Beyond species: understanding the spatial dynamics of ecological networks

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

Working paper

Community ecology is tasked with the considerable challenge of predicting the structure, and properties, of emerging ecosystems triggered by species movement, environmental change, and rapid adaptive response. This task requires the ability to understand how and why species establish interactions, as this will allow the development of mechanism-based predictive models. Despite multiple arguments to the contrary, we argue that the current conceptualisation of species interaction networks is ill-suited for this task. Instead, we propose that future research must start to account for the intrinsic variability of interaction networks. By shifting the scale towards population-based processes, we show that this new approach will improve our predictive ability and mechanistic understanding of species interactions.

Introduction

Ecological interactions are the driving force behind ecological dynamics within communities (Berlow et al. 2009). Likely for this reason more than any, the structure of communities have been described by species interaction networks for over a century (Dunne 2006). Formally an ecological network is a mathematical and conceptual representation of both *species*, and the *interactions* they establish. Behind this conceptual framework is a rich and expanding literature whose primary focus has been how certain quantifiable numerical and statistical properties of the network relate 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 has proved particularly successful because it can be applied equally to all types of ecological interactions (Kéfi et al. 2012).

This body of literature generally assumes that, short of changes in local densities due to ecological dynamics, networks are inherently *static* objects. More explicitly, if two species are known to interact at one location, it is often assumed that they will interact whenever and wherever they co-occur (see *e.g.* Havens 1992). More recently, however, it has been established that networks are *dynamic* objects that have structured variation in α, β, and γ diversity, not only to the change of species composition at different locations but also to the fact that the same species will interact in different ways over time or across space. Of these sources of variation in networks, the change of species composition has been addressed by previous literature either explicitly in the context of networks (Gravel et al. 2011, Dáttilo et al. 2013), or within classical meta-community theory. 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.

Within the current paradigm, interactions are established between species, and are an immutable "property" of a species pair. 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, @piechnick_oikos_2008; 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.

In contrast to the current paradigm, 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 realization of these regional probabilities. This approach is outlined in **Box 1**. Although this proposal is an intuitive yet radical change in the way we think about ecological network structure, we demonstrate in this paper that it is well supported by empirical and theoretical results alike. What's more, our new perspective is well placed to open the door to novel predictive approaches integrating over a range of key ecological mechanisms. Notably, we propose in **Box 2** that this approach facilitates the study of indirect interactions, for which predictive approaches have long been proved elusive [@tack_can_2011].

The dynamic nature of ecological interaction networks

Recent studies on the sensitivity of network structure to environmental change provide some context for the study of dynamic networks. Menke et al. (2012) showed that the structure of a plant–frugivore network changed along a forest–farmland gradient. At the edges between two habitats, species were on average less specialized and interacted more evenly with a larger number of partners than they did in habitat cores. Differences in network structure have also been observed within forest strata that differ in their proximity to the canopy and visitation by birds (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 realized infection; when the species were moved from high to medium to low productivity, some interactions were lost and others were gained. As a whole, these results suggest that the existence, and properties, of an interaction are not only contingent on the presence of the two species involved, but may also require particular environmental conditions, including the presence or absence of species not directly involved in the interaction.
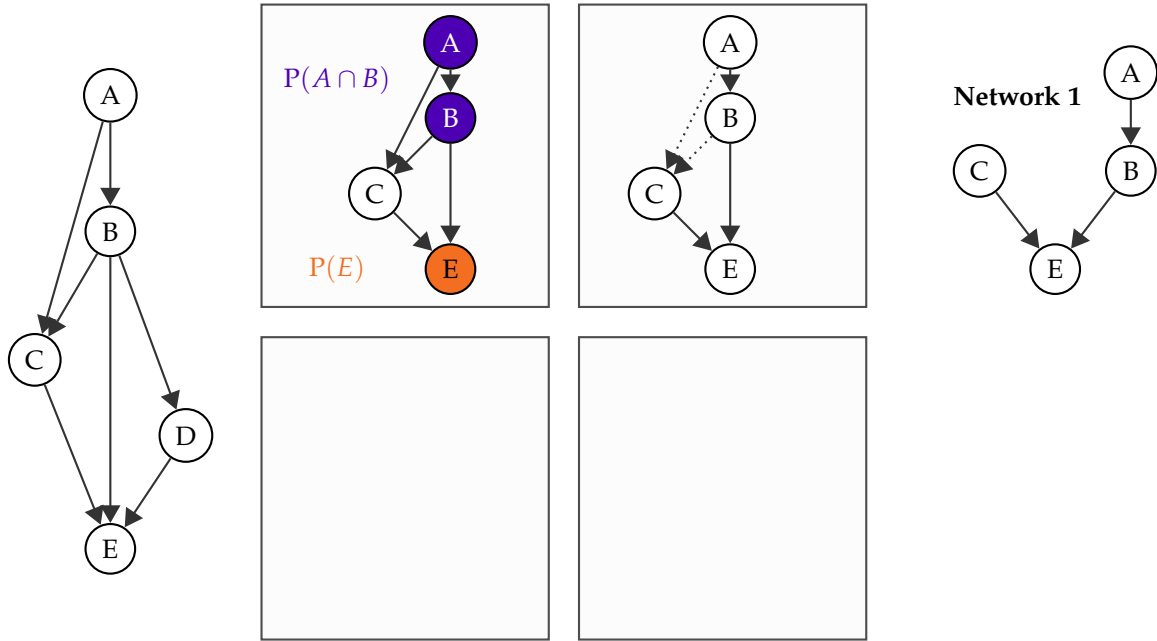
Figure 1: An illustration of the metaweb concept. In its simplest form, a metaweb is the list of all possible species and interactions between them for the system being studied, at the regional level (far left side). Everything that is ultimately observed in nature is a *realisation* of the metaweb (far right side), *i.e.* the resulting network after several sorting proccesses have occurred (central panel). First, species and species pairs have different probabilities to be observed (top panels). Second, as a consequence of the mechanisms we outline in this paper, not all interactions have the same probability to occur at any given site (bottom panels, see **Box 1**).

We argue here that there are three broadly-defined classes of mechanisms that ultimately determine the realization of species interactions. First, individuals must be in high enough local relative abundances to meet; this is the so-called "neutral" perspective of interactions. Second, there must be phenological matching between individuals, such that an interaction will actually occur given that the encounter takes place. Finally, the realization of an interaction is regulated by the interacting organisms' surroundings, and should be studied in the context of indirect interactions. Below, we examine each of these mechanisms in turn, and we show how they integrate into a robust statistical framework in **Box 1**, and more broadly into network context in **Box 2**. We propose that shifting our approach from the species level to the population level will result in a better appreciation of the mechanisms of network variations, which will allow to develop mechanistic hypotheses for the comparison of community structure in space, time, or over environmental gradients.

Population dynamics and neutral processes

Over the recent years, the idea of neutrality has left a clear imprint on the analysis of ecological network structure, most notably in bipartite networks (Blüthgen et al. 2006). Re-analysis of several host–parasite datasets, for example, showed that changes in local species abundances triggers variation in parasite specificity (Vazquez et al. 2005). More broadly, it is possible to predicting the structure of trophic interactions given minimal assumptions about the distribution of species abundance (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 directly to interaction turnover.

The basic processes

As noted previously, for an interaction to occur between individuals from two populations, these individuals must first meet, then interact. Assuming that two populations occupy the

same location 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 (Vázquez et al. 2007). This means that individuals from two large populations are more likely to interact than individuals from two small populations, simply because they tend to 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. The neutral perspective predicts that locally-abundant species should have more partners, and locally-rare species should appear more specialized. In a purely neutral model (*i.e.* interactions happen entirely by chance, although the determinants of abundance can still be non-neutral), the identities of species do not matter, and it becomes easy to understand how this can lead to a situation where the structure of local networks will vary since species vary regionally in abundance. Canard et al. (2012) proposed the term of "neutrally forbidden link" to refer to interactions that are phenologically feasible but not realized because of the underlying 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 responds 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, whether neutral or not, cascade to the structure of interaction networks. One approach is to use simple statistical models to quantify the effect of population sizes on local interaction occurrence or strength (see *e.g.* Krishna et al. 2008). 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 (Box 1). Doing so allows us to compare the variation of neutral and non-neutral components of network structure over space and time. To achieve this goal, however, it is essential the future sampling of interaction networks (i) are replicated and (ii) include independent measurements of population sizes.

An additional benefit is that these data will also help refine 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, albeit intentionally, absent from the original formulation of the theory [@hubbell]. Merging the two views will increase our explanatory power, and provide new ways to test neutral theory in interactive communities. It will also offer 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); @stouffer_pnas_2011; @saavedra_nature_2011]. Adopting this neutral perspective allows to bring things full circle since the abundance of a species will also dictate its position in the network: changes in abundance can lead to interactions being gained or lost, and these changes in abundance are in part caused by existing interactions (Box 2). For this reason, there is a potential to link species and interaction dynamics and, more importantly, to do so in a way which accounts for the interplay between the two. 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, embracing the neutral view will force us to reconsider the causal relationship between resource dynamics and interaction strength; in a neutral context, both are necessarily interdependent, a fact which likely further increases the complexity of the feedbacks between them.

Traits matching in space and time

Once individuals meet, whether they will interact is widely thought to be the product of an array of behavioral, phenotypic, cultural aspects, that can conveniently be referred to as "trait-based process". 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 interaction networks will consequently vary along with variation in local trait distribution. In this section, we review how trait-based processes impact network structure, how they can create variation, and the perspective they open for an evolutionary approach.

The basic processes

There is considerable evidence 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 [Williams and Martinez (2000); @stouffer_ecology_2005]. Trait values, however, 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 it has also reinforced the need to understand intra-specific trait variation to describe the structure and dynamics of communities (Bolnick et al. 2011). Nevertheless, this notion has yet to percolate into the literature on network structure, despite its most profound consequence: a species appearing generalist at the regional scale can easily be specialized in *each* of the patches it occupies.

Empirically, there are several examples of intraspecific trait variation resulting in extreme interaction turnover. A particularly spectacular example is identified by Ohba (2011) who

describes how : 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; their 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 the trait-based perspective, the existence of an interaction is an emergent property of the trait distribution of local populations: variations in one or both of these distributions, regardless of the mechanism involved (development, selection, plasticity), are likely to alter the interaction. Importantly, when interaction-driving traits are subject to 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 gradients is a central concern at present if we are to understand, for example, network variation and its subsequent response to environmental change.
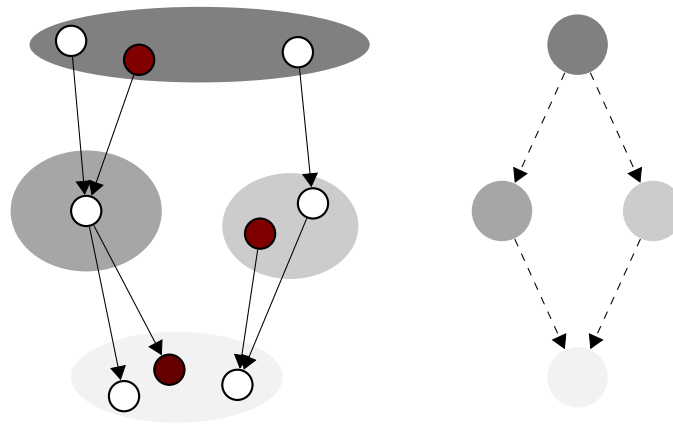

Figure 2: The left-hand side of this figure represents possible interactions between populations (circles) of four species (ellipses), and the aggregated species interaction network on the right. In this example, the populations and species level networks have divergent properties, and the inference on the system dynamics are likely to be different depending on the level of observation. More importantly, if the three populations highlighted in red were to co-occur, there would be no interactions between them, whereas the species-level network would predict a linear chain..

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 requires that, when interaction are recorded, they are coupled with trait measurements. Importantly, these measurements cannot merely be extracted from a reference database because interactions are driven by *local* trait values and their matching across populations from different species. Within our overarching statistical framework (Box 1), we 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 depend on the *covariance* between species traits. Although its requires considerably larger quantities of data to test, this approach should allow us to infer an *a priori* estimate of network variation. Given this next generation of data will also help link variation of network structure to variation of environmental conditions. Price (in press) shows how specific biomechanical responses to water input in shrubs can have pleiotropic effects on traits involved in the interaction with insects. In their 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. We have little doubt that future empirical studies will provide additional mechanistic narratives.

At a larger temporal scales, current distribution of traits also reflects past evolutionary history (Diniz-Filho and Bini 2008). Recognizing this important fact offers us 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), creating patchiness in the processes and outcomes of coevolution. Trait structure and traits correlations are also disrupted by migration (Gandon et al. 2008, Burdon and Thrall 2009). Ultimately, 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 [Eklof et al. (2011); Baskerville et al. (2011); @stouffer_science_2012].

Beyond direct interactions

In this section, we argue that, although networks are built around observations of direct interactions like predation or pollination, they also offer a compelling tool with which to address indirect effects on the existence of interactions. Any direct interaction originates in the "physical" interaction of two species, and as we have already detailed, these can be modified by local relative abundances and/or species traits 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 exudate increase the bio-availability of iron for all bacterial species; plants with large foliage provide shade for smaller species). As we discuss in this section, the fact that many (if not all) interactions are indirectly affected by the presence of other species (i) has relevance for understanding the variation of interaction network structure and (ii) can be studied within the classical network-theory formalism.

The basic processes

Several authors (Golubski and Abrams 2011) have demonstrated 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. This doesn't actually mean pairwise approaches are bound to fail, but it does harken for a larger scale approach that accounts 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.

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 inter-action turnover is the patchiness of species distribution; this helps emphasize why the two concepts would benefit from further integration. 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 results 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 ef-fects are thus likely to act on components of dissimilarity. A common feature of the examples mentioned here is that pinpointing the exact mechanism through which species interactions interfere often requires a good working 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 and Loreau 2008, 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. Recent experimental work by Sanders and van Veen (2012) showed that some predator species can only be maintained if another predator species is present, since the latter regulates a competitively superior prey and allows for 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_can_2011], and can only be understood by comparing communities in which different species are present/absent. Looking at figure 1, it is also clear that the probability of having an interaction between species i and j ($P(\mathbf{L}_{ij})$) is ultimately constrained by the probability of simultaneously observing i and

j together, *i.e.* P($i \cap j$). Thus, the existence of any ecological interaction will be contingent upon *other* ecological interactions driving local co-occurrence [@araujo_using_2001]. Based on this arguments, ecological networks cannot be a collection of pairwise interactions. Our view of them needs be updated to account for the importance of the context surrounding these interactions (Box 2). From a biogeographic standpoint, it requires us to 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 that competitive interactions can leave a trace in species co-occurrence network. A direct consequence of this result is that, for example, trophic interactions are constrained by species competition outcome *before* they are even constrained by predation-related traits. Appreciating such an effect requires a spatial or replicated sampling (**Box 1**) at the population level (**Box 2**).

Conclusions

Overall, we argue here that 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 are several direct (abundance-based and trait-based) and indirect (biotic modifiers, indirect effects of co-occurrence) effects to account for. On the surface, we expect that the relative importance of each of these factors, and how precisely they affect the probability of establishing an interaction, are likely system-specific; nonetheless, we have proposed a unified mathematical approach to understand them better.

At the moment, the field of community ecology is severely data-limited if we are to tackle this challenge. 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 information has been measured independently. It was recently concluded, however, that even a reasonably small subset of data can be enough to draw inferences at larger scales (Gravel

et al. 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 extremely-detailed characterisation of a more modest number of interactions [@rodriguezcabal_pnas_2013]. Assuming that there are indeed statistical invariants in the rules governing interactions, this information will allow us to make verifiable predictions on the structure of the networks. Better still, this approach has the potential to substantially strengthen our understanding of the interplay 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 here (e.g, Box 2), their approach is of limited generality, as the abudance of a species itself can be directly driven by factors such as 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].

<!–DBS: It seems to me that we need a punchier concluding paragraph. . .->

Species 1

Can species ...

Species 2
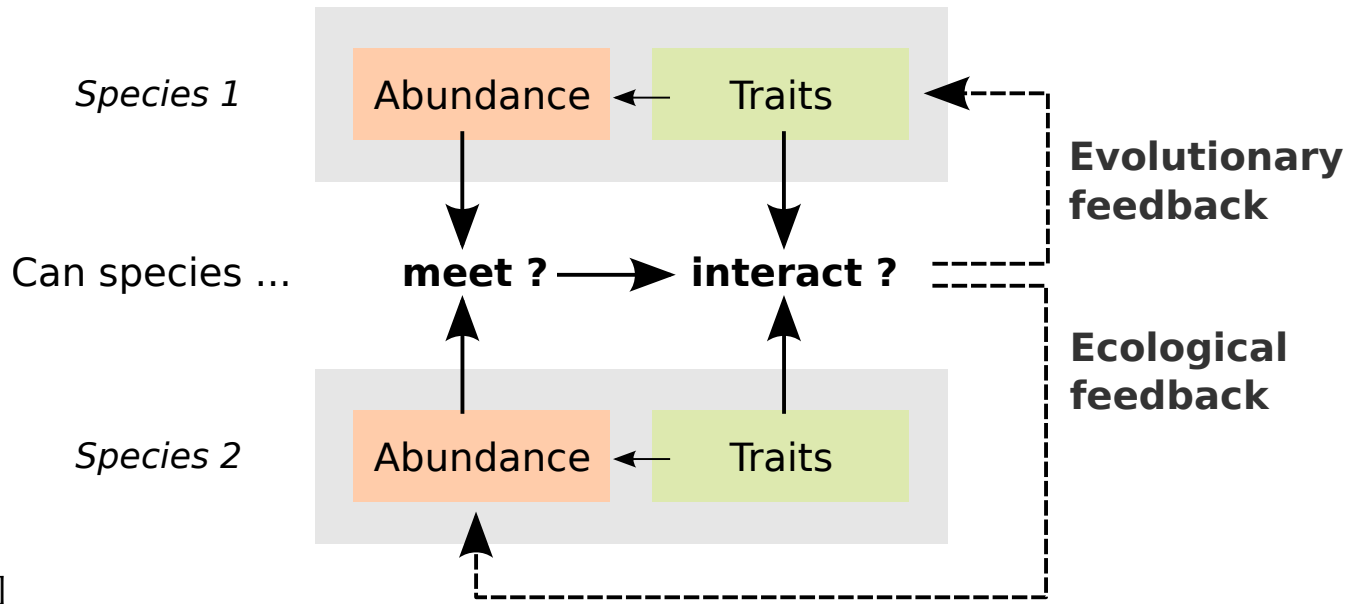
[tb]

[fig:synth]

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 abudances*, 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 (Vázquez et al. 2007, Canard et al. 2012). 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 $\alpha_{ij} N)iN_j$). 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.

References

Allesina, S. and Levine, J. M. 2011. A competitive network theory of species diversity. - Proceedings of the National Academy of Sciences of the United States of America 108: 5638.

Angilletta, M. J. et al. 2004. Temperature, Growth Rate, and Body Size in Ectotherms: Fitting Pieces of a Life-History Puzzle. - Integrative and Comparative Biology 44: 498–509.

Araújo, M. B. et al. 2011. Using species co-occurrence networks to assess the impacts of climate change. - Ecography in press.

Baiser, B. et al. 2012. Geographic variation in network structure of a nearctic aquatic food web. - Global Ecology and Biogeography 21: 579–591.

Baskerville, E. B. et al. 2011. Spatial Guilds in the Serengeti Food Web Revealed by a Bayesian Group Model (LA Meyers, Ed.). - PLoS Computational Biology 7: e1002321.

Berlow, E. L. et al. 2009. Simple prediction of interaction strengths in complex food webs. - Proceedings of the National Academy of Sciences of the United States of America 106: 187–91.

Blüthgen, N. et al. 2006. Measuring specialization in species interaction networks. - BMC ecology 6: 9.

Blüthgen, N. et al. 2008. What do interaction network metrics tell us about specialization and biological traits? - Ecology 89: 3387–99.

Bolnick, D. I. et al. 2003. The ecology of individuals: incidence and implications of individual specialization. - The American Naturalist 161: 1–28.

Bolnick, D. I. et al. 2011. Why intraspecific trait variation matters in community ecology. - Trends in Ecology & Evolution 26: 183–192.

Brose, U. et al. 2006. Allometric scaling enhances stability in complex food webs. - Ecology letters 9: 1228–1236.

Burdon, J. J. and Thrall, P. H. 2009. Coevolution of plants and their pathogens in natural habitats. - Science 324: 755.

Canard, E. et al. 2012. Emergence of Structural Patterns in Neutral Trophic Networks. - PLoS ONE 7: e38295.

Choh, Y. et al. 2012. Predator-prey role reversals, juvenile experience and adult antipredator behaviour. - Scientific Reports in press.

Devictor, V. et al. 2010. Defining and measuring ecological specialization. - Journal of Applied Ecology 47: 15–25.

Diniz-Filho, J. A. F. and Bini, L. M. 2008. Macroecology, global change and the shadow of forgotten ancestors. - Global Ecology and Biogeography 17: 11–17.

Duffy, J. E. et al. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. - Ecology Letters 10: 522–538.

Dunne, J. A. 2006. The Network Structure of Food Webs. - In: Dunne, J. A. and Pascual, M. (eds), Ecological networks: Linking structure and dynamics. Oxford University Press, ppp. 27–86.

Dunne, J. A. et al. 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. - Ecology Letters 5: 558–567.

Dáttilo, W. et al. 2013. Spatial structure of ant–plant mutualistic networks. - Oikos: no–no.

Eklof, A. et al. 2011. Relevance of evolutionary history for food web structure. - Proceedings of the Royal Society B: Biological Sciences 279: 1588–1596.

Eveleigh, E. S. et al. 2007. Fluctuations in density of an outbreak species drive diversity cascades in food webs. - Proceedings of the National Academy of Sciences of the United States of America 104: 16976–16981.

Gandon, S. et al. 2008. Host-parasite coevolution and patterns of adaptation across time and space. - Journal of Evolutionary Biology 21: 1861–1866.

Golubski, A. J. and Abrams, P. A. 2011. Modifying modifiers: what happens when interspecific interactions interact? - Journal of Animal Ecology 80: 1097–1108.

Gomulkiewicz, R. et al. 2000. Hot spots, cold spots, and the geographic mosaic theory of coevolution. - The American Naturalist 156: 156–174.

Goudard, A. and Loreau, M. 2008. Nontrophic interactions, biodiversity, and ecosystem functioning: an interaction web model. - The American Naturalist 171: 91–106.

Gravel, D. et al. 2011. Trophic theory of island biogeography. - Ecology Letters 14: 1010–1016.

Gravel, D. et al. 2013. Inferring food web structure from predator-prey body size relationships. - Methods in Ecology and Evolution in press.

Havens, K. 1992. Scale and structure in natural food webs. - Science in press.

Heil, M. and McKey, D. 2003. Protective ant-plant interactions as model systems in ecological and evolutionary research. - Annual Review of Ecology, Evolution, and Systematics 34: 425–553.

Ings, T. C. et al. 2009. Ecological networks–beyond food webs. - Journal of Animal Ecology in press.

Koch, H. and Schmid-Hempel, P. 2011. Socially transmitted gut microbiota protect bumble bees against an intestinal parasite. - PNAS in press.

Krishna, A. et al. 2008. A neutral-niche theory of nestedness in mutualistic networks. - Oikos 117: 1609–1618.

Kéfi, S. et al. 2012. More than a meal\textbackslashldots integrating non-feeding interactions into food webs. - Ecology letters in press.

Memmott, J. et al. 2004. Tolerance of pollination networks to species extinctions. - Proceedings of the Royal Society B: Biological Sciences 271: 2605–2611.

Menke, S. et al. 2012. Plant-frugivore networks are less specialized and more robust at forest-farmland edges than in the interior of a tropical forest. - Oikos 121: 1553–1566.

Mouritsen, K. N. et al. 2011. Food web including metazoan parasites for an intertidal ecosystem in New Zealand. - Ecology 92: 2006–2006.

Nuismer, S. L. et al. 2003. Coevolution between hosts and parasites with partially overlapping geographic ranges. - Journal of Evolutionary Biology 16: 1337–1345.

Ohba, S.-y. 2011. Field observation of predation on a turtle by a giant water bug. - Entomological Science 14: 364–365.

Olesen, J. M. et al. 2011. Missing and forbidden links in mutualistic networks. - Proceedings. Biological sciences / The Royal Society 278: 725–32.

Olivier, L. 2012. Are Opportunistic Pathogens Able to Sense the Weakness of Host through Specific Detection of Human Hormone? - Journal of Bacteriology & Parasitology in press.

Poisot, T. et al. 2011. Resource availability affects the structure of a natural bacteria-bacteriophage community. - Biology Letters 7: 201–204.

Poisot, T. et al. 2012. The dissimilarity of species interaction networks. - Ecology Letters 15: 1353–1361.

Price, P. W. Macroevolutionary Theory on Macroecological Patterns. - Cambridge University Press.

Rohr, R. P. et al. 2010. Modeling food webs: exploring unexplained structure using latent traits. - The American naturalist 176: 170–7.

Sanders, D. and van Veen, F. J. F. 2012. Indirect commensalism promotes persistence of secondary consumer species. - Biology letters: 960–963.

Schleuning, M. et al. 2011. Specialization and interaction strength in a tropical plant-frugivore network differ among forest strata. - Ecology 92: 26–36.

Schleuning, M. et al. 2012. Specialization of Mutualistic Interaction Networks Decreases toward Tropical Latitudes. - Current biology 22: 1925–31.

Singer, M. C. et al. 2004. Disentangling food quality from resistance against parasitoids: diet choice by a generalist caterpillar. - The American Naturalist 164: 423–429.

Singer, M. S. et al. 2012. Tritrophic interactions at a community level: effects of host plant species quality on bird predation of caterpillars. - The American naturalist 179: 363–74.

Thompson, J. N. 2005. The Geographic Mosaic of Coevolution. - University Of Chicago Press.

Vazquez, D. P. et al. 2005. Species abundance and the distribution of specialization in host-parasite interaction networks. - Journal of Animal Ecology 74: 946–955.

Vázquez, D. P. et al. 2007. Species abundance and asymmetric interaction strength in ecological networks. - Oikos 116: 1120–1127.

Williams, R. J. and Martinez, N. D. 2000. Simple rules yield complex food webs. - Nature 404: 180–183.

Woodward, G. et al. 2012. Climate change impacts in multispecies systems: drought alters food web size structure in a field experiment. - Philosophical Transactions of the Royal Society B: Biological Sciences 367: 2990–2997.

Wootton, J. T. 2005. Field parameterization and experimental test of the neutral theory of biodiversity. - Nature 433: 309–12.

Yeakel, J. D. et al. 2012. Probabilistic patterns of interaction: the effects of link-strength variability on food web structure. - Journal of The Royal Society Interface: rsif.2012.0481.

Zander, C. D. et al. 2011. Food web including metazoan parasites for a brackish shallow water ecosystem in Germany and Denmark. - Ecology 92: 2007–2007.