

The causes of species interactions variability

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Introduction

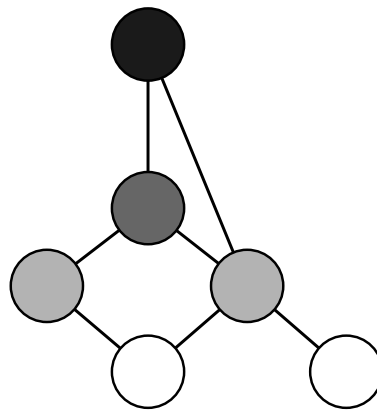
Describing the structure of ecological communities requires to know not only the identity of species, but also their interactions (Dunne 2006). Because interactions drive ecological dynamics within communities (Berlow et al. 2009), their organization will confer certain ecological properties. Defining the “structure” of interactions is made easier by seeing ecological communities as graphs (West 2001). A graph is a collection of nodes (species, populations, individuals) linked two-by-two through edges (direct ecological interactions). Ecological research over the last two decades focused on how certain mathematical properties of this graph 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, up to the point where all of them are included in the same network (Kéfi et al. 2012). Recently, empirical evidences point to the fact that the structure of ecological networks is affected by global changes, at both short (Dossena et al. 2012) and long (Dalsgaard et al. 2013) time-scales. Although it is tempting to forecast the future structure of these networks, because it will allow us to predict the properties of future communities, doing so is notoriously difficult except in some well-described, well-controlled experimental systems (Sarmiento et al. 2010). One of the source of complexity is that, following changes in species range, extinctions, and micro-evolutionary events induced by global changes, future networks will not

be a simple aggregation of the contemporary ones, and will truly be emergent systems, in that they will be made of both old and new species, and different interactions between these species. In this perspective, it becomes important to identify the reasons for which ecological interactions will occur in a given species assemblage, but not in another.

Recent studies on the sensitivity of network structure to environmental change provide some context for this question. Menke et al. (2012) showed that a plant–frugivore network changed its structure on a forest–farmland gradient. Even within different forest strata, differences in network structure were observed (Schleuning et al. 2011). Eveleigh et al. (2007) demonstrated 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, which suggest complex genotype-by-genotype-by-environment relationships. These results can be explained by assuming that any observation of an ecological network is the realization of *potential* interactions. These potential species and interactions represent a *metaweb* (Figure 1). Recent results suggest different filtering of species and their interactions (Poisot et al. 2012), which confers both a dynamic and a variability to networks, even though the species within them are the same. It is therefore important to better understand why two species are not always interacting in the same way, and how accounting for this phenomenon and the mechanisms triggering it will improve our ability to use networks as predictive tools. In this paper, we argue that this knowledge can be acquired by focusing on populations, rather than species.

To observe that interactions can be gained or lost when the environment changes, requires that sampling be replicated. In other words, to address these problematics, there is a need to shift our focus from species interactions (*i.e.* regional, potential) to populations (*i.e.* local, realized) interactions. This begs the questions of the similarity between these two levels. As argued before, species-level networks reconstructed on the basis of literature survey, expert knowledge, or even potential trait-based relationships (Brose et al. 2006, Heckmann et al.

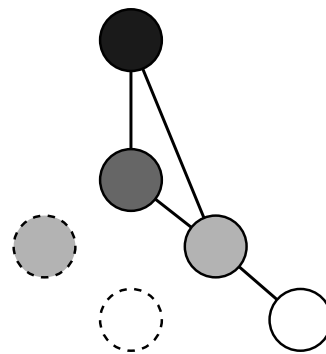
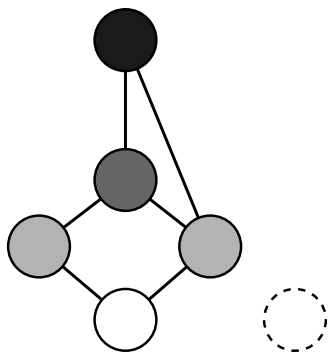
metaweb



Site 1

local species sorting

Site 2



local interaction sorting

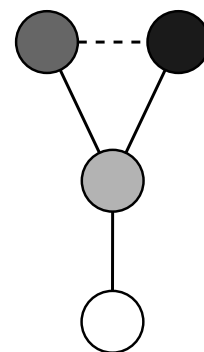
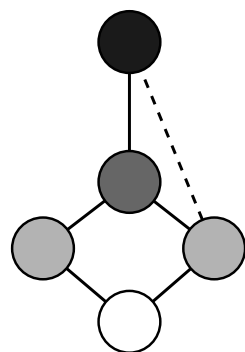


Figure 1: An illustration of the notion of a metaweb. In its simplest form, the metaweb is the list of all possible species and interactions between them for the system studied, whether these interactions were observed or inferred from trait values and previous knowledge. What

2012) , are networks of potential interactions, but can seldom be used to predict whether two populations will interact. When sampling populations enough times, either through time or space, we only gain knowledge of the realized interactions, and it is possible that some potential interactions are not encountered. Take, for example, the iconic dataset of (Havens 1992), which describes the interactions between species in the Adirondack lakes. For each lake, the list of species is known. At the regional level, the interactions between all species were retrieved from literature surveys. With these informations in hand, it is only possible to describe the structure of *potential* interactions at the local scale, but not to describe the *realized* network. The opposite standpoint is to assume that aggregating all realizations will give a good knowledge of the potential interactions in the metaweb. This, however, is the age old problem of proving a negative: we are only certain that no potential interactions were missed insofar that we are confident in our ability to locally detect them (Copi 1953), and have sampled enough combinations of environmental conditions. Some networks will be more sensitive to sampling effects than others. Pollination or frugivory networks are typically sampled through several sessions of observation (Schleuning et al. 2012), and therefore rely on the skill of the observer, or the amount of people available to conduct the survey. On the other hand, macro-parasite networks (Stanko et al. 2002) or food webs (Shaner and Macko 2011) can be conducted by sampling individual hosts, and investigating them in the lab (through e.g. combing or stomach content analysis), meaning that it is harder to miss an interaction if enough individuals are sampled.

Poisot et al. (2012) showed that after more than a hundred independent samplings of a host-ectoparasite system, not all regional interactions are known. This bears two important consequences. First, the adequate sampling of potential interactions (in other words, the knowledge of the metaweb) is a difficult task (Martinez et al. 1999). Second, the compilation of interactions observed at one sampling site between local populations is not the network of species interactions, which can only be reconstructed through numerous samplings (so as to be confident that an absence of link really indicates that the interaction is not possible). However, the realized interactions between populations will impact their local dynamics, and thus drive

local ecological properties of the community (Bascompte 2009, Poisot et al. 2013); this makes them the relevant scale at which to study ecological networks as indicators of ecosystem properties. In addition, because different realizations of a metaweb will show interaction turnover, it is important that we now focus our effort on understanding population-level interaction networks, because this seems the only way to understand the difference between potential and realized interactions, which is required to advance toward a biogeography theory of interactions. So that we can understand the relationship between the structure of potential and realized networks, *i.e.* in the terms of Poisot et al. (2012), the differences between a metaweb and its realizations, it is important to understand the ecological factors involved in making populations interact.

The goal of this paper is to evaluate how several families of mechanisms and ecological processes can create turnover in species interactions at the population level. We evaluate in turn the importance of neutral processes, local traits distribution, and context-dependence, to (i) give a comprehensive overview of how and why they create turnover, and (ii) show how integrating them into our current analyses of networks will result in a more predictive science. Although most of the discussion is, for the sake of simplicity, about whether species will interact or not, the same mechanisms can be used in a probabilistic approach (Yeakel et al. 2012). This leads to an altered view of ecological networks, which is more focused on populations rather than species, as it appears as the natural scale of biological organization at which these mechanisms are expressed (Smallegange and Coulson 2012). Doing so leads to clear recommendations about what to measure in the field when sampling interaction networks, and how we can design statistical approaches to better understand the interactions of the factors of turnover (we present one possible way to do so in *Box 1*). We conclude by discussing how the new knowledge gained this way will be applied to our understanding of species interactions, and how it will help us build more predictive models.

Population dynamics and neutral processes

The *Unified neutral theory of biodiversity* (Hubbell 2001) relies on the assumption that species are ecologically neutral when it comes to their competitive interactions. Neutral (*i.e.* abundance) and non-neutral (*i.e.* trait-based) effects can act simultaneously in a population, albeit with different intensities (Gravel et al. 2006). The development of this theory was an important step into accounting for the importance of ecological drift in structuring horizontal diversity (Rosindell et al. 2012). Over the recent years, the idea of neutrality percolated into the analysis of the structure of ecological networks, and this theory started being used to explain vertical diversity, most notably in bipartite networks (Blüthgen et al. 2006). Several host–parasite datasets were thusly re-analyzed, with the conclusion that changes in local species abundances triggers variation in parasite specificity (Vazquez et al. 2005). Recent results show that this logic also holds predictive power for food webs (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

The reasoning for a neutral approach to species interaction networks is as follows. In order for two species to interact, there are a number of requirements they must jointly meet. Combes (2001) proposed that there are two families of such requirements: ecological (related to species encountering one another), and evolutionary (related to species falling within one another Eltonian fundamental niche, which are addressed in the following section). Assuming that two species occupy the same patch, and are active at the same time of the day, a neutral approach to modeling their encounter probability is to use their local abundance. Two locally abundant species are more likely to interact than two locally rare ones, 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, the identity of species do not matter (*i.e.* there are no trait-based processes involved), and it becomes easy to understand how this can lead to a situation where, because species vary regionally in abundance, some interactions display turnover. In addition, and because of spatial and temporal variation in abundance, the same species can appear to gain or lose partners in different patches.

In a recent work, Canard et al. (2012) showed that simulated networks obtained through a neutral process displayed a realistic structure, which suggest that neutral processes do indeed drive the local organization of interactions. More importantly, this study revealed the possibility for “neutrally forbidden links”: these appear when one species is at an abundance too low to interact to interact with some species (in an individual-based model, over the course of one generation, a given species cannot interact with more other species than it has individuals). Such forbidden links can generate interactions turnover over spatial or temporal extents, even in the presence of trait-based constraints (*Box 2*). 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 their pairwise interactions were measured along a gradient of decreasing availability of the resources used by victims for their growth. This resulted in locally decreasing the abundance of victims, thus diminishing their availability for enemies. As in this system, the abundance of enemies is tied to the abundance of victims (Beretta and Kuang 1998, Rabinovitch et al. 1999), this experiment effectively decreased the encounter probability of the two species. 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

As local variations in the environmental conditions (heterogeneity) can trigger changes in the local abundance of interacting species, it is important to have the ability to understand how this heterogeneity cascades to the structure of species interactions. Simple statistical models can be used to quantify the effect of population sizes on local interaction occurrence or strength, which tells if neutral processes are involved (Krishna et al. 2008). Furthermore, knowing the part of each interaction explained by neutrality, it is possible to *remove* it from the observed values. One can then examine the structure of the networks once neutral effects have been removed, or in the contrary, if only neutral effects are accounted for. This offers an extremely powerful tool to measure the consistency of neutral and trait-based components of interactions through time and space. As most data will now include estimates of population density as well as estimates of interaction strength, it is crucial that we develop standardized methods to isolate the neutral signal on interaction strength. Coming up with such a framework will complement theory surrounding the measurement of interaction strengths in nature (Wootton and Emmerson 2005). Even more importantly, integrating neutral processes in our understanding of networks will benefit 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 species 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).

Traits distribution fluctuation in space and time

Olesen et al. (2011) reported the existence of “forbidden links” in mutualistic interactions, that is interactions whose existence is prevented by the fact that species traits do not match. For example, the proboscis of a pollinator may be too short to reach the pollen of a plant species. Under this perspective, both the existence and absence of interactions can be mapped on trait values. In contrast to the neutral perspective, this can also be linked to evolutionary hypotheses on trait conservatism. Price (2003) proposed that a wide range of current macroecological patterns, including the identity of species that are interacted with, is a consequence of the macroevolutionary dynamics of traits, a view which is also at the core of community phylogenetics interpretation of interaction networks (Ives and Godfray 2006, Mouquet et al. 2012). Polidori et al. (2012) showed that fast-flying preys (a trait which has been evolved under pressures other than predation) were preferentially attacked by generalist parasitoid wasps, while specialist wasps favored slow-flying preys. Clearly trait values have far-reaching consequences on network structure. However, rarely addressed is the fact that at short spatial and temporal scales, trait structure of populations within a species can show great variability. In this section, we review how this granularity in trait distribution can affect network structure. We propose that integrating it our description of networks will (i) increase our ability to predict the existence of interactions, and (ii) allow to better ground the current structure of networks in an evolutionary context.

The basic processes

Much in the same way that across-species matching in trait values will allow the existence of interactions, the value of traits across different populations will determine whether they interact. In [Figure 2](#), we present an illustration of this fact. In short, the species-level interaction network, because it is built by aggregating population-level interactions, which may have a large variability if the morphospace occupied by each species is large, can have unique emerging properties. 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.

There are, however, several examples of trait value shifts 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. This interaction can most likely exist only during a limited time of the “prey” life-span. Similarly, predation role reversal is mostly contingent upon the traits of the individuals being in different configurations. 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. These two examples share a common feature: in interactions strongly regulated by matching trait values, the functional role of an individual is an emergent property of its traits values, taken in combination with the traits values of other individuals, rather than a species characteristic.

Kuwae et al. (2012) showed that local differences in bird morphology led to them not consistently interacting with bacterial biofilm in an intertidal food web. The local stratification of traits result in situations in which two populations will not be able to interact, even though they belong in each other fundamental Eltonian niche (at the species level). Assuming that some interaction-related traits can be under strong environmental forcing (for example, body

size is expected to be lower in warm environments, Angilletta et al. (2004)), there can be co-variation between environmental values, life history traits, and the occurrence of interactions, because of either developmental constraints or phenotypic plasticity. An empirical demonstration of this was provided by Woodward et al. (2012): through the simulation of ecosystem warming, they demonstrate that changes in food-web structure happen at the same time as changes in body mass. Integrating trait variation over spatial or temporal extents is now central if we are to understand network variation and response to environmental change.

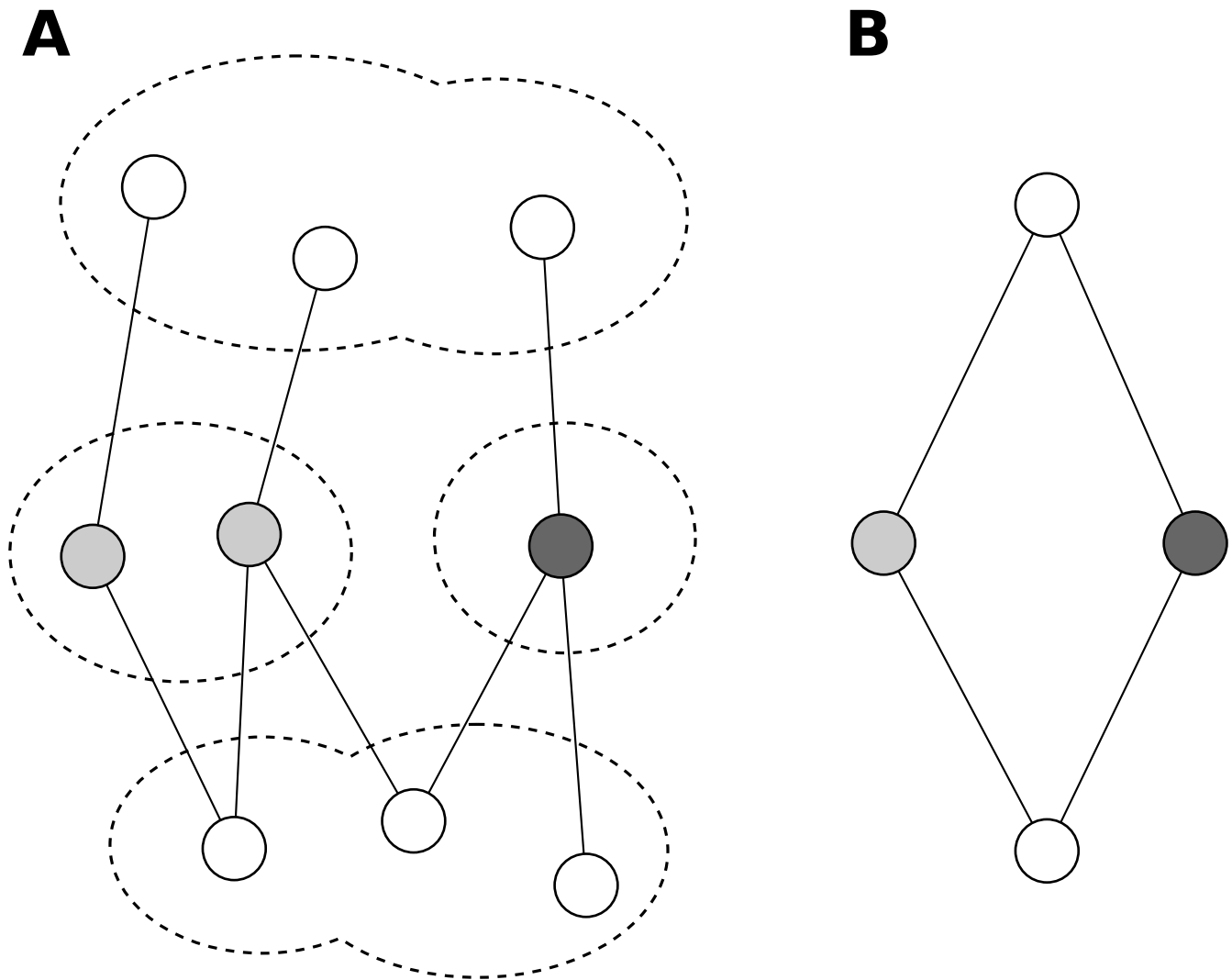


Figure 2: Panel **a** represents the interactions between different populations (circles) of four species, identified by the boundaries of their morphospaces (dashed lines). This network is mostly made of linear food chains, and has one generalist consumer. When aggregated at the species level however, 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 individual population can interact differently than the species it belongs to..

Benefits for network analysis

Although tools now exist to measure the turnover of interactions (Poisot et al. 2012), there is a need to link this turnover in a mechanistic understanding. Intra-specific variation in traits values in space or time is, as we illustrated below, a promising avenue. We propose in *Box 1* a way to understand the impact of traits and neutral effects on the occurrence of interactions. To be put in practice, this requires that when assembling a network locally, trait values of interacting organisms are measured. For obvious reasons, the trait values cannot be extracted from reference databases, as this will assume that all populations of a species are equal. With the accumulation of data, this new perspective will allow to better understand how networks vary along environmental gradients. Price (2003) shows how specific biomechanic response to water input in shrubs can have pleiotropic effects on traits involved in the interaction with insects. So as to make sense of the variation of plant–insect interactions on the gradient, one needs to look at trait interactions, and traits responses to environmental constraints. At a macro scale, since current traits reflect adaptation to past environments (Diniz-Filho and Bini 2008), looking for trait conservatism will help highlight historical contingencies on the structure of current networks.

Finally, paying more attention to local trait distribution and how it impacts the realization of the interaction between two species will contribute to the integration of coevolution and network analysis. Trait-trait correlation, and trait-fitness correlation, are one of the basic ingredients for reciprocal selection (Gomulkiewicz et al. 2000, Nuismer et al. 2003), and needs be studied at the scale of the population, so as to be able to address the spatial dynamics (Thompson 2005). Several authors discussed how migration between patches can disrupt local selection dynamics (Gandon et al. 2008, Burdon and Thrall 2009), which received empirical support in experimental evolution studies (Brockhurst et al. 2007, Morgan et al. 2007). Understanding how the realization of potential interactions are affected by local trait distribution in the two species involved will allow not only to understand how a new species will integrate into the existing network, but also how it can affect its evolutionary dynamics. In parallel, the bulk of community phylogenetics (Webb et al. 2006) was developed to re-analyse community

structure through the phylogenetic conservatism of traits (Cavender-Bares et al. 2009, Mouquet et al. 2012). If enough realizations are sampled, for which we know even coarsely the phylogenetic structure of traits (Chamberlain et al. 2012), we will have a strong database on which to carry out statistical analyses to determine when interactions will occur. This effort will provide a strong mechanistic basis for previous work showing a phylogenetic and ecological structure of complex networks (Baskerville et al. 2011, Eklof et al. 2011). In addition to providing this more mechanistic insight, better linking traits and their phylogenetic structure to the local occurrence of an interactions is a promising way to incorporate more evolutionary hypotheses and mechanisms in the study of network dynamics.

Beyond pairwise interactions

In this section, we argue that although networks offer a direct access to direct intractions, there is potential in adresssing indirect effects to. We present evidences showing that this can be done by understanding the effects that direct interactions have on one another, and outline the benefits of doing so to further reinforce the links between species interactions and species distribution (Thuiller et al. 2013).

The basic processes

Several authors (Golubski and Abrams 2011) showed that biotic interactions themselves interact. The presence or absence of a biotic interaction can affect either the realization of other interactions, or the presence of other species, as we will illustrate below. There are two broad situations which can happen. First, the presence of one interaction will be a necessary condition for the presence of a second. For example, opportunistic pathogens have a greater success of infection on hosts which are already immunocompromised by previous infections Olivier (2012) . Second, already established interactions can prevent future partners from interacting. Such is notably the case in protective symbioses, *i.e.* those in which a resident

symbiont decreases the infection probability of a new pathogen (Heil and McKey 2003, Koch and Schmid-Hempel 2011). Note that in both cases, the driver of interaction turnover is the patchiness of species distribution, emphasizing why the two concepts ought to be integrated. Direct interactions can also interfere with each others when there is preference in the selection of interaction partners. Lafferty (1992) documents some examples of predators avoiding preys infected by parasites. Schmitz (2008) show that two predators, whose difference is the hunting mode, are able to trigger a diet shift in their prey. Similarly, 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). The rich natural history of this relatively simple community module clearly illustrates that interactions between direct interactions needs be accounted for.

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 (i) integrate different types of interactions in ecological networks (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.

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).

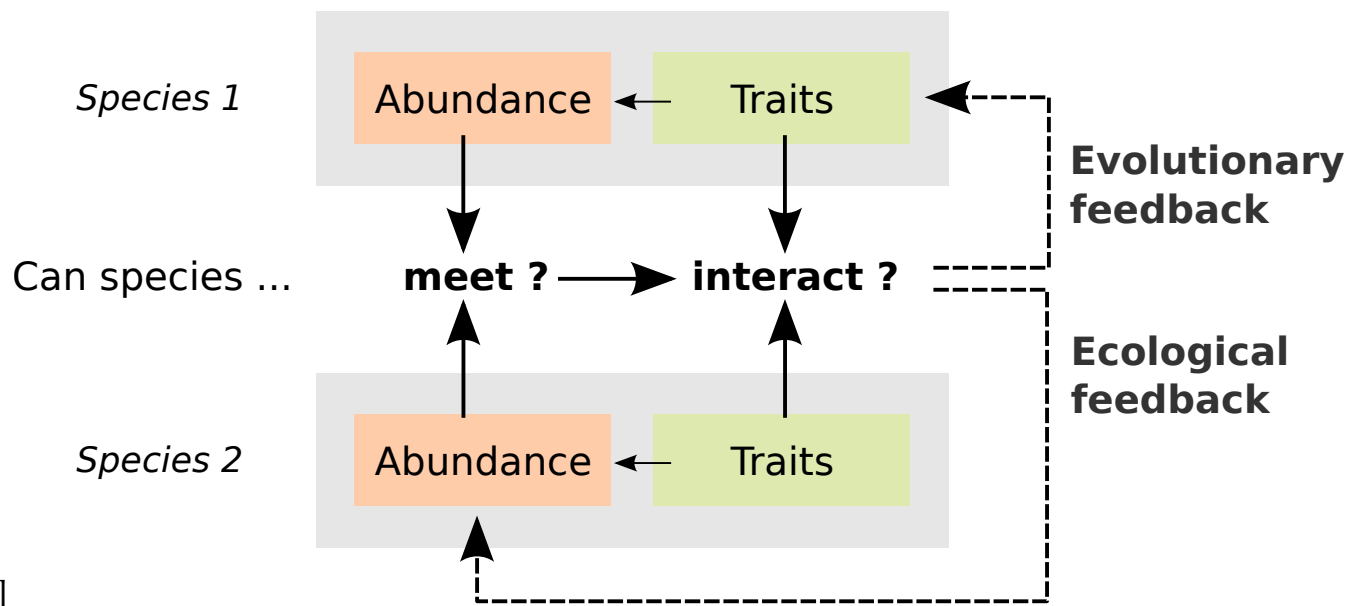
Conclusions

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

$$\mathbf{A}_{ij} = [(N_i \times N_j) \times (T_i \times T_j)] + \epsilon$$

wherein N_k is the local abundance of population k , and T_k is a measure of its position in a trait space; ϵ is an error term. \mathbf{A}_{ij} can take the form of, according to what is measured in the field, either presence and absence of interactions, or a measure of interaction strength. The term $(T_i \times T_j)$ can be as complex as needs be, and can rely on the use of latent variables (Rohr et al. 2010) rather than actual traits values. Re-casting the question of the occurrence of an interaction as a statistical one can at first seems at odd with our goal to incorporate more explicit feedbacks between traits, population sizes, and interactions. However, it bears two important advantages. First, it allows to identify broad patterns, namely which kind of interactions are more affected by neutral and niche processes. Second, it allows to partition the impact of said processes on the occurrence of interactions; this, in turn, allows to derive the structure of interactions *in the absence* of any niche, or neutral effects, which will find useful applications as it is a null model of species interactions. Further, in a multi-site context, we can reformulate the above linear model as

$$\mathbf{A}_{ijx} = [(N_{ix} \times N_{jx}) \times (T_{ix} \times T_{jx})] + \epsilon_{ijx}$$

In which the x indice denotes one site at which the interaction is either present or absent. 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.

Box 2: Between-site variability under neutral and trait-based assumptions

We use a simple conceptual model to generate predictions about the dissimilarity between networks in which only neutral effects, or neutral and traits effects, regulate the existence of interactions. Starting with a pool of 50 species establishing trophic interaction (see the reference to the model for details), we generate 50 replicates run, each starting with equal size of each population. After 2500 timesteps, we record the current state of the network, by pooling all the interactions which occurred over the last 20 timesteps. For the neutral and trait scenario, we reconstructed the metaweb, *i.e.* the regional pool of all species and their realizations. Based on this information, we (1) measure the dissimilarity between the 50 replicated networks (*i.e.* how different do we expect these networks to be in nature – top row of the figure), and (2) measure the distance between each of these networks and their respective metaweb (bottom row), using the β -diversity measures of networks proposed by Poisot et al. (2012). This analysis shows that the networks in which only neutral effects acts are more dissimilar (β_{WN}) than when traits regulate interactions. This also true of the way shared pairs of species (β_{OS}) interact. When measuring the contribution of species turnover to network turnover ($\beta_{contrib}$), it is clear that it is far less important in the neutral situation (*i.e.* because traits are not important, all species are functionally equivalent provided that their abundances are similar). Similarly, networks in the trait-based situation are relatively similar to their metaweb (approx. 20 % of difference), whereas the neutral ones are not (approx. 80 % of difference). This last result allows to estimate the error made when assuming that all interactions reported in the metaweb consistently occur over space (*e.g.* Havens 1992). Finally,

these results assume an homogeneous environment, *i.e.* the feeding niche of the species are not affected by local environmental conditions. Should it be the case, we expect an increased variability in the networks in which traits determine the interactions.

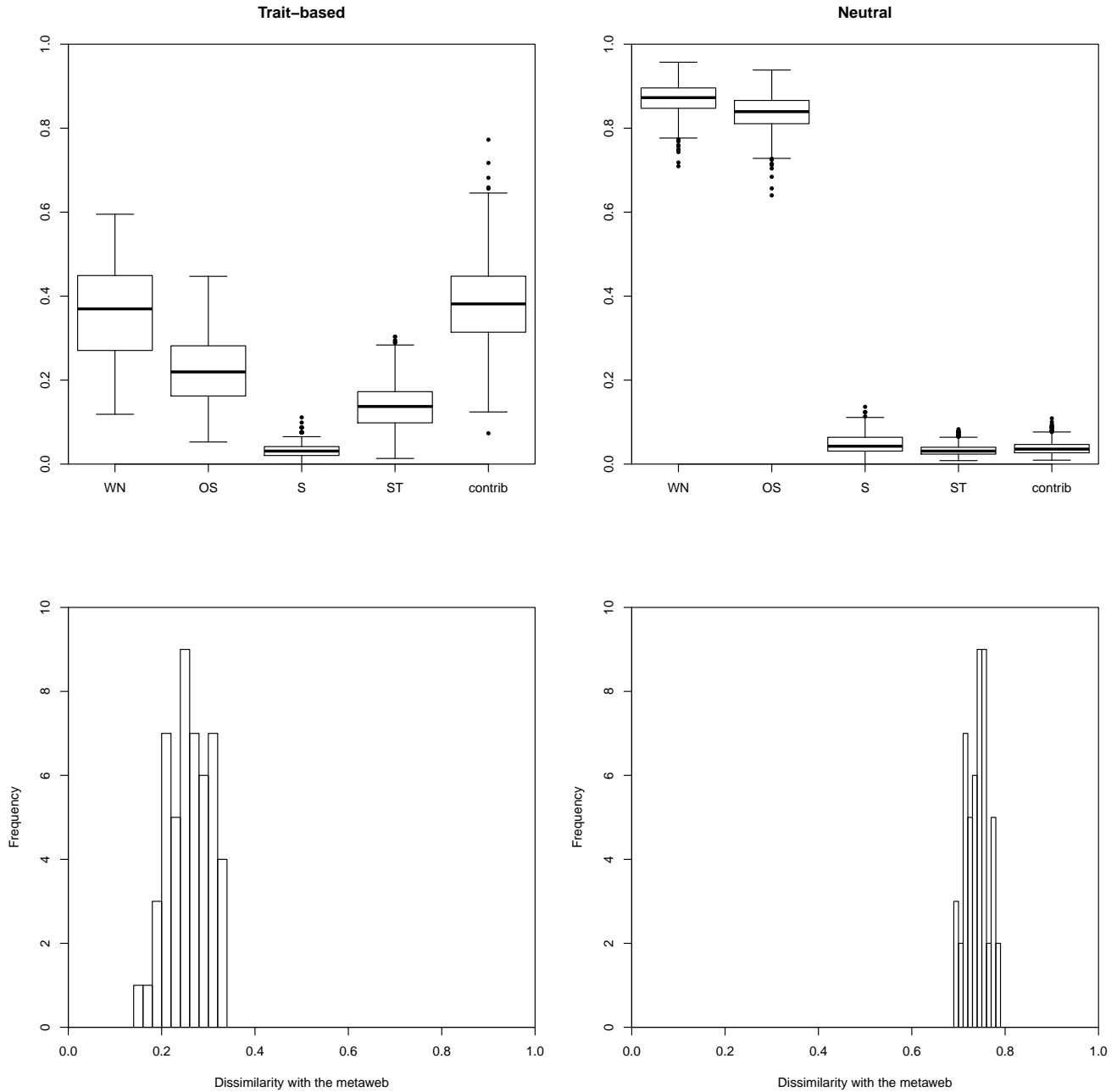


Figure 3: image

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