

Beyond species: why ecological interaction networks vary through space and time

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15 **Abstract:** Community ecology is tasked with the considerable challenge of predicting the struc-
16 ture, and properties, of emerging ecosystems. It requires the ability to understand how and why
17 species interact, as this will allow the development of mechanism-based predictive models, and

1 as such to better characterize how ecological mechanisms act locally on the existence of inter-
2 specific interactions. Here we argue that the current conceptualization of species interaction
3 networks is ill-suited for this task. Instead, we propose that future research must start to ac-
4 count for the intrinsic variability of species interactions, then scale up from here onto complex
5 networks. This can be accomplished simply by recognizing that there exists intra-specific vari-
6 ability, in traits or properties related to the establishment of species interactions. By shifting
7 the scale towards population-based processes, we show that this new approach will improve
8 our predictive ability and mechanistic understanding of how species interact over large spatial
9 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 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
5 *any* location is composed of *all* of the potential interactions known for this species pool. This
6 stands in stark contrast with recent results showing that (i) the identities of interacting species
7 vary over space and (ii) the dissimilarity of interactions is not related to the dissimilarity in
8 species composition (Poisot et al. 2012). The current conceptual and operational tools to study
9 networks therefore leaves us poorly equipped to understand the causes of this variation. In
10 this paper, we propose to shift the research agenda towards understanding the mechanisms
11 involved in the variability of co-occurring species interactions.

12 In contrast to the current paradigm, we propose that future research on interaction networks
13 should be guided by the following principles: the existence of an interaction between two
14 species is the result of a stochastic process involving (i) local traits distributions, (ii) local abun-
15 dances, and (iii) higher-order effects by the local environment or species acting “at a distance”
16 on the interaction; regionally, the observation of interactions results of the accumulation of lo-
17 cal observations. This approach is outlined in **Box 1**. Although this proposal is a radical yet
18 intuitive change in the way we think about ecological network structure, we demonstrate in this
19 paper that it is well supported by empirical and theoretical results alike. Furthermore, our new
20 perspective is well placed to open the door to novel predictive approaches integrating a range
21 of 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 they are in-
26 trinsically variable and exhibit a geographic variability of their own. Indeed, investigating the
27 impact of species interactions on species distributions only makes sense under the implicit
28 assumption that species interactions themselves vary over biogeographical scales. Models of

1 species distributions will therefore increase their predictive ability if they account for the vari-
2 ability of ecological interactions. In turn, tighter coupling between species-distribution and
3 interaction-distribution models will provide more accurate predictions of the properties of
4 emerging ecosystems (Gilman et al. 2010, Estes et al. 2011) and the spatial variability of
5 properties between existing ecosystems. By paying more attention to the variability of species
6 interactions, the field of biogeography will be able to re-visit classical observations typically
7 explained by species-level mechanisms; for example, how does community complexity and
8 function vary along latitudinal gradients, is there information hidden in the co-occurrence or
9 avoidance of species interactions, etc. This predictive effort is made all the more important
10 as both the phenology (Parmesan 2007) and ranges (Devictor et al. 2012) of species occupy-
11 ing different positions in their interactions networks are affected differently by climate change.
12 Predicting that species will move and change while interactions remain the same is probably
13 a very conservative approach to estimating the changes to come, and building explicitly on
14 biological mechanisms is one possible way to overcome this limitation.

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

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

22 Recent studies on the sensitivity of network structure to environmental change provide some
23 context for the study of dynamic networks. Menke et al. (2012) showed that the structure of a
24 plant–frugivore network changed along a forest–farmland gradient. At the edges between two
25 habitats, species were on average less specialized and interacted more evenly with a larger num-
26 ber of partners than they did in habitat cores. Differences in network structure have also been

1 observed within forest strata that differ in their proximity to the canopy and visitation by birds
2 (Schleuning et al. 2011). Tylianakis et al. (2007) reports a *stronger* signal of spatial interaction
3 turnover when working with quantitative rather than binary interactions, highlighting the im-
4 portance of *measuring* rather than assuming (or simply reporting) the existence of interactions.
5 Eveleigh et al. (2007) demonstrated that outbreaks of the spruce budworm were associated
6 with changes in the structure of its trophic network, both in terms of species observed and
7 their interactions. Poisot et al. (2011) used a microbial system of hosts and pathogens to study
8 the impact of productivity gradients on realized infection; when the species were moved from
9 high to medium to low productivity, some interactions were lost and others were gained. As
10 a whole, these results suggest that the existence, and properties, of an interaction are not only
11 contingent on the presence of the two species involved but may also require particular envi-
12 ronmental conditions, including the presence or absence of species not directly involved in the
13 interaction.

14 We argue here that there are three broadly-defined classes of mechanisms that ultimately de-
15 termine the realization of species interactions. First, species must be locally abundant enough
16 for their individuals to meet; this is the so-called “neutral” perspective of interactions. Second,
17 there must be phenological or trait matching between individuals, such that an interaction will
18 actually occur given that the encounter takes place. Finally, the realization of an interaction is
19 regulated by the interacting organisms’ surroundings and should be studied in the context of
20 indirect interactions.

21 **Population dynamics and neutral processes**

22 Over the recent years, the concept of neutral dynamics has left a clear imprint on the analy-
23 sis of ecological network structure, most notably in bipartite networks (Blüthgen et al. 2006).
24 Re-analysis of several host–parasite datasets, for example, showed that changes in local species
25 abundances triggers variation in parasite specificity (Vazquez et al. 2005). More generally, it is
26 possible to predict the structure of trophic interactions (Canard et al. 2012) and host-parasite

1 communities (Canard et al. 2014) given only minimal assumptions about the distribution of
2 species abundance. In this section, we review recent studies investigating the consequences of
3 neutral dynamics on the structure of interaction networks and show how variations in popula-
4 tion size can lead directly to interaction turnover.

5 **The basic processes**

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

1 **Benefits for network analysis**

2 It is important to understand how local variations in abundance, whether neutral or not, cas-
3 cade up to affect the structure of interaction networks. One approach is to use simple statistical
4 models to quantify the effect of population sizes on local interaction occurrence or strength (see
5 *e.g.* Krishna et al. 2008). These models can be extended to remove the contribution of neutral-
6 ity to link strength, allowing us to work directly on the interactions as they are determined by
7 traits (**Box 1**). Doing so allows us to compare the variation of neutral and non-neutral compo-
8 nents of network structure over space and time. To achieve this goal, however, it is essential that
9 empirical interaction networks (i) are replicated and (ii) include independent measurements of
10 population sizes.

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

1 **Traits matching in space and time**

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

12 **The basic processes**

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

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

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

22 **Benefits for network analysis**

23 Linking spatial and temporal trait variation with network variation will help identify the mech-
24 anistic basis of network dissimilarity. From a sampling point of view, having enough data
25 requires that, when interactions are recorded, they are coupled with trait measurements. Im-
26 portantly, these measurements cannot merely be extracted from a reference database because
27 interactions are driven by *local* trait values and their matching across populations from differ-

1 ent species. Within our overarching statistical framework (**Box 1**), we expect that (i) network
2 variability at the *regional* scale will be dependent on the variation of populations' traits, and (ii)
3 variation between any series of networks will depend on the *covariance* between species traits.
4 Although it requires considerably larger quantities of data to test, this approach should allow
5 us to infer *a priori* network variation. This next generation of data will also help link varia-
6 tion of network structure to variation of environmental conditions. Price (2003) shows how
7 specific biomechanical responses to water input in shrubs can have pleiotropic effects on traits
8 involved in the interaction with insects. In this system, the difference in network structure can
9 be explained because (i) trait values determine the existence of an interaction, and (ii) environ-
10 mental features determine trait values. We have little doubt that future empirical studies will
11 provide similar mechanistic narratives.

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

23 **Beyond direct interactions**

24 In this section, we argue that, although networks are built around observations of direct interac-
25 tions like predation or pollination, they also offer a compelling tool with which to address indi-
26 rect effects on the existence and strength of interactions. Any direct interaction arises from the

1 “physical” interaction of only two species, and, as we have already detailed, these can be modi-
2 fied by local relative abundances and/or species traits. Indirect interactions, on the other hand,
3 are established through the involvement of another party than the two focal species, either
4 through cascading effects (herbivorous species compete with insect laying eggs on plants) or
5 through physical mediation of the environment (bacterial exudates increase the bio-availability
6 of iron for all bacterial species; plants with large foliage provide shade for smaller species). As
7 we discuss in this section, the fact that many (if not all) interactions are indirectly affected by
8 the presence of other species (i) has relevance for understanding the variation of interaction
9 network structure and (ii) can be studied within the classical network-theory formalism.

10 **The basic processes**

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

17 The occurrence or absence of a biotic interaction can either affect either the realization of other
18 interactions (thus affecting the “interaction” component of network β -diversity) or the pres-
19 ence of other species. There are several well-documented examples of one interaction allowing
20 new interactions to happen, *e.g.* opportunistic pathogens have a greater success of infection in
21 hosts which are already immunocompromised by previous infections, (Olivier 2012), or con-
22 versely preventing them, *e.g.* a resident symbiont decreases the infection probability of a new
23 pathogen (Heil and McKey 2003, Koch and Schmid-Hempel 2011). In both cases, the driver
24 of interaction turnover is the patchiness of species distribution; the species acting as a “mod-
25 ifier” of the probability of interaction is only partially present throughout the range of the
26 other two species, thus creating a mosaic of different interaction configurations. Variation in
27 interaction structure can happen through both cascading and environmental effects: Singer et

1 al. (2004) show that caterpillars change the proportion of different plant species in their diet
2 when parasitized in order to favor low quality items and load themselves with chemical com-
3 pounds which are toxic for their parasitoids. However, low quality food results in birds having
4 a greater impact on caterpillar populations (Singer et al. 2012). It is noteworthy that in this ex-
5 ample, the existence of a parasitic interaction will affect both the strength, and impact, of other
6 interactions. In terms of their effects on network β -diversity, indirect effects are thus likely to
7 act on components of dissimilarity. A common feature of the examples mentioned here is that
8 pinpointing the exact mechanism through which interactions affect each other often requires a
9 good working knowledge of the system's natural history.

10 **Benefits for network analysis**

11 As discussed in previous sections, improved understanding of why and where species interact
12 should also provide a mechanistic understanding of observed species co-occurrences. How-
13 ever, the presence of species is also regulated by indirect interactions. Recent experimental re-
14 sults showed that some predator species can only be maintained if another predator species is
15 present, since the latter regulates a competitively superior prey and allows for prey coexistence
16 (Sanders and Veen 2012). These effects involving several species and several types of interac-
17 tions across trophic levels are complex (and for this reason, have been deemed unpredictable in
18 the past, Tack et al. (2011)), and can only be understood by comparing communities in which
19 different species are present/absent. Looking at figure 1, it is also clear that the probability of
20 having an interaction between species i and j ($P(\mathbf{L}_{ij})$) is ultimately constrained by the probabil-
21 ity that individuals of species i and j will meet assuming random movement, *i.e.* $P(i \cap j)$. Thus,
22 the existence of any ecological interaction will be contingent upon *other* ecological interactions
23 driving local co-occurrence (Araújo et al. 2011). Based on this argument, ecological networks
24 cannot be limited to a collection of pairwise interactions. Our view of them needs be updated
25 to account for the importance of the context surrounding these interactions (**Box 2**). From a
26 biogeographic standpoint, it requires us to develop a theory based on interaction co-occurrence
27 in addition to the current knowledge encompassing only species co-occurrence. Araújo et al.

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

9 **Conclusions**

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

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

1 deed statistical invariants in the rules governing interactions, this information will allow us
2 to make verifiable predictions on the structure of the networks. Better still, this approach has
3 the potential to substantially strengthen our understanding of the interplay between traits and
4 neutral effects. Blüthgen et al. (2008) claim that the impact of traits distribution on network
5 structure can be inferred simply by removing the impact of neutrality (population densities),
6 based on the idea that many rare links were instances of sampling artifacts. As illustrated here
7 (e.g, **Box 2**), their approach is of limited generality, as the abundance of a species itself can
8 be directly driven by factors such as trait-environment matching. In addition, there are virtu-
9 ally no datasets that follow a collection of interacting species through both space *and* time in
10 a replicated fashion. This type of data, although exceedingly tedious to collect, would provide
11 important indications of which mechanisms should be explored to improve our understanding
12 the variability of species interactions.

13 Assuming that suitable and accessible empirical data will inevitably accumulate in the coming
14 years, these approaches will rapidly expand our ability to predict the re-wiring of networks
15 under environmental change. There are two broad mechanisms linking network structure to
16 environmental change: changes in population sizes due to modification of demographic pa-
17 rameters, and plastic or adaptive responses resulting in shifted or disrupted trait distributions.
18 The framework proposed in **Box 1** predicts interaction probabilities under different scenarios.
19 Ultimately, being explicit about the trait-abundance-interaction feedback will provide a better
20 understanding of short-term and long-term dynamics of interaction networks. We illustrate
21 this in Fig. 3. The notion that population sizes have direct effects on the existence of an interac-
22 tion stands opposed to classical consumer-resource theory, which is one of the bases of network
23 analysis. Considering this an opposition, however, is erroneous. Consumer-resource theory
24 considers a strong effect of abundance on the intensity of interactions (**Box 2**), and itself is a
25 source of (quantitative) variation. Furthermore, these models are entirely determined by varia-
26 tions in population sizes in the limiting case where the coefficient of interactions are similar. As
27 such, any approach seeking to understand the variation of interactions over space ought to con-
28 sider that local densities are not only a consequence, but also a predictor, of the probability of

1 observing an interaction. The same reasoning can be held for local trait distributions, although
2 over micro-evolutionary time-scales. While trait values determine whether two species are able
3 to interact, they will be modified by the selective effect of species interacting. Therefore, con-
4 ceptualizing interactions as the outcome of a probabilistic process regulated by local factors, as
5 opposed to a constant, offers the unprecedented opportunity to investigate feedbacks between
6 different time scales. This is especially important since all of the mechanisms mentioned above
7 are also likely to change rapidly over spatial scales. The situation in which the phenologies of
8 populations are synchronized locally but not regionally (as shown by Singer and McBride 2012)
9 is an excellent example of when we must integrate these mechanisms into our interpretation of
10 spatial and temporal dynamics.

11 Over the past decade, many insights have been gained by looking at the turnover of different
12 facets of biodiversity (taxonomic, functional, and phylogenetic) through space (Devictor et al.
13 2010b, Meynard et al. 2011). Here, we propose that there is another oft-neglected side of bio-
14 diversity: species interactions. The perspective we bring forth allows us to unify these dimen-
15 sions and offers us the opportunity to describe the biogeographic structure of all components
16 of community and ecosystem structure simultaneously.

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22 New Zealand.

23 **Boxes**

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

25 We propose that the occurrence (and intensity) of ecological interactions at the population
26 level relies on several factors, including relative local abundances and local trait distributions.

1 It is important to tease apart these different factors so as to better disentangle neutral and
2 niche processes. We propose that these different effects can adequately be partitioned using the
3 model

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

4 where \mathcal{N} is a function giving the probability that species i and j interact *based only on their local*
5 *abundances* (that is, the probability of encounter), and \mathcal{T} is a function giving the *per encounter*
6 *probability* that species i and j interact *based on their trait values*. The term ϵ accounts for all
7 higher-order effects, such as indirect interactions, local impact of environmental conditions on
8 the interaction, and impact of co-occurring species. Both of these functions can take any form
9 needed. In several papers, $\mathcal{N}(i, j)$ was expressed as $\mathbf{n}_i \times \mathbf{n}_j$, where \mathbf{n} is a vector of relative abun-
10 dances (Canard et al. 2014). The expression of \mathcal{T} can in most cases be derived from mechanistic
11 hypotheses about the observation. For example, Gravel et al. (2013) used the niche model of
12 Williams and Martinez (2000) to predict interactions with the simple rule that $\mathcal{T}(i, j) = 1$ if i
13 can consume j based on allometric rules, and 0 otherwise. Following Rohr et al. (2010), the
14 expression of \mathcal{T} can be based on latent variables rather than actual trait values. This simple
15 formulation could be used to partition, at the level of individual interactions, the relative im-
16 portance of density-dependent and trait-based processes using variance decomposition. Most
17 importantly, it predicts (i) how each of these components will vary over space and (ii) how the
18 structure of the network will be affected by, for example, changes in local abundances or trait
19 distributions. The results provided by this framework will only be as good as the empirical data
20 used, and there is a dire need for a methodological discussion about how “predictor” variables
21 (traits, population sizes, etc.) should be measured in the field, in a way that is not biased by the
22 observation of the interactions. This will prove challenging for some types of interactions; *e.g.*
23 estimating the population size of parasites is often contingent upon catching and examining
24 hosts. Understanding non-independence between these variables in a system-specific way is a
25 crucial point.

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 ϵ 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 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 (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 ϵ 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.

¹ **Figures**

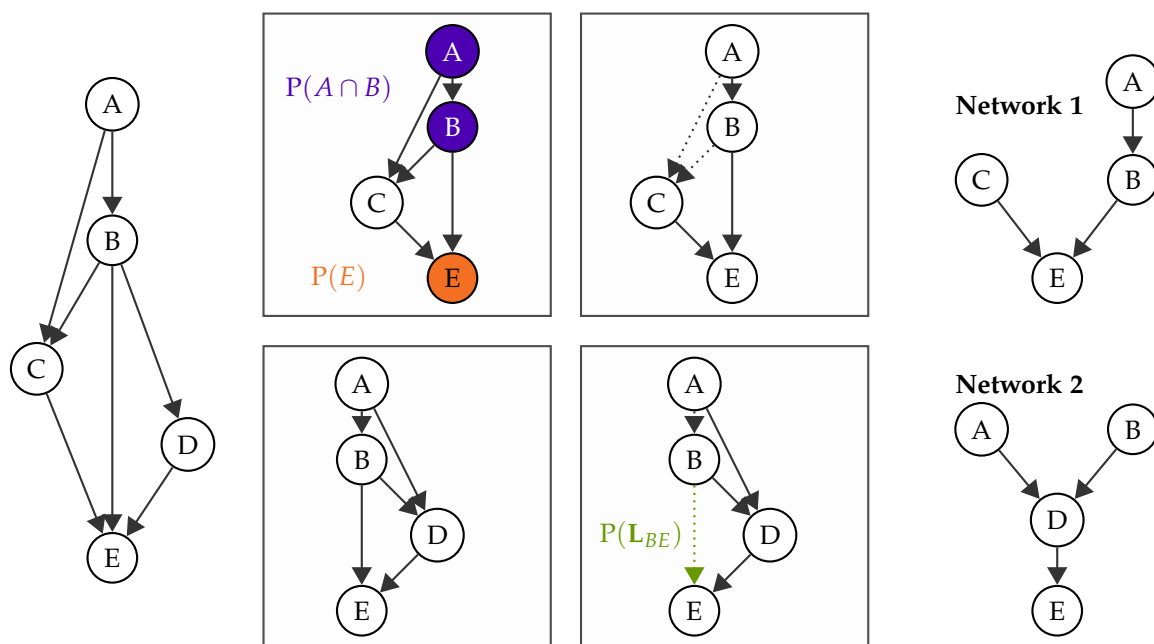


Figure 1: An illustration of the metaweb concept. In its simplest form, a metaweb is the list of all possible species and interactions between them for the system being studied, at the regional level (far left side). Everything that is ultimately observed in nature is a *realisation* of the metaweb (far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

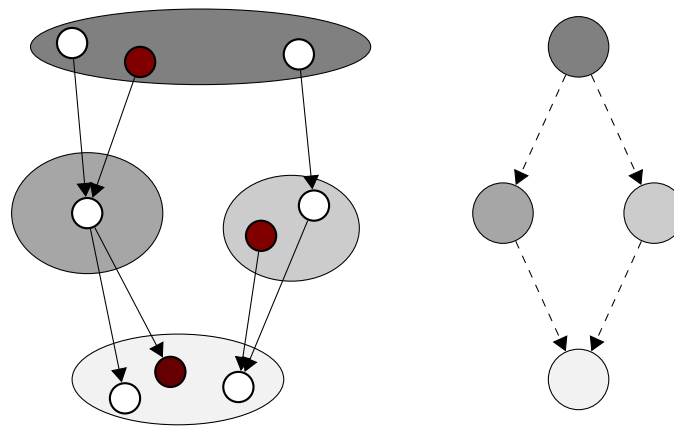


Figure 2: The left-hand side of this figure represents possible interactions between populations (circles) of four species (ellipses), and the aggregated species interaction network on the right. In this example, the populations and species level networks have divergent properties, and the inference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

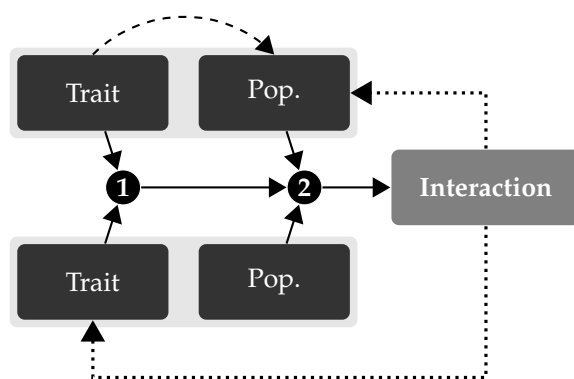


Figure 3: The approach we propose (that populations can interact at the conditions that 1 their trait allow it and 2 they are locally abundant enough for some of their individuals to meet by chance) requires an increased focus on population-level processes. A compelling argument that supports working at this level of organisation is that eco-evolutionary feedbacks are explicit. All of the components of interaction variability we described are potentially related, either through variations of population sizes due to the interaction itself, or due to selection arising 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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