

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

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~~Jan.~~ July 2014

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

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

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20 **Abstract:** Community ecology is tasked with the considerable challenge of predicting the
21 structure, and properties, of emerging ecosystems. It requires the ability to understand how
22 and why species interact, as this will allow the development of mechanism-based predictive
23 models, and as such to better characterize how ecological mechanisms act locally on the
24 existence of inter-specific interactions. Here we argue that the current conceptualization of
25 species interaction networks is ill-suited for this task. Instead, we propose that future research
26 must start to account for the intrinsic variability of ~~interaction~~ species interactions, then scale
27 up from here onto complex networks. This can be ~~accomplished~~ accomplished simply by
28 recognizing that there exists intra-specific variability, in traits or properties related to the
29 establishment of species interactions. By shifting the scale towards population-based
30 processes, we show that this new approach will improve our predictive ability and
31 mechanistic understanding of how species interact over large spatial or temporal scales.

32 Introduction

33 Interactions between species are the driving force behind ecological dynamics within
34 communities (Berlow et al. 2009). Likely for this reason more than any [other](#), the structure of
35 communities have been described by species interaction networks for over a century (Dunne
36 2006). Formally an ecological network is a mathematical and conceptual representation of
37 both *species*, and the *interactions* they establish. Behind this conceptual framework is a rich
38 and expanding literature whose primary focus has been to quantify how numerical and
39 statistical properties of networks relate to their robustness (Dunne et al. 2002), productivity
40 (Duffy et al. 2007), or tolerance to extinction (Memmott et al. 2004). Although this approach
41 classically focused on food webs (Ings et al. 2009), it has proved particularly successful
42 because it can be applied equally to all types of ecological interactions (Kéfi et al. 2012).

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

59 Within the current paradigm, interactions are established between species and are an
60 immutable “property” of a species pair. Starting from empirical observations, expert
61 knowledge, or literature surveys, one could collect a list of interactions for any given species
62 pool. Several studies used this approach to extrapolate the structure of networks over time
63 and space (Havens 1992, Piechnik et al. 2008, Baiser et al. 2012) by considering that the
64 network at *any* location is composed of *all* of the potential interactions known for this species
65 pool. This stands in stark contrast with recent results showing that (i) the identities of
66 interacting species vary over space and (ii) the dissimilarity of interactions is not related to the
67 dissimilarity in species composition (Poisot et al. 2012). The current conceptual and
68 operational tools to study networks therefore ~~leaves~~ leave us poorly equipped to understand
69 the causes of this variation. In this paper, we propose ~~a general research agenda to understand~~
70 to shift the research agenda towards understanding the mechanisms involved in the
71 variability of co-occurring species interactions.

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

84 Since the next generation of predictive biogeographic models will need to account for species
85 interactions (Thuiller et al. 2013), it is crucial not to underestimate the fact that ~~these~~

86 ~~interactions~~ they are intrinsically variable and exhibit a geographic variability of their own.
87 Indeed, investigating the impact of species interactions on species distributions only makes
88 sense under the implicit assumption that species interactions themselves vary over
89 biogeographical scales. Models of species distributions will therefore increase their predictive
90 ~~potential~~ ability if they account for the variability of ecological interactions. In turn, tighter
91 coupling between species-distribution and interaction-distribution models will provide more
92 accurate predictions of the properties of emerging ecosystems (Gilman et al. 2010, Estes et al.
93 2011) and the spatial variability of properties between existing ecosystems. By paying more
94 attention to the variability of species interactions, the field of biogeography will be able to
95 re-visit classical observations typically explained by species-level mechanisms; for example,
96 how does community complexity and function vary along latitudinal gradients, is there
97 information hidden in the co-occurrence or avoidance of species interactions, etc. This
98 predictive effort is made all the more important as both the phenology (Parmesan 2007) and
99 ranges (Devictor et al. 2012) of species occupying different positions in their interactions
100 networks are affected differently by climate change. Predicting that species will move and
101 change while interactions remain the same is probably a very conservative approach to
102 estimating the changes to come, and building explicitly on biological mechanisms is one
103 possible way to overcome this limitation.

104 In this paper, we outline the mechanisms that are involved in the variability of species
105 interactions over time, space, and environmental gradients. We discuss how they will affect
106 the structure of ecological networks, and how these mechanisms can be integrated into new
107 predictive and statistical models (**Box 1**). Most importantly, we show that this approach
108 integrates classical community ecology thinking and biogeographic questions (**Box 2**) and will
109 ultimately result in a better understanding of the structure of ecological communities.

110 The dynamic nature of ecological interaction networks

111 Recent studies on the sensitivity of network structure to environmental change provide some
112 context for the study of dynamic networks. Menke et al. (2012) showed that the structure of a
113 plant–frugivore network changed along a forest–farmland gradient. At the edges between two
114 habitats, species were on average less specialized and interacted more evenly with a larger
115 number of partners than they did in habitat cores. Differences in network structure have also
116 been observed within forest strata that differ in their proximity to the canopy and visitation by
117 birds (Schleuning et al. 2011). Tylianakis et al. (2007) reports a *stronger* signal of spatial
118 interaction turnover when working with quantitative rather than binary interactions,
119 highlighting the importance of *measuring* rather than assuming (or simply reporting) the
120 existence of interactions. Eveleigh et al. (2007) demonstrated that outbreaks of the spruce
121 budworm were associated with changes in the structure of its trophic network, both in terms
122 of species observed and their interactions. Poisot et al. (2011) used a microbial system of hosts
123 and pathogens to study the impact of productivity gradients on realized infection; when the
124 species were moved from high to medium to low productivity, some interactions were lost and
125 others were gained. As a whole, these results suggest that the existence, and properties, of an
126 interaction are not only contingent on the presence of the two species involved but may also
127 require particular environmental conditions, including the presence or absence of species not
128 directly involved in the interaction.

129 We argue here that there are three broadly-defined classes of mechanisms that ultimately
130 determine the realization of species interactions. First, ~~individuals must be in high enough~~
131 ~~local relative abundances~~ species must be locally abundant enough for their individuals to
132 meet; this is the so-called “neutral” perspective of interactions. Second, there must be
133 phenological or trait matching between individuals, such that an interaction will actually
134 occur given that the encounter takes place. Finally, the realization of an interaction is
135 regulated by the interacting organisms’ surroundings and should be studied in the context of
136 indirect interactions.

137 **Population dynamics and neutral processes**

138 Over the recent years, the concept of neutral dynamics has left a clear imprint on the analysis
139 of ecological network structure, most notably in bipartite networks (Blüthgen et al. 2006).
140 Re-analysis of several host–parasite datasets, for example, showed that changes in local species
141 abundances triggers variation in parasite specificity (Vazquez et al. 2005). More generally, it is
142 possible to predict the structure of trophic interactions (Canard et al. 2012) and host-parasite
143 communities (Canard et al. 2014) given only minimal assumptions about the distribution of
144 species abundance. In this section, we review recent studies investigating the consequences of
145 neutral dynamics on the structure of interaction networks and show how variations in
146 population size can lead directly to interaction turnover.

147 **The basic processes**

148 As noted previously, for an interaction to occur between individuals from two populations,
149 these individuals must first meet, then interact. Assuming that two populations occupy the
150 same location and are active at the same time of the day/year, then the likelihood of an
151 interaction is roughly proportional to the product of their relative abundance (Vázquez et al.
152 2007). This means that individuals from two large populations are more likely to interact than
153 individuals from two small populations, simply because they tend to meet more often. This
154 approach can also be extended to the prediction of interaction strength (Blüthgen et al. 2006,
155 Vázquez et al. 2007), *i.e.* how strong the consequences of the interaction will be. The neutral
156 perspective predicts that locally-abundant species should have more partners and that
157 locally-rare species should appear more specialized. In a purely neutral model (*i.e.*
158 interactions happen entirely by chance, although the determinants of abundance can still be
159 non-neutral), the identities of species do not matter, and it becomes easy to understand how
160 the structure of local networks can vary since species vary regionally in abundance. Canard et
161 al. (2012) proposed the term of “neutrally forbidden links” to refer to interactions that are

phenologically feasible but not realized because of the underlying population size distribution. The identity of these neutrally forbidden links will vary over time and space, either due to stochastic changes in population sizes or because population size responds deterministically (*i.e.* non-neutrally) to extrinsic drivers.

Benefits for network analysis

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

An additional benefit of such sampling is that these data will also help refine neutral theory. Wootton (2005) made the point that deviations of empirical communities from neutral predictions were most often explained by species trophic interactions which are notoriously, albeit intentionally, absent from the original formulation of the theory (Hubbell 2001). Merging the two views will increase our explanatory power, and provide new ways to test neutral theory in interactive communities; it will also offer a new opportunity, namely to complete the integration of network structure with population dynamics. To date, most studies have focused on the effects of a species' position within a food web on the dynamics of its biomass or abundance (Brose et al. 2006, Berlow et al. 2009, Stouffer et al. 2011, Saavedra et al. 2011). Adopting this neutral perspective brings things full circle since the abundance of a species will also dictate its position in the network: changes in abundance can lead to interactions being gained or lost, and these changes in abundance are in part caused by

existing interactions (**Box 2**). For this reason, there is a potential to link species and interaction dynamics and, more importantly, to do so in a way which accounts for the interplay between the two. From a practical point of view, this requires repeated sampling of a system through time, so that changes in relative abundances can be related to changes in interaction strength (Yeakel et al. 2012). Importantly, embracing the neutral view will force us to reconsider the causal relationship between resource dynamics and interaction strength since, in a neutral context, both are necessarily interdependent.

Traits matching in space and time

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

The basic processes

There is considerable evidence that, at the species level, interaction partners are selected on the grounds of matching trait values. Random networks built on these rules exhibit realistic structural properties (Williams and Martinez 2000, Stouffer et al. 2005). Trait values, however, vary from population to population within species; it is therefore expected that the

211 local interactions will be contingent upon ~~traits spatial distribution~~ the spatial distribution of
212 the traits (??). The fact that a species' niche can appear large if it is the aggregation of narrow
213 but differentiated individual or population niches is now well established (Bolnick et al. 2003,
214 Devictor et al. 2010a) and has also reinforced the need to understand intra-specific trait
215 variation to describe the structure and dynamics of communities (Woodward et al. 2010,
216 Bolnick et al. 2011). Nevertheless, this notion has yet to percolate into the literature on
217 network structure despite its most profound consequence: a species appearing generalist at
218 the regional scale can easily be specialized in *each* of the patches it occupies. This reality has
219 long been recognized by functional ecologists, which are now increasingly predicting the
220 *variance* in traits of different populations within a species (Violle et al. 2012).

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

232 From a trait-based perspective, the existence of an interaction is an emergent property of the
233 trait distribution of local populations: variations in one or both of these distributions,
234 regardless of the mechanism involved (development, selection, plasticity, environment), are
235 likely to alter the interaction. Importantly, when interaction-driving traits are subject to
236 environmental forcing (for example, body size is expected to be lower in warm environments,
237 Angilletta et al. (2004)), there can be covariation between environmental conditions and the

238 occurrence of interactions. Woodward et al. (2012) used macrocosms to experimentally
239 demonstrate that changes in food-web structure happen at the same time as changes in species
240 body mass distribution. Integrating trait variation over gradients will provide more predictive
241 power to models of community response to environmental change.

242 **Benefits for network analysis**

243 Linking spatial and temporal trait variation with network variation will help identify the
244 mechanistic basis of network dissimilarity. From a sampling point of view, having enough
245 data requires that, when interactions are recorded, they are coupled with trait measurements.
246 Importantly, these measurements cannot merely be extracted from a reference database
247 because interactions are driven by *local* trait values and their matching across populations
248 from different species. Within our overarching statistical framework (**Box 1**), we expect that (i)
249 network variability at the *regional* scale will be dependent on the variation of populations'
250 traits, and (ii) variation between any series of networks will depend on the *covariance* between
251 species traits. Although it requires considerably larger quantities of data to test, this approach
252 should allow us to infer *a priori* network variation. This next generation of data will also help
253 link variation of network structure to variation of environmental conditions. Price (2003)
254 shows how specific biomechanical responses to water input in shrubs can have pleiotropic
255 effects on traits involved in the interaction with insects. In this system, the difference in
256 network structure can be explained because (i) trait values determine the existence of an
257 interaction, and (ii) environmental features determine trait values. We have little doubt that
258 future empirical studies will provide similar mechanistic narratives.

259 At larger temporal scales, the current distribution of traits also reflects past evolutionary
260 history (Diniz-Filho and Bini 2008). Recognizing this important fact offers an opportunity to
261 approach the evolutionary dynamics and variation of networks. Correlations between
262 different species' traits, and between traits and fitness, drive coevolutionary dynamics
263 (Gomulkiewicz et al. 2000, Nuismer et al. 2003). Both of these correlations vary over space

and time (Thompson 2005), creating patchiness in the processes and outcomes of coevolution. Trait structure and trait correlations are also disrupted by migration (Gandon et al. 2008, Burdon and Thrall 2009). Ultimately, understanding of how ecological and evolutionary trait dynamics affect network structure will provide a mechanistic basis for the historical signal found in contemporary network structures (Rezende et al. 2007, Eklof et al. 2011, Baskerville et al. 2011, Stouffer et al. 2012).

Beyond direct interactions

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

The basic processes

Biotic interactions themselves interact (Golubski and Abrams 2011); in other words, interactions are contingent on the occurrence of species other than those interacting. Because

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

The occurrence or absence of a biotic interaction can either affect either the realization of other interactions (thus affecting the “interaction” component of network β -diversity) or the presence of other species. There are several well-documented examples of one interaction allowing new interactions to happen (e.g. opportunistic pathogens have a greater success of infection in hosts which are already immunocompromised by previous infections, (Olivier 2012), or conversely preventing them (e.g. a resident symbiont decreases the infection probability of a new pathogen (Heil and McKey 2003, Koch and Schmid-Hempel 2011, @hei03). In both cases, the driver of interaction turnover is the patchiness of species distribution; the species acting as a “modifier” of the probability of interaction is only partially present throughout the range of the other two species, thus creating a mosaic of different interaction configurations. Variation in interaction structure can happen through both cascading and environmental effects: Singer et al. (2004) show that caterpillars change the proportion of different plant species in their diet when parasitized in order to favor low quality items and load themselves with chemical compounds which are toxic for their parasitoids. However, low quality food results in birds having a greater impact on caterpillar populations (Singer et al. 2012). It is noteworthy that in this example, the existence of an a parasitic interaction will affect both the strength, and impact, of other interactions. In terms of their effects on network β -diversity, indirect effects are thus likely to act on components of dissimilarity. A common feature of the examples mentioned here is that pinpointing the exact mechanism through which interactions affect each other often requires a good working knowledge of the system’s natural history.

313 Benefits for network analysis

314 As discussed in previous sections, improved understanding of why and where species interact
315 should also provide a mechanistic understanding of observed species co-occurrences.
316 However, the presence of species is also regulated by indirect interactions. Recent
317 experimental [results](#) showed that some predator species can only be maintained if another
318 predator species is present, since the latter regulates a competitively superior prey and allows
319 for prey coexistence (Sanders and Veen 2012). These effects involving several species and
320 several types of interactions across trophic levels are complex (and for this reason, have been
321 deemed unpredictable in the past, Tack et al. (2011)), and can only be understood by
322 comparing communities in which different species are present/absent. Looking at figure ??, it
323 is also clear that the probability of having an interaction between species i and j ($P(L_{ij})$) is
324 ultimately constrained by the probability ~~of simultaneously observing that individuals of~~
325 [species \$i\$ and \$j\$ together will meet assuming random movement](#), i.e. $P(i \cap j)$. Thus, the existence
326 of any ecological interaction will be contingent upon *other* ecological interactions driving local
327 co-occurrence (Araújo et al. 2011). Based on this argument, ecological networks cannot be
328 limited to a collection of pairwise interactions. Our view of them needs be updated to account
329 for the importance of the context surrounding these interactions (**Box 2**). From a
330 biogeographic standpoint, it requires us to develop a theory based on interaction
331 co-occurrence in addition to the current knowledge encompassing only species co-occurrence.
332 Araújo et al. (2011) and Allesina and Levine (2011) introduced the idea that competitive
333 interactions can leave a signal in species co-occurrence network. A direct consequence of this
334 result is that, for example, trophic interactions are constrained by species' competitive
335 outcomes *before* they are ever constrained by e.g. predation-related traits. In order to fully
336 understand interactions and their indirect effects, however, there is a need to develop new
337 conceptual tools to *represent* effects that interactions have on one another. In a graph
338 theoretical perspective, this would amount to establishing edges between pairs of edges, a task
339 for which there is limited conceptual or methodological background.

Conclusions

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

At the moment, the field of community ecology is severely data-limited to tackle this perspective. Despite the existence of several spatially- or temporally-replicated datasets (*e.g.* Schleuning et al. 2011 2012 Menke et al. 2012), it is rare that all relevant information has been measured independently. It was recently concluded, however, that even a reasonably small subset of data can be enough to draw inferences at larger scales (Gravel et al. 2013). Paradoxically, as tempting as it may be to sample a network in its entirety, the goal of establishing global predictions might be better furthered by extremely-detailed characterization of a more modest number of interactions (Rodriguez-Cabal et al. 2013). Assuming that there are indeed statistical invariants in the rules governing interactions, this information will allow us to make verifiable predictions on the structure of the networks. Better still, this approach has the potential to substantially strengthen our understanding of the interplay between traits and neutral effects. Blüthgen et al. (2008) claim that the impact of traits distribution on network structure can be inferred simply by removing the impact of neutrality (population densities), based on the idea that many rare links were instances of sampling artifacts. As illustrated here (*e.g.* **Box 2**), their approach is of limited generality, as the abundance of a species itself can be directly driven by factors such as trait-environment matching. In addition, there are virtually no datasets that follow a collection of interacting

species through both space *and* time in a replicated fashion. This type of data, although exceedingly tedious to collect, would provide important indications of which mechanisms should be explored to improve our understanding the variability of species interactions.

~~With the accumulation of data~~ Assuming that suitable and accessible empirical data will inevitably accumulate in the coming years, these approaches will rapidly expand our ability to predict the re-wiring of networks under environmental change. ~~The effect of environmental change is expected to occur because (i) population sizes will be affected by the change and (ii) either~~ There are two broad mechanisms linking network structure to environmental change: changes in population sizes due to modification of demographic parameters, and plastic or adaptive responses ~~will shift or disrupt the~~ resulting in shifted or disrupted trait distributions.

The framework proposed in **Box 1** predicts interaction probabilities under different scenarios. Ultimately, being explicit about the trait-abundance-interaction feedback will provide a better understanding of short-term and long-term dynamics of interaction networks. We illustrate this in Fig. ??.

The notion that population sizes have direct effects on the existence of an interaction stands opposed to classical consumer-resource theory, which is one of the bases of network analysis. Considering this an opposition, however, is erroneous. Consumer-resource theory considers a strong effect of abundance on the intensity of interactions (**Box 2**), and itself is a source of (quantitative) variation. Furthermore, these models are entirely determined by variations in population sizes in the limiting case where the coefficient of interactions are similar. As such, any approach seeking to understand the variation of interactions over space ought to consider that local densities are not only a consequence, but also a predictor, of the probability of observing an interaction. The same reasoning can be held for local trait distributions, although over micro-evolutionary time-scales. While trait values determine whether two species are able to interact, they will be modified by the selective effect of species interacting. Therefore, conceptualizing interactions as the outcome of a probabilistic ~~process~~ process regulated by local factors, as opposed to a constant, offers the unprecedented opportunity to investigate feedbacks between different time scales. This is especially important since all of the mechanisms mentioned above are also likely to change rapidly over

spatial scales. The situation in which the phenologies of populations are synchronized locally but not regionally (as shown by Singer and McBride 2012) is an excellent example of when we must integrate these mechanisms into our interpretation of spatial and temporal dynamics.

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

Acknowledgements: We thank Michael C. Singer and one anonymous referee for insightful comments on this manuscript. TP, DBS, and DG received financial support from the Canadian Institute of Ecology and Evolution (*Continental Scale Variation of Ecological Networks* thematic working group). TP was funded by a FRQNT-MELS PBEE post-doctoral scholarship. DBS was funded by a Marsden Fund Fast-Start grant (UOC-1101) administered by the Royal Society of New Zealand.

Boxes

Box 1: A mathematical framework for population-level interactions

We propose that the occurrence (and intensity) of ecological interactions at the population level relies on several factors, including relative local abundances and local trait distributions. It is important to tease apart these different factors so as to better disentangle neutral and niche processes. We propose that these different effects can adequately be partitioned using ~~the model~~ a model for the adjacency matrix A , where the probability of an interaction between species i and j is

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

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

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

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

442 in which i_x is the population of species i at site x . In this formulation, the ϵ term could include
 443 the spatial variation of interaction between i and j over sites, and the covariance between the
 444 observed presence of this interaction and the occurrence of species i and j . This can, for
 445 example, help address situations in which the selection of prey items is determined by traits,
 446 but also by behavioral choices. Most importantly, this model differs from the previous one in
 447 that each site x is characterized by a set of functions $\mathcal{N}_x, \mathcal{T}_x$ that may not be identical for all
 448 sites considered. For example, the same predator may prefer different prey items in different
 449 locations, which will require the use of a different form for \mathcal{T} across the range of locations.
 450 [\(Gravel et al. \(2013\)\)](#) show that it is possible to derive robust approximation for the \mathcal{T}
 451 function even with [an](#) incomplete set of data, which gives hope that this framework can be
 452 applied even when all species information is not known at all sites (which would be an
 453 unrealistic requirement for most realistic systems). Both of these models can be used to
 454 partition the variance from existing data or to test which trait-matching function best
 455 describes the observed interactions. They also provide a solid platform for dynamical
 456 simulations in that they will allow re-wiring the interaction network as a function of trait
 457 change and to generate simulations that are explicit about the variability of interactions.

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

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

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

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

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

477 Since dynamic models demonstrate quite clearly that non-interacting species can alter each
478 others' abundances (*e.g.* via apparent competition (Holt and Kotler 1987)), this is a
479 deeply-ingrained inconsistency between the two approaches. Such a simplification does
480 increase the analytical tractability of the problem (Allesina and Tang 2012), but there is little,

481 if any, guarantee that it is ecologically accurate. In our opinion, the “higher-effects” term ϵ in
482 the models presented in **Box 1** is the one with the least straightforward expectations, but it
483 may also prove to be the most important if we wish to accurately describe all of these indirect
484 effects.

485 A similar problem actually arises in the typical statistical framework for predicting
486 interaction occurrence. Often, one attempts to “decompose” interactions into the component
487 that is explained by species’ abundances and the component explained by species’ traits (e.g.,
488 Box 1). Just like how the underlying functions \mathcal{N} and \mathcal{T} could vary across sites, there could
489 also be feedback between species’ abundances and traits, in the same way that we have
490 outlined the feedback between interactions and species’ abundances. In fact, given the
491 increasing evidence for the evolutionary role of species-species interactions in explaining
492 extant biodiversity and their underlying traits (Janzen and Martin 1982, Herrera et al. 2002), a
493 framework which assumes relative independence of these different phenomenon is likely
494 starting from an overly-simplified perspective.

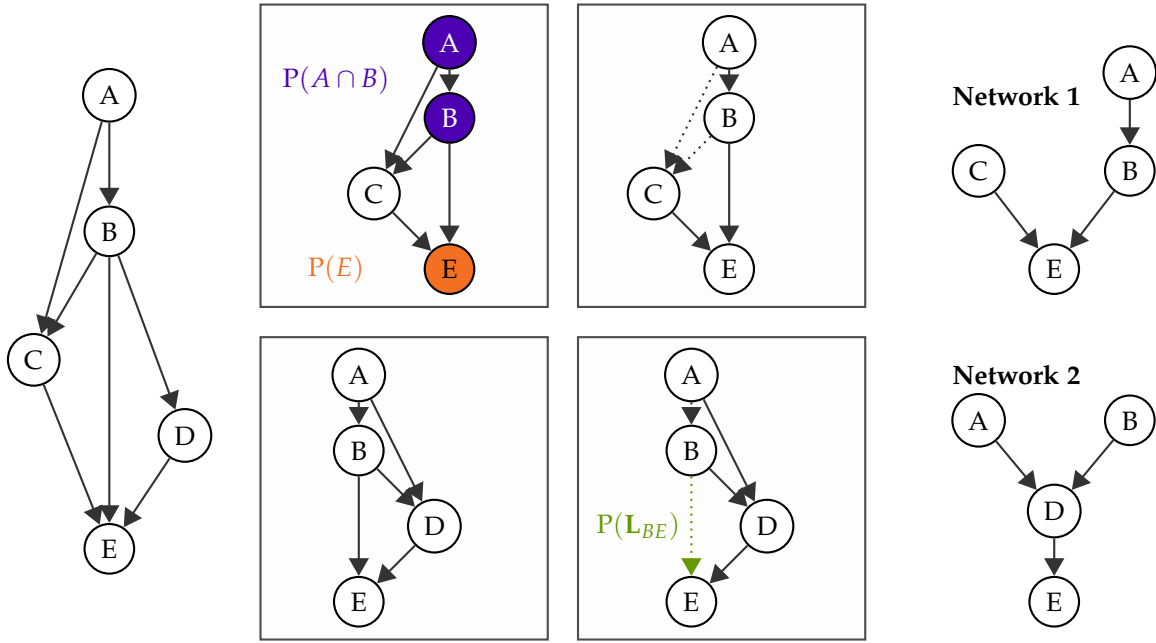


Figure 1: An illustration of the metaweb concept. In its simplest form, a metaweb is the list of all possible species and interactions between them for the system being studied, at the regional level (far left side). Everything that is ultimately observed in nature is a *realisation* of the metaweb (far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

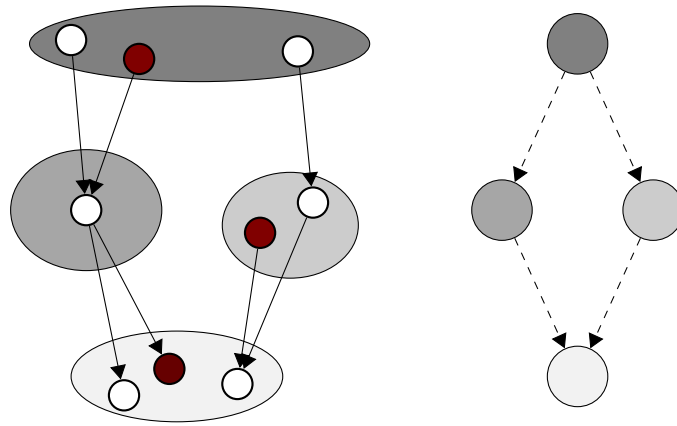


Figure 2: The left-hand side of this figure represents possible interactions between populations (circles) of four species (ellipses), and the aggregated species interaction network on the right. In this example, the populations and species level networks have divergent properties, and the inference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

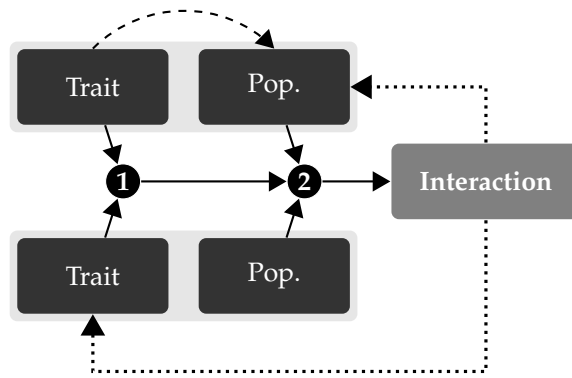


Figure 3: The approach we propose (that populations can interact at the conditions that 1 their trait allow it and 2 they are locally abundant enough for some of their individuals to meet by chance) requires ~~to shift our~~ an increased focus ~~to on~~ population-level processes. A compelling argument ~~to work 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 ~~stemming 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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