

Beyond species: why ecological interactions vary through space and time

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

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

28 Introduction

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

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

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

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

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

83 Models of species distributions will therefore increase their predictive potential if they ac-
84 count for the variability of ecological interactions. In turn, tighter coupling between species-
85 distribution and interaction-distribution models will provide more accurate predictions of the
86 properties of emerging ecosystems (Gilman et al. 2010, Estes et al. 2011) and the spatial vari-
87 ability of properties between existing ecosystems. By paying more attention to the variability of
88 species interactions, the field of biogeography will be able to re-visit classical observations typ-
89 ically explained by species-level mechanisms; for example, how does community complexity
90 and function vary along latitudinal gradients, is there information hidden in the co-occurrence
91 or avoidance of species interactions, etc. This predictive effort is made all the more important
92 as both the phenology PARMESAN07 and ranges (Devictor et al. 2012) of species occupying
93 different positions in their interactions networks change are affected differently by climate
94 change. Predicting that species will move and change while interactions remain the same is
95 probably a very conservative estimation of actual changes to come, and building explicitly on
96 biological mechanisms is one possible way to overcome this limitation.

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

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

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

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

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

129 **Population dynamics and neutral processes**

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

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

139 **The basic processes**

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

158 **Benefits for network analysis**

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

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

186 **Traits matching in space and time**

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

197 **The basic processes**

198 There is considerable evidence that, at the species level, interaction partners are selected on the
199 grounds of matching trait values. Random networks built on these rules exhibit realistic struc-
200 tural properties (Williams and Martinez 2000, Stouffer et al. 2005). Trait values, however, vary
201 from population to population within species; it is therefore expected that the local interactions
202 will be contingent upon traits spatial distribution (??). The fact that a species’ niche can ap-
203 pear large if it is the aggregation of narrow but differentiated individual or population niches
204 is now well established (Bolnick et al. 2003, Devictor et al. 2010a) and has also reinforced
205 the need to understand intra-specific trait variation to describe the structure and dynamics of
206 communities (Woodward et al. 2010, Bolnick et al. 2011). Nevertheless, this notion has yet
207 to percolate into the literature on network structure despite its most profound consequence: a
208 species appearing generalist at the regional scale can easily be specialized in *each* of the patches
209 it occupies. This reality has long been recognized by functional ecologists, which are now in-
210 creasingly predicting the *variance* in traits of different populations within a species (Violle et
211 al. 2012).

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

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

233 **Benefits for network analysis**

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

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

At larger temporal scales, the current distribution of traits also reflects past evolutionary history (Diniz-Filho and Bini 2008). Recognizing this important fact offers an opportunity to approach the evolutionary dynamics and variation of networks. Correlations between different species' traits, and between traits and fitness, drive coevolutionary dynamics (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

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

274 The basic processes

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

281 The occurrence or absence of a biotic interaction can either affect either the realization of other
 282 interactions (thus affecting the “interaction” component of network β -diversity) or the pres-
 283 ence of other species. There are several well-documented examples of one interaction allowing
 284 new interactions to happen (e.g. opportunistic pathogens have a greater success of infection in
 285 hosts which are already immunocompromised by previous infections, (Olivier 2012), or con-
 286 versely preventing them (e.g. a resident symbiont decreases the infection probability of a new
 287 pathogen (Heil and McKey 2003, Koch and Schmid-Hempel 2011~~op. @hei03~~). In both cases,
 288 the driver of interaction turnover is the patchiness of species distribution; the species acting as
 289 a “modifier” of the probability of interaction is only partially present throughout the range of
 290 the other two species, thus creating a mosaic of different interaction configurations. Variation
 291 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 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.

Benefits for network analysis

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

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

345 deed statistical invariants in the rules governing interactions, this information will allow us
346 to make verifiable predictions on the structure of the networks. Better still, this approach has
347 the potential to substantially strengthen our understanding of the interplay between traits and
348 neutral effects. Blüthgen et al. (2008) claim that the impact of traits distribution on network
349 structure can be inferred simply by removing the impact of neutrality (population densities),
350 based on the idea that many rare links were instances of sampling artifacts. As illustrated
351 here (e.g, **Box 2**), their approach is of limited generality, as the abundance of a species itself
352 can be directly driven by factors such as trait-environment matching. In addition, there are
353 virtually no datasets that follow a complex of interacting species both through space and time
354 in a replicated way. This type of data, although certainly tedious to collect, would provide
355 important insights about which mechanisms should be looked at to understand the variability
356 of species interactions.

357 ~~With the accumulation of data~~ Assuming that empirical data will indeed accumulate in the
358 coming years, these approaches will rapidly expand our ability to predict the re-wiring of net-
359 works under environmental change. The effect of environmental change is expected to occur
360 because (i) population sizes will be affected by the change and (ii) either plastic or adaptive
361 responses will shift or disrupt the trait distributions. The framework proposed in **Box 1** pre-
362 dicts interaction probabilities under different scenarios. Ultimately, being explicit about the
363 trait-abundance-interaction feedback will provide a better understanding of short-term and
364 long-term dynamics of interaction networks. We illustrate this in Fig. ???. The notion that
365 population sizes have direct effects on the existence of an interaction stands opposed to classi-
366 cal consumer-resource theory, which is one of the bases of network analysis. Considering this
367 an opposition, however, is erroneous. Consumer-resource theory considers a strong effect of
368 abundance on the intensity of interactions (**Box 2**), and itself is a source of (quantitative) vari-
369 ation. Furthermore, these models are entirely determined by variations in population sizes in
370 the limiting case where the coefficient of interactions are similar. As such, any approach seek-
371 ing to understand the variation of interactions over space ought to consider that local densities
372 are not only a consequence, but also a predictor, of the probability of observing an interaction.

373 The same reasoning can be held for local trait distributions, although over micro-evolutionary
374 time-scales. While trait values determine whether two species are able to interact, they will be
375 modified by the selective effect of species interacting. Therefore, conceptualizing interactions
376 as the outcome of a probabilistic ~~process~~process regulated by local factors, as opposed to a
377 constant, offers the unprecedented opportunity to investigate feedbacks between different time
378 scales. This is especially important since all of the mechanisms mentioned above are also likely
379 to change rapidly over spatial scales. The situation in which populations are synchronized in
380 their phenology at the local, but not at the regional scale (as shown by Singer and McBride
381 2012), is a good example of when the integration of these mechanisms to our interpretation of
382 spatial and temporal dynamics is required.

383 Over the past decade, many insights have been gained by looking at the turnover of different
384 facets of biodiversity (taxonomic, functional, and phylogenetic) through space (Devictor et al.
385 2010b, Meynard et al. 2011). Here, we propose that there is another oft-neglected side of bio-
386 diversity: species interactions. The perspective we bring forth allows us to unify these dimen-
387 sions and offers us the opportunity to describe the biogeographic structure of all components
388 of community and ecosystem structure simultaneously.

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393 **Boxes**

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

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

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

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

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

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

425 in which i_x is the population of species i at site x . In this formulation, the ϵ term could include
426 the spatial variation of interaction between i and j over sites, and the covariance between the
427 observed presence of this interaction and the occurrence of species i and j . This can, for ex-
428 ample, help address situations in which the selection of prey items is determined by traits, but
429 also by behavioral choices. Most importantly, this model differs from the previous one in that
430 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-
431 sidered. For example, the same predator may prefer different prey items in different locations,
432 which will require the use of a different form for \mathcal{T} across the range of locations. [\(Gravel](#)
433 [et al. \(2013\)](#) show that it is possible to derive robust approximation for the \mathcal{T} function even
434 with incomplete set of data, which gives hope that this framework can be applied even when
435 all species information is not known at all sites (which would be an unrealistic requirement for
436 most realistic systems). Both of these models can be used to partition the variance from exist-
437 ing data or to test which trait-matching function best describes the observed interactions. They
438 also provide a solid platform for dynamical simulations in that they will allow re-wiring the
439 interaction network as a function of trait change and to generate simulations that are explicit
440 about the variability of interactions.

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

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

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

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

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

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

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

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

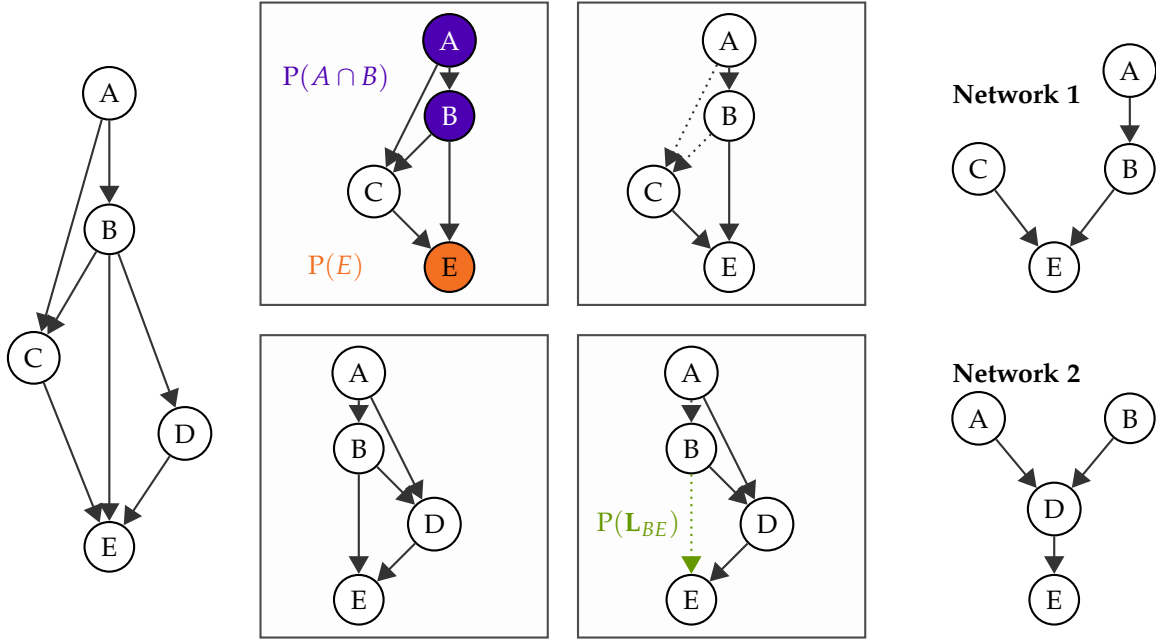


Figure 1: An illustration of the metaweb concept. In its simplest form, a metaweb is the list of all possible species and interactions between them for the system being studied, at the regional level (far left side). Everything that is ultimately observed in nature is a *realisation* of the metaweb (far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

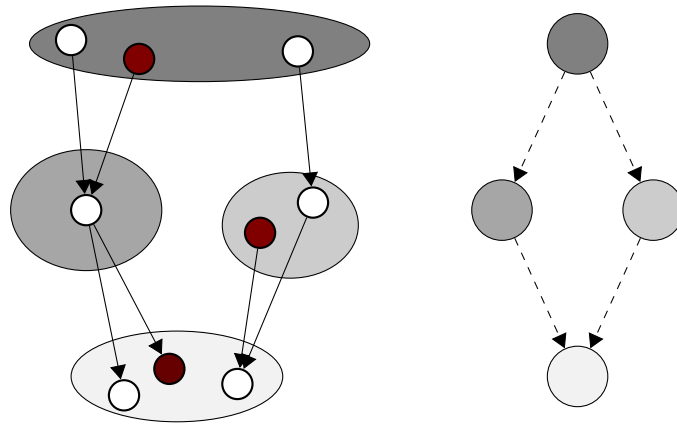


Figure 2: The left-hand side of this figure represents possible interactions between populations (circles) of four species (ellipses), and the aggregated species interaction network on the right. In this example, the populations and species level networks have divergent properties, and the inference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

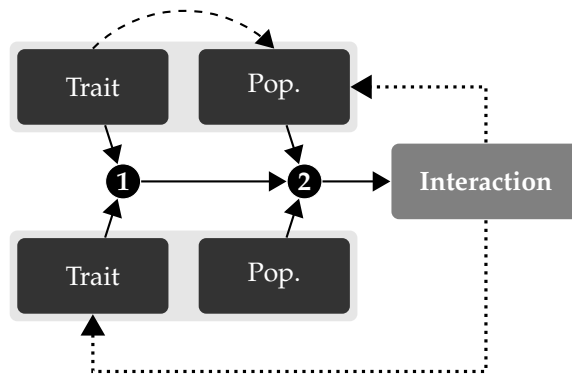


Figure 3: The approach we propose (that populations can interact at the conditions that 1 their trait allow it and 2 they are locally abundant enough for some of their individuals to meet by chance) requires ~~to shift our~~ an increased focus ~~to on~~ population-level processes. A compelling argument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