The causes of species interactions variability

T. Poisot & D. Gravel

May 2013

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 the dynamics within this community (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 (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 were 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 (Sarmento 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 truely be emergent systems. 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. (2011b) 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 change, requires that the sampling of network be replicated. In other words, to address these problematics, there is a need to shift our focus from species to populations 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. 2012) , are networks of potential interactions, but can seldom be used to predict whether two populations will interact. When sampling popula-
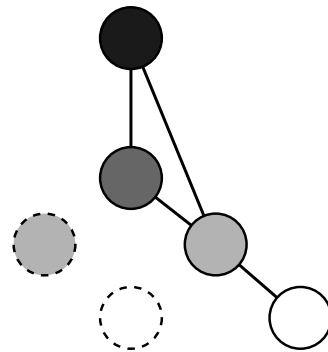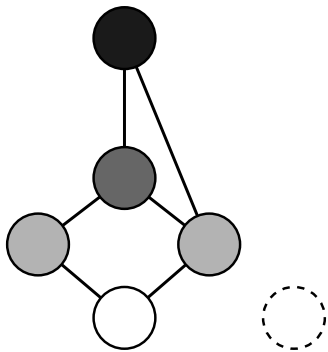
metaweb
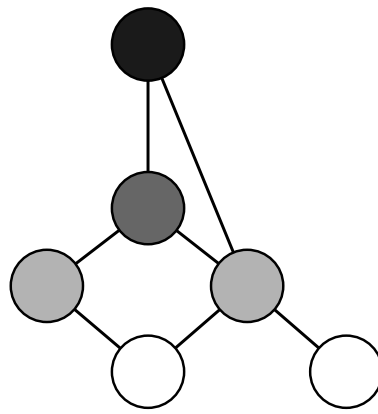
Site 1   local species sorting   Site 2
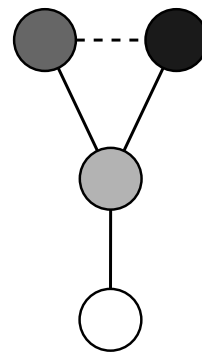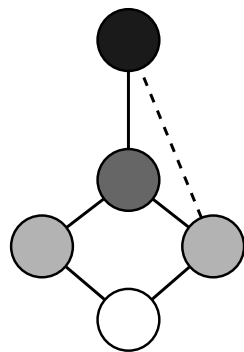
local interaction sorting

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. What is observed locally, here in sites 1 and 2, is *realizations* of this metaweb, after the action of

tions 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 an 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). 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's harder to miss an interaction if enough individuals are sampled.

Poisot et al. (2012) showed that after more than a hundred independent sampling of a host–ectoparasite system, not all regional interactions are known. This bears two important consequences. First, the adequate sampling of potential interactions is a difficult task. 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). In addition, because different realizations of a metaweb will show interaction turnover, it is important than we now focus our effort on understanding population-level interaction networks, because this seems the only way to understand the different 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. 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 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, notably in food webs. 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). 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_parasitism:_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 that two locally rare ones. 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 niche 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 models, 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. A similar phenomenon was observed by Poisot et al. (2011b). 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. 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) madde the point that deviations of empirical communities from neutral

predictions were explained by species interactions. 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.

Traits distribution fluctuation in space and time

Intro into the section: some studies found a niche signal through phylogenetic analysis, and a strong consequence of traits values, e.g. forbidden links. Both makes sense in that species interact as a function of the current state of their evolved traits. Discuss Price briefly.

Examples abound of species traits driving the number of interactions. For example, parasitic wasps targeting high-speed flying preys showed a larger niche, and less specialization, than sister species targeting slower preys [@Polidori2012]. When traits

Take-home: need to account for local structure of populations to explain, probabilistic approach can be based on something else than link strength, see Guimera in Proc R Soc Interfaces paper.

The basic processes

The logic of forbidden links also exists at the population level – local variation in traits

examples of predation reversal when juv and mature do not share the same site / ontogenetic changes

- Ohba 2011 - bug eat turtle

- Choh 2012 - juv experience has long lasting consequences

An interaction requires traits matching or mismatching, can be strongly locally stratified – as for neutrality, requires a population-level approach

@Kuwae2012 showed that local differences in bird morphology led to them not consistently interacting with bacterial biofilm in an intertidal food wed. The local stratification of traits will 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).

Wood paper ELE on traits vs. environment

can be disrupted by local adaptation to the environment – needs for a population rather than species level approach

expand on the idea that this can change the *nature* of the interaction, thompson paper

Allesina Eklof

Benefits for network analysis

quantify how much turnover is linked to trait distribution, through spatial analysis – propose some tools in the betalink paper

also temporal dynamics, and impact of environment through changes in traits – examples of water input in Price

@Price2003 proposed that, since the response of organisms to current environmental conditions and changes is dictated by the state of evolved traits, historical contingencies on the evolution of these traits should be better integrated into ecological studies. **to be continued**
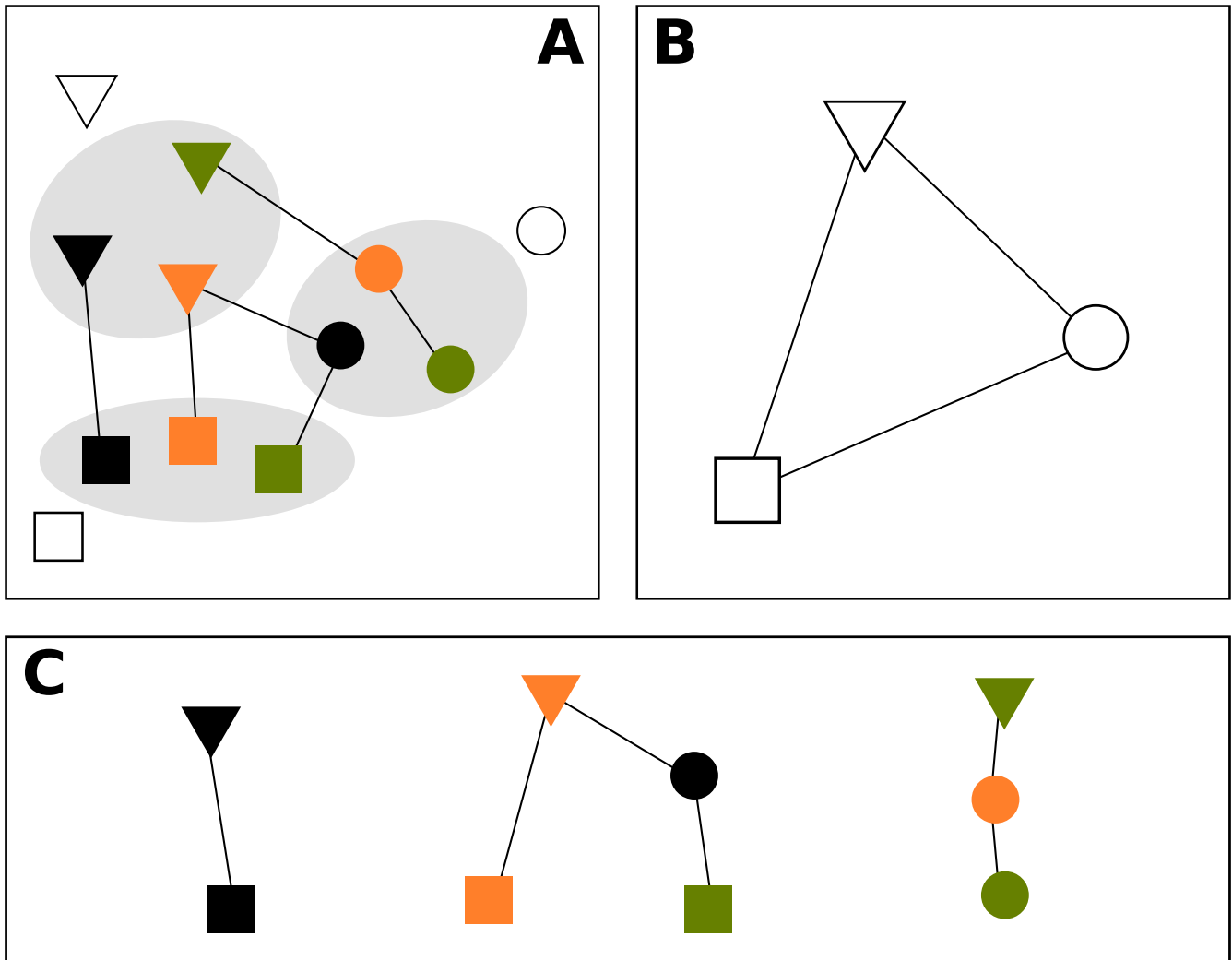
Figure 2: Assuming that species interact based on the value of their traits, looking at the inter-population variance of trait values is important. In the above example, three populations of each three secies interact (**A**). Aggregated at the species level, this yields a network represented in **B**. However, if one is to examine each population separately, the *actual* network shares no properties with its species-level counterpart (**C**).

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 [@Gomulkiewicz2000;@Nuismer2003], and needs be studied at the scale of the population, so as to be able to address the spatial dynamics [@Thompson2005a]. Several authors discussed how migration between patches can disrupt local selection dynamics [@Gandon2008;@Burdon2009], 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

The basic processes

Several authors (Golubski and Abrams 2011) showed that biotic interactions themselves interact. 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. 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.

— facilitation

Lafferty (1992) documents some examples of predators avoiding preys infected by parasites. In this case, the interaction is not established in the presence of a third species.

Hay et al. (2004) shows how "apparent mutualism" can emerge. When a predator or competitor of a focal species becomes involved in another antagonistic interaction with a third species, this third species can appear as a mutualist of the focal one, as its effects negates the original antagonistic interaction.

- trait change in response to predation: change outcome of competition

— prevention

Of course, these multiple symbioses or interactions can have consequences beyond the existence of pairwise interactions. The biotic interactions received by an organism will often affect its environmental tolerance, and modify its realized Grinnelian niche (Poisot et al. 2011a).

need for better resolved data
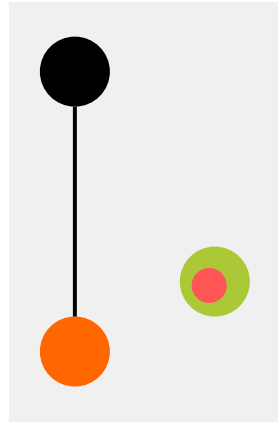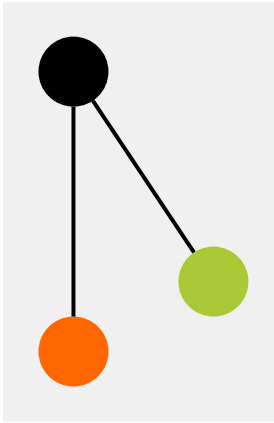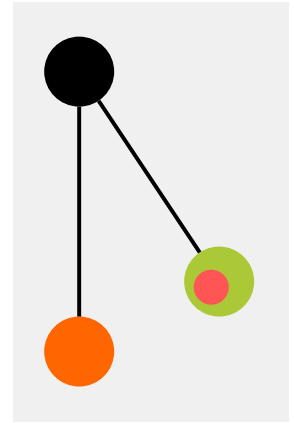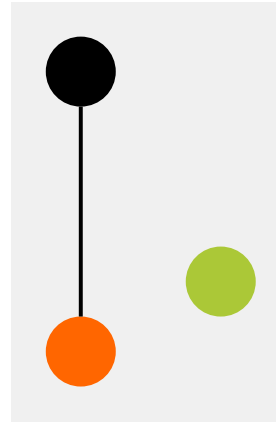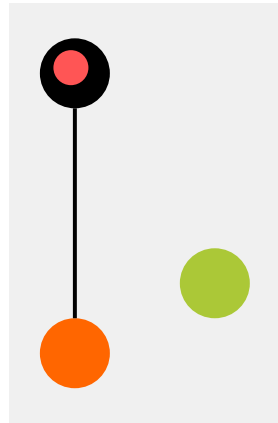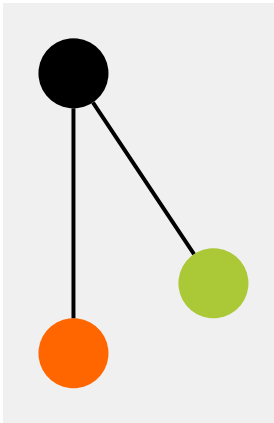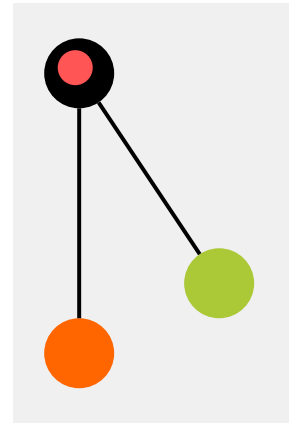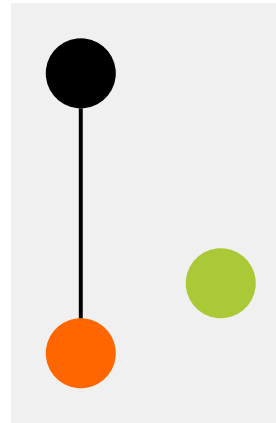
somehow linked to species persistence, Pillai et al. (2011)

— environmental mediations

Benefits for network analysis

In addition, 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 can only be understood by (i) comparing communities in which different species are present/absent, and (ii) accounting for multiple interaction types (Kéfi et al. 2012).

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.

Finally, the widespread impacts of interactions involving more than two species bears important consequences for some experimental approaches. Microbial systems, notably, use pairwise interactions to infer the structure of interaction networks (**ref me, buckling, daphnia papers**). While at reduced taxonomical scales, when we expect interactions to be relatively consistent, this process might not introduce too much bias, it is likely to under-report interactions when working on more complex systems. For example, **XXX** used pairwise assays to reproduce some of the interactions in the **ccc** metaweb. Especially in the context of multi-interaction networks, one should keep in mind the possibility that this approach is not unbiased.

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.
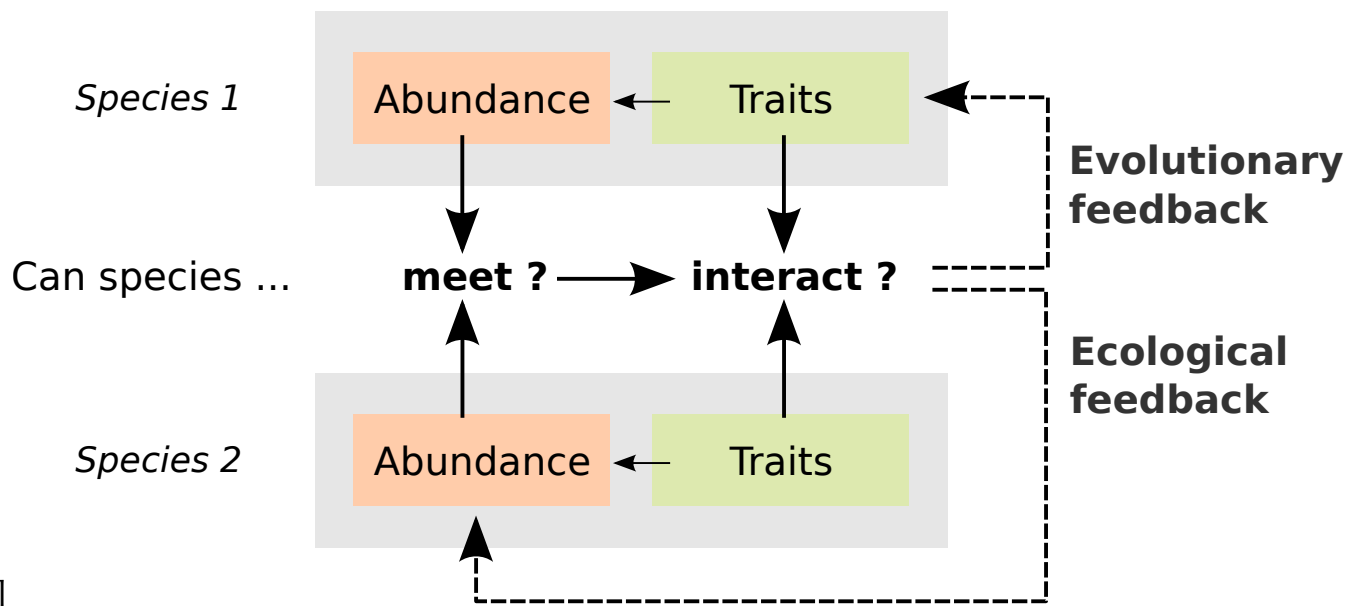
[tb]

[fig:synth]

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 by 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 nest 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.

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

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

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 $\left(T_i \times T_j\right)$ 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

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

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 (β_{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.
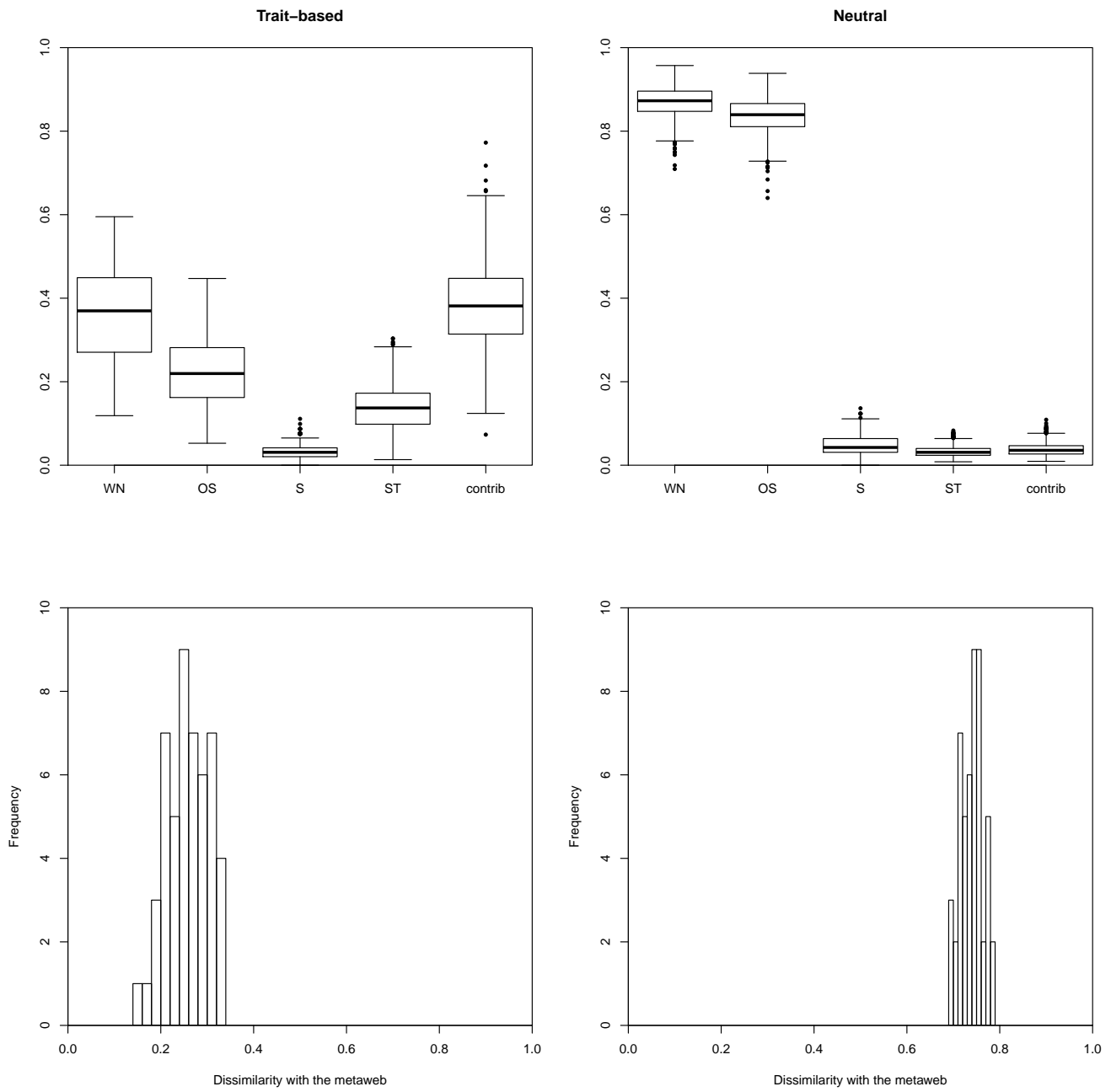
Figure 3: image

References

Bascompte, J. 2009. Mutualistic networks. - Frontiers in Ecology and the Environment 7: 429–436.

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: 1002321.

Beretta, E. and Kuang, Y. 1998. Modeling and analysis of a marine bacteriophage infection. - Mathematical Biosciences 149: 57–76.

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.

Brockhurst, M. A. et al. 2007. The impact of migration from parasite-free patches on antagonistic host-parasite coevolution. - Evolution 61: 1238–1243.

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

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: 38295.

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.

Copi, I. M. 1953. Introduction to logic. - Macmillian.

Cumming, G. S. et al. 2010. Network analysis in conservation biogeography: challenges and opportunities. - Diversity and Distributions 16: 414–425.

Dalsgaard, B. et al. 2013. Historical climate-change influences modularity and nestedness of pollination networks. - Ecography in press.

Dossena, M. et al. 2012. Warming alters community size structure and ecosystem functioning. - Proceedings. Biological sciences / The Royal Society 279: 3011–9.

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.

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

Gravel, D. et al. 2006. Reconciling niche and neutrality: the continuum hypothesis. - Ecology Letters 9: 399–409.

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.

Hay, M. E. et al. 2004. MUTUALISMS AND AQUATIC COMMUNITY STRUCTURE: The Enemy of My Enemy Is My Friend. - Annual Review of Ecology, Evolution, and Systematics 35: 175–197.

Heckmann, L. et al. 2012. Interactive effects of body-size structure and adaptive foraging on food-web stability. - Ecology Letters in press.

Hubbell, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. - Princeton University Press.

Ings, T. C. et al. 2009. Ecological networks–beyond food webs. - Journal of Animal Ecology 78: 253–269.

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.

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, ppp. 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.

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. 2011a. A conceptual framework for the evolution of ecological specialisation. - Ecology Letters 14: 841–851.

Poisot, T. et al. 2011b. 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.

Rabinovitch, A. et al. 1999. Bacterial Lysis by Phage–A Theoretical Model. - Journal of Theoretical Biology 201: 209–213.

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

Rosindell, J. et al. 2012. The case for ecological neutral theory. - Trends in Ecology & Evolution in press.

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

Sarmento, H. et al. 2010. Warming effects on marine microbial food web processes: how far can we go when it comes to predictions? - Philosophical Transactions of the Royal Society B: Biological Sciences 365: 2137–49.

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.

Shaner, P.-J. L. and Macko, S. A. 2011. Trophic Shifts of a Generalist Consumer in Response to Resource Pulses (J Wright, Ed.). - PLoS One 6: 17970.

Smallegange, I. M. and Coulson, T. 2012. Towards a general, population-level understanding of eco-evolutionary change. - Trends in Ecology & Evolution in press.

Stanko, M. et al. 2002. Mammal density and patterns of ectoparasite species richness and abundance. - Oecologia 131: 289–295.

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.

West, D. B. 2001. Introduction to graph theory. in press.

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

Wootton, J. T. and Emmerson, M. 2005. Measurement of Interaction Strength in Nature. - Annual Review of Ecology, Evolution, and Systematics 36: 419–444.

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: 2012.