

Beyond species: why ecological interactions vary through space and time

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Jan. 2014

1 **Running headline:** Variability of species interactions

2 5900 words, 3 figures, 2 boxes, no tables

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17 **Abstract:**

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

1 and its relevance for biogeographical studies.

2 2. Location - Worldwide.

3 3. Methods - Analysis of the litterature.

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

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

6 the variation in species interactions is explained by population-level processes.

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

8 in population size, trait distribution, and indirect biotic interactions. We propose a statistical

9 framework to understand and separate these effects.

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

11 ory; functional traits; intra-specific variance

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 α , β , and γ 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 (???, ???) and the spatial variability of properties between ex-
5 isting ecosystems. By paying more attention to the variability of species interactions, the field
6 of biogeography will be able to re-visit classical observations typically explained by species-
7 level mechanisms; for example, how does community complexity and function vary along lat-
8 itudinal gradients, is there information hidden in the co-occurrence or avoidance of species
9 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. (???) showed that the structure of a plant–frugivore
19 network changed along a forest–farmland gradient. At the edges between two habitats, species
20 were on average less specialized and interacted more evenly with a larger number of partners
21 than they did in habitat cores. Differences in network structure have also been observed within
22 forest strata that differ in their proximity to the canopy and visitation by birds (???). (???) re-
23 ports a *stronger* signal of spatial interaction turnover when working with quantitative rather
24 than binary interactions, highlighting the importance of *measuring* rather than assuming the
25 existence of interactions. (???) demonstrated that outbreaks of the spruce budworm were asso-
26 ciated with changes in the structure of its trophic network, both in terms of species observed

1 and their interactions. (???) used a microbial system of hosts and pathogens to study the im-
2 pact of productivity gradients on realized infection; when the species were moved from high to
3 medium to low productivity, some interactions were lost and others were gained. As a whole,
4 these results suggest that the existence, and properties, of an interaction are not only contin-
5 gent on the presence of the two species involved but may also require particular environmental
6 conditions, including the presence or absence of species not directly involved in the interaction.
7 We argue here that there are three broadly-defined classes of mechanisms that ultimately de-
8 termine the realization of species interactions. First, individuals must be in high enough local
9 relative abundances to meet; this is the so-called “neutral” perspective of interactions. Sec-
10 ond, there must be phenological matching between individuals, such that an interaction will
11 actually occur given that the encounter takes place. Finally, the realization of an interaction is
12 regulated by the interacting organisms’ surroundings and should be studied in the context of
13 indirect interactions.

14 **Population dynamics and neutral processes**

15 Over the recent years, the concept of neutral dynamics has left a clear imprint on the analysis
16 of ecological network structure, most notably in bipartite networks (???). Re-analysis of several
17 host–parasite datasets, for example, showed that changes in local species abundances triggers
18 variation in parasite specificity (???). More generally, it is possible to predict the structure of
19 trophic interactions given minimal assumptions about the distribution of species abundance
20 (???). In this section, we review recent studies investigating the consequences of neutral dy-
21 namics on the structure of interaction networks and show how variations in population size
22 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 in-
5 teraction is roughly proportional to the product of their relative abundance (???). This means
6 that individuals from two large populations are more likely to interact than individuals from
7 two small populations, simply because they tend to meet more often. This approach can also
8 be extended to the prediction of interaction strength (???), *i.e.* how strong the consequences of
9 the interaction will be. The neutral perspective predicts that locally-abundant species should
10 have more partners and that locally-rare species should appear more specialized. In a purely
11 neutral model (*i.e.* interactions happen entirely by chance, although the determinants of abun-
12 dance can still be non-neutral), the identities of species do not matter, and it becomes easy to
13 understand how the structure of local networks can vary since species vary regionally in abun-
14 dance. (???) proposed the term of “neutrally forbidden links” to refer to interactions that are
15 phenologically feasible but not realized because of the underlying population size distribution.
16 The identity of these neutrally forbidden links will vary over time and space, either due to
17 stochastic changes in population sizes or because population size responds deterministically
18 (*i.e.* non-neutrally) to extrinsic drivers.

19 Benefits for network analysis

20 It is important to understand how local variations in abundance, whether neutral or not, cas-
21 cade up to affect the structure of interaction networks. One approach is to use simple statistical
22 models to quantify the effect of population sizes on local interaction occurrence or strength
23 (see *e.g.* ???). These models can be extended to remove the contribution of neutrality to link
24 strength, allowing us to work directly on the interactions as they are determined by traits (**Box**
25 **1**). Doing so allows us to compare the variation of neutral and non-neutral components of
26 network structure over space and time. To achieve this goal, however, it is essential that em-

1 pirical interaction networks (i) are replicated and (ii) include independent measurements of
2 population sizes.

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

20 **Traits matching in space and time**

21 Once individuals meet, whether they will interact is widely thought to be the product of an
22 array of behavioral, phenotypic, and cultural aspects that can conveniently be referred to as
23 a “trait-based process”. Two populations can interact when their traits values allow it, *e.g.*
24 viruses are able to overcome host resistance, predators can capture the preys, trees provide
25 enough shading for shorter grasses to grow. Non-matching traits will effectively prevent the
26 existence of an interaction, as demonstrated by (???). Under this perspective, the existence

1 of interactions can be mapped onto trait values, and interaction networks will consequently
2 vary along with variation in local trait distribution. In this section, we review how trait-based
3 processes impact network structure, how they can create variation, and the perspective they
4 open for an evolutionary approach.

5 **The basic processes**

6 There is considerable evidence that, at the species level, interaction partners are selected on
7 the grounds of matching trait values. Random networks built on these rules exhibit realistic
8 structural properties (???). Trait values, however, vary from population to population within
9 species; it is therefore expected that the local interactions will be contingent upon traits spatial
10 distribution (Figure 2). The fact that a species' niche can appear large if it is the aggregation
11 of narrow but differentiated individual or population niches is now well established (???) and
12 has also reinforced the need to understand intra-specific trait variation to describe the struc-
13 ture and dynamics of communities (???). Nevertheless, this notion has yet to percolate into the
14 literature on network structure despite its most profound consequence: a species appearing
15 generalist at the regional scale can easily be specialized in *each* of the patches it occupies. This
16 reality has long been recognized by functional ecologists, which are now increasingly predict-
17 ing the *variance* in traits of different populations within a species (???)

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

1 From a trait-based perspective, the existence of an interaction is an emergent property of the
2 trait distribution of local populations: variations in one or both of these distributions, regard-
3 less of the mechanism involved (development, selection, plasticity, environment), are likely to
4 alter the interaction. Importantly, when interaction-driving traits are subject to environmental
5 forcing (for example, body size is expected to be lower in warm environments, (???)), there can
6 be covariation between environmental conditions and the occurrence of interactions. (???) used
7 macrocosms to experimentally demonstrate that changes in food-web structure happen at the
8 same time as changes in species body mass distribution. Integrating trait variation over gradi-
9 ents will provide more predictive power to models of community response to environmental
10 change.

11 **Benefits for network analysis**

12 Linking spatial and temporal trait variation with network variation will help identify the mech-
13 anistic basis of network dissimilarity. From a sampling point of view, having enough data
14 requires that, when interactions are recorded, they are coupled with trait measurements. Im-
15 portantly, these measurements cannot merely be extracted from a reference database because
16 interactions are driven by *local* trait values and their matching across populations from differ-
17 ent species. Within our overarching statistical framework (**Box 1**), we expect that (i) network
18 variability at the *regional* scale will be dependent on the variation of populations' traits, and (ii)
19 variation between any series of networks will depend on the *covariance* between species traits.
20 Although it requires considerably larger quantities of data to test, this approach should allow
21 us to infer *a priori* network variation. This next generation of data will also help link variation
22 of network structure to variation of environmental conditions. (???) shows how specific biome-
23 chanical responses to water input in shrubs can have pleiotropic effects on traits involved in the
24 interaction with insects. In their system, the difference in network structure can be explained
25 because (i) trait values determine the existence of an interaction, and (ii) environmental fea-
26 tures determine trait values. We have little doubt that future empirical studies will provide
27 similar mechanistic narratives.

1 At larger temporal scales, the current distribution of traits also reflects past evolutionary his-
2 tory (???). Recognizing this important fact offers an opportunity to approach the evolutionary
3 dynamics and variation of networks. Correlations between different species' traits, and be-
4 tween traits and fitness, drive coevolutionary dynamics (???). Both of these correlations vary
5 over space and time (???), creating patchiness in the processes and outcomes of coevolution.
6 Trait structure and trait correlations are also disrupted by migration (???). Ultimately, un-
7 derstanding of how ecological and evolutionary trait dynamics affect network structure will
8 provide a mechanistic basis for the historical signal found in contemporary network structures
9 (???).

10 **Beyond direct interactions**

11 In this section, we argue that, although networks are built around observations of direct interac-
12 tions like predation or pollination, they also offer a compelling tool with which to address indi-
13 rect effects on the existence and strength of interactions. Any direct interaction arises from the
14 “physical” interaction of only two species, and, as we have already detailed, these can be modi-
15 fied by local relative abundances and/or species traits. Indirect interactions, on the other hand,
16 are established through the involvement of another party than the two focal species, either
17 through cascading effects (herbivorous species compete with insect laying eggs on plants) or
18 through physical mediation of the environment (bacterial exudates increase the bio-availability
19 of iron for all bacterial species; plants with large foliage provide shade for smaller species). As
20 we discuss in this section, the fact that many (if not all) interactions are indirectly affected by
21 the presence of other species (i) has relevance for understanding the variation of interaction
22 network structure and (ii) can be studied within the classical network-theory formalism.

23 **The basic processes**

24 Several authors (see (???) and references therein) have demonstrated that biotic interactions
25 themselves interact; in other words, interactions are contingent on the occurrence of species

1 other than those interacting. Because the outcome of an interaction ultimately affects local
2 abundances (over ecological time scales) and population trait structure (over evolutionary time
3 scales), all interactions happening within a community will impact one another. This does
4 not actually mean pairwise approaches are bound to fail, but it does clamor for a larger scale
5 approach that accounts for indirect effects.

6 The occurrence or absence of a biotic interaction can either affect either the realization of other
7 interactions (thus affecting the “interaction” component of network β -diversity) or the presence
8 of other species. There are several well-documented examples of one interaction allowing new
9 interactions to happen (e.g. opportunistic pathogens have a greater success of infection in hosts
10 which are already immunocompromised by previous infections (???)), or conversely preventing
11 them (a resident symbiont decreases the infection probability of a new pathogen (???)). In both
12 cases, the driver of interaction turnover is the patchiness of species distribution; the species
13 acting as a “modifier” of the probability of interaction is only partially present throughout the
14 range of the other two species, thus creating a mosaic of different interaction configurations.
15 Variation in interaction structure can happen through both cascading and environmental ef-
16 fects: (???) show that caterpillars change the proportion of different plant species in their diet
17 when parasitized in order to favor low quality items and load themselves with chemical com-
18 pounds which are toxic for their parasitoids. However, low quality food results in birds having
19 a greater impact on caterpillar populations (???). It is noteworthy that in this example, the exis-
20 tence of an interaction will affect both the strength, and impact, of other interactions. In terms
21 of their effects on network β -diversity, indirect effects are thus likely to act on components
22 of dissimilarity. A common feature of the examples mentioned here is that pinpointing the
23 exact mechanism through which interactions affect each other often requires a good working
24 knowledge of the system’s natural history.

25 **Benefits for network analysis**

26 As discussed in previous sections, improved understanding of why and where species interact
27 should also provide a mechanistic understanding of observed species co-occurrences. However,

1 the presence of species is also regulated by indirect interactions. Recent experimental work by
 2 (???) showed that some predator species can only be maintained if another predator species is
 3 present, since the latter regulates a competitively superior prey and allows for prey coexistence.
 4 These effects involving several species and several types of interactions across trophic levels are
 5 complex (and for this reason, have been deemed unpredictable in the past, (???)), and can only
 6 be understood by comparing communities in which different species are present/absent. Look-
 7 ing at figure 1, it is also clear that the probability of having an interaction between species i
 8 and j ($P(L_{ij})$) is ultimately constrained by the probability of simultaneously observing i and j
 9 together, *i.e.* $P(i \cap j)$. Thus, the existence of any ecological interaction will be contingent upon
 10 other ecological interactions driving local co-occurrence (???). Based on this argument, ecologi-
 11 cal networks cannot be limited to a collection of pairwise interactions. Our view of them needs
 12 be updated to account for the importance of the context surrounding these interactions (**Box**
 13 2). From a biogeographic standpoint, it requires us to develop a theory based on interaction
 14 co-occurrence in addition to the current knowledge encompassing only species co-occurrence.
 15 (???) and (???) introduced the idea that competitive interactions can leave a signal in species
 16 co-occurrence network. A direct consequence of this result is that, for example, trophic inter-
 17 actions are constrained by species' competitive outcomes *before* they are ever constrained by
 18 predation-related traits. In order to fully understand interactions and their indirect effects,
 19 however, there is a need to develop new conceptual tools to *represent* effects that interactions
 20 have on one another. In a graph theoretical perspective, this would amount to establishing
 21 edges between pairs of edges, a task for which there is limited conceptual or methodological
 22 background.

23 Conclusions

24 Overall, we argue here that the notion of “species interaction networks” shifts our focus away
 25 from the level of organization at which most of the relevant biogeographic processes happen
 26 — populations. In order to make reliable predictions about the structure of networks, we need

1 to understand what triggers variability of ecological interactions. In this contribution, we have
2 outlined that there are several direct (abundance-based and trait-based) and indirect (biotic
3 modifiers, indirect effects of co-occurrence) effects to account for. We expect that the relative
4 importance of each of these factors and how precisely they affect the probability of establishing
5 an interaction are likely system-specific; nonetheless, we have proposed a unified conceptual
6 approach to understand them better.

7 At the moment, the field of community ecology is severely data-limited to tackle this perspec-
8 tive. Despite the existence of several spatially- or temporally-replicated datasets (*e.g.* ??? ???
9 ???), it is rare that all relevant information has been measured independently. It was recently
10 concluded, however, that even a reasonably small subset of data can be enough to draw in-
11 ferences at larger scales (???). Paradoxically, as tempting as it may be to sample a network in
12 its entirety, the goal of establishing global predictions might be better furthered by extremely-
13 detailed characterization of a more modest number of interactions (???). Assuming that there
14 are indeed statistical invariants in the rules governing interactions, this information will allow
15 us to make verifiable predictions on the structure of the networks. Better still, this approach
16 has the potential to substantially strengthen our understanding of the interplay between traits
17 and neutral effects. (???) claim that the impact of traits distribution on network structure can
18 be inferred simply by removing the impact of neutrality (population densities), based on the
19 idea that many rare links were instances of sampling artifacts. As illustrated here (*e.g.* **Box**
20 **2**), their approach is of limited generality, as the abundance of a species itself can be directly
21 driven by factors such as trait-environment matching.

22 With the accumulation of data, these approaches will rapidly expand our ability to predict the
23 re-wiring of networks under environmental change. The effect of environmental change is ex-
24 pected to occur because (i) population sizes will be affected by the change and (ii) either plastic
25 or adaptive responses will shift or disrupt the trait distributions. The framework proposed in
26 **Box 1** predicts interaction probabilities under different scenarios. Ultimately, being explicit
27 about the trait-abundance-interaction feedback will provide a better understanding of short-
28 term and long-term dynamics of interaction networks. We illustrate this in Fig. 3. The notion

1 that population sizes have direct effects on the existence of an interaction stands opposed to
2 classical consumer-resource theory, which is one of the bases of network analysis. Considering
3 this an opposition, however, is erroneous. Consumer-resource theory considers a strong effect
4 of abundance on the intensity of interactions (**Box 2**), and itself is a source of (quantitative) vari-
5 ation. Furthermore, these models are entirely determined by variations in population sizes in
6 the limiting case where the coefficient of interactions are similar. As such, any approach seek-
7 ing to understand the variation of interactions over space ought to consider that local densities
8 are not only a consequence, but also a predictor, of the probability of observing an interaction.
9 The same reasoning can be held for local trait distributions, although over micro-evolutionary
10 time-scales. While trait values determine whether two species are able to interact, they will be
11 modified by the selective effect of species interacting. Therefore, conceptualizing interactions
12 as the outcome of a probabilistic process regulated by local factors, as opposed to a constant,
13 offers the unprecedented opportunity to investigate feedbacks between different time scales.
14 Over the past decade, many insights have been gained by looking at the turnover of different
15 facets of biodiversity (taxonomic, functional, and phylogenetic) through space (???, ???). Here,
16 we propose that there is another oft-neglected side of biodiversity: species interactions. The
17 perspective we bring forth allows us to unify these dimensions and offers us the opportunity to
18 describe the biogeographic structure of all components of community and ecosystem structure
19 simultaneously.

20 **Boxes**

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

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

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

1 where \mathcal{N} is a function giving the probability that species i and j interact *based on their relative*
 2 *abundances*, and \mathcal{T} is a function giving the *per encounter* probability that species i and j interact
 3 *based on their trait values*. The term ϵ accounts for all higher-order effects, such as indirect
 4 interactions, local impact of environmental conditions on the interaction, and impact of co-
 5 occurring species. Both of these functions can take any form needed. In several papers, $\mathcal{N}(i, j)$
 6 was expressed as $\mathbf{n}_i \times \mathbf{n}_j$, where \mathbf{n} is a vector of relative abundances (???). The expression of \mathcal{T}
 7 can in most cases be derived from mechanistic hypotheses about the observation. For example,
 8 (???) used the niche model of (???) to predict interactions with the simple rule that $\mathcal{T}(i, j) = 1$
 9 if i can consume j based on allometric rules, and 0 otherwise. Following (???), the expression
 10 of \mathcal{T} can be based on latent variables rather than actual trait values. This simple formulation
 11 could be used to partition, at the level of individual interactions, the relative importance of
 12 density-dependent and trait-based processes using variance decomposition. Most importantly,
 13 it predicts (i) how each of these components will vary over space and (ii) how the structure of
 14 the network will be affected by, for example, changes in local abundances or trait distributions.
 15 This model can further be extended in a spatial context, as

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

16 in which i_x is the population of species i at site x . In this formulation, the ϵ term could include
 17 the spatial variation of interaction between i and j over sites, and the covariance between the
 18 observed presence of this interaction and the occurrence of species i and j . This can, for ex-
 19 ample, help address situations in which the selection of prey items is determined by traits, but
 20 also by behavioral choices. Most importantly, this model differs from the previous one in that
 21 each site x is characterized by a set of functions $\mathcal{N}_x, \mathcal{T}_x$ that may not be identical for all sites con-
 22 sidered. For example, the same predator may prefer different prey items in different locations,
 23 which will require the use of a different form for \mathcal{T} across the range of locations. (???) show

1 that it is possible to derive robust approximation for the \mathcal{T} function even with incomplete set of
2 data, which gives hope that this framework can be applied even when all species information is
3 not known at all sites (which would be an unrealistic requirement for most realistic systems).
4 Both of these models can be used to partition the variance from existing data or to test which
5 trait-matching function best describes the observed interactions. They also provide a solid plat-
6 form for dynamical simulations in that they will allow re-wiring the interaction network as a
7 function of trait change and to generate simulations that are explicit about the variability of
8 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 α_{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 α_{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 (??).

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 oth-
19 ers' abundances (e.g. via apparent competition (??)), this is a deeply-ingrained inconsistency
20 between the two approaches. Such a simplification does increase the analytical tractability of
21 the problem (??), but there is little, if any, guarantee that it is ecologically accurate. In our
22 opinion, the “higher-effects” term ϵ in the models presented in **Box 1** is the one with the least
23 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

1 occurrence. Often, one attempts to “decompose” interactions into the component that is ex-
2 plained by species’ abundances and the component explained by species’ traits (e.g., Box 1).
3 Just like how the underlying functions \mathcal{N} and \mathcal{T} could vary across sites, there could also be
4 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, ???), a framework which assumes rela-
8 tive independence of these different phenomenon is likely starting from an overly-simplified
9 perspective.

Biosketch

Timothée Poisot (Twitter: @tpoi), Daniel B Stouffer and Dominique Gravel are network ecologists, interested in understanding how spatial and meta-community processes influence the structure of ecological interactions, with the goal of building more accurate predictive models.

Figures

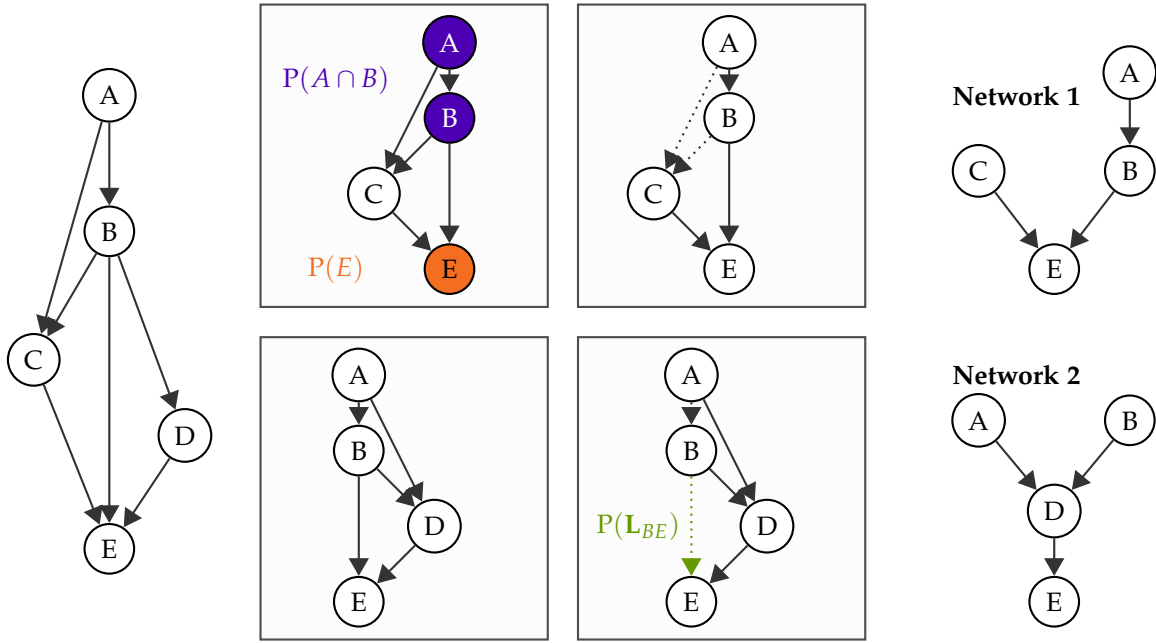


Figure 1: An illustration of the metaweb concept. In its simplest form, a metaweb is the list of all possible species and interactions between them for the system being studied, at the regional level (far left side). Everything that is ultimately observed in nature is a *realisation* of the metaweb (far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

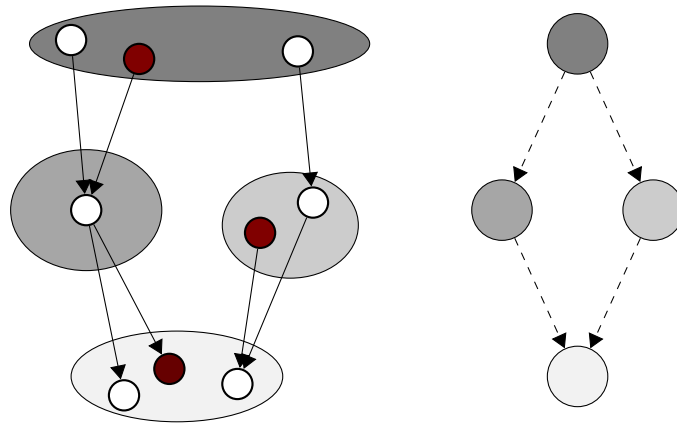


Figure 2: The left-hand side of this figure represents possible interactions between populations (circles) of four species (ellipses), and the aggregated species interaction network on the right. In this example, the populations and species level networks have divergent properties, and the inference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

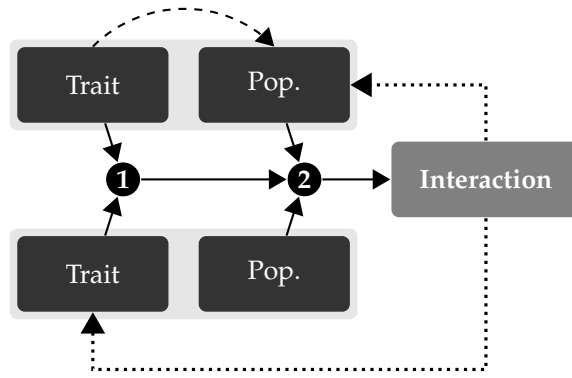


Figure 3: The approach we propose (that populations can interact at the conditions that 1 their trait allow it and 2 they are locally abundant enough to meet) requires to shift our focus to population-level processes. A compelling argument to work at this level of organisation is that eco-evolutionary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