

Expanding the paradigm of ecological network research

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Introduction

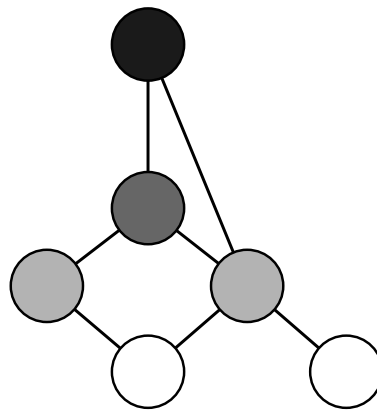
Describing the structure of ecological communities requires to know not only the identity of species, but also their interactions. Because interactions drive ecological dynamics within communities (Berlow et al. 2009), their organization will confer certain ecological properties. The structure of interactions has been described by species interaction networks (Dunne 2006), that is, a mathematical and conceptual representation of both *species*, and the *interactions* they establish. This view generated a rich literature primarily focused on how certain mathematical properties of the network related to the robustness (Dunne et al. 2002), productivity (Duffy et al. 2007), or tolerance to extinction (Memmott et al. 2004) of the community it represents. Although this approach classically focused on food webs (Ings et al. 2009), it can be applied equally to all types of ecological interactions (Kéfi et al. 2012). By large, this literature assumes that, short of changes in local densities due to ecological dynamics, networks are *static* objects. If two species are known to interact at one location, it is assumed that they will interact whenever they co-occur (see *e.g.* Havens 1992). Recently, we proposed 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); others refs]. 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 to be supplemented with new concepts and mechanisms.

Recent studies on the sensitivity of network structure to environmental change provide some context for this question. 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.

Understanding these results requires a major change in the conceptualization of an ecological network: any observation of an ecological network is the realization of *potential* interactions, much in the same way that the observation of a community is a realization of a *potential* species pool in the meta-community theory (Leibold et al. 2004). Further, there is a need to identify and conceptualize the new mechanisms involved in giving networks their dynamics. We argue that this can be done within a simple framework describing the sources of network variation. Following Dunne (2006) and Poisot et al. (2012), the pool of potential interactions at the regional level is a *metaweb* (Figure 1). The composition of *realized* networks, *i.e.* those observed in nature, is determined by a series of sorting processes (on the species being present, then on the way they interact). As the mechanisms of species sorting have been described by meta-community theory (Leibold et al. 2004), there is a need to tear apart the mechanisms of interaction sorting.

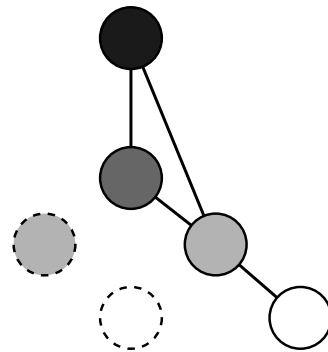
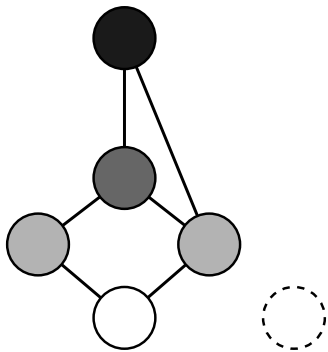
metaweb



Site 1

local species sorting

Site 2



local interaction sorting

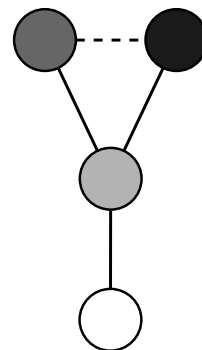
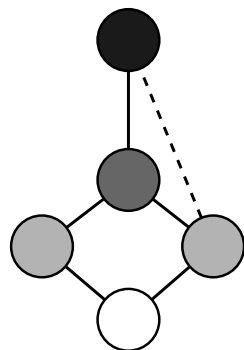


Figure 1: An illustration of the metaweb. In its simplest form, the metaweb is the list of all possible species and interactions between them for the system studied. The interactions could be based on observations or inferred from trait values and previous knowledge

There are two broad families classes of mechanisms involved in the establishment of an interaction. First, individuals of both species should be in a large enough number to meet, giving interactions a density or frequency-dependant component. Second, there should be some degree of phenological matching between the individuals, so that their traits allow the interaction to occur (for example, pollinators must have a proboscis long enough to reach the pollen, predators should have a jaw large or wide enough to eat their prey). These mechanisms (to which we will refer as “neutral” and “trait-based” henceforth) will then be altered by the surrounding, *i.e.* environmental conditions, presence of other species, and so forth. As show in *Box 1*, this conceptualization of an interaction lends itself to a statistical approach. However, it requires that our attention be shifted from *species*-level interactions to *population*-level ones, so that variation between sites is grounded in a mechanistic approach.

In this article, we will show that focusing on population level networks have several benefits from our understanding of species interactions both at the local, regional, and global scales. Specifically, it (i) integrates across a range of mechanisms, linking community ecology to biogeography, functional ecology, and evolutionary biology. (ii) It will guide the gathering of new data, and give a better pitcure of how they should be analyzed. We will shortly review evidences supporting the role of neutral and trait-based processes involved in network variation, and discuss how they should be accounted for in network studies. Finally, we will show that these mechanisms also pertain to the studies of indirect interactions. We conclude by providing a global framework situating these different processes, and showing their relevance for ecological and evolutionary feedbacks.

% DG: might be useful to refer to McGill et al. 2005 (TREE) here. He makes the argument that the study of pairwise interactions has been a waste of time with no general rules. I strongly disagree, I think we could achieve the equivalent for networks to the framework he is proposing for plants

Population dynamics and neutral processes

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

The basic processes

% DG: I like the structure of each section, but I would almost try to limit it to one good paragraph per subsection. There are already three families of processes (and I propose a fourth one, see below), times 3 paragraphs per process, it already makes 9-12 paragraphs, which is considerable.

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 interact is 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 model (*i.e.* interactions happen entirely by chance, although abundance can be not neutral), the identity of species do not matter, and it becomes easy to understand how this can lead to a situation where, because species vary regionally in abundance, the structure of local

networks will vary. Canard et al. (2012) proposed the term of “neutrally forbidden link” to refer to interactions that are feasible from a phenologic standpoint, but not realized because of population size distribution. The identity of these neutrally forbidden links will vary over time and space, either by stochastic changes in population sizes, or because population size respond deterministically to extrinsic drivers. A similar phenomenon was observed by Poisot et al. (2011). A soil community of bacteria (victims) and bacteriophages (enemies) was isolated from its natural environment, and all pairwise interactions were measured along a gradient of decreasing resource availability. The resulting lower abundance of the bacteria significantly decreased the encounter probability of the two species and thereby the network structure. This resulted in a strong link turnover, with some species being able to interact in the resource-rich environment, but not in the resource-poor ones. % DG: I did reduced the paragraph quite a lot. Much more compact now.

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 stud-

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

The basic processes

There are evidences that at the species level, interaction partners are selected on the grounds of matching trait values. Random networks built on these rules exhibit realistic structural properties [Williams 2000]. However, trait values vary from population to population within species, and so it is expected that the local interactions will be contingent upon trait distributions (Figure 2). The fact that the niche of species can appear large if it is the aggregation of narrow but differentiated individual or population niches is now well established (Bolnick et al. 2003, Devictor et al. 2010), and reinforced the need to understand intra-specific trait variation to describe the structure and dynamics of communities (Bolnick et al. 2011). This notion is yet, however, to percolate the literature on network structure, despite an immediate consequence: a species appearing generalist at the regional scale, can be specialized in each of the patches it occupies. There are several examples of intraspecific trait variation resulting in extreme interaction turnover. A particularly spectacular example is described by Ohba (2011): a giant waterbug is able to get hold of, and eventually consume, juveniles from a turtle species. Choh et al. (2012) demonstrated through behavioral assays that preys which evaded predation when young, were more likely to predate juvenile predators, than the “naive” individuals: the past interactions shaped behavioral traits that alter the network structure over time. These examples show that trait-based effects on networks can be observed even in the absence of genotypic variation (although we discuss this in the next section). In this perspective, the existence of an interaction is an emergent property of the trait distribution of local populations: variations in one or both of these distributions, regardless of the mechanism involved (development, selection, plasticity), is likely to alter the interaction. Importantly, when interaction-driving traits are under environmental forcing (for example, body size is expected to be lower in warm environments, Angilletta et al. (2004)), there can be covariation between environmental conditions and the occurrence of interactions. Woodward et al. (2012) demonstrate that changes in food-web structure happen at the same time as changes in body mass in experimental macrocosms. Integrating trait variation over spatial or temporal extents is now central if we are to understand network variation and response to environmental change.

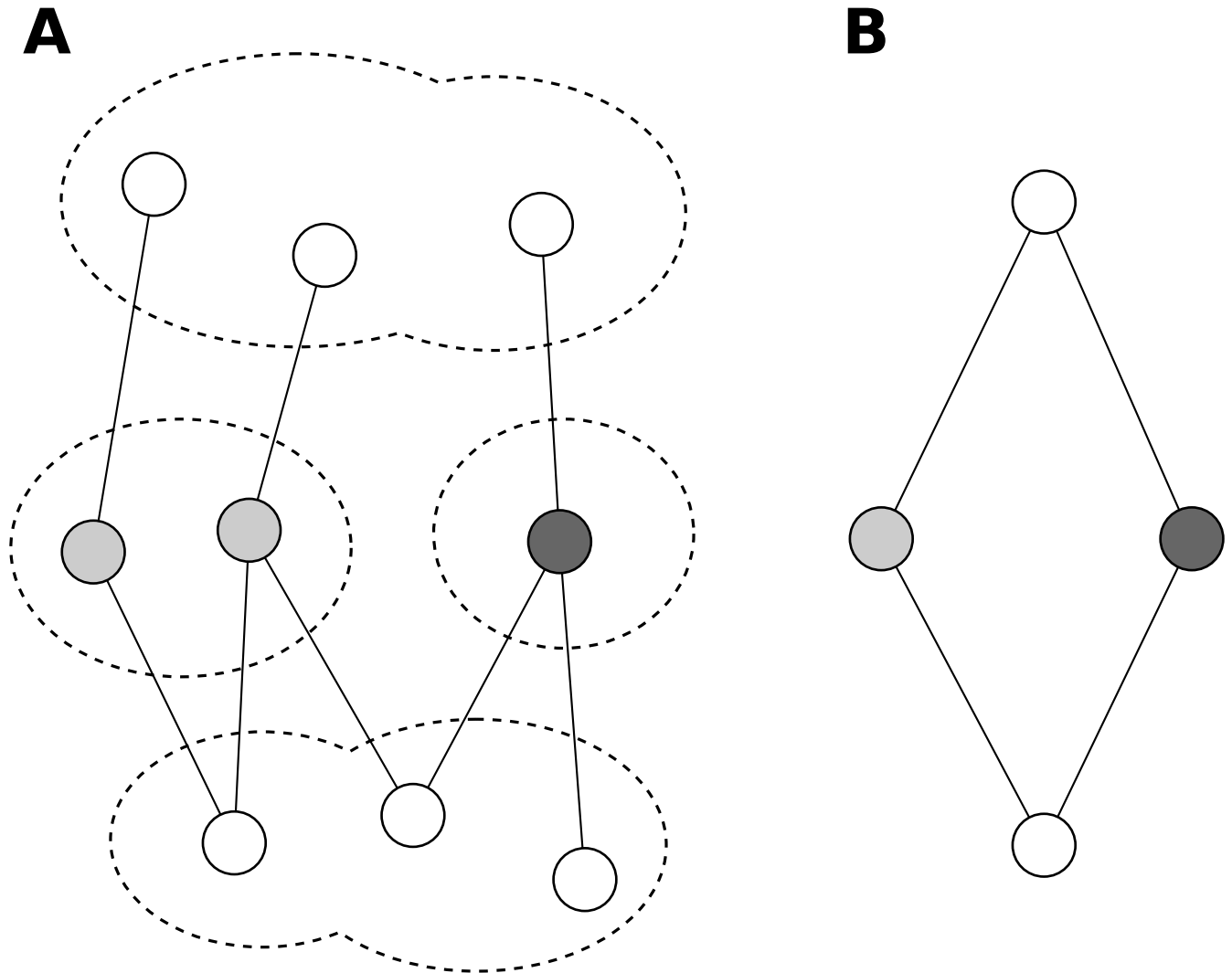


Figure 2: Panel **a** represents the interactions between different populations (circles) of four species, identified by the boundaries of their morphospaces (dashed lines). This network is mostly made of linear food chains, and has one generalist consumer. When aggregated at the species level however,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

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 because (i) traits values determine the existence of an interaction, and (ii) environmental features determine trait values. Accumulating empirical evidences will increase our ability to come-up with such mechanistic narratives. At a larger temporal scales, current distribution of traits also reflects past evolutionary history (Diniz-Filho and Bini 2008), looking for trait conservatism will help highlight historical contingencies on the structure of current networks. % DG: I think we will need to brainstorm more on those concepts. I find that the right ideas are there, but they still need to be develop more, I have the feeling that the thinking is not completely accomplished.

% DG: I like the ideas of the next paragraph, but the logic still needs to be further developped. There is a bunch of ideas, but they are not fully accomplished. Finally, paying more attention to trait variation and how it impacts the realization of ecological interactions 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). % DG: too much stuff and jargon in the previous sentence. You want to say too many things at once. Several authors discussed how migration between populations can disrupt local selection dynamics (brockhurst_impact_2007; Morgan et al. 2007, Gandon et al. 2008, Burdon and Thrall 2009). Understanding how the realization of potential interactions are affected by local trait distribution will allow not only to understand how a new species will integrate into the existing network of interactions, but also how it can affect its evolutionary dynamics. %DG: last sentence redundant 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). %DG: this idea is not fully developed, I don't understand where you are going. 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.

% DG: there is not much on the environmental dependance of interactions. How do you account for the fact that, for instance, a lemming is protected from the fox by the snow cover. Low snow fall one year will promote predation; it's not a neutral effect, it's not an effect of traits, it's simply environmental dependance of interactions. Should we have an extra section on this? I would see at least two effects of the environment: one on the abundance, the other on the strenght of the interaction. And perhaps even a third one, at the regional level on the species pool

Beyond direct interactions

In this section, we argue that although networks offer a direct access to direct interactions, there is potential in addressing indirect effects too. % DG: define what you mean by direct vs indirect interactions % DG: as I told you, I think this section is particularly relevant and original. 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. % DG: again, a definition would be useful. The occurrence or absence of a biotic interaction can either 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 occurrence 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. % DG: be careful, there is a big difference between an interaction changing the strenght of another, to an interaction changing the abundance of another species and thus the likelihood of an interaction. The first one will have an effect on the beta link, while the second will only have an effect on the species turnover part of the beta. % DG: But just made me thought that all of indirect interactions (in the traditional sense, with a cascade of interactions) are drivers of beta diversity of interactions. It's a purely species composition component, but still it is very interesting.

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. % DG: you have to go further than a ref to Kefi here, this section adress interactions that are not considered by Kefi. You can have a look instead at Goudard and Loreau Goudard, A. & Loreau, M. (2008). Non-trophic interactions, biodiversity and ecosystem functioning : an interaction web model. *The American Naturalist*, 171 : 91–106.

Benefits for network analysis

Accounting for the relationships between biotic interactions can be a powerful explanation for species co-occurrence. A recent experimental work by Sanders and van Veen (2012) showed that some predators species can only be maintained if another predator species is present, which regulates a competitively superior prey, hence allowing prey coexistence. These effects involving several species and several types of interactions across trophic levels are complex

(and for this reason, have been deemed unpredictable in the past, Tack et al. 2011), and can only be understood by comparing communities in which different species are present/absent. To better understand these effects, it is important that several networks with similar species compositions are sampled. Assuming that interactions are present is obviously not enough, and the data needed to characterize these mechanism need to include a precise measure of interaction strength between each species. It is true that such data are orders of magnitude more difficult to gather than literature surveys or expert knowledge, but they are the only way to go beyond the current paradigm of seeing networks as mostly a collection of pairwise interactions.

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

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

% 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)

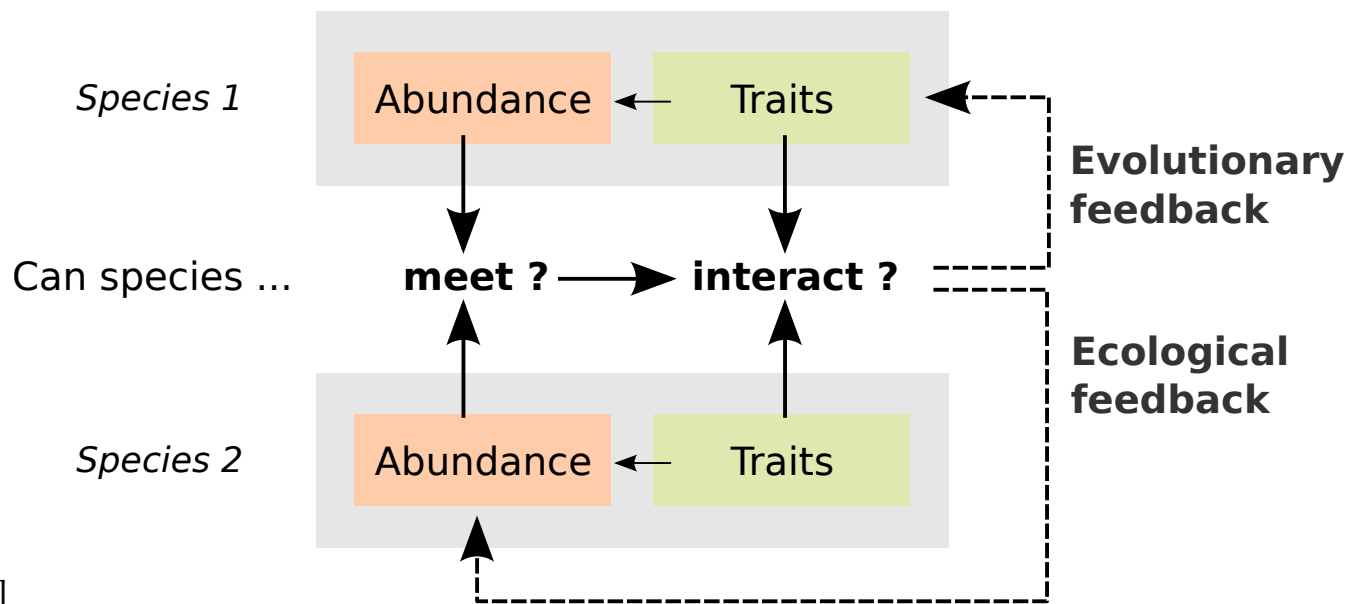
Conclusions

The notion of "species interaction networks" is an epistemological obstacle, 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.



[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. Following the approach put forth by Boulangeat et al. (2012), it is possible to apply this logic to the presence/absence of interactions, or to their strength, to further understand the dynamics of networks.

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.

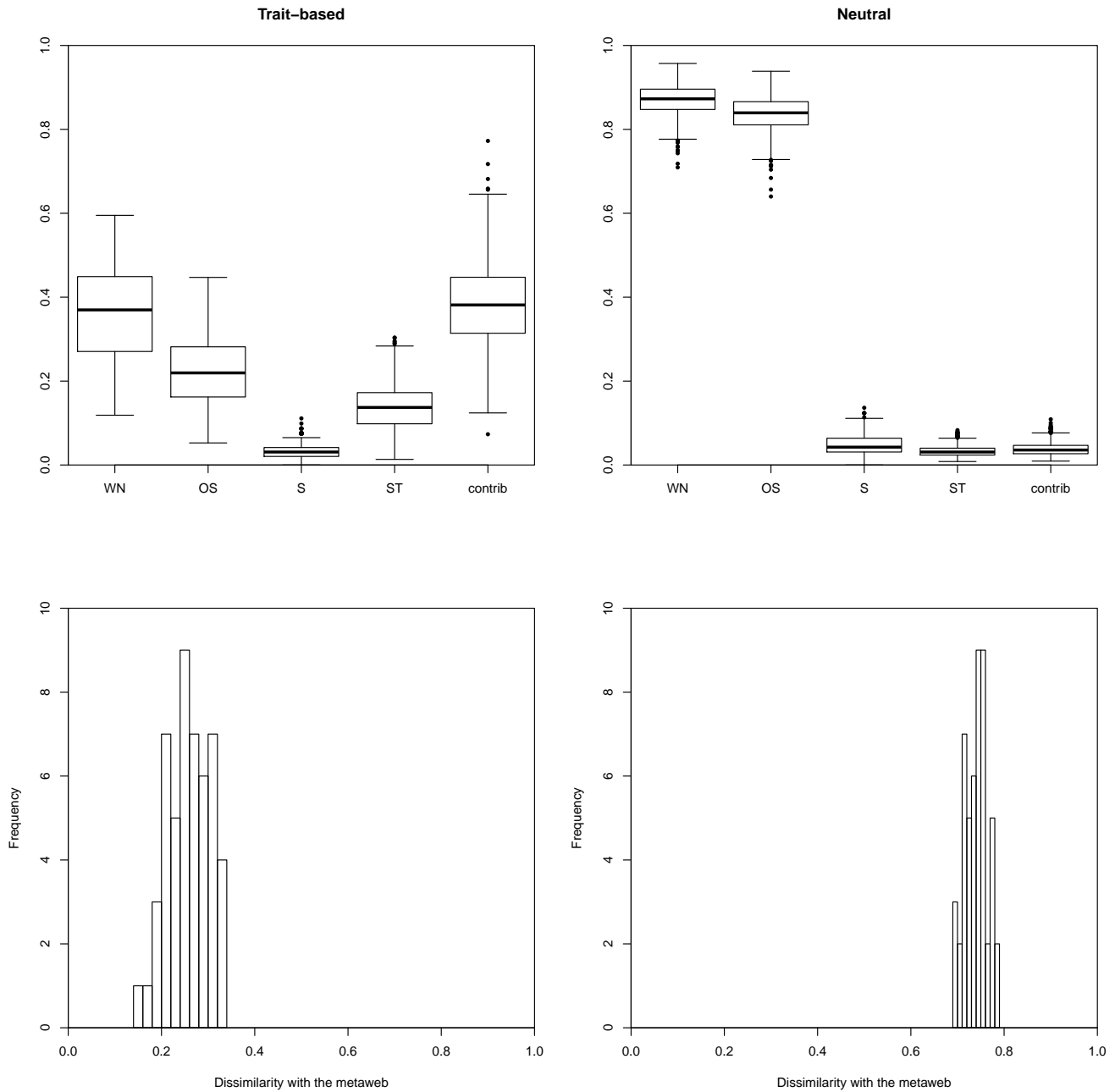


Figure 3: image

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* 34: 897–908.
- 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.
- Boulangeat, I. et al. 2012. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. - *Ecology Letters* 15: 584–593.
- 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.

- Calcagno, V. et al. 2011. Constraints on food chain length arising from regional metacommunity dynamics. - *Proceedings of the Royal Society B: Biological Sciences* 278: 3042–3049.
- Canard, E. et al. 2012. Emergence of Structural Patterns in Neutral Trophic Networks. - *PLoS ONE* 7: e38295.
- Cavender-Bares, J. et al. 2009. The merging of community ecology and phylogenetic biology. - *Ecology Letters* 12: 693–715.
- Chamberlain, S. a et al. 2012. Does phylogeny matter? Assessing the impact of phylogenetic information in ecological meta-analysis. - *Ecology Letters* 15: 627–636.
- Choh, Y. et al. 2012. Predator-prey role reversals, juvenile experience and adult antipredator behaviour. - *Scientific Reports* in press.
- Cumming, G. S. et al. 2010. Network analysis in conservation biogeography: challenges and opportunities. - *Diversity and Distributions* 16: 414–425.
- 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.
- 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.

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

Havens, K. 1992. Scale and structure in natural food webs. - *Science* 257: 1107–1109.

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* 78: 253–269.

Koch, H. and Schmid-Hempel, P. 2011. Socially transmitted gut microbiota protect bumble bees against an intestinal parasite. - *PNAS*: 1110474108.

Krasnov, B. R. et al. 2004. Geographical variation in host specificity of fleas (Siphonaptera) parasitic on small mammals: the influence of phylogeny and local environmental conditions. - *Ecography* 27: 787–797.

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* 15: 291–300.

Lafferty, K. D. 1992. Foraging on prey that are modified by parasites. - *American Naturalist* 140: 854–867.

- Leibold, M. A. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. - *Ecology Letters* 7: 601–613.
- MacArthur, R. H. and Wilson, E. O. 2001. *The Theory of Island Biogeography*. - Princeton University Press.
- Melián, C. J. et al. 2011. Eco-evolutionary dynamics of individual-based food webs. - In: Belgramo, A. and Reiss, J. (eds), *Advances in Ecological Research*. Academic Press, pp. 225–268.
- 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.
- Morgan, A. D. et al. 2007. Differential impact of simultaneous migration on coevolving hosts and parasites. - *BMC Evolutionary Biology* in press.
- Mouquet, N. et al. 2012. Ecophylogenetics - advances and perspectives. - *Biological reviews of the Cambridge Philosophical Society* 87: 769–785.
- 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.

- Pillai, P. et al. 2011. Metacommunity theory explains the emergence of food web complexity. - *Proceedings of the National Academy of Sciences of the United States of America* 108: 19293–8.
- 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. 2003. *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.
- Schmitz, O. J. 2008. Effects of Predator Hunting Mode on Grassland Ecosystem Function. - *Science* 319: 952–954.
- 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.
- Stanko, M. et al. 2002. Mammal density and patterns of ectoparasite species richness and abundance. - *Oecologia* 131: 289–295.
- Tack, A. J. M. et al. 2011. Can we predict indirect interactions from quantitative food webs?—an experimental approach. - *The Journal of animal ecology* 80: 108–118.

- Thompson, J. N. 2005. *The Geographic Mosaic of Coevolution*. - University Of Chicago Press.
- Thuiller, W. et al. 2013. A road map for integrating eco-evolutionary processes into biodiversity models. - *Ecology Letters* 16: 94–105.
- 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.
- Webb, C. O. et al. 2006. Integrating phylogenies into community ecology. - *Ecology* 87: 1–2.
- 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.