

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 vary in space and time, metaweb as a large scale synthesis. We don't know yet the mechanisms of variation

The metaweb concept is making its way through the network literature even though it has never been formally and technically defined. It is usually conceived as a network of interactions among species that could potentially co-occur, and represented by a binary matrix, *i.e.* a probabilistic matrix in which the probability of observing an interaction is either 0 or 1. As the metaweb is usually constructed by aggregating observations, it assigns a probability of 0 to the interaction of species that never co-occurred, and is unable to factor-out the effect of co-occurrence. The main problem with that approach is that the co-occurrence of rare species is extremely unlikely and thus most often appear as an absence of interactions in the metaweb. A rarefaction analysis previously shown that interactions accumulate with the addition of networks at a slower rate than species richness (Poisot et al. 2012) – this is because interactions cannot accumulate faster than the rate of species observations, and ultimately the rate of co-occurrence observations. The only way to build a metaweb *only* based on observational data is to compensate for the inflation of 0 due to lack of co-occurrence through manipulative experiments (REF). As this is impracticable for all but the smallest organisms, predictive probabilistic methods are needed.

No theory to explain and interpret the meaning of network variation in space. Current interpretation of species turnover involves the effect of the environment and

55 stochasticity.

56 Objective: Propose a theoretical framework to understand and predict the spatial
57 and temporal variation in network structure.

A probabilistic representation of ecological interactions networks in space

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 $X_{i,y}$ as a stochastic variable representing the occurrence of a species i at location y , and similarly $X_{ij,y}$ the co-occurrence of species i and j . The quantity we seek to understand is the probability of a joint event:

$$P(X_{i,y}, X_{j,y}, L_{ij,y},) \quad (1)$$

Or simply said, the probability of observing both species i and j , and an interaction from i to j . This probability could be further decomposed in two parts using the product rule of probabilities:

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

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

104 to the metaweb signifies that the pairwise interaction is conditional on higher order
105 interactions. An interaction modifier occurs for instance when the predation risk by
106 species j might be impacted by a parasite k changing the behaviour of the prey i . We
107 note that a conditional probability approach could thus be used represent non-trophic
108 interactions into ecological networks (REF). This topic is however beyond the scope
109 of the current paper.

110 There are also variants to the co-occurrence matrix. Akin to the metaweb, co-
111 occurrence could be conditional or not. The simplest model relates co-occurrence
112 probability directly to the environment. In this situation there is no underlying
113 assumption about the ecological processes responsible for co-occurrence. Alterna-
114 tively, the co-occurrence probability could be a function of the environment because
115 of shared ecological requirements by the two species. Species are independently dis-
116 tributed, but co-occur more often than expected by chance alone because they are
117 found on the same environments. We call this model later neutral because species are
118 specifically responding to the environment but are independently distributed. Co-
119 occurrence is then simply obtained by multiplying the result of two independent and
120 specific species distribution models (SDM).

121 Finally, the co-occurrence probability itself could be dependent on ecological inter-
122 actions. Direct pairwise interactions such as competition, facilitation and predation
123 have long been studied for their impact on co-distribution. Second and higher order
124 interactions (e.g. trophic cascade) could also impact co-occurrence. There is how-
125 ever currently no general theory on the expected co-occurrence in complex ecological
126 networks. For instance, we do not know how far co-occurrence is not-random when
127 going along the chain of indirect interactions. Berlow (2009) shown previously that
128 almost only first and second order interactions do matter in ecological networks, but
129 we don't know for co-distribution. We neither know what is the sensitivity to species

¹³⁰ richness: do interactions tend to buffer each other? Generalizing knowledge acquired
¹³¹ by the study of small community modules will require future research.

132 Interpretation: the integrated niche

133 Correctly describing the ecological niche is key to understand and predict species
134 distribution. Despite several attempts to refresh the conceptual basis of what ecolog-
135 ical niches are, ecologists haven't moved far past the "n-dimensional hypervolume"
136 formalism (Holt 2009) introduced by Hutchinson (1961). Despite its intuitive inter-
137 pretation and translation into species distribution models (Blonder et al. 2014), the
138 concept has been constantly criticized (Hardin, 1960; Peters, 1991; Chase2003; Sil-
139 vertown, 2004; Soberon, 2007) and several attempts have been made to expand and
140 reinforce it.

141 Part of the problem surrounding the definition of the niche has been clarified
142 with the distinction between Eltonian and Grinnellian definitions (Chase & Leibold
143 2003). The Grinnellian dimension of the niche is the effect of the environment on the
144 demography of a species, while the Eltonian dimension is the effect of a species on
145 its environment *sensu lato*. The Grinnellian niche is the most intuitive one to apply
146 and is the conceptual backbone of species distribution models. The Eltonian niche is
147 well known by community ecologists, but is trickier to turn into predictive models
148 (Devictor et al. 2010). Nonetheless, the development of the niche model of food web
149 structure (Williams2000) and its parameterization (Williams2010; Gravel2013) made it
150 more operational, although it has yet to be applied to more than trophic interactions.

151 Chase & Leibold (2003) attempted this representation in their definition: [*The niche*
152 *is] the joint description of the environmental conditions that allow a species to satisfy its*
153 *minimum requirements so that the birth rate of a local population is equal or greater than*
154 *its death rate along with the set of per capita effects of that species on these environmental*
155 *conditions*. Their representation merges zero-net growth figuring the Grinnellian niche
156 (when do the population persist) with impact vectors figuring the Eltonian niche
157 (what is the population impact). While this representation has been very influential in

community ecology at the local scale, it remains impracticable at the biogeographical one. The absence of any mathematical representation of the niche that could easily be fit to ecological data perhaps explain why biogeographers are still struggling to develop species distribution models taking into account ecological interactions.

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

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

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

- We propose that the metaweb is the Eltonian dimension of the niche, while the matrix of co-occurrence is the Grinnellian dimension.

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

- This approach radically change the representation of the niche, putting species distribution and ecological interactions at the same level.

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

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

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; Dyptera: 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 whether 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 were 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 the probaweb package for R (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

206 interface facilitating the development of different species and link distribution mod-
 207 els. It is also built to facilitate the interaction with themangal database of ecological
 208 interactions (REF). The first step consists of fitting a probabilistic model from the ob-
 209 servation of a pairwise interaction (binary) and the environment (could be categorical
 210 or continuous) from the subset of the data where the two species are co-occurring.
 211 In other words, it fits the equation $P(L_{ijy}|X_{iy}, X_{jy}, E_y)$ to the data where $X_{iy} = 1$ and
 212 $X_{jy} = 1$. Logistic regression was used and is currently programmed, but alternative
 213 models could be used as well. The second steps consists of fitting a probabilistic
 214 model for co-occurrence over the whole dataset, $P(X_{iy}, X_{jy}|E_y)$, independently of the
 215 observation of an interaction. The two probabilities are then multiplied to obtain the
 216 probability of observing an interaction (Eq. 2). We used this probability to com-
 217 pute the likelihood of each observation ($\zeta(\theta|D) = P(L_{ijy}, X_{iy}, X_{jy})$ if $L_{ijy} = 1$ and
 218 $\zeta(\theta|D) = 1 - P(L_{ijy}, X_{iy}, X_{jy})$ otherwise). We then after compare the models by their
 219 AIC.

220 We considered the gradient of habitat modification as a ordered categorical vari-
 221 able and compared XX models (results are summarized at Table 2). Not surprisingly
 222 the best model takes into account the effect of the environment on both the metaweb
 223 and co-occurrence. What is most interesting are the comparisons to the best model.
 224 First, we find that using a constant metaweb has a dramatic impact on the fit of the
 225 model to the data (the AIC drops from X for model 1 to X for model 2), indicating a
 226 strong effect of the environment on pairwise interactions. Secondly, we find that the
 227 deterministic metaweb is the worst model (model 3, AIC =). This result indicate that
 228 the traditional approach to consider that species interact as soon as they co-occur is
 229 definitely wrong. Thirdly, we also find that using a constant co-occurrence does have
 230 a significant impact on the model (the AIC drops to X, model 4), indicating there is a
 231 non-random change in community composition with habitat modification. Taken to-

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 high for the estimation of a probability with a 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 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.

Applications

Network descriptors

Partitionning beta diversity

Guidance for empirical studies

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

279 **Null model testing**

280 **Species & interactions distribution models**

281 Conclusion

- 282 • New research agenda

283

- 284 • List of new questions

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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).

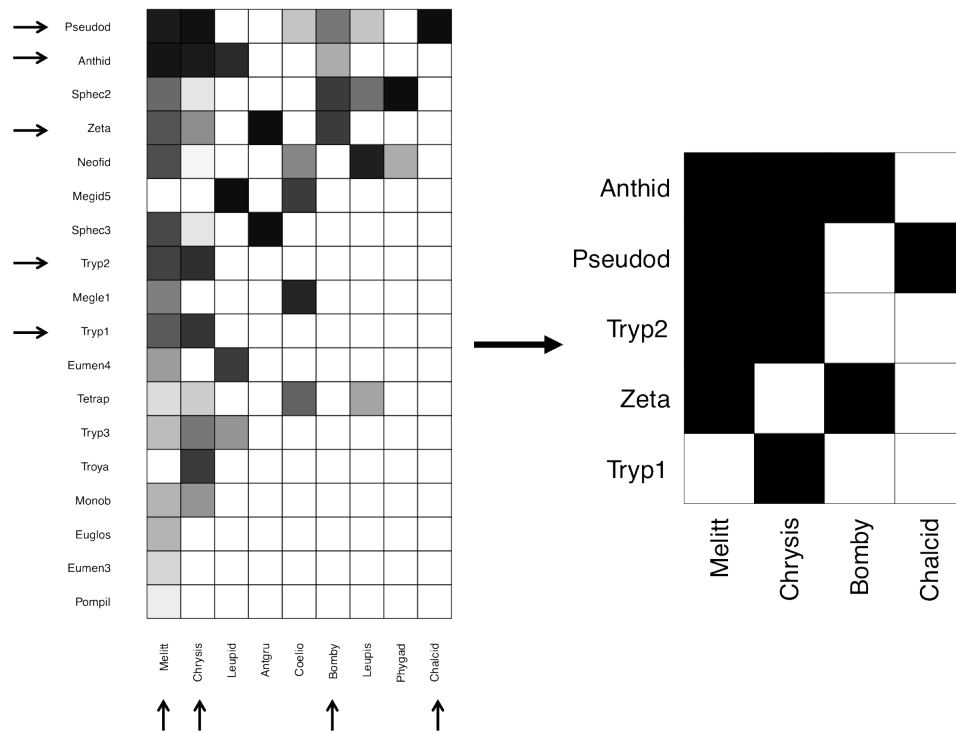
Figure 2

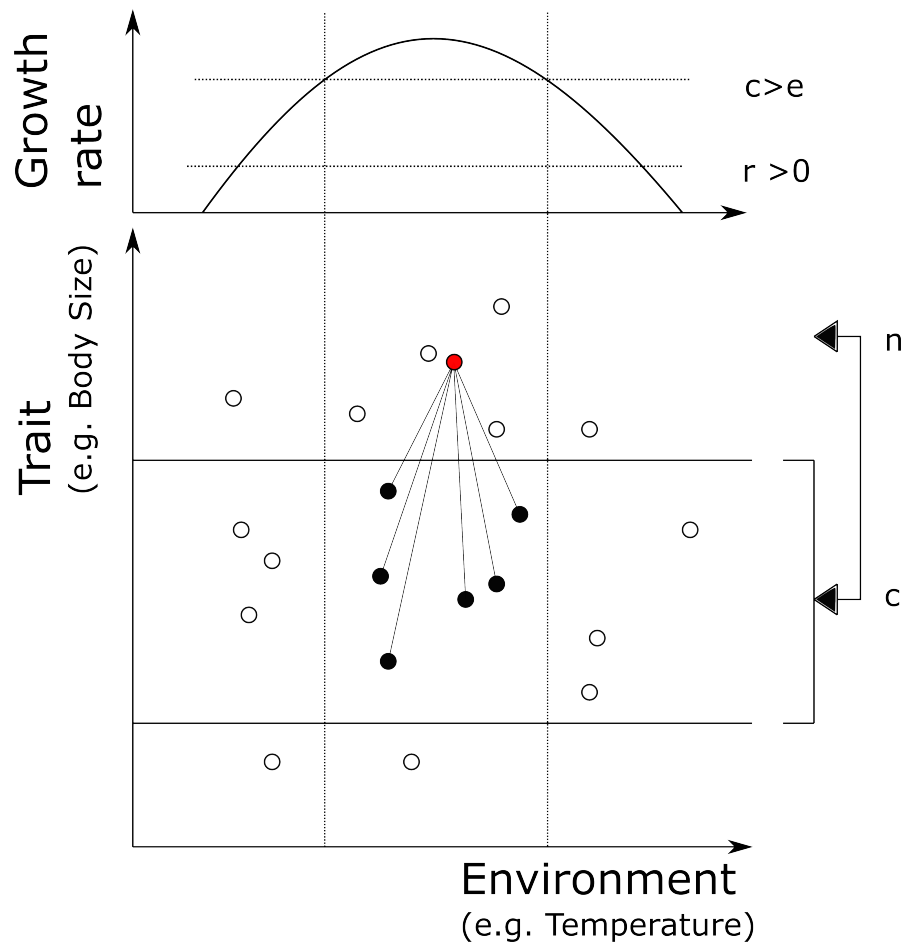
The integrated niche. The Grinnellian niche is the set of environmental conditions where the intrinsic growth rate r is positive (axioms i, ii & iii). Contingencies (axiom iv) such as disturbances and stochastic extinctions, in conjunction with limited dispersal (axiom v), restrict species distribution 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.

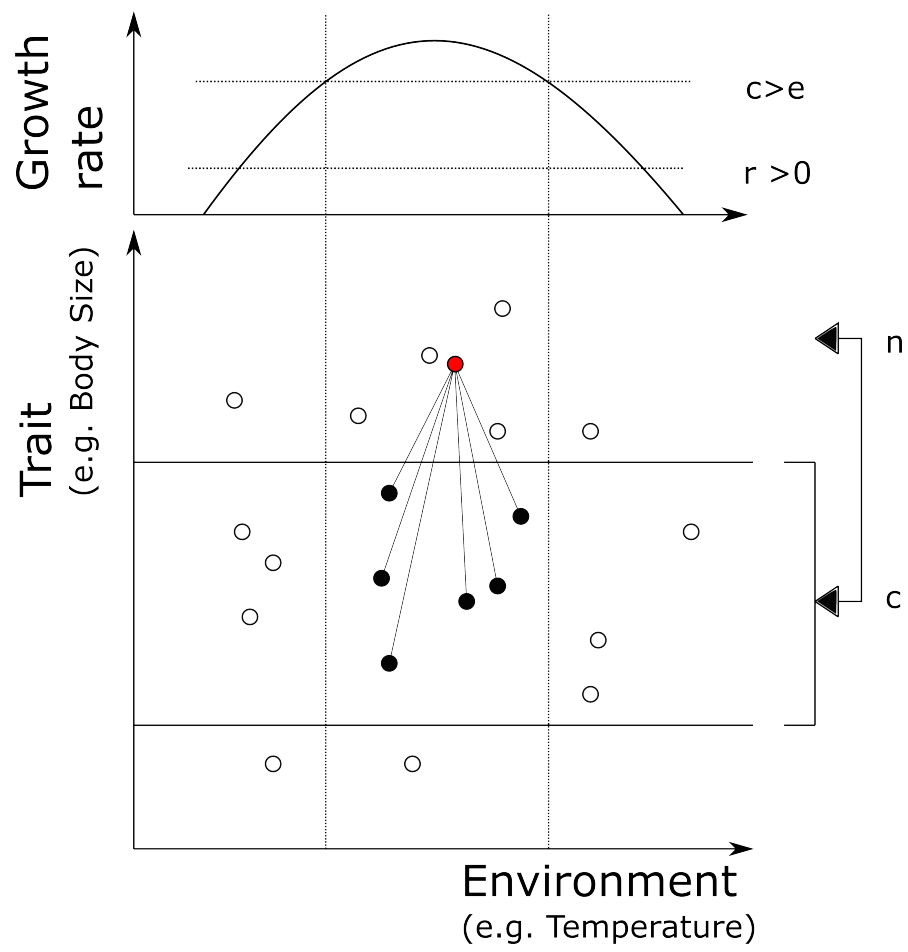
Figure 3

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

³²⁹ 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.