

Title: A quantitative framework for network biogeography

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Introduction

Ecology textbooks define the structure of an ecological community as *the pool of species occupying a given location at a given time, and the way these species interact* (ref to Morin?). It is therefore surprising that ecological research on the variation of community structure has focused on species turnover (refs), almost entirely neglecting variation in the way species interact (refs).

- Network structure do vary in space in time.
- We don't know yet to what extent interactions are varying with the environment.
- No theory to explain and interpret the meaning of network variation in space. Current interpretation fo species turnover involves the effect of the environment and stochasticity.
- Objective: Propose a theoretical framework to understand and predict the spatial and temporal variation in network structure.

A probabilistic representation of ecological interactions networks

Networks of species interactions vary in space and time because any given pairwise interaction could either occur or not at any particular location. Understanding this variation amounts to be able to determine the probability that two species (i and j) will interact at a given time/location (y); the existence of an interaction in this situation is thus essentially a stochastic variable, which we note $L_{ij,y}$. It takes a value of 1 where the interaction occurs, and 0 elsewhere. We note $P(L_{ij,y})$ the probability of this event. There are several factors that could impact the occurrence of an interaction and we will describe them below. But ultimately, this probability depends on the spatial and temporal scale of observation. As long as the probability of a particular interaction is not null, the probability of observing it at least once will become asymptotically closer to 1 when the scale of observation increases.

The occurrence of an interaction requires the co-occurrence of species i and j . This argument might seem trivial at first, but the explicit consideration of this condition in the probabilistic representation of ecological networks will prove fundamental to understand their variation. We thus define X_{iy} as a stochastic variable representing the occurrence of a species i at location y , and similarly X_{jy} the co-occurrence of species i and j . The quantity we seek to understand is the probability of a joint event:

$$P(X_{iy}, X_{jy}, L_{ijy},) \quad (1)$$

Which reads as the probability of observing species i , species j and an interaction between them. This probability could be further decomposed in two parts using the

67 product rule of probabilities:

$$P(X_{iy}, X_{jy}, L_{ijy}) = P(L_{ijy} | X_{iy}, X_{jy}, E_y) P(X_{iy}, X_{jy} | E_y) \quad (2)$$

68 We will refer to the left term as the metaweb. It is a conditional probability, represent-
69 ing the probability that an interaction occurs if species i and j are co-occurring. The
70 right term is the probability of observing the two species co-occurring at location y .

71 The metaweb concept is making its way through the network literature even though
72 it has never been formally and technically defined. It is usually conceived as a network
73 of interactions among species that could potentially co-occur. It is usually represented
74 by a binary matrix and thus deterministically. Here we define it as the matrix of inter-
75 action probabilities between co-occurring species. It thus represents potential interac-
76 tions and should therefore include interactions between species that never co-occurred
77 but are susceptible to. The problem with most representations of metawebs to date is
78 that the effect of co-occurrence is never factored out. The traditional approach to build
79 a metaweb is to cumulate observations across replicated networks. The main problem
80 with that approach is that the co-occurrence of rare species is extremely unlikely and
81 thus most often appear as an absence of interactions in the metaweb. This approach is
82 inappropriate because the observed co-occurrence will have a strong signature on the
83 evaluation of interactions. A rarefaction analysis previously shown that interactions
84 accumulate with the addition of networks at a slower rate than species richness. It in-
85 dicates that it is harder to have a direct evaluation of interactions from observation
86 than it is to evaluate species richness. If built from the observation of interactions, then
87 the only way to fill a metaweb is by running cafeteria experiments between all pairs of
88 species. Otherwise, the metaweb should be inferred using traits and phylogenetic in-
89 formation. Most of the published metawebs are therefore incomplete because of their
90 sensitivity to sampling heterogeneity. We will come back to the issue of evaluating the

metaweb in the sections Example and Applications

There are many variants of the metaweb representing different hypotheses about the origin of temporal and spatial variation in network structure (see the explicit formulations at Table 1). First, the interaction could be deterministic instead of probabilistic. In other words, $P(L_{ijy}) = 1$ if $X_{ijy} = 1$, and 0 otherwise. This representation of the metaweb is the one mostly used so far, as soon as the species are found together they are assumed to interact. It is also the only way to represent interactions when there is not enough information available to evaluate the interaction probability. It should be a reasonable approximation when the sampling and inference scales are large enough and that the only variation of networks considered arises from species distribution.

Ecological interactions could also depend on the environment. Although it is not common to see a conditional representation of ecological interactions, experimental studies of pairwise interactions revealing their sensitivity to the environment are common (REF). For instance, it has been documented that the predation risks of shorebirds do vary at the continental scale, from the south to the north (REF). The effect of the environment on interactions propagate up the community and influence network structure (REF). Here the environment is considered in a very broad sense, as any factor potentially influencing the probability of a pairwise interaction, provided that the species co-occur. It thus includes both the biotic and the abiotic components of environment. We note however that here the biotic environment includes organisms that are not considered in the co-occurrence matrix. Including a biotic component to the metaweb signifies that the pairwise interaction is conditional on higher order interactions. An interaction modifier occurs for instance when the predation risk by species j might be impacted by a parasite k changing the behaviour of the prey i . We note that a conditional probability approach could thus be used represent non-trophic in-

117 teractions into ecological networks (REF). This topic is however beyond the scope of
118 the current paper.

119 There are also variants to the co-occurrence matrix. Akin to the metaweb, co-
120 occurrence could be conditional or not. The simplest model relates co-occurrence
121 probability directly to the environment. In this situation there is no underlying as-
122 sumption about the ecological processes responsible for co-occurrence. Alternatively,
123 the co-occurrence probability could be a function of the environment because of shared
124 ecological requirements by the two species. Species are independently distributed,
125 but co-occur more often than expected by chance alone because they are found on the
126 same environments. We call this model later neutral because species are specifically
127 responding to the environment but are independently distributed. Co-occurrence
128 is then simply obtained by multiplying the result of two independent and specific
129 species distribution models (SDM).

130 Finally, the co-occurrence probability itself could be dependent on ecological inter-
131 actions. Direct pairwise interactions such as competition, facilitation and predation
132 have long been studied for their impact on co-distribution. Second and higher order
133 interactions (e.g. trophic cascade) could also impact co-occurrence. There is how-
134 ever currently no general theory on the expected co-occurrence in complex ecological
135 networks. For instance, we do not know how far co-occurrence is not-random when
136 going along the chain of indirect interactions. Berlow(2009) shown previously that
137 almost only first and second order interactions do matter in ecological networks, but
138 we don't know for co-distribution. We neither know what is the sensitivity to species
139 richness: do interactions tend to buffer each other? Generalizing knowledge acquired
140 by the study of small community models will require future research.

141 Interpretation: the integrated niche

142 The niche concept is key to understand and predict species distribution. Several at-
143 tempts have been made to refresh it, but its main usage still follows Hutchinson's idea
144 that species interactions restrict the fundamental niche to a realized one, and ecolo-
145 gists haven't moved far past the n-dimensional hypervolume formalism (Blonder et
146 al. 2014). Despite its intuitive interpretation and translation into species distribu-
147 tion models, the concept has been constantly criticized (Hardin, 1960; Peters, 1991;
148 Chase2003; Silvertown, 2004; Soberon, 2007) and several attempts have been made to
149 expand and reinforce it.

150 Part of the problem surrounding the definition of the niche has been clarified with
151 the distinction between Eltonian and Grinnellian definitions (ChaseLeibold 2003).
152 The Grinnellian dimension of the niche is the effect of the environment on the de-
153 mography of a species, while the Eltonian dimension is the effect of a species on its
154 environment *sensu lato*. The Grinnellian niche is the most intuitive one to apply and
155 is the conceptual backbone of species distribution models. The Eltonian niche is well
156 known by community ecologists, but is trickier to turn into predictive models (De-
157 victor et al. 2010). Nonetheless, the development of the niche model of food web
158 structure (Williams2000) and its parameterization (Williams2010; Gravel2013) made
159 it more operational, although it has yet to be applied to more than trophic interactions.

160 While it is straightforward to represent statistically the hyper volume where a
161 species occurs, it is much more challenging to account for ecological interactions.
162 Chase and Leibold (2003) attempted this representation in their definition: [*The niche*
163 *is*] *the joint description of the environmental conditions that allow a species to satisfy its*
164 *minimum requirements so that the birth rate of a local population is equal or greater than*
165 *its death rate along with the set of per capita effects of that species on these environmental*
166 *conditions*. They represented the niche graphically with zero-net growth isoclines (the

167 Grinnelian niche) and impact vectors (the Eltonian niche). While this representation
168 has been very influential in community ecology at the local scale, it remains unprac-
169 ticable at the biogeographical one. The absence of any mathematical representation
170 of the niche that could easily be fit to ecological data perhaps explain why biogeog-
171 raphers are still struggling to develop species distribution models taking into account
172 ecological interactions.

173 The key point to integrate dimensions of the niche is to represent the Eltonian
174 niche into a Grinnelian space. - We do so by considering that the Eltonian niche is the
175 hyper volume in the trait-space allowing an interaction.

176 - Doing so, we could project both niches in a plane and find the hypervolume where
177 an interaction should occur (Fig. 2).

178 - This visual representation is parallel to the probabilistic definition of interaction
179 probability.

180 - We propose that the metaweb is the Eltonian dimension of the niche, while the ma-
181 trix of co-occurrence is the Grinnellian dimension.

182 - Feedbacks between dimensions occur through the inclusion of co-occurrence in the
183 metaweb, and interactions in the co-occurrence matrix.

184 - This approach radically change the representation of the niche, putting species dis-
185 tribution and ecological interactions at the same level.

186 - Fitting the probabilistic model allows the evaluation of link distribution and species
187 distribution models.

188 - Moreover, the integrated niche concept facilitates the formulation of species distri-
189 bution models taking into account biotic interactions (see the section Applications)

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Example: network structure in different habitats

In this section we provide an analysis illustrating the framework with an empirical dataset of host-parasitoid networks. Data come from the study of Tylianakis(2007) on the impacts of habitat modifications to the network structure. The data consists of 48 networks with 4090 recorded interactions. The advantage of replicated host-parasitoid networks is that usually every interaction is observed, not inferred from a stationary metaweb. It thus allows to evaluate interaction probability and to factor out the effect of co-occurrence. Five habitats were sampled along a gradient of habitat modification: forest, abandoned coffee agroforest, coffee agroforest, pasture and rice culture. The metaweb consists of 9 parasitoids and kleptoparasites (Hymenoptera: Eulophidae, Ichneumonidae, Leucospidae, Megachilidae and Chrysididae; Diptera: Bombyliidae) of 33 species of bees and wasps (Hymenoptera: Apidae, Megachilidae, Mutilidae, Pompilidae, Sphecidae, Vespidae). The metaweb is illustrated at Fig. 2, along with an example of one iteration of the metaweb.

Tylianakis (2007) investigated if habitat modification affects the structure of these networks. They found a significant impact of the habitat on their structure, despite little variation in species richness. Increasing habitat modification led to a higher parasitoid to host species ratio and a parasitoid was also more specialized, thus impacting considerably vulnerability. A closer inspection of the networks revealed that intensive agricultural systems were dominated by a strong interaction and a specialization of the most abundant parasitoid. Although the discussion made clear that both the turnover in species composition and the interaction probability changed with habitat modification, it was not possible to partition these components.

We developed a R package (REF) to fit alternative formulations of the metaweb and the co-occurrence matrix along an environmental gradient and run it to re-interpret the data of Tylianakis (2007). The package provides a general interface facilitating the

217 development of different species and link distribution models. It is also built to fa-
 218 cilitate the interaction iwth the Mangal database of ecological interactions (REF). The
 219 first step consists of fitting a probablistic model from the observation of a pairwise in-
 220 teraction (binary) and the environment (could be categorical or continuous) from the
 221 subset of the data where the two species are co-occurring. In other words, it fits the
 222 equation $P(L_{ijy}|X_{iy}, X_{jy}, E_y)$ to the data where $X_{iy} = 1$ and $X_{jy} = 1$. Logistic regression
 223 was used and is currently programmed, but alternative models could be used as well.
 224 The second steps consists of fitting a a probabilistic model for co-occurrence over the
 225 whole dataset, $P(X_{iy}, X_{jy}|E_y)$, independently of the observation of an interaction. The
 226 two probabilities are then multiplied to obtain the probability of observing an inter-
 227 action (Eq. 2). We used this probability to compute the likelihood of each observation
 228 ($\zeta(\theta|D) = P(L_{ijy}, X_{iy}, X_{jy})$ if $L_{ijy} = 1$ and $\zeta(\theta|D) = 1 - P(L_{ijy}, X_{iy}, X_{jy})$ otherwise). We
 229 then after compare the models by their AIC.

230 We considered the gradient of habitat modification as a ordered categorical vari-
 231 able and compared XX models (results are summarized at Table 2). Not surprisingly
 232 the best model takes into account the effect of the environment on both the metaweb
 233 and co-occurrence. What is most interesting are the comparisons to the best model.
 234 First, we find that using a constant metaweb has a dramatic impact on the fit of the
 235 model to the data (the AIC drops from X for model 1 to X for model 2), indicating a
 236 strong effect of the environment on pairwise interactions. Secondly, we find that the
 237 deterministic metaweb is the worst model (model 3, AIC =). This result indicate that
 238 the traditional appraoch to consider that species interact as soon as they co-occur is
 239 definitely wrong. Thirdly, we also find that using a constant co-occurrence does have
 240 a significant impact on the model (the AIC drops to X, model 4), indicating there is a
 241 non-random change in community composition with habitat modification. Taken to-
 242 gether, these two results better explain why network structured changed with habitat

modification, even though here we only used binary information about the network structure. Another interesting result is that considering a neutral co-occurrence did not impact much the fit of the model. The AIC drops to XX with model 6, indicating that considering independent SDMs yields similar networks over this environmental gradient. This means that for this particular dataset, ecological interactions does not have a strong impact on species distribution since; a strong dependence of parasitoids to the host for instance would have a occurrence probability higher than expected by chance, while a repulsion would have had the opposite.

An important output of this analysis is a more explicit representation of the uncertainty in the evaluation of the metaweb. We find that among the XX pairs of host and parasitoids, XX did not co-occur. There were therefore many forbidden links based on co-occurrence. These might never occur in reality, but we do not know without doing extra experiments. Therefore, any analysis of the structure of the metaweb would be inappropriate without filling those gaps. In addition to specific experiments, the gaps could be filled with a trait-based approach, using phylogenies or with a null hypothesis (e.g. the interaction probability is equal to connectance computed on the observed interactions).

It is also possible to obtain for each pairwise interaction an estimate of the uncertainty. Not surprisingly, the confidence interval is usually very high for the estimation of a probability with a very small sample size. The standard error on the evaluation of the interaction probability is provided along with the metaweb at Fig. 3. It reveals that the uncertainty is very high for most interactions, even if 48 networks were sampled. Such an approach could be used to detect which pairwise interaction requires additional sampling in order to reduce the uncertainty to a manageable level.

267 Applications

268 Network descriptors

269 Partitionning beta diversity

270 Guidance for empirical studies

271 Ecological networks are known to be extremely sparse, *i.e.* having far more absences
272 of interactions than they have interactions. These absences of interactions, however,
273 can come from different sources. The fact that unequal sampling at the local scale
274 can affect our understanding of network structure is well documented (Martinez et al.
275 1999). However, in a spatial context, some interactions may be undocumented be-
276 cause the species involved have never been observed in co-occurrence. Although these
277 are reported as a lack of interactions, in actuality we cannot make inference about
278 them seeing that they have never been observed: it is possible that this interaction
279 may happen should the two species co-occur. A second category of absences of inter-
280 actions are those that are reported after multiple observations of species co-occurrence.
281 However, so as to have a confidence in the fact that the probability of an interaction
282 is low, extensive sampling (that is, several co-occurrences) is needed. Generally, our
283 confidence that the interaction is indeed impossible will increase when the number of
284 observations of the species pair. Seeing that this is essentially a Bernoulli process (what
285 is the probability that the species will interact given their presence), the breadth of the
286 confidence interval is expected to saturate after a fixed number of observations, which
287 can be set as a threshold above which a species pair has been observed "often enough".

288 **Null model testing**

289 **Species & interactions distribution models**

Conclusion

- New research agenda

- List of new questions

Acknowledgements

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Figure legends

Figure 1

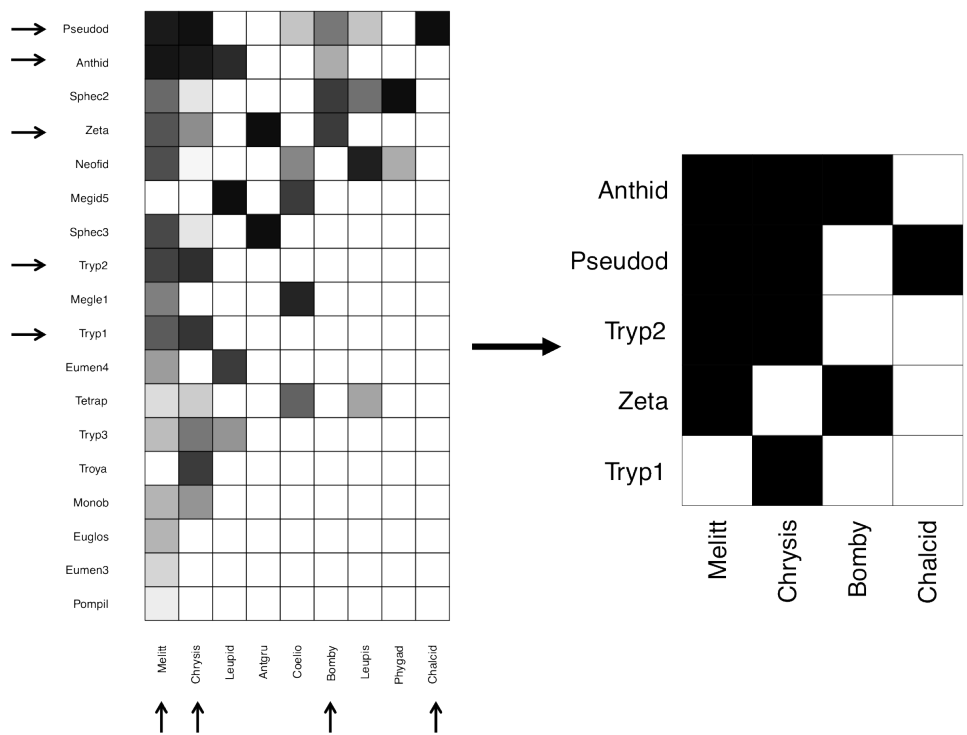
Non-random sampling of the metaweb. The sampling of the metaweb is illustrated with a local interaction network from the Tylianakis et al (2007) dataset. Here the metaweb is simply the number of observed interactions over the 48 networks. Arrows points to species that are present in the local network #34 (represented on the right).

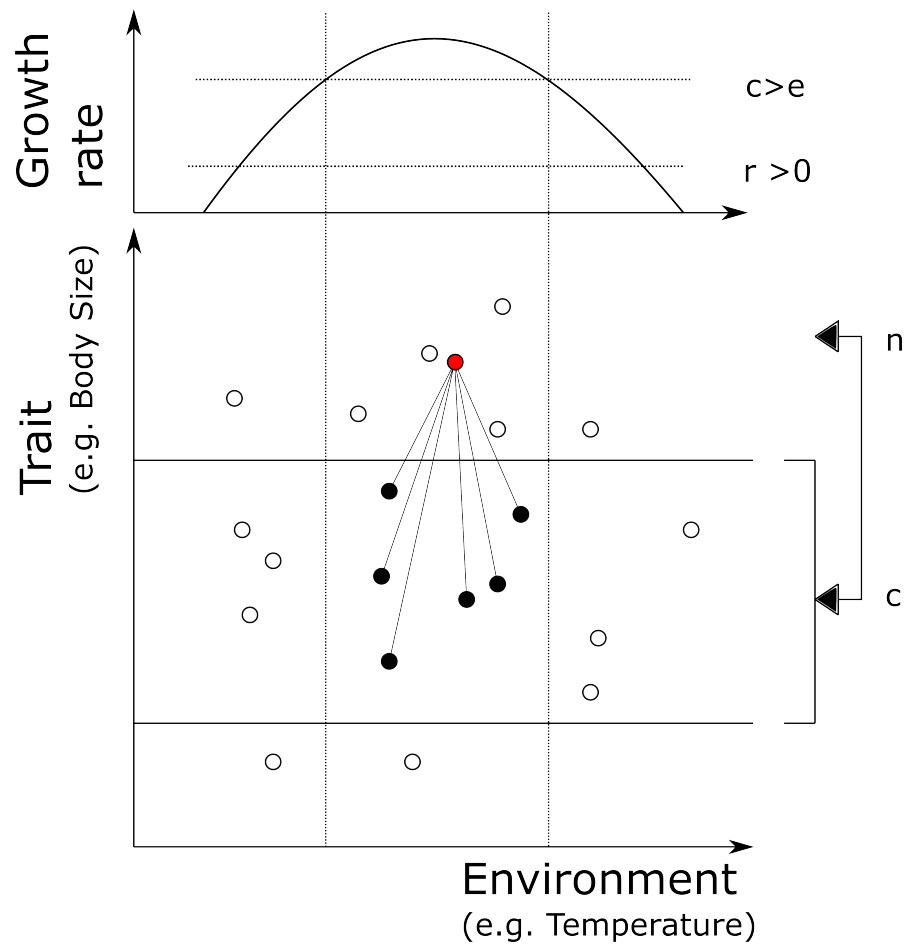
Figure 2

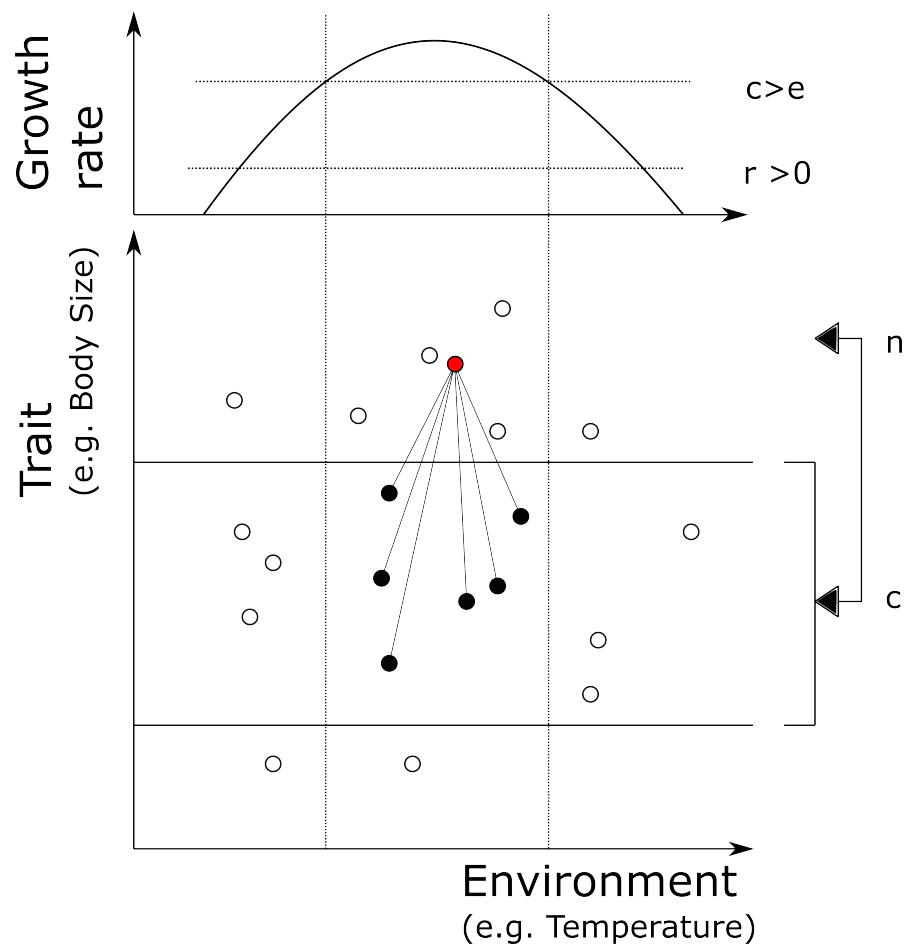
The integrated niche. The Grinnellian niche is the set of environmental conditions where the intrinsic growth rate r is positive (axioms i, ii & iii). Contingencies (axiom iv) such as disturbances and stochastic extinctions, in conjunction with limited dispersal (axiom v), restrict species distribution to the conditions where the colonization rate c is larger than extinction rate e . The Eltonian niche on the other dimension is represented by the set of traits allowing species to interact (axiom viii). The red species is a predator with a trophic position n , feeding on species whose niche is within a certain range around the niche optimum c . The integrated niche combines the effects of the environment and ecological interactions. The central square represents the area where the joint probability of observing interactions and co-occurrence is positive.

Figure 3

Uncertainty in the evaluation of the metaweb. The inferred metaweb for the XX environment is represented (left), along with the uncertainty in the evaluation of the interaction probability (right). Note that the standard error for probabilities is not symmetric and thus only the upper bound is represented.







Name	Equation	Details
Metaweb		
Constant	$P(L_{ijy} X_{iy}, X_{jy})$	Interaction probability is invariant to the environment
Conditional	$P(L_{ijy} X_{iy}, X_{jy}, E_y)$	Interaction probability is a function of the local environment
Deterministic	$P(L_{ijy}^* X_{iy}, X_{jy})$	Interaction occurs whenever both species are present
Co-occurrence		
Constant	$P(X_{iy}, X_{jy})$	Species distribution independent of E
Conditional on E	$P(X_{iy}, X_{jy} E_y)$	Similar to a SDM applied to co-occurrence
Neutral	$P(X_{ix} E_y)P(X_{jy} E_y)$	Independent SDMs fit to both species; could be independent of E
Conditional on L_y	$P(X_{iy}, X_{jy} L_y)$	Could account for first and higher order interactions

Table 1: List of different models

	Model	Metaweb		Cond. on E	Deterministic	Co-occurrence		Cond. on E	Neutral	$L(H D)$	AIC
		Constant	Cond. on E			Constant	Constant				
1.		X						X		0	0
2.			X					X		0	0
3.				X				X		0	0
4.			X			X				0	0
5.			X					X		0	0
6.			X						X	0	0

Table 2: Model comparison with the host-parasitoid networks. The 48 networks were fitted to different models of interaction networks. Note that for the computation of the likelihood all null interaction probabilities, co-occurrences and the pairwise interactions without observed co-occurrences were removed.