

Beyond species: why ecological interactions vary through space and time

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

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3 **Affiliations:**

4 **TP:**

5 (1) Université du Québec à Rimouski, Department of Biology, Rimouski (QC) G5L 3A1, Canada

6 (2) Québec Centre for Biodiversity Sciences, Montréal (QC), Canada (3) University of Canterbury,

7 School of Biological Sciences, Christchurch, New Zealand

8 **DG:**

9 (1) Université du Québec à Rimouski, Department of Biology, Rimouski (QC) G5L 3A1, Canada

10 (2) Québec Centre for Biodiversity Sciences, Montréal (QC), Canada

11 **DBS:**

12 (3) University of Canterbury, School of Biological Sciences, Christchurch, New Zealand

13 **Short title:** Variability of species interactions

14 **Correspondence:** Timothée Poisot, t.poisot@gmail.com, @tpoi – Université du Québec à Rimouski,

15 300 Allée des Ursulines, Département de Biologie. G5L 3A1 Rimouski (QC) Canada. Phone: 001 (418)

16 723 1986, ext. 1968

17 **Abstract:**

18 1. Aim - Establishing a formal framework to understand the variability of species interactions and its

1 relevance for biogeographical studies.

2 2. Location - Worldwide.

3 3. Methods - Analysis of the literature.

4 4. Results - The current paradigm of species-level interaction networks is ill-suited to adress the chal-

5 lenges associated with accounting for species interactions in a spatial context. Most of the variation

6 in species interactions is explained by population-level proccesses.

7 5.Main conclusions - Species interactions vary over time and space because of local variations in pop-

8 ulation size, trait distribution, and indirect biotic interactions. We propose a statistical framework to

9 understand and separate these effects.

10 6. Keywords - Ecological networks; biotic interactions; coevolutionary dynamics; neutral theory;

11 functional traits; intra-specific variance

1 Introduction

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

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

25 Within the current paradigm, interactions are established between species and are an immutable
26 “property” of a species pair. Starting from empirical observations, expert knowledge, or literature
27 surveys, one could collect a list of interactions for any given species pool. Several studies used this

1 approach to extrapolate the structure of networks over time and space (Havens 1992, Piechnik et al.
2 2008, Baiser et al. 2012) by considering that the network at *any* location is composed of *all* of the
3 potential interactions known for this species pool. This stands in stark contrast with recent results
4 showing that (i) the identities of interacting species vary over space and (ii) the dissimilarity of in-
5 teractions is not related to the dissimilarity in species composition (Poisot et al. 2012). The current
6 conceptual and operational tools to study networks therefore leaves us poorly equipped to under-
7 stand the causes of this variation. In this paper, we propose a general research agenda to understand
8 the mechanisms involved in the variability of species interactions.

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

20 Since the next generation of predictive biogeographic models will need to account for species inter-
21 actions (Thuiller et al. 2013), it is crucial not to underestimate the fact that these interactions are
22 intrinsically variable and exhibit a geographic variability of their own. Indeed, investigating the im-
23 pact of species interactions on species distributions only makes sense under the implicit assumption
24 that species interactions themselves vary over biogeographical scales. Models of species distributions
25 will therefore increase their predictive potential if they account for the variability of ecological inter-
26 actions. In turn, tighter coupling between species-distribution and interaction-distribution models
27 will provide more accurate predictions of the properties of emerging ecosystems (Gilman et al. 2010,
28 Estes et al. 2011) and the spatial variability of properties between existing ecosystems. By paying

1 more attention to the variability of species interactions, the field of biogeography will be able to re-
2 visit classical observations typically explained by species-level mechanisms; for example, how does
3 community complexity and function vary along latitudinal gradients, is there information hidden in
4 the co-occurrence or avoidance of species interactions, etc.

5 In this paper, we outline the mechanisms that are involved in the variability of species interactions
6 over time, space, and environmental gradients. We discuss how they will affect the structure of eco-
7 logical networks, and how these mechanisms can be integrated into new predictive and statistical
8 models (**Box 1**). Most importantly, we show that this approach integrates classical community ecol-
9 ogy thinking and biogeographic questions (**Box 2**) and will ultimately result in a better understanding
10 of the structure of ecological communities.

11 **The dynamic nature of ecological interaction networks**

12 Recent studies on the sensitivity of network structure to environmental change provide some context
13 for the study of dynamic networks. Menke et al. (2012) showed that the structure of a plant–frugivore
14 network changed along a forest–farmland gradient. At the edges between two habitats, species were
15 on average less specialized and interacted more evenly with a larger number of partners than they
16 did in habitat cores. Differences in network structure have also been observed within forest strata
17 that differ in their proximity to the canopy and visitation by birds (Schleuning et al. 2011). Tylianakis
18 et al. (2007) reports a *stronger* signal of spatial interaction turnover when working with quantitative
19 rather than binary interactions, highlighting the importance of *measuring* rather than assuming the
20 existence of interactions. Eveleigh et al. (2007) demonstrated that outbreaks of the spruce budworm
21 were associated with changes in the structure of its trophic network, both in terms of species ob-
22 served and their interactions. Poisot et al. (2011) used a microbial system of hosts and pathogens to
23 study the impact of productivity gradients on realized infection; when the species were moved from
24 high to medium to low productivity, some interactions were lost and others were gained. As a whole,
25 these results suggest that the existence, and properties, of an interaction are not only contingent on
26 the presence of the two species involved but may also require particular environmental conditions,

1 including the presence or absence of species not directly involved in the interaction.

2 We argue here that there are three broadly-defined classes of mechanisms that ultimately determine
3 the realization of species interactions. First, individuals must be in high enough local relative abun-
4 dances to meet; this is the so-called “neutral” perspective of interactions. Second, there must be
5 phenological matching between individuals, such that an interaction will actually occur given that
6 the encounter takes place. Finally, the realization of an interaction is regulated by the interacting
7 organisms’ surroundings and should be studied in the context of indirect interactions.

8 **Population dynamics and neutral processes**

9 Over the recent years, the concept of neutral dynamics has left a clear imprint on the analysis of eco-
10 logical network structure, most notably in bipartite networks (Blüthgen et al. 2006). Re-analysis of
11 several host–parasite datasets, for example, showed that changes in local species abundances trig-
12 gers variation in parasite specificity (Vazquez et al. 2005). More generally, it is possible to predict
13 the structure of trophic interactions (Canard et al. 2012) and host-parasite communities (Canard et
14 al. 2014) given only minimal assumptions about the distribution of species abundance. In this sec-
15 tion, we review recent studies investigating the consequences of neutral dynamics on the structure
16 of interaction networks and show how variations in population size can lead directly to interaction
17 turnover.

18 **The basic processes**

19 As noted previously, for an interaction to occur between individuals from two populations, these indi-
20 viduals must first meet, then interact. Assuming that two populations occupy the same location and
21 are active at the same time of the day/year, then the likelihood of an interaction is roughly propor-
22 tional to the product of their relative abundance (Vázquez et al. 2007). This means that individuals
23 from two large populations are more likely to interact than individuals from two small populations,
24 simply because they tend to meet more often. This approach can also be extended to the prediction

1 of interaction strength (Blüthgen et al. 2006, Vázquez et al. 2007), *i.e.* how strong the consequences
2 of the interaction will be. The neutral perspective predicts that locally-abundant species should have
3 more partners and that locally-rare species should appear more specialized. In a purely neutral model
4 (*i.e.* interactions happen entirely by chance, although the determinants of abundance can still be non-
5 neutral), the identities of species do not matter, and it becomes easy to understand how the structure
6 of local networks can vary since species vary regionally in abundance. Canard et al. (2012) proposed
7 the term of “neutrally forbidden links” to refer to interactions that are phenologically feasible but not
8 realized because of the underlying population size distribution. The identity of these neutrally for-
9 bidden links will vary over time and space, either due to stochastic changes in population sizes or
10 because population size responds deterministically (*i.e.* non-neutrally) to extrinsic drivers.

11 **Benefits for network analysis**

12 It is important to understand how local variations in abundance, whether neutral or not, cascade up
13 to affect the structure of interaction networks. One approach is to use simple statistical models to
14 quantify the effect of population sizes on local interaction occurrence or strength (see *e.g.* Krishna
15 et al. 2008). These models can be extended to remove the contribution of neutrality to link strength,
16 allowing us to work directly on the interactions as they are determined by traits (**Box 1**). Doing so
17 allows us to compare the variation of neutral and non-neutral components of network structure over
18 space and time. To achieve this goal, however, it is essential that empirical interaction networks (i) are
19 replicated and (ii) include independent measurements of population sizes.

20 An additional benefit of such sampling is that these data will also help refine neutral theory. Woot-
21 ton (2005) made the point that deviations of empirical communities from neutral predictions were
22 most often explained by species trophic interactions which are notoriously, albeit intentionally, ab-
23 sent from the original formulation of the theory (Hubbell 2001). Merging the two views will increase
24 our explanatory power, and provide new ways to test neutral theory in interactive communities; it will
25 also offer a new opportunity, namely to complete the integration of network structure with population
26 dynamics. To date, most studies have focused on the effects of a species’ position within a food web
27 on the dynamics of its biomass or abundance (Brose et al. 2006, Berlow et al. 2009, Stouffer and Bas-

1 compte 2011, Saavedra et al. 2011). Adopting this neutral perspective brings things full circle since
2 the abundance of a species will also dictate its position in the network: changes in abundance can
3 lead to interactions being gained or lost, and these changes in abundance are in part caused by exist-
4 ing interactions (**Box 2**). For this reason, there is a potential to link species and interaction dynamics
5 and, more importantly, to do so in a way which accounts for the interplay between the two. From
6 a practical point of view, this requires repeated sampling of a system through time, so that changes
7 in relative abundances can be related to changes in interaction strength (Yeakel et al. 2012). Impor-
8 tantly, embracing the neutral view will force us to reconsider the causal relationship between resource
9 dynamics and interaction strength since, in a neutral context, both are necessarily interdependent.

10 **Traits matching in space and time**

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

20 **The basic processes**

21 There is considerable evidence that, at the species level, interaction partners are selected on the
22 grounds of matching trait values. Random networks built on these rules exhibit realistic structural
23 properties (Williams and Martinez 2000, Stouffer et al. 2005). Trait values, however, vary from popu-
24 lation to population within species; it is therefore expected that the local interactions will be contin-
1 gent upon traits spatial distribution ([Figure 2](#)). The fact that a species’ niche 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. 2010a) and has also reinforced the need to understand intra-specific trait variation to describe the structure and dynamics of communities (Woodward et al. 2010, Bolnick et al. 2011). Nevertheless, this notion has yet to percolate into the literature on network structure despite its most profound consequence: a species appearing generalist at the regional scale can easily be specialized in *each* of the patches it occupies. This reality has long been recognized by functional ecologists, which are now increasingly predicting the *variance* in traits of different populations within a species (Violle et al. 2012).

Empirically, there are several examples of intraspecific trait variation resulting in extreme interaction turnover. A particularly spectacular example was identified by Ohba (2011) who describes how a giant waterbug is able to get hold of, and eventually consume, juveniles from a turtle species. This interaction can only happen when the turtle is small enough for the morphotraits of the bug to allow it to consume the turtle, and as such will vary throughout the developmental cycle of both species. Choh et al. (2012) demonstrated through behavioral assays that prey which evaded predation when young were more likely to consume juvenile predators than the “naive” individuals; their past interactions shaped behavioral traits that alter the network structure over time. These examples show that trait-based effects on networks can be observed even in the absence of genotypic variation (although we discuss this in the next section).

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

1 **Benefits for network analysis**

2 Linking spatial and temporal trait variation with network variation will help identify the mechanistic
3 basis of network dissimilarity. From a sampling point of view, having enough data requires that, when
4 interactions are recorded, they are coupled with trait measurements. Importantly, these measure-
5 ments cannot merely be extracted from a reference database because interactions are driven by *local*
6 trait values and their matching across populations from different species. Within our overarching sta-
7 tistical framework (**Box 1**), we expect that (i) network variability at the *regional* scale will be dependent
8 on the variation of populations' traits, and (ii) variation between any series of networks will depend
9 on the *covariance* between species traits. Although it requires considerably larger quantities of data
10 to test, this approach should allow us to infer *a priori* network variation. This next generation of data
11 will also help link variation of network structure to variation of environmental conditions. Price (2003)
12 shows how specific biomechanical responses to water input in shrubs can have pleiotropic effects on
13 traits involved in the interaction with insects. In their system, the difference in network structure can
14 be explained because (i) trait values determine the existence of an interaction, and (ii) environmental
15 features determine trait values. We have little doubt that future empirical studies will provide similar
16 mechanistic narratives.

17 At larger temporal scales, the current distribution of traits also reflects past evolutionary history (Diniz-
18 Filho and Bini 2008). Recognizing this important fact offers an opportunity to approach the evolution-
19 ary dynamics and variation of networks. Correlations between different species' traits, and between
20 traits and fitness, drive coevolutionary dynamics (Gomulkiewicz et al. 2000, Nuismer et al. 2003).
21 Both of these correlations vary over space and time (Thompson 2005), creating patchiness in the pro-
22 cesses and outcomes of coevolution. Trait structure and trait correlations are also disrupted by migra-
23 tion (Gandon et al. 2008, Burdon and Thrall 2009). Ultimately, understanding of how ecological and
24 evolutionary trait dynamics affect network structure will provide a mechanistic basis for the historical
25 signal found in contemporary network structures (Rezende et al. 2007, Eklof et al. 2011, Baskerville et
26 al. 2011, Stouffer et al. 2012).

1 **Beyond direct interactions**

2 In this section, we argue that, although networks are built around observations of direct interactions
3 like predation or pollination, they also offer a compelling tool with which to address indirect effects
4 on the existence and strength of interactions. Any direct interaction arises from the “physical” inter-
5 action of only two species, and, as we have already detailed, these can be modified by local relative
6 abundances and/or species traits. Indirect interactions, on the other hand, are established through
7 the involvement of another party than the two focal species, either through cascading effects (her-
8 bivorous species compete with insect laying eggs on plants) or through physical mediation of the
9 environment (bacterial exudates increase the bio-availability of iron for all bacterial species; plants
10 with large foliage provide shade for smaller species). As we discuss in this section, the fact that many
11 (if not all) interactions are indirectly affected by the presence of other species (i) has relevance for un-
12 derstanding the variation of interaction network structure and (ii) can be studied within the classical
13 network-theory formalism.

14 **The basic processes**

15 Biotic interactions themselves interact (Golubski and Abrams 2011); in other words, interactions are
16 contingent on the occurrence of species other than those interacting. Because the outcome of an in-
17 teraction ultimately affects local abundances (over ecological time scales) and population trait struc-
18 ture (over evolutionary time scales), all interactions happening within a community will impact one
19 another. This does not actually mean pairwise approaches are bound to fail, but it does clamor for a
20 larger scale approach that accounts for indirect effects.

21 The occurrence or absence of a biotic interaction can either affect either the realization of other inter-
22 actions (thus affecting the “interaction” component of network β -diversity) or the presence of other
23 species. There are several well-documented examples of one interaction allowing new interactions to
24 happen (*e.g.* opportunistic pathogens have a greater success of infection in hosts which are already
25 immunocompromised by previous infections, Olivier 2012), or conversely preventing them (a resident
26 symbiont decreases the infection probability of a new pathogen, Koch and Schmid-Hempel 2011 op.

1 @heil2003). In both cases, the driver of interaction turnover is the patchiness of species distribution;
 2 the species acting as a “modifier” of the probability of interaction is only partially present throughout
 3 the range of the other two species, thus creating a mosaic of different interaction configurations. Vari-
 4 ation in interaction structure can happen through both cascading and environmental effects: Singer
 5 et al. (2004) show that caterpillars change the proportion of different plant species in their diet when
 6 parasitized in order to favor low quality items and load themselves with chemical compounds which
 7 are toxic for their parasitoids. However, low quality food results in birds having a greater impact on
 8 caterpillar populations (Singer et al. 2012). It is noteworthy that in this example, the existence of an
 9 interaction will affect both the strength, and impact, of other interactions. In terms of their effects
 10 on network β -diversity, indirect effects are thus likely to act on components of dissimilarity. A com-
 11 mon feature of the examples mentioned here is that pinpointing the exact mechanism through which
 12 interactions affect each other often requires a good working knowledge of the system’s natural history.

13 **Benefits for network analysis**

14 As discussed in previous sections, improved understanding of why and where species interact should
 15 also provide a mechanistic understanding of observed species co-occurrences. However, the presence
 16 of species is also regulated by indirect interactions. Recent experimental showed that some preda-
 17 tor species can only be maintained if another predator species is present, since the latter regulates a
 18 competitively superior prey and allows for prey coexistence (Sanders and Veen 2012). These effects
 19 involving several species and several types of interactions across trophic levels are complex (and for
 20 this reason, have been deemed unpredictable in the past, Tack et al. (2011)), and can only be under-
 21 stood by comparing communities in which different species are present/absent. Looking at figure 1,
 22 it is also clear that the probability of having an interaction between species i and j ($P(L_{ij})$) is ulti-
 23 mately constrained by the probability of simultaneously observing i and j together, *i.e.* $P(i \cap j)$. Thus,
 24 the existence of any ecological interaction will be contingent upon *other* ecological interactions driv-
 25 ing local co-occurrence (Araújo et al. 2011). Based on this argument, ecological networks cannot be
 26 limited to a collection of pairwise interactions. Our view of them needs be updated to account for
 27 the importance of the context surrounding these interactions (**Box 2**). From a biogeographic stand-

1 point, it requires us to develop a theory based on interaction co-occurrence in addition to the current
2 knowledge encompassing only species co-occurrence. Araújo et al. (2011) and Allesina and Levine
3 (2011) introduced the idea that competitive interactions can leave a signal in species co-occurrence
4 network. A direct consequence of this result is that, for example, trophic interactions are constrained
5 by species' competitive outcomes *before* they are ever constrained by *e.g.* predation-related traits. In
6 order to fully understand interactions and their indirect effects, however, there is a need to develop
7 new conceptual tools to *represent* effects that interactions have on one another. In a graph theoretical
8 perspective, this would amount to establishing edges between pairs of edges, a task for which there is
9 limited conceptual or methodological background.

10 **Conclusions**

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

19 At the moment, the field of community ecology is severely data-limited to tackle this perspective. De-
20 spite the existence of several spatially- or temporally-replicated datasets (*e.g.* Schleuning et al. 2011
21 2012 Menke et al. 2012), it is rare that all relevant information has been measured independently.
22 It was recently concluded, however, that even a reasonably small subset of data can be enough to
23 draw inferences at larger scales (Gravel et al. 2013). Paradoxically, as tempting as it may be to sam-
24 ple a network in its entirety, the goal of establishing global predictions might be better furthered by
25 extremely-detailed characterization of a more modest number of interactions (Rodriguez-Cabal et
26 al. 2013). Assuming that there are indeed statistical invariants in the rules governing interactions,

1 this information will allow us to make verifiable predictions on the structure of the networks. Better
2 still, this approach has the potential to substantially strengthen our understanding of the interplay
3 between traits and neutral effects. Blüthgen et al. (2008) claim that the impact of traits distribution
4 on network structure can be inferred simply by removing the impact of neutrality (population densi-
5 ties), based on the idea that many rare links were instances of sampling artifacts. As illustrated here
6 (e.g, **Box 2**), their approach is of limited generality, as the abundance of a species itself can be directly
7 driven by factors such as trait-environment matching.

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

27 Over the past decade, many insights have been gained by looking at the turnover of different facets
28 of biodiversity (taxonomic, functional, and phylogenetic) through space (Devictor et al. 2010b, Mey-

1 nard et al. 2011). Here, we propose that there is another oft-neglected side of biodiversity: species
 2 interactions. The perspective we bring forth allows us to unify these dimensions and offers us the
 3 opportunity to describe the biogeographic structure of all components of community and ecosystem
 4 structure simultaneously.

5 **Boxes**

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

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

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

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

1 work will be affected by, for example, changes in local abundances or trait distributions.

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

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

3 in which i_x is the population of species i at site x . In this formulation, the ϵ term could include the
4 spatial variation of interaction between i and j over sites, and the covariance between the observed
5 presence of this interaction and the occurrence of species i and j . This can, for example, help address
6 situations in which the selection of prey items is determined by traits, but also by behavioral choices.
7 Most importantly, this model differs from the previous one in that each site x is characterized by a set
8 of functions $\mathcal{N}_x, \mathcal{T}_x$ that may not be identical for all sites considered. For example, the same predator
9 may prefer different prey items in different locations, which will require the use of a different form for
10 \mathcal{T} across the range of locations. Gravel et al. (2013) show that it is possible to derive robust approxi-
11 mation for the \mathcal{T} function even with incomplete set of data, which gives hope that this framework can
12 be applied even when all species information is not known at all sites (which would be an unrealistic
13 requirement for most realistic systems). Both of these models can be used to partition the variance
14 from existing data or to test which trait-matching function best describes the observed interactions.
15 They also provide a solid platform for dynamical simulations in that they will allow re-wiring the in-
16 teraction network as a function of trait change and to generate simulations that are explicit about the
17 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 the
3 adjacency matrix **A** as a fixed entity that specifies observable interactions on the basis of whether two
4 species co-occur or not. Given this assumption, there is a lengthy history of trying to understand how
5 the strength or organization of these interactions influence the dynamic behavior of species abun-
6 dance (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' abundances
8 N) and α_{ij} is the strength of the effect of j on i . In this or just about any related model, direct species-
9 species interaction can influence species abundances but their abundances *never* feedback and in-
10 fluence the *per capita* interaction coefficients α_{ij} . They do, however, affect the realized interactions,
11 which are defined by $\alpha_{ij} N_i(t) N_j(t)$, something which is also the case when considering more com-
12 plicated functional responses (Koen-Alonso 2007).

13 More recently, there have been multiple attempts to approach the problem from the other side. Namely,
14 to understand how factors such as species' abundance and/or trait distributions influence the occur-
15 rence of the interactions themselves (**Box 1**). One potential drawback to that approach, however, is
16 that it still adopts the assumption that the observation of any interaction A_{ij} is only an explicit func-
17 tion 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 others'
19 abundances (*e.g.* via apparent competition (Holt and Kotler 1987)), this is a deeply-ingrained incon-
20 sistency between the two approaches. Such a simplification does increase the analytical tractability
21 of the problem (Allesina and Tang 2012), but there is little, if any, guarantee that it is ecologically ac-
22 curate. In our opinion, the “higher-effects” term ϵ in the models presented in **Box 1** is the one with
23 the least straightforward expectations, but it may also prove to be the most important if we wish to
24 accurately describe all of these indirect effects.

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

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

¹ **Figures**

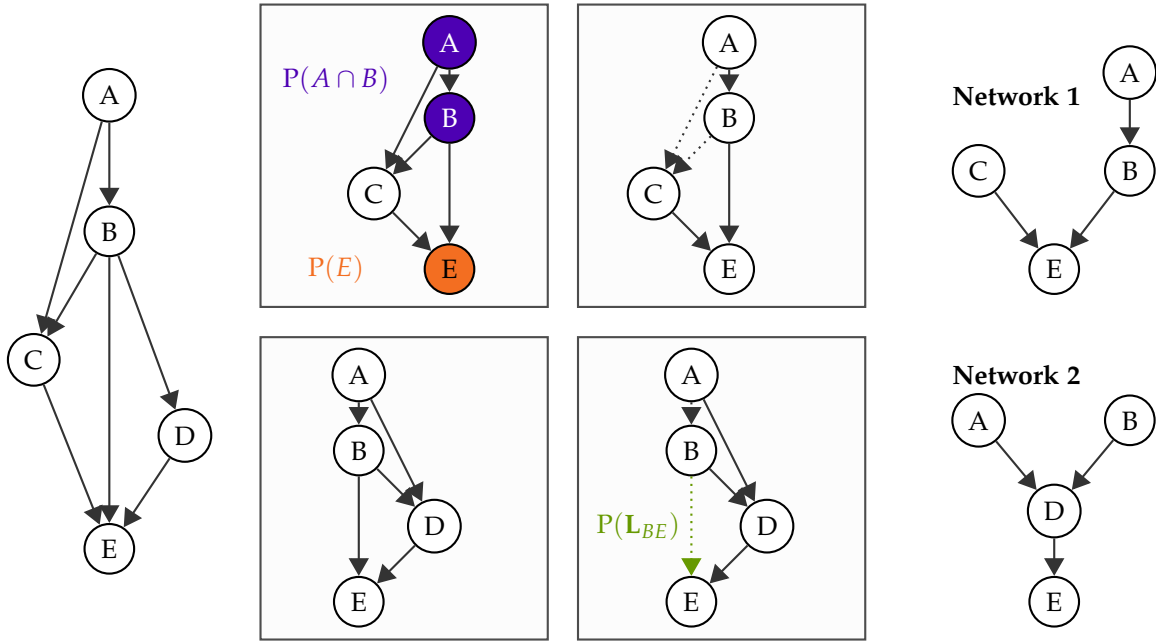


Figure 1: An illustration of the metaweb concept. In its simplest form, a metaweb is the list of all possible species and interactions between them for the system being studied, at the regional level (far left side). Everything that is ultimately observed in nature is a *realisation* of the metaweb (far 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**).

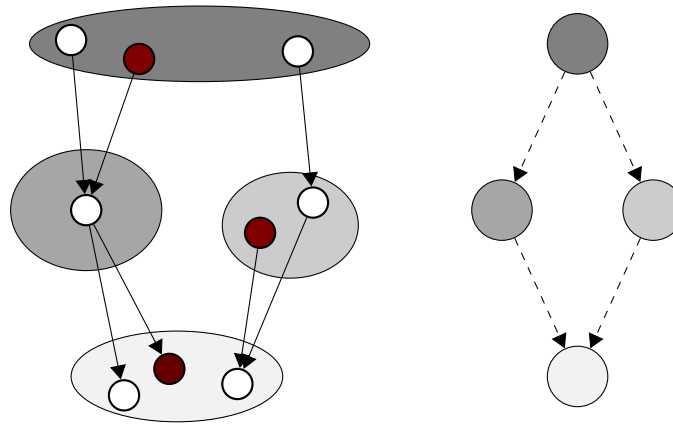


Figure 2: The left-hand side of this figure represents possible interactions between populations (circles) of four species (ellipses), and the aggregated species interaction network on the right. In this example, the populations and species level networks have divergent properties, and the inference 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..

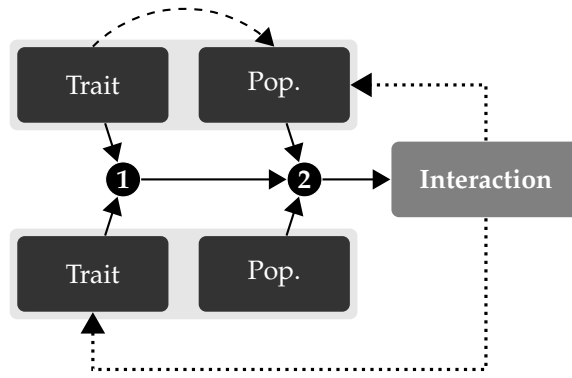


Figure 3: The approach we propose (that populations can interact at the conditions that **1** their trait allow it and **2** they are locally abundant enough to meet) requires to shift our focus to population-level processes. A compelling argument to work at this level of organisation is that eco-evolutionary 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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