

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

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

30 Introduction

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

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

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

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

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

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

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

The dynamic nature of ecological interaction networks

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

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

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

131 **Population dynamics and neutral processes**

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

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

141 **The basic processes**

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

188 **Traits matching in space and time**

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

199 **The basic processes**

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

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

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

235 **Benefits for network analysis**

236 Linking spatial and temporal trait variation with network variation will help identify the mech-
237 anistic basis of network dissimilarity. From a sampling point of view, having enough data
238 requires that, when interactions are recorded, they are coupled with trait measurements. Im-
239 portantly, these measurements cannot merely be extracted from a reference database because
240 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

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

276 The basic processes

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

283 The occurrence or absence of a biotic interaction can either affect either the realization of other
 284 interactions (thus affecting the “interaction” component of network β -diversity) or the pres-
 285 ence of other species. There are several well-documented examples of one interaction allowing
 286 new interactions to happen (e.g. opportunistic pathogens have a greater success of infection in
 287 hosts which are already immunocompromised by previous infections, (Olivier 2012), or con-
 288 versely preventing them (e.g. a resident symbiont decreases the infection probability of a new
 289 pathogen (Heil and McKey 2003, Koch and Schmid-Hempel 2011~~op. @hei03~~). In both cases,
 290 the driver of interaction turnover is the patchiness of species distribution; the species acting as
 291 a “modifier” of the probability of interaction is only partially present throughout the range of
 292 the other two species, thus creating a mosaic of different interaction configurations. Variation
 293 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.

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-

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

359 ~~With the accumulation of data~~ Assuming that suitable and accessible empirical data will inevitably
 360 accumulate in the coming years, these approaches will rapidly expand our ability to predict
 361 the re-wiring of networks under environmental change. ~~The effect of environmental change is~~
 362 ~~expected to occur because (i) population sizes will be affected by the change and (ii) either~~
 363 There are two broad mechanisms linking network structure to environmental change: changes
 364 in population sizes due to modification of demographic parameters, and plastic or adaptive
 365 responses ~~will shift or disrupt the~~ resulting in shifted or disrupted trait distributions. The
 366 framework proposed in **Box 1** predicts interaction probabilities under different scenarios. Ul-
 367 timately, being explicit about the trait-abundance-interaction feedback will provide a better
 368 understanding of short-term and long-term dynamics of interaction networks. We illustrate
 369 this in Fig. ???. The notion that population sizes have direct effects on the existence of an in-
 370 teraction stands opposed to classical consumer-resource theory, which is one of the bases of
 371 network analysis. Considering this an opposition, however, is erroneous. Consumer-resource
 372 theory considers a strong effect of abundance on the intensity of interactions (**Box 2**), and it-
 373 self is a source of (quantitative) variation. Furthermore, these models are entirely determined
 374 by variations in population sizes in the limiting case where the coefficient of interactions are

375 similar. As such, any approach seeking to understand the variation of interactions over space
376 ought to consider that local densities are not only a consequence, but also a predictor, of the
377 probability of observing an interaction. The same reasoning can be held for local trait distri-
378 butions, although over micro-evolutionary time-scales. While trait values determine whether
379 two species are able to interact, they will be modified by the selective effect of species interact-
380 ing. Therefore, conceptualizing interactions as the outcome of a probabilistic ~~process~~ process
381 regulated by local factors, as opposed to a constant, offers the unprecedented opportunity to
382 investigate feedbacks between different time scales. This is especially important since all of
383 the mechanisms mentioned above are also likely to change rapidly over spatial scales. The
384 situation in which the phenologies of populations are synchronized locally but not regionally
385 (as shown by Singer and McBride 2012) is an excellent example of when we must integrate
386 these mechanisms into our interpretation of spatial and temporal dynamics.

387 Over the past decade, many insights have been gained by looking at the turnover of different
388 facets of biodiversity (taxonomic, functional, and phylogenetic) through space (Devictor et al.
389 2010b, Meynard et al. 2011). Here, we propose that there is another oft-neglected side of bio-
390 diversity: species interactions. The perspective we bring forth allows us to unify these dimen-
391 sions and offers us the opportunity to describe the biogeographic structure of all components
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399 **Boxes**

400 **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

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

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 environmental 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. Following 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 individual interactions, the relative importance of density-dependent and trait-based processes using 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 example, changes in local abundances or trait distributions. The results provided by this framework will only be as good as the empirical data used, and there is a dire need for a methodological discussion about how “predictor” variables (traits, population sizes, etc.) 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

427 system-specific way is a crucial point.

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

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

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

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

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

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

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

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

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

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.

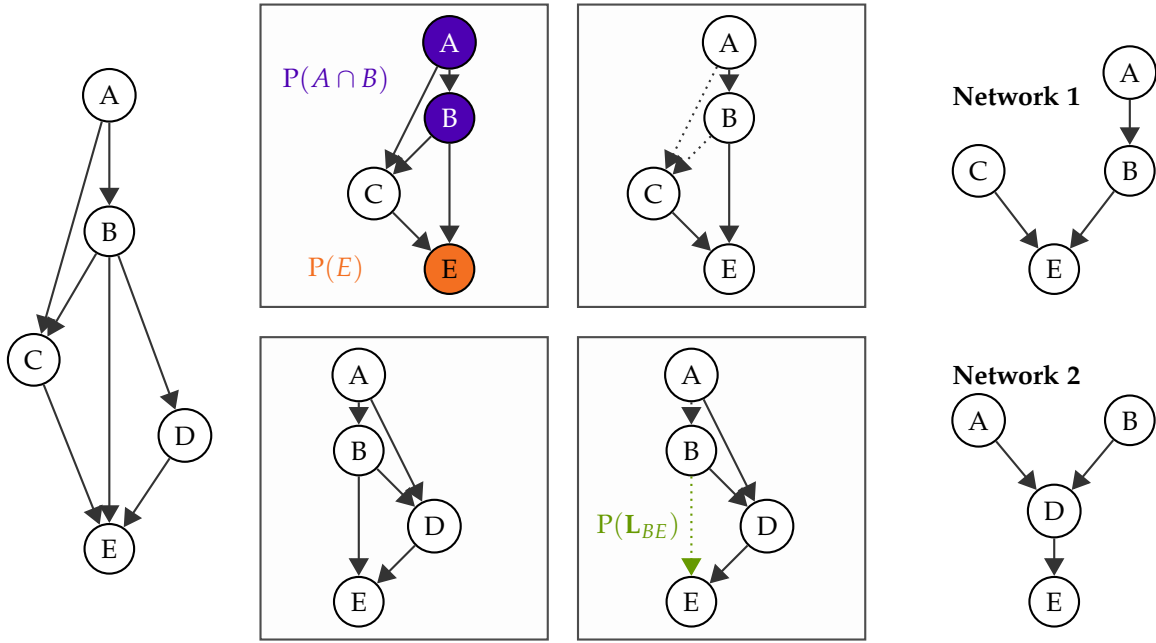


Figure 1: An illustration of the metaweb concept. In its simplest form, a metaweb is the list of all possible species and interactions between them for the system being studied, at the regional level (far left side). Everything that is ultimately observed in nature is a *realisation* of the metaweb (far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

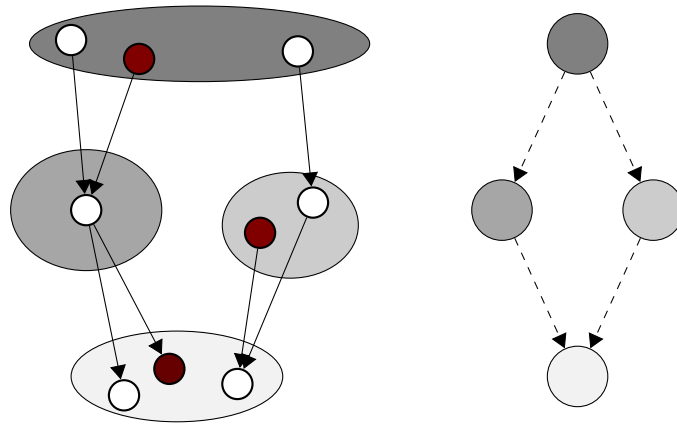


Figure 2: The left-hand side of this figure represents possible interactions between populations (circles) of four species (ellipses), and the aggregated species interaction network on the right. In this example, the populations and species level networks have divergent properties, and the inference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

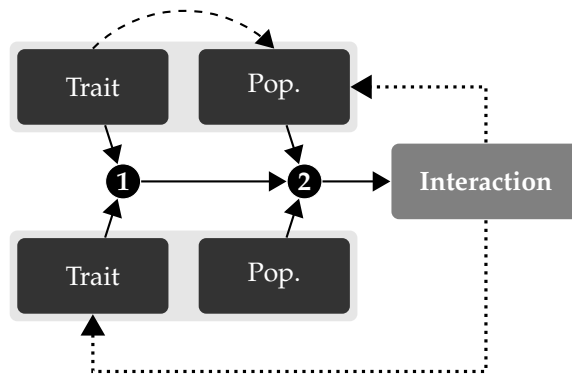


Figure 3: The approach we propose (that populations can interact at the conditions that 1 their trait allow it and 2 they are locally abundant enough for some of their individuals to meet by chance) requires ~~to shift our~~ an increased focus ~~to on~~ population-level processes. A compelling argument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