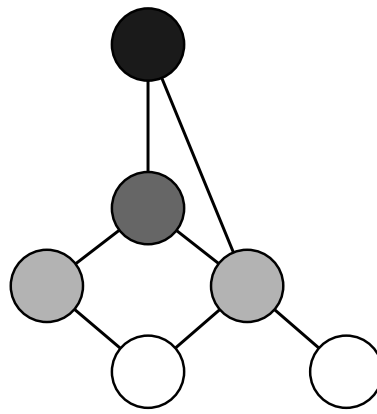
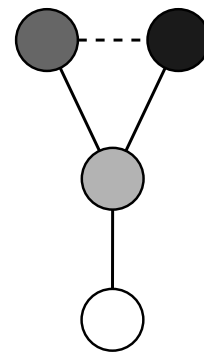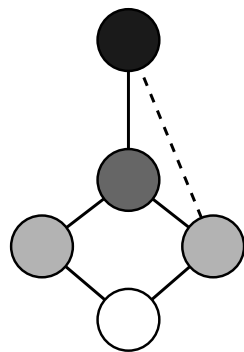Site 1   local species sorting   Site 2

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

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 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 modeli (*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 interdependant, thus potentially complexifying our view of the feedbacks between them.

Traits matching in space and time

Once individuals meet, wether they will interact is determined by an array of behavioral, phenotyic, cultural aspects, that can convenientyl be refered to as "trait-based procsse". 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 [@williwams_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 differenciated 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, ca be specialized in each of the patches it occupies. There are several examples of intraspecific trait variation resulting in extreme interaction tunrover. 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 occurence 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.
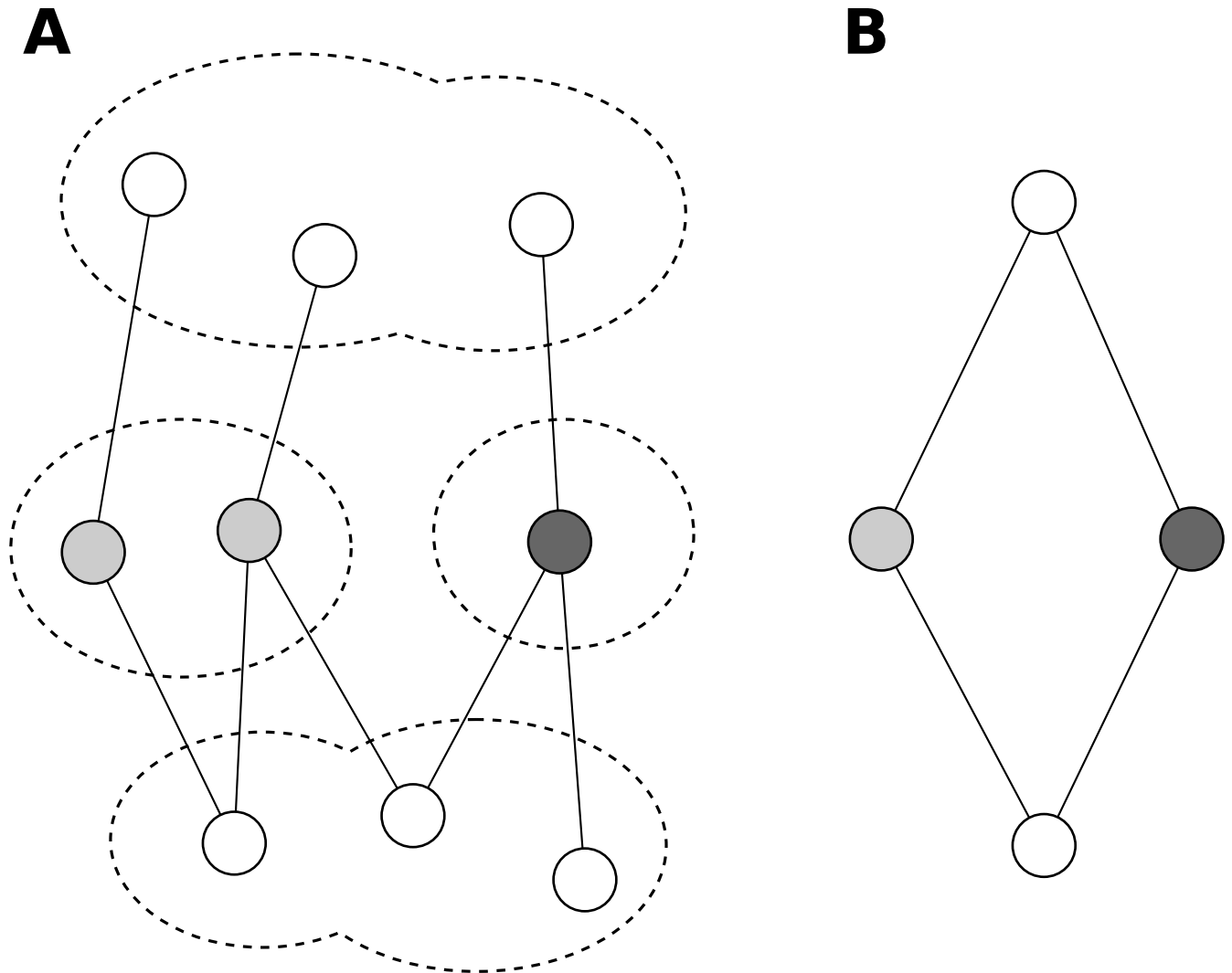
Figure 2: Panel **A** represents the interactions between different populations (circles) of four species, identified by the boundaries of their morphospaces (dashed lines). This network is mostly made of linear food chains, and has one generalist consumer. When aggregated at the species level however, 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 indivudal population can interact differently than the species it belongs to..

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* 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 sytem, the difference in network structure can be explained be- cause (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 vari- ation 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. Ad- ditionally, trait structure and traits correlations are disrupted by migration (Gandon et al. 2008, Burdon and Thrall 2009). Developping 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 adressing indirect effects on the existence of interactions too. A direct interaction originates in the "physical" interaction of two species, and as we argued before, these can be modified by species traits or local relative abundances. For example, predation, or pollination, are instances of direct interactions. Indirect interactions, on the other hand, are established "at a distance", either through cascading effet (herbivorous species compete with insect laying eggs on plants), or through physical mediation by the environment (bacterial exudates increase the bio-disponbility of iron for all bacterial species; plants with large foliage provide shade for smaller species). As we discuss in this section, the fact that interactions are indirectly affected by the presence of other species (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 abudances (on ecological times) and population trait structure (over evolutionary times), all interactions happenning 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 mentionned 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 unpredictible 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 interac-

tions 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-occurence 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).

% DG: I dropped here, there is considerable work to be done above before going back to the conclusions. We'll talk more about it. There is interesting stuff though below that might worth being moving up (e.g. the effect of the environment on the beta)

Conclusions

The notion of "species interaction networks" is an epistemological obstacle shifting our focus away from the level of organization at which most of the relevant processes happen — populations. In order to make reliable predictions on the structure of networks, we need to understand what triggers variability in ecological interactions. In this contribution, we outlined that there were direct (abundance-related, and trait-based) and indirect (biotic modifiers, indirect effects of co-ocurence) effects to account for. The relative importance of each of these factors, and how exactly the affect the probability of establishing an interaction, are most-likely system-specific; nonetheless, we propose a unified mathematical approach to better understand them.

At the moment, the field is data-limited. Despite the existence of several spatially or temporally replicated datasets (*e.g.* Schleuning et al. 2011 , Menke et al. 2012, Schleuning et al. 2012), it is rare that all relevant informations have been measured. However, we recently showed that only a reasonably small subset of data is enough to draw inferences at larger scales [@gravel_infering_2013]. Paradoxically, as tempting as it may be to sample a network in its entirety, the goal of establishing global predictions might be better furthered by characterising extremely well a more modest number of interactions. Assuming that there

are indeed statistical invariants in the rules of interactions, this information will allow to make predictions on the structure of the networks. Better still, this approach has the potential to substantially strengthen our understanding of the relationships between traits and neutral effects. 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. As illustrated in Box 2, their approach is of limited generality, as the abudance of a species can be directly driven by trait-environment matching.

With the accumulation of data, these approaches will rapidly expand our ability to predict the re-wiring of networks under environmental change. The effect of environmental change is expected to occur because (i) population sizes will be affected by the change and (ii) either plastic or adaptive responses will shoft or disrupt the traits distributions. The framework proposed in Box 1 allows to generate new probabilities of interactions under different scenarios. Ultimately, being explicit on the trait-abundance-interaction feedback will provide a better understanding of short-term and long-term dynamics of interaction networks. We illsutrate this in Fig. [fig:synth].
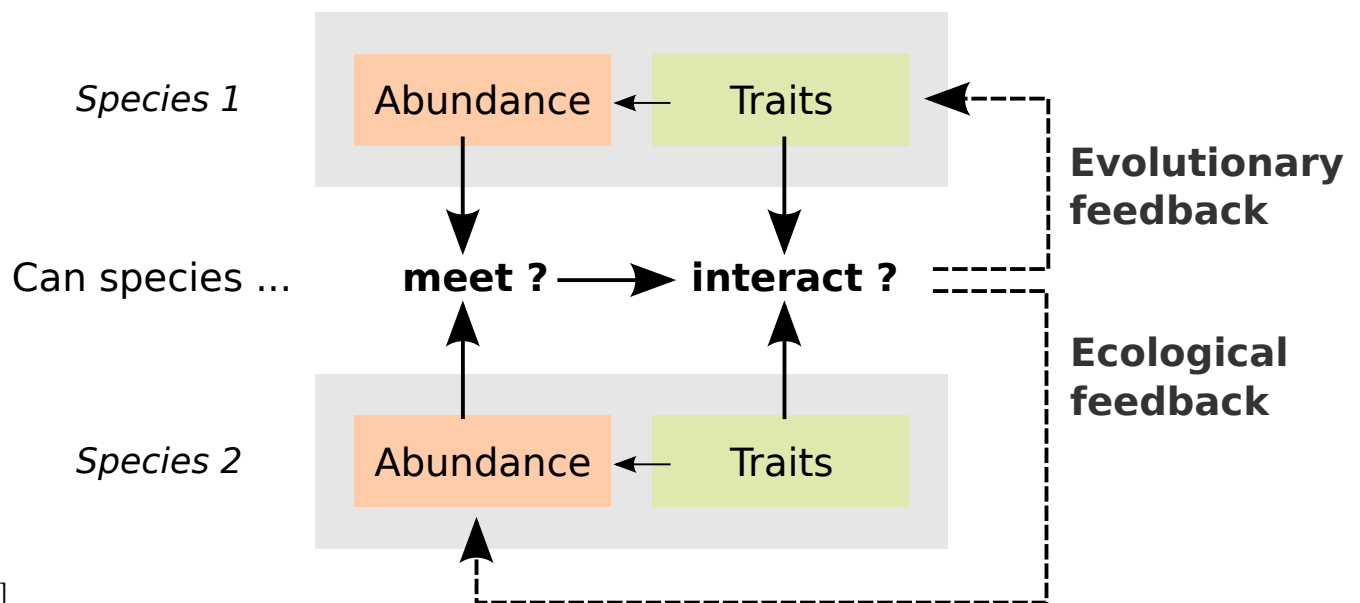
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Boxes

Box 1: A mathematical 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 and local trait distribution. It is important to tell apart these different factors, so as to better disentangle neutral and niche processes. We propose that these different effects can adequately be partitionned using the model,

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

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 *per encounter* probability that species i and j interact *based on their trait values*. The term ϵ accounts for all higher-order effects, such as indirect interactions, local impact of environmental conditions on the interaction, and impact of co-occuring species. 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 abudances (@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 index denotes sites, and i_x is the population of species i at site x. In this formulation,

the ϵ term can be made to include the spatial variation of interaction between i and j over sites, and the covariance between the observed presence of this interaction and the occurence of species i and j. 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). The strength of these models is that they can be used in a variance partitionning approach (in which case they measure the multiplicative and additive contributions of abundance, traits, and other factors), or within dynamical simulations, to generate realistic rewiring of the networks as a function of environmental changes.

Box 2: Why population-level (or individual-level) interactions are critically important

As noted in the main text, most studies of ecological networks—particularly food webs—regard the adjacency matrix **A** as a fixed entity that specifies observable interactions on the basis of whether two species co-occur or not. Given this assumption, there is a long history, dating back at least to the Lotka-Volterra model, of trying to understand how the strength or organization of these interactions influence the dynamic behavior of species abundance. Often, such models take the form

$$\frac{dN_i}{dt} = N_i \left(g_i - \sum_{j \neq i} \alpha_{ij} A_{ij} N_j \right),$$

where g_i is the growth rate of species i (and could, in principle, depend on all other species' abundances **N**) and α_{ij} is the strength of the effect of j on i. It is important to note that, in this or just about any related model, direct species-species interaction can influence species' abundances but their abundances *never* feedback and influence the *per capita* interactions (although they do affect the *realized* interactions, which are here defined by $\alpha_{ij} N) i N_j$). Moreover, the only manner in which non-directly-interacting species could "influence" the abundances of other species is via indirect mechanisms like apparent or exploitative competition.

More recently, there have been multiple attempts to approach the problem from the other way around. Namely, to understand how factors such as species' abundance and/or trait distributions influence the occurrence of the interactions themselves (see Box 1). One drawback to the standard approach here, however, is that it still depends on the fundamental assumption that the observation of any interaction A_{ij} is a function of the properties of species i and j alone. Since dynamic models can demonstrate quite clearly that non-interacting species can alter each others' abundances, this is a surprisingly pertinent inconsistency between the two approaches. Such a simplification *does* increase the analytical tractability of the problem, but there is little if any guarantee that it is scientifically or ecologically correct. In our opinion, the "higher-effects" term ϵ in the models presented in Box 1 is the one with the least straightforward expectations, but the most important to accurately describe as its encompasses all of these indirect effects.

It could also be argued that a similar problem arises in the typical statistical framework for predicting interaction occurrence. Often, attempts are made to "decompose" interactions into the component that

is explained by species' abundances and the component explained by species' traits (e.g., Box 1). Just like how the underlying functions could vary across sites, there should also be interplay between species' abundances and traits, in the same way that we have outlined the feedback between interactions and species' abundances. What's more, given the increasing evidence for the evolutionary role of species-species interactions in explaining extant biodiversity and their underlying traits, any framework which depends on the relative independence of these different phenomenon is likely starting from an overly reductionist perspective. Importantly, we will have *no* hope in successfully piecing apart the effects of each of these drivers, or robustly assessing the degree to which they are interrelated, without adopting a broader perspective on ecological- network data that is fully replicated at the site, population, or individual level.

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