

# Beyond species: why ecological interactions vary through space and time

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17 **Abstract:** Community ecology is tasked with the considerable challenge of predicting the struc-  
18 ture, and properties, of emerging ecosystems. It requires the ability to understand how and

1 why species interact, as this will allow the development of mechanism-based predictive mod-  
2 els, and as such to better characterize how ecological mechanisms act locally on the existence  
3 of inter-specific interactions. Here we argue that the current conceptualization of species in-  
4 teraction networks is ill-suited for this task. Instead, we propose that future research must  
5 start to account for the intrinsic variability of interaction networks. This can be accomplished  
6 simply by recognizing that there exists intra-specific variability, in traits or properties related  
7 to the establishment of species interactions. By shifting the scale towards population-based  
8 processes, we show that this new approach will improve our predictive ability and mechanistic  
9 understanding of how species interact over large spatial or temporal scales.

# 1 Introduction

2 Interactions between species are the driving force behind ecological dynamics within commu-  
3 nities (Berlow et al. 2009). Likely for this reason more than any, the structure of communities  
4 have been described by species interaction networks for over a century (Dunne 2006). Formally  
5 an ecological network is a mathematical and conceptual representation of both *species*, and the  
6 *interactions* they establish. Behind this conceptual framework is a rich and expanding literature  
7 whose primary focus has been to quantify how numerical and statistical properties of networks  
8 relate to their robustness (Dunne et al. 2002), productivity (Duffy et al. 2007), or tolerance to  
9 extinction (Memmott et al. 2004). Although this approach classically focused on food webs  
10 (Ings et al. 2009), it has proved particularly successful because it can be applied equally to all  
11 types of ecological interactions (Kéfi et al. 2012).

12 This body of literature generally assumes that, short of changes in local densities due to eco-  
13 logical dynamics, networks are inherently *static* objects. This assumption calls into question  
14 the relevance of network studies at biogeographic scales. More explicitly, if two species are  
15 known to interact at one location, it is often assumed that they will interact whenever and  
16 wherever they co-occur (see *e.g.* Havens 1992); this neglects the fact that local environmental  
17 conditions, species states, and community composition can intervene in the realization of in-  
18 teractions. More recently, however, it has been established that networks are *dynamic* objects  
19 that have structured variation in  $\alpha$ ,  $\beta$ , and  $\gamma$  diversity, not only with regard to the change of  
20 species composition at different locations but also to the fact that the same species will interact  
21 in different ways over time or across their area of co-occurrence (Poisot et al. 2012). Of these  
22 sources of variation in networks, the change of species composition has been addressed explic-  
23 itly in the context of networks (Gravel et al. 2011, Dáttilo et al. 2013) and within classical  
24 meta-community theory. However, because this literature still tends to assume that interac-  
25 tions happen consistently between species wherever they co-occur, it is ill-suited to address  
26 network variation as a whole and needs be supplemented with new concepts and mechanisms.  
27 Within the current paradigm, interactions are established between species and are an im-

1 mutable “property” of a species pair. Starting from empirical observations, expert knowledge,  
2 or literature surveys, one could collect a list of interactions for any given species pool. Sev-  
3 eral studies used this approach to extrapolate the structure of networks over time and space  
4 (Havens 1992, Piechnik et al. 2008, Baiser et al. 2012) by considering that the network at *any*  
5 location is composed of *all* of the potential interactions known for this species pool. This stands  
6 in stark contrast with recent results showing that (i) the identities of interacting species vary  
7 over space and (ii) the dissimilarity of interactions is not related to the dissimilarity in species  
8 composition (Poisot et al. 2012). The current conceptual and operational tools to study net-  
9 works therefore leaves us poorly equipped to understand the causes of this variation. In this  
10 paper, we propose a general research agenda to understand the mechanisms involved in the  
11 variability of species interactions.

12 In contrast to the current paradigm, we propose that future research on interaction networks  
13 be guided by the following principle: the existence of an interaction between two species is  
14 the result of a stochastic process involving (i) local traits distributions, (ii) local abundances,  
15 and (iii) higher-order effects by the local environment or species acting “at a distance” on the  
16 interaction; regionally, the observation of interactions results of the accumulation of local ob-  
17 servations. This approach is outlined in **Box 1**. Although this proposal is a radical yet intuitive  
18 change in the way we think about ecological network structure, we demonstrate in this paper  
19 that it is well supported by empirical and theoretical results alike. Furthermore, our new per-  
20 spective is well placed to open the door to novel predictive approaches integrating a range of  
21 key ecological mechanisms. Notably, we propose in **Box 2** that this approach facilitates the  
22 study of indirect interactions, for which predictive approaches have long proved elusive (Tack  
23 et al. 2011).

24 Since the next generation of predictive biogeographic models will need to account for species  
25 interactions (Thuiller et al. 2013), it is crucial not to underestimate the fact that these in-  
26 teractions are intrinsically variable and exhibit a geographic variability of their own. Indeed,  
27 investigating the impact of species interactions on species distributions only makes sense under  
28 the implicit assumption that species interactions themselves vary over biogeographical scales.

1 Models of species distributions will therefore increase their predictive potential if they ac-  
2 count for the variability of ecological interactions. In turn, tighter coupling between species-  
3 distribution and interaction-distribution models will provide more accurate predictions of the  
4 properties of emerging ecosystems (Gilman et al. 2010, Estes et al. 2011) and the spatial vari-  
5 ability of properties between existing ecosystems. By paying more attention to the variability of  
6 species interactions, the field of biogeography will be able to re-visit classical observations typ-  
7 ically explained by species-level mechanisms; for example, how does community complexity  
8 and function vary along latitudinal gradients, is there information hidden in the co-occurrence  
9 or avoidance of species interactions, etc.

10 In this paper, we outline the mechanisms that are involved in the variability of species inter-  
11 actions over time, space, and environmental gradients. We discuss how they will affect the  
12 structure of ecological networks, and how these mechanisms can be integrated into new pre-  
13 dictive and statistical models (**Box 1**). Most importantly, we show that this approach integrates  
14 classical community ecology thinking and biogeographic questions (**Box 2**) and will ultimately  
15 result in a better understanding of the structure of ecological communities.

## 16 **The dynamic nature of ecological interaction networks**

17 Recent studies on the sensitivity of network structure to environmental change provide some  
18 context for the study of dynamic networks. Menke et al. (2012) showed that the structure of a  
19 plant–frugivore network changed along a forest–farmland gradient. At the edges between two  
20 habitats, species were on average less specialized and interacted more evenly with a larger num-  
21 ber of partners than they did in habitat cores. Differences in network structure have also been  
22 observed within forest strata that differ in their proximity to the canopy and visitation by birds  
23 (Schleuning et al. 2011). Tylianakis et al. (2007) reports a *stronger* signal of spatial interaction  
24 turnover when working with quantitative rather than binary interactions, highlighting the im-  
25 portance of *measuring* rather than assuming (or simply reporting) the existence of interactions.  
26 Eveleigh et al. (2007) demonstrated that outbreaks of the spruce budworm were associated

1 with changes in the structure of its trophic network, both in terms of species observed and  
2 their interactions. Poisot et al. (2011) used a microbial system of hosts and pathogens to study  
3 the impact of productivity gradients on realized infection; when the species were moved from  
4 high to medium to low productivity, some interactions were lost and others were gained. As  
5 a whole, these results suggest that the existence, and properties, of an interaction are not only  
6 contingent on the presence of the two species involved but may also require particular envi-  
7 ronmental conditions, including the presence or absence of species not directly involved in the  
8 interaction.

9 We argue here that there are three broadly-defined classes of mechanisms that ultimately de-  
10 termine the realization of species interactions. First, individuals must be in high enough local  
11 relative abundances to meet; this is the so-called “neutral” perspective of interactions. Second,  
12 there must be phenological or trait matching between individuals, such that an interaction will  
13 actually occur given that the encounter takes place. Finally, the realization of an interaction is  
14 regulated by the interacting organisms’ surroundings and should be studied in the context of  
15 indirect interactions.

## 16 **Population dynamics and neutral processes**

17 Over the recent years, the concept of neutral dynamics has left a clear imprint on the analy-  
18 sis of ecological network structure, most notably in bipartite networks (Blüthgen et al. 2006).  
19 Re-analysis of several host–parasite datasets, for example, showed that changes in local species  
20 abundances triggers variation in parasite specificity (Vazquez et al. 2005). More generally, it is  
21 possible to predict the structure of trophic interactions (Canard et al. 2012) and host-parasite  
22 communities (Canard et al. 2014) given only minimal assumptions about the distribution of  
23 species abundance. In this section, we review recent studies investigating the consequences of  
24 neutral dynamics on the structure of interaction networks and show how variations in popula-  
25 tion size can lead directly to interaction turnover.

## 1 The basic processes

2 As noted previously, for an interaction to occur between individuals from two populations,  
3 these individuals must first meet, then interact. Assuming that two populations occupy the  
4 same location and are active at the same time of the day/year, then the likelihood of an inter-  
5 action is roughly proportional to the product of their relative abundance (Vázquez et al. 2007).  
6 This means that individuals from two large populations are more likely to interact than individ-  
7 uals from two small populations, simply because they tend to meet more often. This approach  
8 can also be extended to the prediction of interaction strength (Blüthgen et al. 2006, Vázquez et  
9 al. 2007), *i.e.* how strong the consequences of the interaction will be. The neutral perspective  
10 predicts that locally-abundant species should have more partners and that locally-rare species  
11 should appear more specialized. In a purely neutral model (*i.e.* interactions happen entirely  
12 by chance, although the determinants of abundance can still be non-neutral), the identities of  
13 species do not matter, and it becomes easy to understand how the structure of local networks  
14 can vary since species vary regionally in abundance. Canard et al. (2012) proposed the term  
15 of “neutrally forbidden links” to refer to interactions that are phenologically feasible but not  
16 realized because of the underlying population size distribution. The identity of these neutrally  
17 forbidden links will vary over time and space, either due to stochastic changes in population  
18 sizes or because population size responds deterministically (*i.e.* non-neutrally) to extrinsic  
19 drivers.

## 20 Benefits for network analysis

21 It is important to understand how local variations in abundance, whether neutral or not, cas-  
22 cade up to affect the structure of interaction networks. One approach is to use simple statistical  
23 models to quantify the effect of population sizes on local interaction occurrence or strength (see  
24 *e.g.* Krishna et al. 2008). These models can be extended to remove the contribution of neutral-  
25 ity to link strength, allowing us to work directly on the interactions as they are determined by  
26 traits (**Box 1**). Doing so allows us to compare the variation of neutral and non-neutral compo-

1 nents of network structure over space and time. To achieve this goal, however, it is essential that  
2 empirical interaction networks (i) are replicated and (ii) include independent measurements of  
3 population sizes.

4 An additional benefit of such sampling is that these data will also help refine neutral theory.  
5 Wootton (2005) made the point that deviations of empirical communities from neutral predic-  
6 tions were most often explained by species trophic interactions which are notoriously, albeit  
7 intentionally, absent from the original formulation of the theory (Hubbell 2001). Merging the  
8 two views will increase our explanatory power, and provide new ways to test neutral theory in  
9 interactive communities; it will also offer a new opportunity, namely to complete the integra-  
10 tion of network structure with population dynamics. To date, most studies have focused on the  
11 effects of a species' position within a food web on the dynamics of its biomass or abundance  
12 (Brose et al. 2006, Berlow et al. 2009, Stouffer and Bascompte 2011, Saavedra et al. 2011).  
13 Adopting this neutral perspective brings things full circle since the abundance of a species  
14 will also dictate its position in the network: changes in abundance can lead to interactions  
15 being gained or lost, and these changes in abundance are in part caused by existing interac-  
16 tions (**Box 2**). For this reason, there is a potential to link species and interaction dynamics and,  
17 more importantly, to do so in a way which accounts for the interplay between the two. From  
18 a practical point of view, this requires repeated sampling of a system through time, so that  
19 changes in relative abundances can be related to changes in interaction strength (Yeakel et al.  
20 2012). Importantly, embracing the neutral view will force us to reconsider the causal relation-  
21 ship between resource dynamics and interaction strength since, in a neutral context, both are  
22 necessarily interdependent.

## 23 **Traits matching in space and time**

24 Once individuals meet, whether they will interact is widely thought to be the product of an  
25 array of behavioral, phenotypic, and cultural aspects that can conveniently be referred to as  
26 a “trait-based process”. Two populations can interact when their traits values allow it, *e.g.*



1 viruses are able to overcome host resistance, predators can capture the preys, trees provide  
2 enough shading for shorter grasses to grow. Non-matching traits will effectively prevent the  
3 existence of an interaction, as demonstrated by Olesen et al. (2011). Under this perspective,  
4 the existence of interactions can be mapped onto trait values, and interaction networks will  
5 consequently vary along with variation in local trait distribution. In this section, we review  
6 how trait-based processes impact network structure, how they can create variation, and the  
7 perspective they open for an evolutionary approach.

## 8 **The basic processes**

9 There is considerable evidence that, at the species level, interaction partners are selected on  
10 the grounds of matching trait values. Random networks built on these rules exhibit realistic  
11 structural properties (Williams and Martinez 2000, Stouffer et al. 2005). Trait values, however,  
12 vary from population to population within species; it is therefore expected that the local inter-  
13 actions will be contingent upon traits spatial distribution (Figure 2). The fact that a species'  
14 niche can appear large if it is the aggregation of narrow but differentiated individual or pop-  
15 ulation niches is now well established (Bolnick et al. 2003, Devictor et al. 2010a) and has  
16 also reinforced the need to understand intra-specific trait variation to describe the structure  
17 and dynamics of communities (Woodward et al. 2010, Bolnick et al. 2011). Nevertheless, this  
18 notion has yet to percolate into the literature on network structure despite its most profound  
19 consequence: a species appearing generalist at the regional scale can easily be specialized in  
20 *each* of the patches it occupies. This reality has long been recognized by functional ecologists,  
21 which are now increasingly predicting the *variance* in traits of different populations within a  
22 species (Violle et al. 2012).

23 Empirically, there are several examples of intraspecific trait variation resulting in extreme in-  
24 teraction turnover. A particularly spectacular example was identified by Ohba (2011) who  
25 describes how a giant waterbug is able to get hold of, and eventually consume, juveniles from  
26 a turtle species. This interaction can only happen when the turtle is small enough for the  
27 morphotraits of the bug to allow it to consume the turtle, and as such will vary throughout

1 the developmental cycle of both species. Choh et al. (2012) demonstrated through behavioral  
2 assays that prey which evaded predation when young were more likely to consume juvenile  
3 predators than the “naive” individuals; their past interactions shaped behavioral traits that al-  
4 ter the network structure over time. These examples show that trait-based effects on networks  
5 can be observed even in the absence of genotypic variation (although we discuss this in the next  
6 section).

7 From a trait-based perspective, the existence of an interaction is an emergent property of the  
8 trait distribution of local populations: variations in one or both of these distributions, regard-  
9 less of the mechanism involved (development, selection, plasticity, environment), are likely to  
10 alter the interaction. Importantly, when interaction-driving traits are subject to environmen-  
11 tal forcing (for example, body size is expected to be lower in warm environments, Angilletta  
12 et al. (2004)), there can be covariation between environmental conditions and the occurrence  
13 of interactions. Woodward et al. (2012) used macrocosms to experimentally demonstrate that  
14 changes in food-web structure happen at the same time as changes in species body mass distri-  
15 bution. Integrating trait variation over gradients will provide more predictive power to models  
16 of community response to environmental change.

## 17 **Benefits for network analysis**

18 Linking spatial and temporal trait variation with network variation will help identify the mech-  
19 anistic basis of network dissimilarity. From a sampling point of view, having enough data  
20 requires that, when interactions are recorded, they are coupled with trait measurements. Im-  
21 portantly, these measurements cannot merely be extracted from a reference database because  
22 interactions are driven by *local* trait values and their matching across populations from differ-  
23 ent species. Within our overarching statistical framework (**Box 1**), we expect that (i) network  
24 variability at the *regional* scale will be dependent on the variation of populations’ traits, and (ii)  
25 variation between any series of networks will depend on the *covariance* between species traits.  
26 Although it requires considerably larger quantities of data to test, this approach should allow  
27 us to infer *a priori* network variation. This next generation of data will also help link variation

1 of network structure to variation of environmental conditions. Price (2003) shows how specific  
2 biomechanical responses to water input in shrubs can have pleiotropic effects on traits involved  
3 in the interaction with insects. In their system, the difference in network structure can be ex-  
4 plained because (i) trait values determine the existence of an interaction, and (ii) environmental  
5 features determine trait values. We have little doubt that future empirical studies will provide  
6 similar mechanistic narratives.

7 At larger temporal scales, the current distribution of traits also reflects past evolutionary his-  
8 tory (Diniz-Filho and Bini 2008). Recognizing this important fact offers an opportunity to  
9 approach the evolutionary dynamics and variation of networks. Correlations between different  
10 species' traits, and between traits and fitness, drive coevolutionary dynamics (Gomulkiewicz  
11 et al. 2000, Nuismer et al. 2003). Both of these correlations vary over space and time (Thomp-  
12 son 2005), creating patchiness in the processes and outcomes of coevolution. Trait structure  
13 and trait correlations are also disrupted by migration (Gandon et al. 2008, Burdon and Thrall  
14 2009). Ultimately, understanding of how ecological and evolutionary trait dynamics affect net-  
15 work structure will provide a mechanistic basis for the historical signal found in contemporary  
16 network structures (Rezende et al. 2007, Eklof et al. 2011, Baskerville et al. 2011, Stouffer et  
17 al. 2012).

## 18 **Beyond direct interactions**

19 In this section, we argue that, although networks are built around observations of direct interac-  
20 tions like predation or pollination, they also offer a compelling tool with which to address indi-  
21 rect effects on the existence and strength of interactions. Any direct interaction arises from the  
22 “physical” interaction of only two species, and, as we have already detailed, these can be modi-  
23 fied by local relative abundances and/or species traits. Indirect interactions, on the other hand,  
24 are established through the involvement of another party than the two focal species, either  
25 through cascading effects (herbivorous species compete with insect laying eggs on plants) or  
26 through physical mediation of the environment (bacterial exudates increase the bio-availability

1 of iron for all bacterial species; plants with large foliage provide shade for smaller species). As  
2 we discuss in this section, the fact that many (if not all) interactions are indirectly affected by  
3 the presence of other species (i) has relevance for understanding the variation of interaction  
4 network structure and (ii) can be studied within the classical network-theory formalism.

## 5 **The basic processes**

6 Biotic interactions themselves interact (Golubski and Abrams 2011); in other words, interac-  
7 tions are contingent on the occurrence of species other than those interacting. Because the  
8 outcome of an interaction ultimately affects local abundances (over ecological time scales) and  
9 population trait structure (over evolutionary time scales), all interactions happening within  
10 a community will impact one another. This does not actually mean pairwise approaches are  
11 bound to fail, but it does clamor for a larger scale approach that accounts for indirect effects.

12 The occurrence or absence of a biotic interaction can either affect either the realization of other  
13 interactions (thus affecting the “interaction” component of network  $\beta$ -diversity) or the pres-  
14 ence of other species. There are several well-documented examples of one interaction allow-  
15 ing new interactions to happen (*e.g.* opportunistic pathogens have a greater success of infec-  
16 tion in hosts which are already immunocompromised by previous infections, Olivier 2012), or  
17 conversely preventing them (a resident symbiont decreases the infection probability of a new  
18 pathogen, Koch and Schmid-Hempel 2011 op. @heil2003). In both cases, the driver of inter-  
19 action turnover is the patchiness of species distribution; the species acting as a “modifier” of  
20 the probability of interaction is only partially present throughout the range of the other two  
21 species, thus creating a mosaic of different interaction configurations. Variation in interaction  
22 structure can happen through both cascading and environmental effects: Singer et al. (2004)  
23 show that caterpillars change the proportion of different plant species in their diet when para-  
24 sitized in order to favor low quality items and load themselves with chemical compounds which  
25 are toxic for their parasitoids. However, low quality food results in birds having a greater im-  
26 pact on caterpillar populations (Singer et al. 2012). It is noteworthy that in this example, the  
27 existence of an interaction will affect both the strength, and impact, of other interactions. In

1 terms of their effects on network  $\beta$ -diversity, indirect effects are thus likely to act on compo-  
2 nents of dissimilarity. A common feature of the examples mentioned here is that pinpointing  
3 the exact mechanism through which interactions affect each other often requires a good work-  
4 ing knowledge of the system's natural history.

## 5 **Benefits for network analysis**

6 As discussed in previous sections, improved understanding of why and where species interact  
7 should also provide a mechanistic understanding of observed species co-occurrences. However,  
8 the presence of species is also regulated by indirect interactions. Recent experimental showed  
9 that some predator species can only be maintained if another predator species is present, since  
10 the latter regulates a competitively superior prey and allows for prey coexistence (Sanders and  
11 Veen 2012). These effects involving several species and several types of interactions across  
12 trophic levels are complex (and for this reason, have been deemed unpredictable in the past,  
13 Tack et al. (2011)), and can only be understood by comparing communities in which different  
14 species are present/absent. Looking at figure 1, it is also clear that the probability of having  
15 an interaction between species  $i$  and  $j$  ( $P(L_{ij})$ ) is ultimately constrained by the probability of  
16 simultaneously observing  $i$  and  $j$  together, *i.e.*  $P(i \cap j)$ . Thus, the existence of any ecological  
17 interaction will be contingent upon *other* ecological interactions driving local co-occurrence  
18 (Araújo et al. 2011). Based on this argument, ecological networks cannot be limited to a collec-  
19 tion of pairwise interactions. Our view of them needs be updated to account for the importance  
20 of the context surrounding these interactions (**Box 2**). From a biogeographic standpoint, it re-  
21 quires us to develop a theory based on interaction co-occurrence in addition to the current  
22 knowledge encompassing only species co-occurrence. Araújo et al. (2011) and Allesina and  
23 Levine (2011) introduced the idea that competitive interactions can leave a signal in species  
24 co-occurrence network. A direct consequence of this result is that, for example, trophic inter-  
25 actions are constrained by species' competitive outcomes *before* they are ever constrained by  
26 *e.g.* predation-related traits. In order to fully understand interactions and their indirect effects,  
27 however, there is a need to develop new conceptual tools to *represent* effects that interactions

1 have on one another. In a graph theoretical perspective, this would amount to establishing  
2 edges between pairs of edges, a task for which there is limited conceptual or methodological  
3 background.

## 4 **Conclusions**

5 Overall, we argue here that the notion of “species interaction networks” shifts our focus away  
6 from the level of organization at which most of the relevant biogeographic processes happen  
7 — populations. In order to make reliable predictions about the structure of networks, we need  
8 to understand what triggers variability of ecological interactions. In this contribution, we have  
9 outlined that there are several direct (abundance-based and trait-based) and indirect (biotic  
10 modifiers, indirect effects of co-occurrence) effects to account for. We expect that the relative  
11 importance of each of these factors and how precisely they affect the probability of establishing  
12 an interaction are likely system-specific; nonetheless, we have proposed a unified conceptual  
13 approach to understand them better.

14 At the moment, the field of community ecology is severely data-limited to tackle this perspec-  
15 tive. Despite the existence of several spatially- or temporally-replicated datasets (*e.g.* Schle-  
16 uning et al. 2011 2012 Menke et al. 2012), it is rare that all relevant information has been  
17 measured independently. It was recently concluded, however, that even a reasonably small  
18 subset of data can be enough to draw inferences at larger scales (Gravel et al. 2013). Para-  
19 doxically, as tempting as it may be to sample a network in its entirety, the goal of establishing  
20 global predictions might be better furthered by extremely-detailed characterization of a more  
21 modest number of interactions (Rodriguez-Cabal et al. 2013). Assuming that there are indeed  
22 statistical invariants in the rules governing interactions, this information will allow us to make  
23 verifiable predictions on the structure of the networks. Better still, this approach has the poten-  
24 tial to substantially strengthen our understanding of the interplay between traits and neutral  
25 effects. Blüthgen et al. (2008) claim that the impact of traits distribution on network structure  
26 can be inferred simply by removing the impact of neutrality (population densities), based on

1 the idea that many rare links were instances of sampling artifacts. As illustrated here (e.g, **Box**  
2 2), their approach is of limited generality, as the abundance of a species itself can be directly  
3 driven by factors such as trait-environment matching.

4 With the accumulation of data, these approaches will rapidly expand our ability to predict the  
5 re-wiring of networks under environmental change. The effect of environmental change is ex-  
6 pected to occur because (i) population sizes will be affected by the change and (ii) either plastic  
7 or adaptive responses will shift or disrupt the trait distributions. The framework proposed in  
8 **Box 1** predicts interaction probabilities under different scenarios. Ultimately, being explicit  
9 about the trait-abundance-interaction feedback will provide a better understanding of short-  
10 term and long-term dynamics of interaction networks. We illustrate this in Fig. 3. The notion  
11 that population sizes have direct effects on the existence of an interaction stands opposed to  
12 classical consumer-resource theory, which is one of the bases of network analysis. Considering  
13 this an opposition, however, is erroneous. Consumer-resource theory considers a strong effect  
14 of abundance on the intensity of interactions (**Box 2**), and itself is a source of (quantitative) vari-  
15 ation. Furthermore, these models are entirely determined by variations in population sizes in  
16 the limiting case where the coefficient of interactions are similar. As such, any approach seek-  
17 ing to understand the variation of interactions over space ought to consider that local densities  
18 are not only a consequence, but also a predictor, of the probability of observing an interaction.  
19 The same reasoning can be held for local trait distributions, although over micro-evolutionary  
20 time-scales. While trait values determine whether two species are able to interact, they will be  
21 modified by the selective effect of species interacting. Therefore, conceptualizing interactions  
22 as the outcome of a probabilistic process regulated by local factors, as opposed to a constant,  
23 offers the unprecedented opportunity to investigate feedbacks between different time scales.

24 Over the past decade, many insights have been gained by looking at the turnover of different  
25 facets of biodiversity (taxonomic, functional, and phylogenetic) through space (Devictor et al.  
26 2010b, Meynard et al. 2011). Here, we propose that there is another oft-neglected side of bio-  
27 diversity: species interactions. The perspective we bring forth allows us to unify these dimen-  
28 sions and offers us the opportunity to describe the biogeographic structure of all components

1 of community and ecosystem structure simultaneously.

## 2 **Boxes**

### 3 **Box 1: A mathematical framework for population-level interactions**

4 We propose that the occurrence (and intensity) of ecological interactions at the population  
5 level relies on several factors, including relative local abundances and local trait distributions.  
6 It is important to tease apart these different factors so as to better disentangle neutral and  
7 niche processes. We propose that these different effects can adequately be partitioned using the  
8 model

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

9 where  $\mathcal{N}$  is a function giving the probability that species  $i$  and  $j$  interact *based on their relative*  
10 *abundances*, and  $\mathcal{T}$  is a function giving the *per encounter* probability that species  $i$  and  $j$  inter-  
11 *act based on their trait values*. The term  $\epsilon$  accounts for all higher-order effects, such as indirect  
12 interactions, local impact of environmental conditions on the interaction, and impact of co-  
13 occurring species. Both of these functions can take any form needed. In several papers,  $\mathcal{N}(i, j)$   
14 was expressed as  $\mathbf{n}_i \times \mathbf{n}_j$ , where  $\mathbf{n}$  is a vector of relative abundances (Canard et al. 2014). The  
15 expression of  $\mathcal{T}$  can in most cases be derived from mechanistic hypotheses about the observa-  
16 tion. For example, Gravel et al. (2013) used the niche model of Williams and Martinez (2000)  
17 to predict interactions with the simple rule that  $\mathcal{T}(i, j) = 1$  if  $i$  can consume  $j$  based on allo-  
18 metric rules, and 0 otherwise. Following Rohr et al. (2010), the expression of  $\mathcal{T}$  can be based  
19 on latent variables rather than actual trait values. This simple formulation could be used to  
20 partition, at the level of individual interactions, the relative importance of density-dependent  
21 and trait-based processes using variance decomposition. Most importantly, it predicts (i) how  
22 each of these components will vary over space and (ii) how the structure of the network will be  
23 affected by, for example, changes in local abundances or trait distributions.



1 This model can further be extended in a spatial context, as

$$\mathbf{A}_{ijx} \propto [\mathcal{N}_x(i_x, j_x) \times \mathcal{T}_x(i_x, j_x)] + \epsilon_{ijx},$$

2 in which  $i_x$  is the population of species  $i$  at site  $x$ . In this formulation, the  $\epsilon$  term could include  
3 the spatial variation of interaction between  $i$  and  $j$  over sites, and the covariance between the  
4 observed presence of this interaction and the occurrence of species  $i$  and  $j$ . This can, for ex-  
5 ample, help address situations in which the selection of prey items is determined by traits, but  
6 also by behavioral choices. Most importantly, this model differs from the previous one in that  
7 each site  $x$  is characterized by a set of functions  $\mathcal{N}_x, \mathcal{T}_x$  that may not be identical for all sites  
8 considered. For example, the same predator may prefer different prey items in different loca-  
9 tions, which will require the use of a different form for  $\mathcal{T}$  across the range of locations. Gravel  
10 et al. (2013) show that it is possible to derive robust approximation for the  $\mathcal{T}$  function even  
11 with incomplete set of data, which gives hope that this framework can be applied even when  
12 all species information is not known at all sites (which would be an unrealistic requirement for  
13 most realistic systems). Both of these models can be used to partition the variance from exist-  
14 ing data or to test which trait-matching function best describes the observed interactions. They  
15 also provide a solid platform for dynamical simulations in that they will allow re-wiring the  
16 interaction network as a function of trait change and to generate simulations that are explicit  
17 about the variability of interactions.

## 1 **Box 2: Population-level interactions in the classical modelling framework**

2 As noted in the main text, most studies of ecological networks—particularly food webs—regard  
3 the adjacency matrix **A** as a fixed entity that specifies observable interactions on the basis of  
4 whether two species co-occur or not. Given this assumption, there is a lengthy history of trying  
5 to understand how the strength or organization of these interactions influence the dynamic  
6 behavior of species abundance (May 1973). Often, such models take the form

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

7 where  $a_i$  is the growth rate of species  $i$  (and could, in principle, depend on other species' abun-  
8 dances  $N$ ) and  $\alpha_{ij}$  is the strength of the effect of  $j$  on  $i$ . In this or just about any related model,  
9 direct species-species interaction can influence species abundances but their abundances *never*  
10 feedback and influence the *per capita* interaction coefficients  $\alpha_{ij}$ . They do, however, affect the  
11 realized interactions, which are defined by  $\alpha_{ij} N_i(t) N_j(t)$ , something which is also the case when  
12 considering more complicated functional responses (Koen-Alonso 2007).

13 More recently, there have been multiple attempts to approach the problem from the other side.  
14 Namely, to understand how factors such as species' abundance and/or trait distributions in-  
15 fluence the occurrence of the interactions themselves (**Box 1**). One potential drawback to that  
16 approach, however, is that it still adopts the assumption that the observation of any interaction  
17  $A_{ij}$  is only an explicit function of the properties of species  $i$  and  $j$  (traits and co-occurrence).

18 Since dynamic models demonstrate quite clearly that non-interacting species can alter each  
19 others' abundances (*e.g.* via apparent competition (Holt and Kotler 1987)), this is a deeply-  
20 ingrained inconsistency between the two approaches. Such a simplification does increase the  
21 analytical tractability of the problem (Allesina and Tang 2012), but there is little, if any, guar-  
22 antee that it is ecologically accurate. In our opinion, the “higher-effects” term  $\epsilon$  in the models  
23 presented in **Box 1** is the one with the least straightforward expectations, but it may also prove  
24 to be the most important if we wish to accurately describe all of these indirect effects.

25 A similar problem actually arises in the typical statistical framework for predicting interac-

1 tion occurrence. Often, one attempts to “decompose” interactions into the component that is  
2 explained by species’ abundances and the component explained by species’ traits (e.g., Box  
3 1). Just like how the underlying functions  $\mathcal{N}$  and  $\mathcal{T}$  could vary across sites, there could also  
4 be feedback between species’ abundances and traits, in the same way that we have outlined  
5 the feedback between interactions and species’ abundances. In fact, given the increasing evi-  
6 dence for the evolutionary role of species-species interactions in explaining extant biodiversity  
7 and their underlying traits (Janzen and Martin 1982, Herrera et al. 2002), a framework which  
8 assumes relative independence of these different phenomenon is likely starting from an overly-  
9 simplified perspective.

## <sup>1</sup> **Figures**

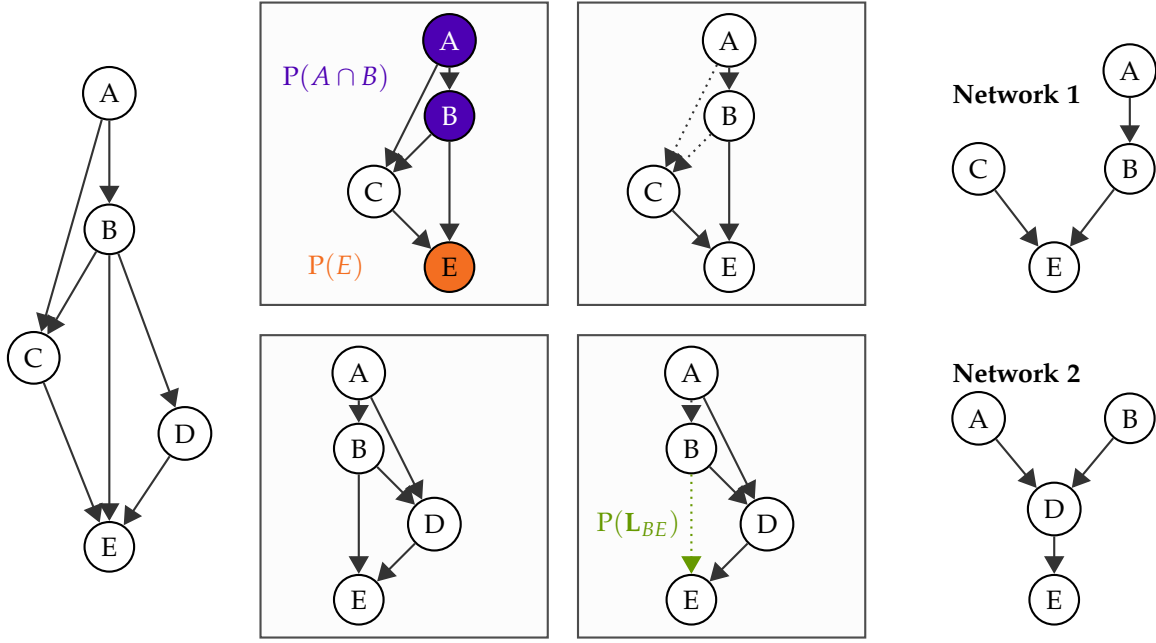


Figure 1: An illustration of the metaweb concept. In its simplest form, a metaweb is the list of all possible species and interactions between them for the system being studied, at the regional level (far left side). Everything that is ultimately observed in nature is a *realisation* of the metaweb (far right side), *i.e.* the resulting network after several sorting processes have occurred (central panel). First, species and species pairs have different probabilities to be observed (top panels). Second, as a consequence of the mechanisms we outline in this paper, not all interactions have the same probability to occur at any given site (bottom panels, see **Box 1**).

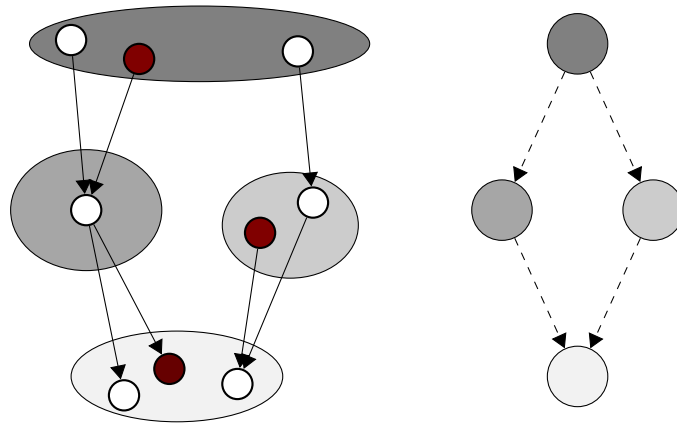


Figure 2: The left-hand side of this figure represents possible interactions between populations (circles) of four species (ellipses), and the aggregated species interaction network on the right. In this example, the populations and species level networks have divergent properties, and the inference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

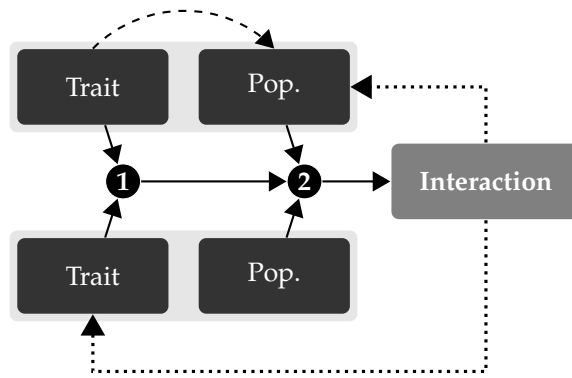


Figure 3: The approach we propose (that populations can interact at the conditions that 1 their trait allow it and 2 they are locally abundant enough to meet) requires to shift our focus to population-level processes. A compelling argument to work at this level of organisation is that eco-evolutionary feedbacks explicit. All of the components of interaction variability we described are potentially related, either through variations of population sizes due to the interaction, or due to selection stemming from these variations in population size. In addition, some traits involved in the existence of the interaction may also affect local population abundance.

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