

# Deciphering probabilistic species interaction networks

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Representing species interactions probabilistically (how likely are they to occur?) as opposed to deterministically (are they occurring?) conveys uncertainties in our knowledge of interactions. The sources of uncertainty captured by interaction probabilities depend on the method used to evaluate them: uncertainty of predictive models, subjective assessment of experts, or empirical measurement of interaction spatiotemporal variability. However, guidelines for the estimation and documentation of probabilistic interaction data are still lacking. This is concerning because our understanding and analysis of interaction probabilities depend on their sometimes elusive definition and uncertainty sources. We review how probabilistic interactions are defined at different spatial scales, from local interactions to regional networks (metawebs), with a strong emphasis on host-parasite and trophic (predatory and herbivory) interactions. These definitions are based on the distinction between the realization of an interaction at a specific time and space (local) and its biological feasibility (regional). Using host-parasite interactions in Europe, we illustrate how these two network representations differ in their statistical properties, specifically: how local networks and metawebs differ in their spatial and temporal scaling of probabilistic interactions, but not in their taxonomic scaling. We present two approaches to inferring binary interactions from probabilistic ones that account for these differences and show that systematic biases arise when directly inferring local networks from metawebs. Our results underscore the importance of more rigorous descriptions of probabilistic species interaction networks that specify their type of interaction (local or regional) and uncertainty sources.

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## **1 Introduction**

### **2 Species interactions are uncertain**

3 As we try to navigate global biodiversity change, filling in knowledge gaps about biodiversity becomes  
4 instrumental to monitoring and mitigating those changes (Abrego *et al.* 2021; Gonzalez & Londoño 2022;  
5 Hortal *et al.* 2015). However, cataloging species, populations and, in particular, ecological interactions (e.g.,  
6 predation, parasitism, and pollination) is a substantial challenge (Pascual *et al.* 2006; Polis 1991). There are  
7 methodological and biological constraints that hinder our ability to document species interactions, inevitably  
8 leading to uncertainty in our knowledge of interactions. For example, the spatial and temporal uncoupling of  
9 species (e.g., nocturnal and diurnal species coexisting in the same space with different daily activity timings,  
10 Jordano 1987) and the large number of rare and cryptic interactions in a community, contribute to these  
11 knowledge gaps (Jordano 2016).

12 Several conditions must be satisfied for an interaction to be observed locally. First, both species must have  
13 overlapping geographic ranges, i.e. they must co-occur within the region of interest (Cazelles *et al.* 2016;  
14 Morales-Castilla *et al.* 2015). Second, they must have some probability of meeting (Poisot *et al.* 2015).  
15 Probabilities of interspecific encounters are typically low, especially for rare species with low abundances.  
16 While species' absolute abundances may impact interaction frequencies (Vázquez *et al.* 2007), encounter  
17 probabilities are determined by their relative abundances (Canard *et al.* 2012). The probability that species  
18 meet also depends on their biology, such as their phenology (Olesen *et al.* 2010; Singer & McBride 2012) and  
19 discoverability (Broom & Ruxton 2005). Finally, when species do come into contact, an interaction occurs only  
20 if their traits are locally compatible (Poisot *et al.* 2015), including their phenotypes (Bolnick *et al.* 2011; Gravel  
21 *et al.* 2013; Stouffer *et al.* 2011) and behavior (Choh *et al.* 2012; Pulliam 1974).

22 Documenting the location and timing of interactions becomes more difficult when accounting for the  
23 spatiotemporal variability of ecological interactions (Poisot *et al.* 2012, 2015). Environmental factors, such as  
24 temperature (Angilletta *et al.* 2004), drought (Woodward *et al.* 2012), climate change (Araujo *et al.* 2011;  
25 Gilman *et al.* 2010; Woodward *et al.* 2010), and habitat modifications (Tylianakis *et al.* 2007), contribute to this  
26 spatiotemporal variability by impacting species abundance and traits. Interactions may also be influenced by a  
27 third species (e.g., a more profitable prey species, Golubski & Abrams 2011; Sanders & van Veen 2012). Even  
28 under favorable circumstances, there remains a possibility that the interaction does not occur locally, either due  
29 to the intricate nature of the system or simply by chance. If it does occur, it might go undetected, particularly if

30 it happens infrequently. In this context, it is unsurprising that our knowledge of ecological interactions remains  
31 limited (Hortal *et al.* 2015) despite extensive biodiversity data collection (Schmeller *et al.* 2015).

## 32 Species interactions as probabilistic objects

33 Knowing the biological capacity of two species to interact directly (via e.g., trophic interactions) is necessary  
34 but not sufficient for inferring their interaction at a specific time and space. The recognition of the intrinsic  
35 variability of species interactions has led ecologists to expand their representation of ecological networks to  
36 include a probabilistic view of interactions (Dallas *et al.* 2017; Fu *et al.* 2021; Poisot *et al.* 2016). This allows  
37 filling in the Eltonian shortfall (Hortal *et al.* 2015) by modeling the probability of occurrence of interactions  
38 (e.g., Gravel *et al.* 2019), which can be an important tool for directing efforts and taking action (Carlson *et al.*  
39 2021), especially in places where access and resources for research are scarce. The probabilistic representation  
40 of interactions has been applied to direct interactions, which are conceptually and mathematically analogous  
41 regardless of their biological type (e.g., predation and pollination). This is in contrast with indirect interactions  
42 (e.g., interspecific competition), which arise from distinct ecological processes and are often not directly  
43 observable (Kéfi *et al.* 2015, 2016). Representing direct interactions probabilistically can capture the  
44 spatiotemporal variability of the aforementioned ecological processes and the uncertainty in our knowledge of  
45 interactions. By accounting for the uncertainty of interactions, networks of probabilistic interactions may  
46 provide a more realistic portrait of species interactions.

47 Networks of probabilistic interactions, within a Bayesian perspective, express our degree of belief (or  
48 confidence) regarding the occurrence or observation of interactions. In contrast, interactions are simply  
49 regarded as either occurring or not in networks of deterministic binary interactions. Based on the scale at which  
50 they are estimated, interaction probabilities may reflect our level of confidence in whether interactions will be  
51 observed, realized locally, or biologically feasible. As an illustration, we could outline a situation in which there  
52 is a 50% certainty that an interaction occurs 50% of the time. Our level of confidence should be more definitive  
53 (approaching either 0 or 1) as we extend our sampling to a broader area and over a longer time period, thereby  
54 diminishing the uncertainty of our knowledge of interactions (but not necessarily the estimation of their  
55 variability). In the broadest sense, binary interactions are also a type of probabilistic interaction, in which the  
56 numerical value of an interaction is restrained to 0 (non-occurring) or 1 (occurring). In networks of  
57 probabilistic interactions, only forbidden interactions (i.e., interactions prohibited by biological traits or species  
58 absence, Jordano *et al.* 2003; Olesen *et al.* 2010) have a probability value of zero, provided that intraspecific

59 trait variability is considered (Gonzalez-Varo & Traveset 2016).

60 The application and development of computational methods in network ecology, often based on a probabilistic  
61 representation of interactions, can alleviate (and guide) the sampling efforts required to document species  
62 interactions (Strydom *et al.* 2021). For example, statistical models can be used to estimate the uncertainty of  
63 pairwise interactions (Cirtwill *et al.* 2019) and the probability of missing (false negatives) and spurious (false  
64 positives) interactions (Guimerà & Sales-Pardo 2009). Statistical models can generate predictions of ecological  
65 networks without prior knowledge of pairwise interactions. They may do so using body size (Caron *et al.* 2024;  
66 Gravel *et al.* 2013; Petchey *et al.* 2008), phylogeny (Elmasri *et al.* 2020; Strydom *et al.* 2022), or a combination  
67 of niche and neutral processes (Bartomeus *et al.* 2016; Pomeranz *et al.* 2019) for inference. Topological null  
68 models, which generate networks of probabilistic interactions by preserving chosen characteristics of the  
69 adjacency matrix of binary interactions while intentionally omitting others (Bascompte *et al.* 2003; Fortuna &  
70 Bascompte 2006), are examples of common probabilistic interaction models. Null models can be used to  
71 produce underlying distributions of network measures for null hypothesis significance testing. However, how  
72 the uncertainty of pairwise interactions propagates to network structure (i.e., community-level properties  
73 driving the functioning, dynamics, and resilience of ecosystems, McCann 2007; McCann 2011; Proulx *et al.*  
74 2005; Rooney & McCann 2012) remains to be elucidated. Many measures have been developed to describe the  
75 structure (Poisot *et al.* 2016) and diversity (Godsoe *et al.* 2022; Ohlmann *et al.* 2019) of probabilistic  
76 interaction networks. These models and measures support the use of this approach for the study of a wide range  
77 of ecological questions, from making better predictions of species distribution (Cazelles *et al.* 2016) to  
78 forecasting the impact of climate change on ecological networks (Gilman *et al.* 2010).

## 79 We lack clear definitions of probabilistic species interactions

80 Yet, a precise definition of probabilistic interactions appears to be lacking, making the estimation and use of  
81 these data more difficult. In this manuscript, we aim to take a step back by outlining different ways in which  
82 probabilistic interactions are defined and used in network ecology. We distinguish two broad categories of  
83 probabilistic interaction networks that necessitate distinct approaches: local networks describing probabilities  
84 of realized interactions, and regional networks (metawebs) describing probabilities of potential interactions. We  
85 highlight the distinctions in the ecological meaning of these two representations and examine their properties  
86 and relationships (particularly with space, time, and between each other).

87 The lack of clear guidelines on the use of probabilistic interaction data is worrisome, as it affects both data  
88 producers and re-users who generate and manipulate these numbers. This is concerning because sampling  
89 strategies and decisions regarding network construction can affect our understanding of network properties  
90 (Brimacombe *et al.* 2023). There is currently no reporting standard that could guide the documentation of all  
91 types of probabilistic interactions (although Salim *et al.* 2022 discuss data standards for deterministic  
92 mutualistic networks). Clear reporting standards for probabilistic interactions would support more adequate  
93 manipulation and integration of interaction data from different sources and guard against possible  
94 misinterpretations arising from ambiguous definitions of probabilistic interaction networks. This  
95 documentation should outline the nature (i.e., local or regional) and type (e.g., predatory or pollination) of the  
96 interactions, provide information regarding the taxonomic level, identities, and characteristics (e.g., life stages)  
97 of the individuals involved in an interaction, present the mathematical formulation of probabilities, including  
98 clearly identified conditional variables (e.g., spatial and temporal scales), and describe the methods and contexts  
99 (e.g., location, time, environmental conditions) in which interactions were estimated. Inadequately documented  
100 probabilistic interaction data should be used with caution when analyzing ecological networks. The broad  
101 principles underlying our findings remain relevant and applicable across diverse ecological contexts involving  
102 direct interactions. In the following sections, we delve into the definitions of probabilistic interactions as we  
103 scale up from pairwise interactions to higher-level representations of ecological networks, i.e. local networks  
104 and metawebs.

## 105 **Pairwise interactions: the building blocks of ecological networks**

### 106 **Probabilistic interactions have different interpretations**

107 Consider a scenario where an avian predator has just established itself in a northern habitat home to a small  
108 rodent. Suppose these species have never co-occurred before, and as a result, their interaction has not been  
109 previously observed. What is the probability that the rodent is part of the diet of the avian predator, or put  
110 differently, what is the probability that they interact? Answering this question requires some clarification, as  
111 there are multiple ways to interpret and calculate interaction probabilities. We could calculate the probability  
112 that the traits of these species match, i.e. that the avian predator possesses the biological attributes to capture  
113 and consume the rodent. We could also calculate the probability that their traits support an interaction under the  
114 typical environmental conditions of the new habitat. For example, because avian predators hunt by sight,

115 predation could be possible in the absence of snow but highly improbable when snow is present, as rodents may  
116 use it as a shelter to hide from predators. Finally, we could calculate the probability that the avian predator will  
117 consume the rodent at *that* particular location, for which the spatial and temporal boundaries need to be  
118 specified. The estimation of interaction probabilities, whether through predictive models or prior distributions,  
119 hinges on our understanding of these probabilities and the specific ecological processes we aim to capture.

120 An important aspect to consider when using interaction probabilities is knowing if they describe potential or  
121 realized interactions, as these two types of interactions have distinct conceptual underpinnings and sources of  
122 uncertainty. A potential (regional) interaction is defined as the biological capacity of two taxa to interact (i.e.,  
123 the probability that they interact if they were to encounter each other and given sufficient time) whereas a  
124 realized (local) interaction is the occurrence or observation of this interaction in a well-defined space and time  
125 (i.e., the probability that they interact locally). For two co-occurring taxa and over enough time, the probability  
126 of local interaction is equivalent to the probability of regional (potential) interaction.

127 We use the terms *metaweb* (Dunne 2006) to designate regional networks of potential interactions and *local*  
128 *networks* (Poisot *et al.* 2012) for those of realized interactions. Metawebs are the network analogs of the species  
129 pool, where local networks originate from a subset of both species (nodes) and interactions (edges) of the  
130 regional metaweb (Saravia *et al.* 2022). Without clear documentation, it can be challenging to know if  
131 published probabilistic interaction networks describe local or regional interactions, or if so-called probabilities  
132 are in reality a form of interaction score. When probabilistic regional interactions are used and interpreted  
133 incorrectly as local interactions (and conversely), this may generate misleading findings during data analysis. A  
134 better understanding of probabilistic local and regional interactions would prevent interpretation errors (e.g.,  
135 when studying network-area relationships with metawebs or local networks) and facilitate a more adequate use  
136 of interaction data.

### 137 **The outcome of probabilistic interactions is usually binary**

138 Local networks and metawebs, like any type of network, are made of nodes and edges that may be represented  
139 at different levels of organization. The basic units of ecological networks are individuals that interact with each  
140 other (e.g., by predation in food webs, Elton 2001), forming individual-based networks (Melián *et al.* 2011).  
141 The aggregation of these individuals into more or less homogeneous groups (e.g., populations, species, families,  
142 feeding guilds) allows us to represent nodes at broader taxonomic scales, which affects our interpretation of the

143 properties of these systems (Guimarães 2020; Hemprich-Bennett *et al.* 2021).

144 Ecologists have traditionally represented interactions (edges) as binary objects that were considered realized  
145 after observing at least one individual from group  $i$  interact with at least another individual from group  $j$ . In an  
146 adjacency matrix  $B$  of binary interactions, the presence or absence of an interaction  $B_{i,j}$  between two taxa can  
147 be viewed as the result of a Bernoulli trial  $B_{i,j} \sim \text{Bernoulli}(P(B_{i,j}))$ , with  $P(B_{i,j})$  being the probability of  
148 interaction. This interaction probability characterizes our limited ecological knowledge and/or the intrinsic  
149 spatiotemporal variability of interactions. It may be estimated through predictive models (e.g., those based on  
150 biological traits and species abundances) or expert (prior) knowledge about the interaction. In networks of  
151 probabilistic interactions, the edge values  $P(B_{i,j})$  are probabilistic events whose only two possible outcomes are  
152 the presence ( $B_{i,j} = 1$ ) or absence ( $B_{i,j} = 0$ ) of an interaction between each pair of nodes. Depending on the  
153 type of probabilistic interaction network (local or metaweb), the mathematical formulation and interpretation of  
154 stochastic parameters like  $P(B_{i,j})$  can be linked to environmental and biological factors such as species  
155 abundance, traits, area, and time, for example using logistic regression with continuous explanatory variables.

156 Predicting the number of local networks in which the interaction between two given taxa occurs can be achieved  
157 by using a Binomial distribution, assuming a constant interaction probability and independence between  
158 networks (trials). When considering uncertainties around the estimation of  $P(B_{i,j})$  or its spatiotemporal  
159 variability, a Beta distribution may be used to represent the relative likelihood of different probability values.  
160 For example, when calculating the probability of interaction between two taxa based on their local abundances,  
161 any spatiotemporal fluctuations in their abundances would introduce variability in the interaction probability at  
162 the local scale. If we take into account the stochasticity of the interaction probability, a Beta-Binomial  
163 distribution can be used to predict the number of networks in which the interaction occurs. Empirically  
164 observing an interaction between two taxa at a given location and time provides important information that can  
165 be used to update previous estimates of  $P(B_{i,j})$ , informing us on the biological capacity of both taxa to interact  
166 and the environmental conditions that enabled them to interact locally.

## 167 **Probabilistic interactions may also describe quantitative networks**

168 Even though binary interaction networks constitute a highly valuable source of ecological information (Pascual  
169 *et al.* 2006), they overlook interaction strengths. Represented in a quantitative adjacency matrix  $W$ , interaction  
170 strengths better describe the energy flows, demographic impacts or frequencies of interactions between nodes

171 (Berlow *et al.* 2004; Borrett & Scharler 2019), with  $W_{i,j}$  being a natural  $\mathbb{N}$  or real  $\mathbb{R}$  number depending on the  
172 measure. For example, they may represent local interaction rates between pairs of taxa (e.g., the flower-visiting  
173 rates of pollinators in a mutualistic network, Herrera 1989). When interaction strengths characterize predation  
174 pressure on prey, they can serve as parameters in a Lotka-Volterra model (e.g., Emmerson & Raffaelli 2004).  
175 The extra amount of ecological information in quantitative networks typically comes at a cost of greater  
176 sampling effort and data volume in predictive models (Strydom *et al.* 2021), which can lead to relatively high  
177 levels of uncertainties when inferring quantitative networks with limited data.

178 Like binary interaction networks, the uncertainty and variability of interaction strengths can be represented  
179 probabilistically. Interaction strengths can follow many probability distributions depending on the measure. For  
180 instance, they can follow a Poisson distribution  $W_{i,j} \sim \text{Poisson}(\lambda_{i,j}t_0)$  when predicting the number of  
181 interactions between individuals, with  $\lambda_{i,j}$  being the expected rate at which individuals of taxa  $i$  and  $j$  interact.  
182 The product  $\lambda_{i,j}t_0$  is the expected number of interactions realized by individuals during the time interval  $t_0$   
183 (e.g., the expected number of prey  $j$  consumed by all predators  $i$ ). The Poisson distribution can also be  
184 0-inflated when taking into account non-interacting taxa (e.g., Boulangeat *et al.* 2012 employ a 0-inflated model  
185 to analyze species abundance following the modeling of species presence and absence), which constitute the  
186 majority of taxa pairs in most local networks (Jordano 2016).

187 Because of the methodological difficulties typically encountered when building deterministic quantitative  
188 networks (which are only partially mitigated by models such as Ecopath, Plagányi & Butterworth 2004), binary  
189 interaction networks, which are easier to sample (Jordano 2016) and predict (Strydom *et al.* 2021), have been  
190 more frequently studied and modeled. Moreover, most published probabilistic interaction networks and methods  
191 describe interactions whose outcome is binary (whether interaction probabilities are regarded as constant or  
192 variable, e.g. represented by a Beta distribution), which underlines the need for better guidelines regarding the  
193 interpretation and manipulation of these types of networks first. For these reasons, our primary focus is  
194 interpreting and using interaction probabilities in Bernoulli distributions, in both local networks and metawebs.

195 **Local networks: communities interacting in space and time**

196 **Species interactions occur in a local context**

197 Local networks of probabilistic interactions describe how likely taxa are to interact at a given location and time  
198 period. Local interactions are contingent upon the environmental conditions of the community and the matching  
199 of taxa biological traits. In local networks, edges commonly represent our degree of belief that two taxa interact  
200 in nature, but can also represent the probability of empirically *observing* this interaction (Catchen *et al.* 2023).

201 **Space and time**

202 We define space as the collection of geographic coordinates  $(x, y, z)$ , with  $(x, y)$  representing longitude and  
203 latitude coordinates, and  $z$  denoting either altitudes or depths. These point coordinates delineate the spatial  
204 boundaries of the system, which may be portrayed as a polyhedron. Ecological interactions may exhibit  
205 variations along latitudinal and altitudinal gradients, as evidenced by changes in hummingbird-plant  
206 interactions (Weinstein & Graham 2017a, b) and mosquito biting rates (e.g., Kulkarni *et al.* 2006) at different  
207 elevations. In contrast, time is defined as the specific time period within which interactions were either observed  
208 or predicted. Even though space and time are continuous variables that should yield probability *densities* of  
209 interactions (i.e., relative likelihoods of interactions occurring at infinitesimal locations and instants in time),  
210 these definitions enable them to be conceptualized as distinct patches and time segments. Treating space and  
211 time as discrete dimensions aligns with the common sampling methods of ecological networks and provides  
212 probabilities of interactions, which can be obtained by integrating probability densities over space and time. We  
213 can quantify both an area  $A_0$  and a duration  $t_0$ , which can readily be used in spatiotemporal analyses of  
214 ecological networks (Box 1).

215 **Co-occurrence**

216 The probability that two taxa  $i$  and  $j$  interact in a local network  $L_{x,y,z,t}$  (spatial and temporal subscripts hereafter  
217 replaced by the shorter subscript  $k$  for clarity) can be conditioned on many environmental and biological  
218 factors. In addition to network area (or volume) and duration, they may be conditioned on taxa co-occurrence  
219  $X_{i,j,k}$ , which is usually a Boolean describing if the geographic distributions of both taxa overlap within the study  
220 area. As illustrated in Box 1, co-occurrence may be modeled probabilistically, in which case it may conform to

221 a Bernoulli distribution  $X_{i,j,k} \sim \text{Bernoulli}(P(X_{i,j,k}))$ . The probability of co-occurrence can be calculated using  
222 the individual (marginal) occurrence probabilities  $P(X_{i,k})$  and  $P(X_{j,k})$ . Given that taxa occurrences are not  
223 independent of each other, the probability of co-occurrence can be calculated by multiplying the probability of  
224 occurrence of one taxon by the probability of occurrence of the other given that the first one occurs:

$$P(X_{i,j,k}) = P(X_{i,k}, X_{j,k}) = P(X_{i,k}|X_{j,k})P(X_{j,k}) \quad (1)$$

225 The probability of co-occurrence  $P(X_{i,j,k})$  can be estimated through the application of joint species distribution  
226 models (e.g., Pollock *et al.* 2014), potentially taking into account biotic interactions (Staniczenko *et al.* 2017).  
227 Given that the probability that two non-co-occurring taxa interact locally is zero (i.e.,  $P(L_{i,j,k}|X_{i,j,k} = 0) = 0$ ),  
228 the probability of local interaction can be obtained by multiplying the probability of interaction given  
229 co-occurrence with the probability of co-occurrence:

$$P(L_{i,j,k}) = P(L_{i,j,k}|X_{i,j,k}) \times P(X_{i,j,k}). \quad (2)$$

## 230 Biological and environmental factors

231 Local interactions may also be conditioned on local environmental factors such as temperature (Angilletta *et al.*  
232 2004), precipitation (Woodward *et al.* 2012), habitat structure (Klecka & Boukal 2014), and presence of other  
233 taxa in the network (Kéfi *et al.* 2012; Pilosof *et al.* 2017). We use the variable  $E_k$  to describe the local  
234 environmental context in which interaction probabilities were estimated. For example, in a mesocosm  
235 experiment estimating interaction probabilities between predators and prey with and without shelters,  $E_k$  would  
236 represent the presence or absence of these shelters. Like co-occurrence,  $E_k$  can also be modeled  
237 probabilistically when the stochasticity or uncertainty of environmental factors is considered.  $E_k$  represents all  
238 environmental variables that were taken into consideration when measuring interaction probabilities; it is a  
239 subset of all environmental factors acting on ecological interactions.

240 Other important factors that can impact interaction probabilities at the local scale are taxa local abundances  $N_{i,k}$ ,  
241 and  $N_{j,k}$ , which affect encounter probabilities (Canard *et al.* 2012), and local traits distributions  $T_{i,k}$  and  $T_{j,k}$   
242 (e.g., body mass, longevity, and habitat breadth, Caron *et al.* 2024), which determine the ability of individuals  
243 to interact after encountering each other (Poisot *et al.* 2015). Local interaction probabilities may also be  
244 conditioned on higher-level properties of the network, which we denote by  $f(L)$ . Many topological null models

245 (i.e., statistical models that randomize interactions by retaining certain properties of the network while  
246 excluding others) provide interaction probabilities from selected measures of network structure, such as  
247 connectance (Fortuna & Bascompte 2006) and the degree distribution (Bascompte *et al.* 2003).

## 248 Local interactions must be biologically feasible

249 Local interactions must be biologically feasible before occurring at a specific time and space. A local  
250 probability of interaction  $P(L_{i,j,k})$  can be expressed as the product of the probability of local interaction given  
251 that the two taxa can potentially interact  $P(L_{i,j,k}|M_{i,j} = 1)$ , which we sometimes denote as  $P(L_{i,j,k}|M_{i,j})$  for the  
252 sake of simplicity, with their probability of regional interaction  $P(M_{i,j})$ :

$$P(L_{i,j,k}) = P(L_{i,j,k}|M_{i,j} = 1) \times P(M_{i,j} = 1). \quad (3)$$

253 Low values of  $P(L_{i,j,k}|M_{i,j})$  indicate that feasible interactions rarely occur locally, intermediate values around  
254 50% suggest considerable spatiotemporal variability, while high values indicate that regional interactions are  
255 nearly always realized locally. The local probability of interaction between a given pair of taxa is always equal  
256 to or below their probability of regional interaction.

## 257 Conditional variables must be explicitly stated

258 The probability that two taxa  $i$  and  $j$  interact in a local network  $L$  can thus be conditioned on their co-occurrence  
259  $X_{i,j,k}$  (or more explicitly on their occurrences  $X_{i,k}$  and  $X_{j,k}$ ), local abundances  $N_{i,k}$  and  $N_{j,k}$ , local traits  
260 distributions  $T_{i,k}$  and  $T_{j,k}$ , local environmental conditions  $E_k$ , network area (or volume)  $A_0$ , time interval  $t_0$ ,  
261 network properties  $f(L_k)$ , and biological feasibility  $M_{i,j}$ .

262 Although these variables correspond to distinct ecological inquiries or mechanisms related to ecological  
263 interactions, they may covary with each other, such as the possible dependence of  $X_{i,j,k}$  and  $E_k$  on spatial and  
264 temporal scales. When estimating interaction probabilities using e.g. a generalized linear model with multiple  
265 explanatory variables that might not be independent, it may become important to address collinearity. In such a  
266 case, to mitigate this issue, it may be necessary to use variable selection techniques before fitting the model to  
267 data. The probability that a local interaction is realized is described by the following expression when all these  
268 conditional variables are included:

$$P(L_{i,j,k}|X_{i,k}, X_{j,k}, N_{i,k}, N_{j,k}, T_{i,k}, T_{j,k}, E_k, A_0, t_0, f(L_k), M_{i,j}) \quad (4)$$

269 The representation of the local context in which probabilities are estimated and the variables that should be  
 270 taken into consideration depend on the study system, the objectives of the study, and the resources available to  
 271 the researchers. In other words, these variables do not systematically need to be accounted for. For example,  
 272 Gravel *et al.* (2019) analyzed local European host-parasite networks of willow-galling sawflies and their natural  
 273 enemies, all referenced in space and time, to infer probabilities of local interactions between co-occurring  
 274 species. This was achieved by including temperature and precipitation as conditional variables in their models.  
 275 In Box 2, we reuse these data to show the extent of variation among these local networks. We do so by  
 276 measuring their dissimilarity with the regional network (metaweb aggregating all local interactions), both in  
 277 terms of species composition and interactions. We build local probabilistic networks following eq. 3, showing  
 278 that insufficient local variation (high probability of local interaction among potentially interacting species)  
 279 results in an overestimation in both the number of interactions and connectance (i.e., the proportion of all of the  
 280 non-forbidden links that are realized).  
 281 When accounted for, conditional variables should be clearly described in the documentation of the data  
 282 (Brimacombe *et al.* 2023), preferentially in mathematical terms to avoid any confusion in their interpretation  
 283 and to limit manipulation errors during their re-use. For instance, ecologists should be explicit about their  
 284 consideration of co-occurrence in their estimation of local interaction probabilities. Indeed, it is important to  
 285 specify if probability values are conditional ( $P(L_{i,j,k}|X_{i,j,k} = 1)$ ) or not ( $P(L_{i,j,k})$ ) on co-occurrence, as this can  
 286 change the interpretation of the data. In Tbl. 1, we present examples of studies that used different expressions of  
 287 probabilistic interactions. We have included the probability of empirically observing an interaction that is  
 288 realized locally  $P(O_{i,j,k}|L_{i,j,k})$  to underscore the distinction between local observations and actual realizations  
 289 of interactions.

Table 1: **Mathematical expressions of probabilistic interactions.** The probability of interaction between two taxa  $i$  and  $j$  is interpreted differently in a local network  $L$  of realized interactions, a local network  $O$  of observed interactions, a metaweb  $M$  of potential interactions (representing the *biological* feasibility of interactions), and a metaweb  $M^*$  of potential interactions (representing the *ecological* feasibility of interactions). Each expression emphasizes a different conditional variable, the ellipsis serving as a placeholder for other variables not explicitly stated in the expression. The outcome of each of these probabilistic events, along with common models used for estimation, is presented alongside examples of studies that employed them (with specific variables indicated in parentheses, when applicable). Uncertainty sources include uncertainty of model parameters, model structure, and input data. The study marked with an asterisk has been conducted on binary interaction networks.

Expression	Type	Outcome	Common models	Reference
$P(L_{i,j,k} X_{i,k}, X_{j,k}, \dots)$	local	realization of the interaction given taxa co-occurrence	species distribution models	Gravel <i>et al.</i> (2019), Dansereau <i>et al.</i> (2023)
$P(L_{i,j,k} N_{i,k}, N_{j,k}, \dots)$	local	realization of the interaction given taxa abundances	neutral models	Canard <i>et al.</i> (2014)
$P(L_{i,j,k} T_{i,k}, T_{j,k}, \dots)$	local	realization of the interaction given local traits	trait matching models	Caron <i>et al.</i> (2024)
$P(L_{i,j,k} E_k, \dots)$	local	realization of the interaction given local environmental conditions	environmental- based models	Gravel <i>et al.</i> (2019) (temperature and precipitation)
$P(L_{i,j,k} A_0, \dots)$	local	realization of the interaction in a given area or volume	spatial models	Galiana <i>et al.</i> (2018) *
$P(L_{i,j,k} t_0, \dots)$	local	realization of the interaction during a given time period	temporal models	Weinstein & Graham (2017a)
$P(L_{i,j,k} f(L_k), \dots)$	local	realization of the interaction given network structure	topological models	Fortuna & Bascompte (2006) (connectance), Stock <i>et al.</i> (2017)
$P(L_{i,j,k} M_{i,j}, \dots)$	local	realization of the interaction given that the taxa can biologically interact	spatiotemporal models	Dansereau <i>et al.</i> (2023)
$P(O_{i,j,k} L_{i,j,k}, \dots)$	local	observation of the interaction given that it is realized locally	sampling models	Catchen <i>et al.</i> (2023)

Expression	Type	Outcome	Common models	Reference
$P(M_{i,j} T_i, T_j)$	regional	biological feasibility of the interaction given regional traits (non-forbiddenness)	trait matching models	Strydom <i>et al.</i> (2022)
$P(M_{i,j}^* T_i, T_j, E)$	regional	ecological feasibility of the interaction given regional traits and environmental conditions	trait matching and environmental-based models	this study

290 **Interaction probabilities may be estimated with multiple models**

291 When using multiple models to estimate local interaction probabilities, rather than selecting a single model that  
 292 best fits the data, model averaging may enhance our estimations. In this approach, the weighting is based on the  
 293 likelihood of each model. Model weights represent the probability that each model is the most suitable for  
 294 explaining the data, and may be measured using Akaike weights (Burnham & Anderson 2004; Wagenmakers &  
 295 Farrell 2004). For instance, considering two models  $mod_1$  and  $mod_2$  with respective probabilities (or weights)  
 296  $P(mod_1)$  and  $P(mod_2)$ , the average probability of interaction  $P(L_{i,j,k}|...)$  can be calculated as follows:

$$P(L_{i,j,k}|...) = P(L_{i,j,k}|mod_1, ...) \times P(mod_1) + P(L_{i,j,k}|mod_2, ...) \times P(mod_2), \quad (5)$$

297 where the ellipsis serves as a placeholder for the conditional variables incorporated in these models. Model  
 298 structure constitutes another source of uncertainty that needs to be documented and quantified when estimating  
 299 interaction probabilities.

**Box 1: A spatiotemporally explicit model of interactions**

Ecologists may resort to predictive models to reconstruct local networks across time and space. We introduce and develop a simple generative Bayesian model for probabilistic local interactions, which explicitly accounts for their spatiotemporal variability. Our model is not designed for regional interactions, which do not vary spatially nor temporally. Rather, it could prove valuable for generating new data on local interactions across time and space, following parameter inference.

As indicated by Eq. 2, the probability that two taxa  $i$  and  $j$  interact locally can be obtained by multiplying their probability of interaction given co-occurrence with their probability of co-occurrence. The probability of interaction given co-occurrence can be made temporally explicit by modeling it as a Poisson process with rate parameter  $\lambda_k$ . This parameter represents the local expected frequency of interaction between co-occurring taxa. The probability that two co-occurring taxa interact during a time interval  $t_0$  can be given by:

$$P(L_{i,j,k}|X_{i,j,k}) = 1 - e^{-\lambda_k t_0}, \quad (6)$$

which tends toward 1 as  $t_0 \rightarrow \infty$  if  $\lambda_k > 0$ . In other words, two co-occurring taxa with a nonzero rate of interaction will inevitably interact in a sufficiently long time interval.

The occurrence of an interaction between  $i$  and  $j$  may be the result of a Bernoulli trial with probability  $P(L_{i,j,k})$ . A Bayesian model can be built using the preceding equations to generate new interaction data, following the inference of the  $\lambda_k$  and  $P(X_{i,j,k})$  parameters.

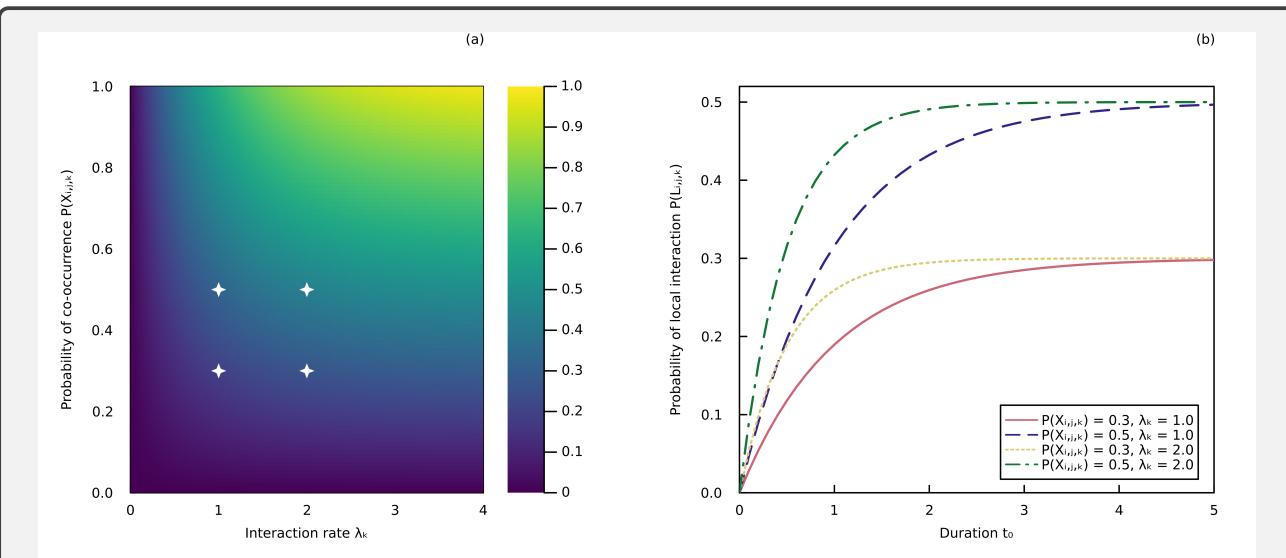
$$L_{i,j,k} \sim \text{Bernoulli}(P(L_{i,j,k})) \quad (7)$$

$$P(L_{i,j,k}) = P(X_{i,j,k})(1 - e^{-\lambda_k t_0}) \quad (8)$$

$$P(X_{i,j,k}) \sim \text{Beta}(2, 2) \quad (9)$$

$$\lambda_k \sim \text{Exponential}(2) \quad (10)$$

In Fig. 1, we show the variation in the probability of interaction under different parameter values. In the right panel, we notice that the probability of interaction always converges toward the probability of co-occurrence  $P(X_{i,j,k})$ , for all positive values of the interaction rate.



**Figure 1: Parameters of the spatiotemporally explicit model of interactions.** (a) Probability of local interaction given by the process model (Eq. 8) under different values of  $\lambda_k$  (interaction rate) and  $P(X_{i,j,k})$  (probability of co-occurrence), with  $t_0 = 1$  (duration). Parameters  $t_0$  and  $\lambda_k$  have complementary units (e.g.,  $t_0$  in months and  $\lambda_k$  in number of interactions per month). The parameter values used in the right panel are denoted by the white stars. (b) Scaling of the probability of interaction with the duration parameter  $t_0$ , for different values of  $\lambda_k$  and  $P(X_{i,j,k})$ .

This model can be customized in different ways, such as linking both parameters to specific environmental or biological variables. For instance, the probability of co-occurrence could be modeled as a function of climatic variables, while the interaction rate parameter could be modeled based on taxa abundances.

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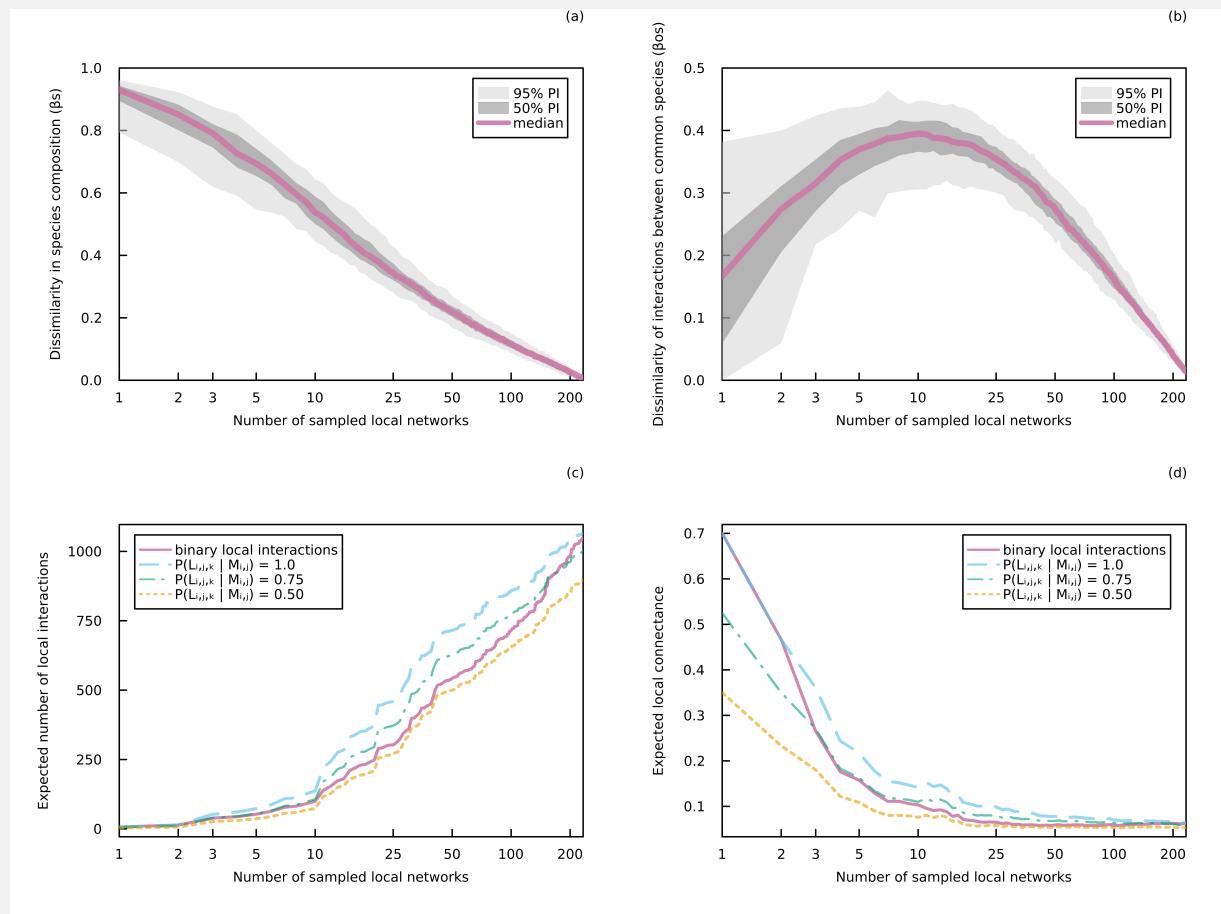
## Box 2: Dissimilarity of local host-parasite networks

We present a way to assess local network variability and dissimilarity regarding species composition and interactions. We do so using the collection of tripartite host-parasite networks of Kopelke *et al.* (2017), consisting of willows, willow-galling sawflies, and their natural enemies sampled across Europe. All data manipulation and methods are described in Appendix 1. All code and data to reproduce these analyses are available at the Open Science Framework (TBD).

In Fig. 2a-b, we show how the dissimilarity between the metaweb of binary interactions and aggregated local networks changes with the number of sampled local networks. We compared the metaweb and the aggregated local networks using the dissimilarity in species composition ( $\beta_S$ , Fig. 2a) and the dissimilarity of interactions between common species ( $\beta_{OS}$ , Fig. 2b) indices (Poisot *et al.* 2012). Expectingly, local networks are highly dissimilar from the metaweb in terms of species composition, especially when only a

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limited number of sites has been sampled. This is because few species from the metaweb (species pool) occur locally. Moreover, we observe a peak in the dissimilarity of interactions between common species at intermediate sampling levels. This suggests that species are collected faster than their interactions. With a limited number of sampled local networks, few regional interactions are observed locally. Adding more sites brings new species, but not always their interactions. Quadratic relationships of network properties with sampling effort were also observed by McLeod *et al.* (2021).



**Figure 2: Network accumulation curves.** (a) Dissimilarity in species composition and (b) dissimilarity of interactions between common species between aggregated local networks and the metaweb of binary host-parasite interactions. In both panels, the colored line represents the median dissimilarity across simulations and the grey areas cover the 50% and 95% percentile intervals. (c) Scaling of the number of interactions and (d) scaling of connectance with the number of sampled (aggregated) binary and probabilistic local interaction networks. For a better comparison with binary interactions, local networks of probabilistic interactions were derived from a metaweb of probabilistic interactions with a false positive and false negative rate of zero. A specific value of  $P(L_{i,j,k} | M_{i,j})$  (the local probability of interaction among potentially interacting species) was used for all non-aggregated local networks within a particular curve. Aggregated local networks were obtained by sequentially and randomly selecting a number of local networks and aggregating both their species and interactions (with the value of  $P(L_{i,j,k} | M_{i,j})$  increasing in aggregated local networks of probabilistic interactions).

Next, we investigate how the number of local interactions and connectance scale with the number of sampled (aggregated) local networks of probabilistic or binary interactions (Fig. 2c-d). By comparing the scaling relationships observed in local networks of binary and probabilistic interactions, we observe that high values of  $P(L_{i,j,k}|M_{i,j})$  lead to systematic overestimations in the number of interactions and connectance, especially when  $P(L_{i,j,k}|M_{i,j}) = 1$  (i.e., when local and regional probabilities of interactions are equivalent). This suggests that high values of  $P(L_{i,j,k}|M_{i,j})$  do not adequately capture the variability of local interactions. However, these biases tend to diminish as the number of sampled networks increases, indicating that most interactions are eventually captured when  $P(L_{i,j,k}|M_{i,j})$  is high. In contrast, low values of  $P(L_{i,j,k}|M_{i,j})$  lead to missing interactions, resulting in an underestimation of the number of interactions and connectance. These results underscore the importance of using the appropriate level of variability when estimating local interaction probabilities.

305

## 306 Metawebs: regional catalogs of interactions

### 307 Unobserved interactions should be probabilistic

308 Metawebs (Dunne 2006) are networks of potential interactions over broad spatial, temporal, and taxonomic  
309 scales (e.g., food webs at the continental scale). Potential interactions describe the biological capacity of taxa to  
310 interact, which is typically assessed at the regional scale. Metawebs of probabilistic interactions are particularly  
311 useful in situations where there is uncertainty in the ability of taxa to interact. This uncertainty frequently arises  
312 due to insufficient interaction data, especially for taxa that have not yet been observed to co-occur, and  
313 uncertainties in trait-matching models. As data accumulates, interactions in metawebs should tend towards  
314 binarity, approaching probability values of 0 (repeatedly failing to observe an interaction between two  
315 co-occurring taxa) and 1 (observing an interaction at least once). Although *neutrally* forbidden interactions  
316 (i.e., between rare species, Canard *et al.* 2012) tend to have low probability values in local networks, they may  
317 have higher probabilities in the metaweb (i.e., when species' biological traits can support an interaction if they  
318 were to encounter each other). Likewise, non-co-occurring taxa may have a non-zero probability of interaction  
319 in the metaweb.

320 The extent of sampling effort influences our evaluation of probabilities of potential interactions, as sampling  
321 over a larger area or for a longer duration enables us to capture a greater number of regional interactions

322 (McLeod *et al.* 2021). However, in contrast with local networks of probabilistic interactions, which describe  
323 local interaction stochasticity, regional interactions are not evaluated for any particular local context. In Box 3,  
324 we discuss the differences in spatial and temporal scaling of regional interactions compared to local interactions.  
325 We do so by using the host-parasite networks of Kopelke *et al.* (2017) as an illustration of spatial scaling.

## 326 Potential interactions are sometimes linked to environmental conditions

### 327 Biological feasibility

328 Potential interactions describe what we refer to as the *biological feasibility* of interactions, which is based solely  
329 on the regional traits distributions  $T_i$  and  $T_j$  of taxa  $i$  and  $j$ , respectively. A probability of potential interaction in  
330 a metaweb  $M$  describing the biological feasibility of interactions may be expressed as:

$$P(M_{i,j}|T_i, T_j), \quad (11)$$

331 which, in contrast with local networks, is not conditioned on any spatial, temporal, co-occurrence or  
332 environmental variables (Tbl. 1). Regional traits may differ from local traits  $T_{i,k}$  and  $T_{j,k}$ , which may vary  
333 spatially and temporally due to phenotypic plasticity (Berg & Ellers 2010). The taxonomic level at which  
334 interactions are evaluated influences the distribution of regional and local traits. However, as explained in Box  
335 4, there is no fundamental difference in the taxonomic scaling of regional and local interactions (i.e., how  
336 interaction probabilities change with taxonomic level), unlike their spatial and temporal scaling.

337 The biological feasibility of interactions expresses our degree of belief that there exists at least one combination  
338 of phenotypes that could support an interaction if they were to encounter each other, assuming they had enough  
339 time to interact. Evaluating this probability is conducted without incorporating the environmental conditions  
340 under which they encounter each other into the model. It is the complement of the probability  $P(F_{i,j}|T_i, T_j)$  of  
341 forbidden interactions (i.e., the probability that their traits do not support an interaction), which is based  
342 uniquely on biological traits:

$$P(M_{i,j}|T_i, T_j) = 1 - P(F_{i,j}|T_i, T_j). \quad (12)$$

343 For example, let  $i$  be a western diamondback rattlesnake (*Crotalus atrox*) and  $j$ , a wood lemming (*Myopus*

344 *schisticolor*). These two taxa never co-occur, the rattlesnake being adapted to warm regions of North America  
 345 (Castoe *et al.* 2007) and the lemming, to northern habitats of Eurasia (Fedorov *et al.* 2008). As we lack direct  
 346 observations of an interaction between these two species, we have to rely on expert knowledge or trait-matching  
 347 models to estimate their probability of potential interaction. To accurately estimate this probability using  
 348 trait-matching models, it is crucial to ensure that the set of traits considered reflects the overall traits  
 349 distributions of both taxa. We could for instance consider their average body mass and the average phylogenetic  
 350 proximity of lemmings to rattlesnakes' prey. Doing so, we might find a high probability of potential interaction  
 351 based on these traits.

### 352 Ecological feasibility

353 The biological feasibility of interactions should not be confused with what we refer to as the *ecological*  
 354 feasibility of interactions. A probability of potential interaction in a metaweb  $M^*$  describing ecological  
 355 feasibility of interactions may be expressed as:

$$P(M_{i,j}^*|T_i, T_j, E), \quad (13)$$

356 where  $E$  is the environmental conditions under which potential interactions are evaluated (Tbl. 1). Unlike  $E_k$ ,  
 357 these environmental conditions do not represent conditions occurring at specific locations. Ecological  
 358 feasibility represents the probability that two taxa interact if they were to encounter each other under given  
 359 environmental conditions, assuming they had enough time to interact. Incorporating environmental conditions  
 360 into a trait-matching model may be important when there is high covariance between the environment and traits.  
 361 For instance, in our example involving rattlesnakes and lemmings, the probability of potential interaction  
 362 between these two species may be low in most environmental conditions. Western diamondback rattlesnakes  
 363 may be unactive under low temperatures (Kissner *et al.* 1997), whereas wood lemmings may have low tolerance  
 364 to high temperatures (Kausrud *et al.* 2008). The probability that an interaction is ecologically feasible is always  
 365 lower than the probability that it is biologically feasible, even across all environmental conditions:

$$\int_E P(M_{i,j}^*|T_i, T_j, E) dE \leq P(M_{i,j}|T_i, T_j). \quad (14)$$

366 This is because the biological feasibility of an interaction is a prerequisite for its ecological feasibility.

367 Biological feasibility is necessary but not sufficient for an interaction to be ecologically feasible. Our discussion  
368 of metawebs will focus on the biological feasibility of interactions since most methods developed for inferring  
369 probabilities of regional interactions do not explicitly take into account environmental conditions (e.g., Strydom  
370 *et al.* 2022).

### 371 Metawebs are built with interaction data and trait-matching models

372 Starting from a selected set of taxa, which are usually distributed within a broad region of interest, metawebs  
373 can be built using different data sources, including literature review (e.g., Maiorano *et al.* 2020), aggregated  
374 interaction data (e.g., Gravel *et al.* 2019; Saravia *et al.* 2022), trait-matching models (e.g., Shaw *et al.* 2024;  
375 Strydom *et al.* 2022), and expert knowledge. Every pair of taxa that have confidently been observed to interact  
376 at least once can be given a probability of 1 (i.e.,  $P(M_{i,j}) = 1$ ) since we know that they *can* interact. This differs  
377 from local networks of probabilistic interactions, where interaction events may remain stochastic (i.e.,  
378  $P(L_{i,j,k}) < 1$ ) even after empirically observing interactions due to their spatiotemporal variability. Interactions  
379 that were never observed typically have low probability values in local networks and vary from low to high  
380 values in metawebs, contingent upon taxa traits distributions (reaching 0 for forbidden links).  
381 When incorporating local network data to estimate probabilities of regional interactions, repeatedly failing to  
382 observe an interaction between two co-occurring taxa (i.e.,  $P(O_{i,j,k} = 0)$ ) should decrease the probability that  
383 the interaction is biologically feasible. Using Bayes' theorem, the probability that the interaction is biologically  
384 feasible given that it was never observed locally,  $P(M_{i,j} = 1|O_{i,j,k} = 0, \dots)$ , may be calculated as follows:

$$P(M_{i,j} = 1|O_{i,j,k} = 0, \dots) = \frac{P(O_{i,j,k} = 0|M_{i,j} = 1, \dots) \times P(M_{i,j} = 1|\dots)}{P(O_{i,j,k} = 0|\dots)}. \quad (15)$$

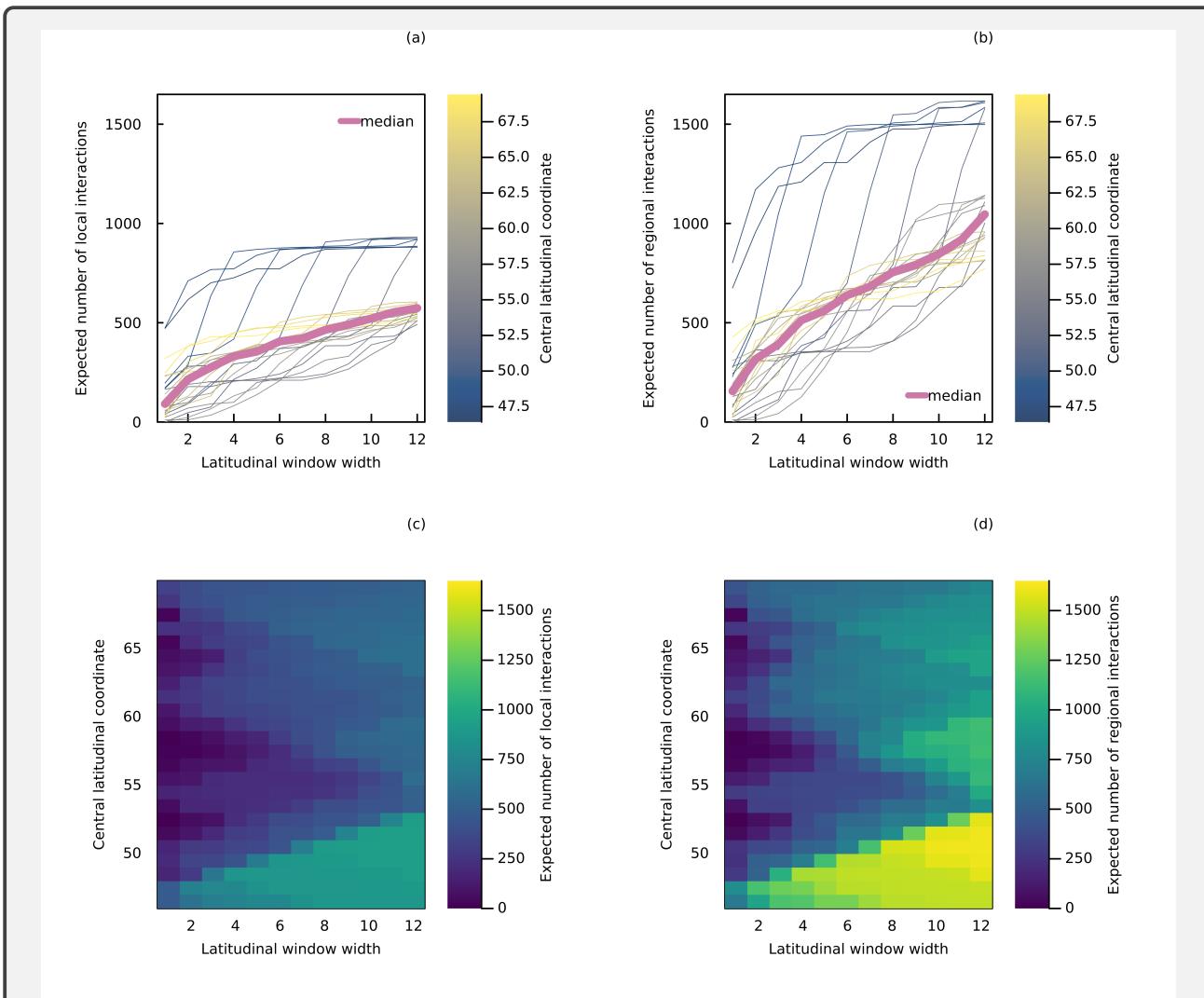
385 The reduction in the probability of regional interaction after considering that it was never observed locally (i.e.,  
386  $P(M_{i,j} = 1|O_{i,j,k} = 0, \dots) < P(M_{i,j} = 1|\dots)$ ) occurs because  $P(O_{i,j,k} = 0|M_{i,j} = 1, \dots)$  must be lower than  
387  $P(O_{i,j,k} = 0, \dots)$ , i.e. there is a higher chance of observing an interaction when it is biologically feasible.  
388 Many observations of interactions are false positives because of observation errors due to taxonomic  
389 misidentifications and ecological misinterpretations (e.g., due to cryptic species and interactions, Pringle &  
390 Hutchinson 2020). Likewise, forbidden interactions may be false negatives, e.g. if they have been evaluated  
391 based on unrepresentative or incomplete traits distributions. Employing Bayesian models proves valuable when  
392 estimating interaction probabilities in metawebs (e.g., Bartomeus *et al.* 2016; Cirtwill *et al.* 2019). This

- 393 improvement is achieved by updating prior information regarding the feasibility of interactions (e.g., experts'  
394 prior assessments of interaction probabilities) with empirical data on interactions and traits.

### Box 3: Spatial and temporal scaling of interactions

Local networks and metawebs have distinct relationships with space (area or volume) and time (sampling effort or duration). Local probabilities of interaction scale both spatially and temporally, because local interactions have more opportunities to be realized in larger areas and longer durations. If a local network of probabilistic interactions  $L_1$  with an area  $A_1$  is compared to a larger network  $L_0$  with an area  $A_0$ , and  $A_1$  is entirely nested within  $A_0$ , interaction probabilities should be lower in the smaller network, i.e.  $P(L_{i,j,1}|A_1 < A_0) \leq P(L_{i,j,0}|A_0)$ . However, if  $A_1$  and  $A_0$  are disjoint, interaction probabilities could be higher in the smaller area, contingent upon local environmental and biological conditions. In contrast, regional probabilities of interaction do not scale with space and time. The probability of two taxa potentially interacting should be the same in all metawebs in which they are present regardless of scale, provided that the data and methods used for estimation are consistent. This is because they depend solely on the biological capacity of two taxa to interact, regardless of co-occurrence and local environmental conditions. However, probabilities of regional interactions may change, tending to become more definitive, with increased sampling effort.

In Fig. 3, we show how the expected *number* of local host-parasite interactions scales with the spatial boundary of the network (represented by an expanding latitudinal window) in comparison with regional interactions. We do so using the host-parasite networks of Kopelke *et al.* (2017). The increase in the number of regional interactions is due to the inclusion of more species in a larger area. To ensure a conservative comparison between aggregated local and regional networks, we employed equal interaction probabilities (i.e., using  $P(L_{i,j,k}|M_{i,j}) = 1$ ) in both types of network. This means that local interaction probabilities could not increase further when aggregating them. Despite this, we notice that the total number of regional interactions scales more rapidly than local interactions. This is because numerous regional interactions involve species that never co-occur, and as a result, these interactions are not captured in local networks. All data manipulation and methods are described in Appendix 1.



**Figure 3: Spatial scaling of interactions.** Expected number of host-parasite interactions in a network aggregating all (a) local and (b) regional probabilistic interactions within a latitudinal window of a given width. Every dashed curve corresponds to a different window centered at a given latitude (color bar), with the pink solid line representing the median number of interactions across windows. Heatmaps of the expected number of (c) local and (d) regional interactions found in windows of specified width and position (central latitude). Probabilities of regional interactions were obtained with a false positive rate of 5% and a false negative rate of 10%. Local probabilistic interactions were derived from regional probabilistic interactions by setting the value of  $P(L_{i,j,k}|M_{i,j})$  (the local probability of interaction among potentially interacting species) to 1. Aggregated local networks were obtained by aggregating both the species and interactions found within a particular latitudinal window, with the values of  $P(L_{i,j,k}|M_{i,j})$  remaining at their maximum value of 1.

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#### Box 4: Taxonomic scaling of interactions

Given that our interpretation of the properties of ecological networks depends on their taxonomic level (Guimarães 2020), investigating the taxonomic scaling of interactions (i.e., how interaction probabilities

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change with taxonomic level) is important. There are no inherent differences between the taxonomic scaling of local and regional interactions. The taxonomic level of interactions impacts the definition of nodes. Local and regional interaction probabilities are not directly conditioned on taxonomic scale. However, some conditional variables (e.g., trait distribution) may covary with taxonomic scale. In such cases, local and regional interaction probabilities would change taxonomically following the scaling of these variables.

In both types of interactions, transitioning to a broader level of organization (e.g., from a species-level network  $S$  to a genus-level network  $G$ ) can be done using interaction probabilities from finer scales. For example, in a network with  $n_1$  species of genus  $g_1$  and  $n_2$  species of genus  $g_2$ , one can calculate the probability that at least one species from genus  $g_1$  interacts with at least one species from genus  $g_2$  (i.e., the probability that the genus-level interaction occurs) as follows:

$$P(G_{g_1,g_2}) = 1 - \prod_{i=1}^{n_1} \prod_{j=1}^{n_2} (1 - P(S_{g_1,i,g_2,j})), \quad (16)$$

where  $g_{1,i}$  and  $g_{2,j}$  are the species of the corresponding genus and assuming independence between species-level interactions. In contrast, a different approach is necessary when transitioning from a broader to a finer level of organization. This is because the knowledge of an interaction between two genera does not guarantee that all possible pairwise species combinations will also interact. One possible method is to build a finer-scale network by generating probabilities of interaction through random sampling from a beta distribution, parameterized by the broader-scale network.

Fundamentally, the taxonomic scaling of interactions involves aggregating interactions between individuals into larger groups. Interaction probabilities at broader taxonomic scales should thus be conform to probabilities of interactions between individuals. For example, Canard *et al.* (2012) built a species-based network using simulated individual-based networks. In local individual-based food webs, the probability that two individuals interact reflects our degree of belief that one individual will consume the other. Likewise, in local species-based food webs, the probability that two species interact represents our degree of belief that *at least* one individual from the predator species will consume at least another individual from the prey species. In that regard, taxonomic scaling is analogous to the spatial and temporal scaling of interactions, as they all represent different ways to aggregate individuals into broader groups (either spatially, temporally, or taxonomically).

### Box 5: Sampling for binary interaction networks

Networks of binary interactions may be predicted by performing independent Bernoulli trials for each probabilistic interaction. This is particularly useful when analyzing the structure of probabilistic interaction networks in the absence of specific analytical formulas (Poisot *et al.* 2016), even though it may introduce biases in our estimations when connectance is low (Chagnon 2015; Poisot & Gravel 2014). There are at least two techniques to sampling binary interaction networks across space, each predicting a binary interaction network for each location  $k$  within a given region. The first technique involves performing a single Bernoulli trial for each pair of taxa based on their regional probability of interaction:

$$M_{i,j} \sim \text{Bernoulli}(P(M_{i,j})).$$

In employing this technique, we predict a single metaweb of binary interactions for each simulation. Every pair of taxa predicted to interact in this metaweb will be treated as interacting in all localized networks where they co-occur, i.e.  $L_{i,j,k} = M_{i,j}$  when  $X_{i,j,k} = 1$ . This will result in local pairwise interactions without spatial variation.

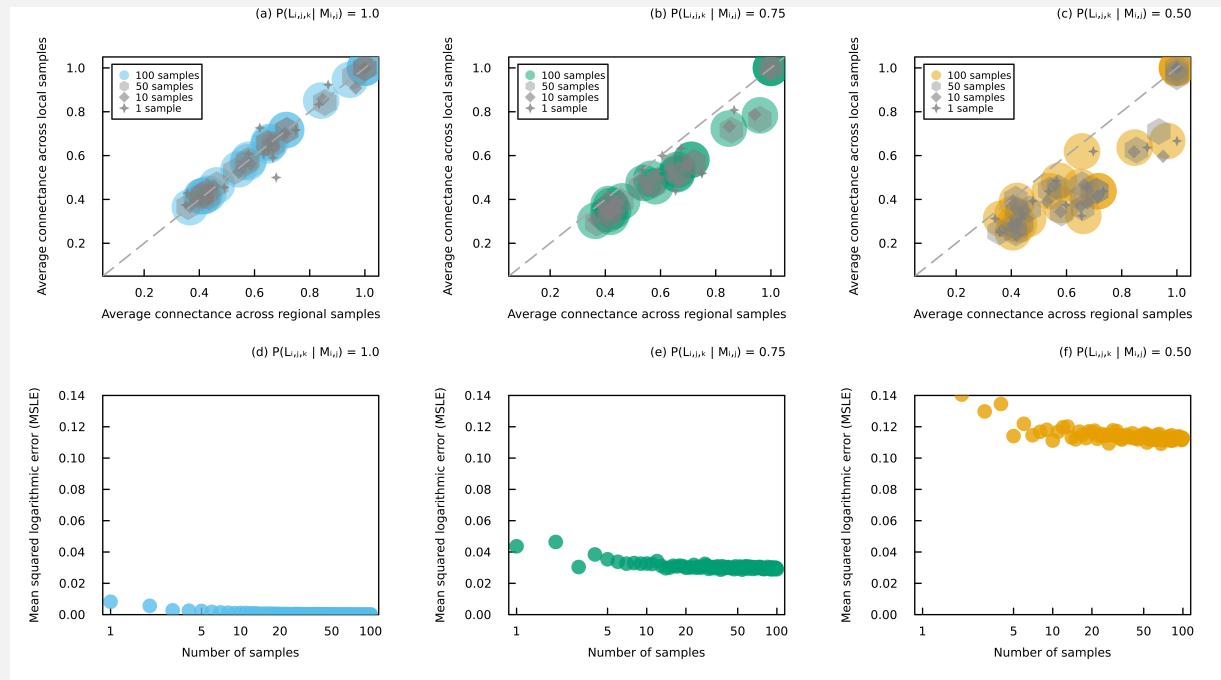
The second technique is to independently sample each local network of probabilistic interactions:

$$L_{i,j,k} \sim \text{Bernoulli}(P(L_{i,j,k})).$$

This can be achieved by first generating distinct probabilistic interaction networks for each location. Because binary interactions are sampled independently for each location, this second technique captures network structure across space and time more effectively. When sampling binary interactions from local interaction probabilities, it is crucial to sample at the same spatial scale for which probabilities were estimated to prevent systematic biases in predictions.

In Fig. 4, we compare the average connectance of binary interaction networks resulting from these two sampling techniques. We sampled regional and local interactions from our host-parasite networks of probabilistic interactions (Kopelke *et al.* 2017), generating a number of binary interaction network realizations for each site in the dataset. These two sampling techniques yield different outcomes, particularly for intermediate values of  $P(L_{i,j,k}|M_{i,j})$  of 0.50, which represent instances where regional

interactions do not consistently manifest locally (i.e., with the largest local variability). As anticipated, we observe that sampling binary interactions from the metaweb tends to overestimate connectance on average compared to sampling them from local networks (Fig. 4). We also observe an increase in the variability of connectance when employing a single simulation (Fig. 4a-c, cross markers), which is a more tangible representation of the process leading to the realization of local interactions in nature. All data manipulation and methods are described in Appendix 1.



**Figure 4: Connectance of sampled binary interaction networks.** (a-c) Average connectance of binary interaction networks obtained from the two sampling techniques for 20 randomly selected host-parasite networks. Cross markers represent the connectance of a single sample for each network, diamond markers the average connectance across 10 samples, hexagon markers the average connectance across 50 samples, and the colored circles the average connectance across 100 samples (marker size proportional to the number of samples). (d-f) Reduction in the mean squared logarithmic error between the average connectance of binary interaction networks (all 233 host-parasite networks) obtained from these two sampling techniques as the number of samples increases. The local probability of interaction between potentially interacting species was set to three different values: (a,d)  $P(L_{i,j,k}|M_{i,j}) = 1.0$ , (b,e)  $P(L_{i,j,k}|M_{i,j}) = 0.75$ , and (c,f)  $P(L_{i,j,k}|M_{i,j}) = 0.50$ . Probabilities of regional interactions were obtained with a false positive rate of 5% and a false negative rate of 10%. Regional samples were obtained by randomly sampling binary interactions from the probabilistic interaction metaweb, and then propagating this result to all local networks that include the species potentially engaged in the interactions. Local samples were obtained by independently sampling binary interactions for each local network of probabilistic interactions.

Both sampling techniques assume independence between interactions, which might not hold true in reality.

Covariation among interactions could exist even if we do not explicitly condition interactions on others. For example, an interaction between two taxa could be more probable when another interaction occurs. The consequences of this assumption of independence on the prediction of network structure have yet to be empirically examined.

401

## 402 Conclusion

403 In this contribution, we underline the importance of network documentation for adequately interpreting and  
404 manipulating probabilistic interaction data. The mathematical representation of probabilities and their statistical  
405 properties depend on the type of interactions (local or regional) and the conditions under which these  
406 interactions were evaluated. We showed that local networks and metawebs of probabilistic interactions differ in  
407 their relationship to spatial and temporal scales (Box 3), with regional interactions remaining consistent across  
408 scales. In contrast with metawebs, local interactions are measured in a specific context (e.g., in a given area,  
409 time, and biological and environmental conditions) and depend on taxa co-occurrence. These differences bring  
410 to light the need to use probabilistic data with caution, for instance when generating network realizations of  
411 binary interactions across space (Box 5). Clear documentation describing the type of interaction and the  
412 variables used in their estimation are required to ensure adequate data manipulation. Sound data practices and  
413 foundations for probabilistic thinking in network ecology facilitate reliable assessments of the spatiotemporal  
414 variability and uncertainty of biotic interactions. Here we identify key research priorities for improving our  
415 understanding of local and regional interactions and their stochasticity.

### 416 Predicting local networks from metawebs

417 Metawebs are a valuable source of ecological information for predicting local networks across time and space.  
418 Local networks of binary interactions can be reconstructed by selecting a subset of taxa and interactions from  
419 the metaweb (Dunne 2006). Metawebs thus contain more interactions than local networks, even though their  
420 connectance is usually much smaller than the one of local networks (Gravel *et al.* 2011). Determining the list of  
421 taxa to select can be achieved empirically (e.g., observed occurrence data for a site) or numerically (e.g., species  
422 distribution models). As species composition is arguably easier to sample or predict than pairwise interactions,  
423 the primary challenge lies in deciding which interactions to select from the metaweb. Inferring the structure of

424 local networks from the metaweb before predicting local pairwise interactions could hold promise (Strydom *et*  
 425 *al.* 2021), considering that the structure of local networks is constrained by the metaweb (Saravia *et al.* 2022).  
 426 Inferring local networks of probabilistic interactions from a metaweb comes with its own set of challenges. For  
 427 example, Dansereau *et al.* (2023) inferred spatially-explicit food webs from a metaweb of probabilistic trophic  
 428 interactions between Canadian mammals. Their predicted localized food webs are downscaled versions of the  
 429 metaweb (i.e., localized metawebs with the same interaction probabilities as those in the regional metaweb). To  
 430 infer local networks as defined in this manuscript (i.e., describing local realizations of interactions), local  
 431 interaction probabilities must be smaller than regional interaction probabilities. This decrease is due to the  
 432 prerequisite that two taxa must initially possess the capacity to interact before engaging in local interactions  
 433 (Eq. 3). Inferring local networks from a metaweb by maintaining identical interaction probability values  
 434 introduces systematic biases into the predictions, as discussed in Box 2 (unless networks are seen as downscaled  
 435 metawebs).

436 As suggested by McLeod *et al.* (2021), although metawebs do not capture the spatiotemporal variability of  
 437 interactions, they establish an upper limit for local interactions (similarly for metawebs of probabilistic  
 438 interactions, Strydom *et al.* 2023). In other words, the probability that two taxa interact at a specific location  
 439 and time is consistently lower or equal to the probability of their regional interaction, regardless of the  
 440 conditional variables considered:

$$P(L_{i,j,k}|...) \leq P(M_{i,j}|T_i, T_j). \quad (17)$$

441 Moreover, the probability that two taxa possess the biological capacity to interact must be higher than the  
 442 probability of them interacting at any location and time because they may never co-occur or encounter locally.  
 443 Specifically, the cumulative probability of local interaction across all spatial, temporal, and environmental  
 444 conditions must be less than the probability of regional interaction, i.e.

$$\int_{E_k} \int_A \int_t P(L_{i,j,k}|E_k, A, t) dt dA dE_k \leq P(M_{i,j}|T_i, T_j). \quad (18)$$

445 Estimating more precisely the probability  $P(L_{i,j,k}|M_{i,j})$  that two taxa interact locally if they can potentially  
 446 interact allows for improved predictions of local networks from the metaweb of probabilistic interactions. This  
 447 task is challenging due to the variability of this probability across space and time, as well as its variability

448 across pairwise interactions within a network. Using simple models of  $P(L_{i,j,k}|M_{i,j})$ , as shown in Box 2,  
449 represents an initial step toward the overarching objective of reconstructing local networks from metawebs.

450 **Quantifying and reducing interaction uncertainty**

451 While sampling biological communities decreases the uncertainty of interactions by accumulating evidence for  
452 their feasibility and local realization, there is a limit to how much we can reduce uncertainty. In metawebs,  
453 probabilities reflect our limited knowledge of interactions (i.e., our degree of belief that interactions are  
454 feasible), which is expected to improve with a larger volume of data. Regional interactions should become more  
455 definitive (with probabilities approaching 0 or 1) as we investigate various conditions, including different  
456 combinations of species traits.

457 In comparison, although local networks can be seen as random instances of metawebs, their stochasticity cannot  
458 be reduced to the same extent. Local interaction probabilities may represent both their uncertainty and  
459 spatiotemporal variability. Owing to environmental heterogeneity, there will invariably be instances in which an  
460 interaction occurs and others in which it does not, across different times and locations, irrespective of the extent  
461 to which we can improve our knowledge of its biological feasibility and the local conditions that facilitate its  
462 occurrence. When local networks describe probabilities of observing interactions rather than their actual  
463 occurrence, we must also consider observation variability (sampling error) as an additional source of  
464 stochasticity. Every ecological process is stochastic but there is also a possibility that a phenomenon goes  
465 undetected. Quantifying and partitioning this stochasticity will enable us to make more accurate predictions  
466 about ecological interactions at various spatial and temporal scales. This will prove to be of vital importance as  
467 our time to understand nature runs out, especially at locations where the impacts of climate change and habitat  
468 loss hit harder.

469 **Relaxing the independence assumption**

470 Estimating local interaction probabilities independently for each taxa pair and assembling them into a network  
471 of probabilistic interactions comes with limitations. Predicting local networks of binary interactions based on  
472 these interaction probabilities assumes independence among interactions, a condition seldom respected in  
473 practice (Golubski & Abrams 2011). Relaxing this assumption is the next logical step in the stochastic  
474 representation of interactions.

475 A more accurate representation of the stochasticity of ecological networks involves creating *probabilistic*  
476 *networks* ( $P(L|...)$  and  $P(M|...)$ ), rather than networks of *probabilistic interactions* ( $P(L_{i,j,k}|...)$  and  $P(M_{i,j}|...)$ ).  
477 Probabilistic networks describe the probability that a particular network of binary (or quantitative) interactions  
478 (its whole adjacency matrix) is realized. For example, Young *et al.* (2021) used a Bayesian approach to estimate  
479 the probability of different plant-pollinator network structures derived from imperfect observational data. A  
480 probability distribution of ecological networks may also be derived using the principle of maximum entropy  
481 given structural constrained (e.g., Cimini *et al.* 2019; Park & Newman 2004).  
  
482 Regardless of the method employed, generating probabilistic local networks could lead to more accurate  
483 predictions of local networks of binary interactions by bypassing the independence assumption. Probabilistic  
484 networks could serve as an alternative to null hypothesis significance testing when comparing the structure of a  
485 local network to some random expectations or, as done in Pellissier *et al.* (2018), to the metaweb. These random  
486 expectations are typically derived by performing a series of Bernoulli trials on probabilistic interactions,  
487 assuming independence, to generate a distribution of networks of binary interactions to calculate their structure  
488 (Poisot *et al.* 2016). One could for instance compare the likelihood of an observed network to the one of the  
489 most likely network structure (according to the probabilistic network distribution), thereby directly obtaining a  
490 measure of discrepancy of the empirical network. Generating probabilistic ecological networks represents a  
491 tangible challenge, one that, in the coming years, promises to unlock doors to more advanced and adequate  
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501 **References**

- 502 Abrego, N., Roslin, T., Huotari, T., Ji, Y., Schmidt, N.M., Wang, J., *et al.* (2021). Accounting for species  
503 interactions is necessary for predicting how arctic arthropod communities respond to climate change.  
504 *Ecography*, 44, 885–896.
- 505 Angilletta, M.J., Jr., Steury, T.D. & Sears, M.W. (2004). Temperature, Growth Rate, and Body Size in  
506 Ectotherms: Fitting Pieces of a Life-History Puzzle<sup>1</sup>. *Integrative and Comparative Biology*, 44, 498–509.
- 507 Araujo, M.B., Rozenfeld, A., Rahbek, C. & Marquet, P.A. (2011). Using species co-occurrence networks to  
508 assess the impacts of climate change. *Ecography*, 34, 897–908.
- 509 Bartomeus, I., Gravel, D., Tylianakis, J.M., Aizen, M.A., Dickie, I.A. & Bernard-Verdier, M. (2016). A  
510 common framework for identifying linkage rules across different types of interactions. *Functional Ecology*,  
511 30, 1894–1903.
- 512 Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003). The nested assembly of plant–animal  
513 mutualistic networks. *Proceedings of the National Academy of Sciences*, 100, 9383–9387.
- 514 Berg, M.P. & Ellers, J. (2010). Trait plasticity in species interactions: A driving force of community dynamics.  
515 *Evolutionary Ecology*, 24, 617–629.
- 516 Berlow, E.L., Neutel, A.-M., Cohen, J.E., De Ruiter, P.C., Ebenman, B., Emmerson, M., *et al.* (2004).  
517 Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73, 585–598.
- 518 Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., *et al.* (2011). Why  
519 intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26, 183–192.
- 520 Borrett, S.R. & Scharler, U.M. (2019). Walk partitions of flow in Ecological Network Analysis: Review and  
521 synthesis of methods and indicators. *Ecological Indicators*, 106, 105451.
- 522 Boulangeat, I., Gravel, D. & Thuiller, W. (2012). Accounting for dispersal and biotic interactions to disentangle  
523 the drivers of species distributions and their abundances. *Ecology Letters*, 15, 584–593.
- 524 Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T. & Fortin, M.-J. (2023). Shortcomings of reusing  
525 species interaction networks created by different sets of researchers. *PLOS Biology*, 21, e3002068.
- 526 Broom, M. & Ruxton, G.D. (2005). You can run—or you can hide: Optimal strategies for cryptic prey against  
527 pursuit predators. *Behavioral Ecology*, 16, 534–540.

- 528 Burnham, K.P. & Anderson, D.R. (2004). [Multimodel Inference: Understanding AIC and BIC in Model](#)  
529 [Selection](#). *Sociological Methods & Research*, 33, 261–304.
- 530 Canard, E.F., Mouquet, N., Mouillot, D., Stanko, M., Miklisova, D. & Gravel, D. (2014). [Empirical Evaluation](#)  
531 [of Neutral Interactions in Host-Parasite Networks](#). *The American Naturalist*, 183, 468–479.
- 532 Canard, E., Mouquet, N., Marescot, L., Gaston, K.J., Gravel, D. & Mouillot, D. (2012). [Emergence of](#)  
533 [Structural Patterns in Neutral Trophic Networks](#). *PLOS ONE*, 7, e38295.
- 534 Carlson, C.J., Farrell, M.J., Grange, Z., Han, B.A., Mollentze, N., Phelan, A.L., et al. (2021). [The future of](#)  
535 [zoonotic risk prediction](#). *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376,  
536 20200358.
- 537 Caron, D., Brose, U., Lurgi, M., Blanchet, F.G., Gravel, D. & Pollock, L.J. (2024). [Trait-matching models](#)  
538 [predict pairwise interactions across regions, not food web properties](#). *Global Ecology and Biogeography*,  
539 33, e13807.
- 540 Castoe, T.A., Spencer, C.L. & Parkinson, C.L. (2007). [Phylogeographic structure and historical demography of](#)  
541 [the western diamondback rattlesnake \(\*Crotalus Atrox\*\): A perspective on North American desert](#)  
542 [biogeography](#). *Molecular Phylogenetics and Evolution*, 42, 193–212.
- 543 Catchen, M.D., Poisot, T., Pollock, L.J. & Gonzalez, A. (2023). [The missing link: Discerning true from false](#)  
544 [negatives when sampling species interaction networks](#).
- 545 Cazelles, K., Araujo, M.B., Mouquet, N. & Gravel, D. (2016). [A theory for species co-occurrence in interaction](#)  
546 [networks](#). *Theoretical Ecology*, 9, 39–48.
- 547 Chagnon, P.-L. (2015). [Characterizing topology of ecological networks along gradients: The limits of metrics'](#)  
548 [standardization](#). *Ecological Complexity*, 22, 36–39.
- 549 Choh, Y., Ignacio, M., Sabelis, M.W. & Janssen, A. (2012). [Predator-prey role reversals, juvenile experience](#)  
550 [and adult antipredator behaviour](#). *Scientific Reports*, 2, 728.
- 551 Cimini, G., Squartini, T., Saracco, F., Garlaschelli, D., Gabrielli, A. & Caldarelli, G. (2019). [The statistical](#)  
552 [physics of real-world networks](#). *Nature Reviews Physics*, 1, 58–71.
- 553 Cirtwill, A.R., Eklöf, A., Roslin, T., Wootton, K. & Gravel, D. (2019). [A quantitative framework for](#)  
554 [investigating the reliability of empirical network construction](#). *Methods in Ecology and Evolution*, 10,  
555 902–911.

- 556 Dallas, T., Park, A.W. & Drake, J.M. (2017). [Predicting cryptic links in host-parasite networks](#). *PLOS Computational Biology*, 13, e1005557.
- 558 Dansereau, G., Barros, C. & Poisot, T. (2023). Spatially explicit predictions of food web structure from regional  
559 level data.
- 560 Dunne, J.A. (2006). The Network Structure of Food Webs. In: *Ecological networks: Linking structure and dynamics* (eds. Dunne, J.A. & Pascual, M.). Oxford University Press, pp. 27–86.
- 562 Elmasri, M., Farrell, M.J., Davies, T.J. & Stephens, D.A. (2020). [A hierarchical Bayesian model for predicting ecological interactions using scaled evolutionary relationships](#). *The Annals of Applied Statistics*, 14, 563 221–240.
- 565 Elton, C.S. (2001). *Animal Ecology*. University of Chicago Press, Chicago, IL.
- 566 Emmerson, M.C. & Raffaelli, D. (2004). [Predator–prey body size, interaction strength and the stability of a real food web](#). *Journal of Animal Ecology*, 73, 399–409.
- 568 Fedorov, V.B., Goropashnaya, A.V., Boeskorov, G.G. & Cook, J.A. (2008). [Comparative phylogeography and demographic history of the wood lemming \(\*Myopus schisticolor\*\): Implications for late Quaternary history of the taiga species in Eurasia](#). *Molecular Ecology*, 17, 598–610.
- 571 Fortuna, M.A. & Bascompte, J. (2006). [Habitat loss and the structure of plant–animal mutualistic networks](#).  
572 *Ecology Letters*, 9, 281–286.
- 573 Fu, X., Seo, E., Clarke, J. & Hutchinson, R.A. (2021). [Link Prediction Under Imperfect Detection: Collaborative Filtering for Ecological Networks](#). *IEEE Transactions on Knowledge and Data Engineering*, 574 33, 3117–3128.
- 576 Galiana, N., Lurgi, M., Claramunt-López, B., Fortin, M.-J., Leroux, S., Cazelles, K., et al. (2018). [The spatial scaling of species interaction networks](#). *Nature Ecology & Evolution*, 2, 782–790.
- 578 Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010). [A framework for community interactions under climate change](#). *Trends in Ecology & Evolution*, 25, 325–331.
- 580 Godsoe, W., Murray, R. & Iritani, R. (2022). [Species interactions and diversity: A unified framework using Hill numbers](#). *Oikos*, n/a, e09282.
- 582 Golubski, A.J. & Abrams, P.A. (2011). [Modifying modifiers: What happens when interspecific interactions interact?](#) *Journal of Animal Ecology*, 80, 1097–1108.

- 584 Gonzalez, A. & Londoño, M.C. (2022). Monitor biodiversity for action. *Science*, 378, 1147–1147.
- 585 Gonzalez-Varo, J.P. & Traveset, A. (2016). The Labile Limits of Forbidden Interactions. *Trends in Ecology &*  
586 *Evolution*, 31, 700–710.
- 587 Gravel, D., Baiser, B., Dunne, J.A., Kopelke, J.-P., Martinez, N.D., Nyman, T., *et al.* (2019). Bringing Elton  
588 and Grinnell together: A quantitative framework to represent the biogeography of ecological interaction  
589 networks. *Ecography*, 42, 401–415.
- 590 Gravel, D., Massol, F., Canard, E., Mouillot, D. & Mouquet, N. (2011). Trophic theory of island biogeography.  
591 *Ecology Letters*, 14, 1010–1016.
- 592 Gravel, D., Poisot, T., Albouy, C., Velez, L. & Mouillot, D. (2013). Inferring food web structure from  
593 predator–prey body size relationships. *Methods in Ecology and Evolution*, 4, 1083–1090.
- 594 Guimarães, P.R. (2020). The Structure of Ecological Networks Across Levels of Organization. *Annual Review  
595 of Ecology, Evolution, and Systematics*, 51, 433–460.
- 596 Guimerà, R. & Sales-Pardo, M. (2009). Missing and spurious interactions and the reconstruction of complex  
597 networks. *Proceedings of the National Academy of Sciences*, 106, 22073–22078.
- 598 Hemprich-Bennett, D.R., Oliveira, H.F.M., Le Comber, S.C., Rossiter, S.J. & Clare, E.L. (2021). Assessing the  
599 impact of taxon resolution on network structure. *Ecology*, 102, e03256.
- 600 Herrera, C.M. (1989). Pollinator abundance, morphology, and flower visitation rate: Analysis of the “quantity”  
601 component in a plant-pollinator system. *Oecologia*, 80, 241–248.
- 602 Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M. & Ladle, R.J. (2015). Seven Shortfalls  
603 that Beset Large-Scale Knowledge of Biodiversity. *Annual Review of Ecology, Evolution, and Systematics*,  
604 46, 523–549.
- 605 Jordano, P. (1987). Patterns of Mutualistic Interactions in Pollination and Seed Dispersal: Connectance,  
606 Dependence Asymmetries, and Coevolution. *The American Naturalist*, 129, 657–677.
- 607 Jordano, P. (2016). Sampling networks of ecological interactions. *Functional Ecology*, 30, 1883–1893.
- 608 Jordano, P., Bascompte, J. & Olesen, J.M. (2003). Invariant properties in coevolutionary networks of  
609 plant–animal interactions. *Ecology Letters*, 6, 69–81.

- 610 Kausrud, K.L., Mysterud, A., Steen, H., Vik, J.O., Østbye, E., Cazelles, B., *et al.* (2008). [Linking climate](#)  
611 [change to lemming cycles](#). *Nature*, 456, 93–97.
- 612 Kéfi, S., Berlow, E.L., Wieters, E.A., Joppa, L.N., Wood, S.A., Brose, U., *et al.* (2015). [Network structure](#)  
613 [beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky shores](#). *Ecology*, 96,  
614 291–303.
- 615 Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., *et al.* (2012). [More than a](#)  
616 [meal... integrating non-feeding interactions into food webs](#). *Ecology Letters*, 15, 291–300.
- 617 Kéfi, S., Miele, V., Wieters, E.A., Navarrete, S.A. & Berlow, E.L. (2016). [How Structured Is the Entangled](#)  
618 [Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks Leads to Increased](#)  
619 [Persistence and Resilience](#). *PLOS Biology*, 14, e1002527.
- 620 Kissner, K.J., Forbes, M.R. & Secoy, D.M. (1997). [Rattling Behavior of Prairie Rattlesnakes \(\*Crotalus viridis\*](#)  
621 [viridis, Viperidae\) in Relation to Sex, Reproductive Status, Body Size, and Body Temperature](#). *Ethology*,  
622 103, 1042–1050.
- 623 Klecka, J. & Boukal, D.S. (2014). [The effect of habitat structure on prey mortality depends on predator and](#)  
624 [prey microhabitat use](#). *Oecologia*, 176, 183–191.
- 625 Kopelke, J.-P., Nyman, T., Cazelles, K., Gravel, D., Vissault, S. & Roslin, T. (2017). [Food-web structure of](#)  
626 [willow-galling sawflies and their natural enemies across Europe](#). *Ecology*, 98, 1730–1730.
- 627 Kulkarni, M.A., Kweka, E., Nyale, E., Lyatuu, E., Mosha, F.W., Chandramohan, D., *et al.* (2006).  
628 [Entomological Evaluation of Malaria Vectors at Different Altitudes in Hai District, Northeastern Tanzania](#).  
629 *Journal of Medical Entomology*, 43, 580–588.
- 630 Maiorano, L., Montemaggiori, A., Ficetola, G.F., O'Connor, L. & Thuiller, W. (2020). [TETRA-EU 1.0: A](#)  
631 [species-level trophic metaweb of European tetrapods](#). *Global Ecology and Biogeography*, 29, 1452–1457.
- 632 McCann, K. (2007). Protecting biostructure. *Nature*, 446, 29–29.
- 633 McCann, K.S. (2011). Food webs (MPB-50). In: *Food Webs (MPB-50)*. Princeton University Press.
- 634 McLeod, A., Leroux, S.J., Gravel, D., Chu, C., Cirtwill, A.R., Fortin, M.-J., *et al.* (2021). [Sampling and](#)  
635 [asymptotic network properties of spatial multi-trophic networks](#). *Oikos*, n/a.
- 636 Melián, C.J., Vilas, C., Baldó, F., González-Ortegón, E., Drake, P. & Williams, R.J. (2011). [Eco-evolutionary](#)  
637 [Dynamics of Individual-Based Food Webs](#). In: *Advances in Ecological Research*, The Role of Body Size in

- 638 Multispecies Systems (ed. Belgrano, A.). Academic Press, pp. 225–268.
- 639 Morales-Castilla, I., Matias, M.G., Gravel, D. & Araújo, M.B. (2015). Inferring biotic interactions from  
640 proxies. *Trends in Ecology & Evolution*, 30, 347–356.
- 641 Ohlmann, M., Miele, V., Dray, S., Chalmandrier, L., O'Connor, L. & Thuiller, W. (2019). Diversity indices for  
642 ecological networks: A unifying framework using Hill numbers. *Ecology Letters*, 22, 737–747.
- 643 Olesen, J.M., Bascompte, J., Dupont, Y.L., Elberling, H., Rasmussen, C. & Jordano, P. (2010). Missing and  
644 forbidden links in mutualistic networks. *Proceedings of the Royal Society B: Biological Sciences*, 278,  
645 725–732.
- 646 Park, J. & Newman, M.E.J. (2004). Statistical mechanics of networks. *Physical Review E*, 70, 066117.
- 647 Pascual, M., Dunne, J.A. & Dunne, J.A. (2006). *Ecological Networks: Linking Structure to Dynamics in Food  
648 Webs*. Oxford University Press, USA.
- 649 Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., et al. (2018). Comparing species  
650 interaction networks along environmental gradients. *Biological Reviews*, 93, 785–800.
- 651 Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2008). Size, foraging, and food web structure.  
652 *Proceedings of the National Academy of Sciences*, 105, 4191–4196.
- 653 Pilosof, S., Porter, M.A., Pascual, M. & Kéfi, S. (2017). The multilayer nature of ecological networks. *Nature  
654 Ecology & Evolution*, 1, 1–9.
- 655 Plagányi, É.E. & Butterworth, D.S. (2004). A critical look at the potential of Ecopath with ecosim to assist in  
656 practical fisheries management. *African Journal of Marine Science*, 26, 261–287.
- 657 Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D. (2012). The dissimilarity of species interaction  
658 networks. *Ecology Letters*, 15, 1353–1361.
- 659 Poisot, T., Cirtwill, A.R., Cazelles, K., Gravel, D., Fortin, M.-J. & Stouffer, D.B. (2016). The structure of  
660 probabilistic networks. *Methods in Ecology and Evolution*, 7, 303–312.
- 661 Poisot, T. & Gravel, D. (2014). When is an ecological network complex? Connectance drives degree  
662 distribution and emerging network properties. *PeerJ*, 2, e251.
- 663 Poisot, T., Stouffer, D.B. & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary  
664 through space and time. *Oikos*, 124, 243–251.

- 665 Polis, G.A. (1991). [Complex Trophic Interactions in Deserts: An Empirical Critique of Food-Web Theory](#). *The  
666 American Naturalist*, 138, 123–155.
- 667 Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O’Hara, R.B., Parris, K.M., *et al.* (2014). [Understanding  
668 co-occurrence by modelling species simultaneously with a Joint Species Distribution Model \(JSDM\)](#).  
669 *Methods in Ecology and Evolution*, 5, 397–406.
- 670 Pomeranz, J.P.F., Thompson, R.M., Poisot, T. & Harding, J.S. (2019). [Inferring predator–prey interactions in  
671 food webs](#). *Methods in Ecology and Evolution*, 10, 356–367.
- 672 Pringle, R.M. & Hutchinson, M.C. (2020). [Resolving Food-Web Structure](#). *Annual Review of Ecology,  
673 Evolution, and Systematics*, 51, 55–80.
- 674 Proulx, S.R., Promislow, D.E.L. & Phillips, P.C. (2005). [Network thinking in ecology and evolution](#). *Trends in  
675 Ecology & Evolution*, SPECIAL ISSUE: BUMPER BOOK REVIEW, 20, 345–353.
- 676 Pulliam, H.R. (1974). [On the Theory of Optimal Diets](#). *The American Naturalist*, 108, 59–74.
- 677 Rooney, N. & McCann, K.S. (2012). [Integrating food web diversity, structure and stability](#). *Trends in Ecology  
678 & Evolution*, 27, 40–46.
- 679 Salim, J.A., Saraiva, A.M., Zermoglio, P.F., Agostini, K., Wolowski, M., Drucker, D.P., *et al.* (2022). [Data  
680 standardization of plant–pollinator interactions](#). *GigaScience*, 11, giac043.
- 681 Sanders, D. & van Veen, F.J.F. (2012). [Indirect commensalism promotes persistence of secondary consumer  
682 species](#). *Biology Letters*, 8, 960–963.
- 683 Saravia, L.A., Marina, T.I., Kristensen, N.P., De Troch, M. & Momo, F.R. (2022). [Ecological network  
684 assembly: How the regional metaweb influences local food webs](#). *Journal of Animal Ecology*, 91, 630–642.
- 685 Schmeller, D.S., Julliard, R., Bellingham, P.J., Böhm, M., Brummitt, N., Chiarucci, A., *et al.* (2015). [Towards a  
686 global terrestrial species monitoring program](#). *Journal for Nature Conservation*, 25, 51–57.
- 687 Shaw, J.O., Dunhill, A.M., Beckerman, A.P., Dunne, J.A. & Hull, P.M. (2024). [A framework for reconstructing  
688 ancient food webs using functional trait data](#).
- 689 Singer, M.C. & McBride, C.S. (2012). [Geographic mosaics of species’ association: A definition and an  
690 example driven by plant–insect phenological synchrony](#). *Ecology*, 93, 2658–2673.

- 691 Staniczenko, P.P.A., Sivasubramaniam, P., Suttle, K.B. & Pearson, R.G. (2017). [Linking macroecology and](#)  
692 [community ecology: Refining predictions of species distributions using biotic interaction networks.](#)
- 693 *Ecology Letters*, 20, 693–707.
- 694 Stock, M., Poisot, T., Waegeman, W. & De Baets, B. (2017). [Linear filtering reveals false negatives in species](#)  
695 [interaction data.](#) *SCIENTIFIC REPORTS*, 7, 45908.
- 696 Stouffer, D.B., Rezende, E.L. & Amaral, L.A.N. (2011). [The role of body mass in diet contiguity and food-web](#)  
697 [structure.](#) *Journal of Animal Ecology*, 80, 632–639.
- 698 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M.J., *et al.* (2022). [Food web](#)  
699 [reconstruction through phylogenetic transfer of low-rank network representation.](#) *Methods in Ecology and*  
700 *Evolution*, 13.
- 701 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M.J., *et al.* (2023). [Graph embedding and](#)  
702 [transfer learning can help predict potential species interaction networks despite data limitations.](#) *Methods in*  
703 *Ecology and Evolution*, 14, 2917–2930.
- 704 Strydom, T., Catchen, M.D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., *et al.* (2021). [A](#)  
705 [roadmap towards predicting species interaction networks \(across space and time\).](#) *Philosophical*  
706 *Transactions of the Royal Society B-Biological Sciences*, 376, 20210063.
- 707 Tylianakis, J.M., Tscharntke, T. & Lewis, O.T. (2007). [Habitat modification alters the structure of tropical](#)  
708 [host-parasitoid food webs.](#) *Nature*, 445, 202–205.
- 709 Vázquez, D.P., Melián, C.J., Williams, N.M., Blüthgen, N., Krasnov, B.R. & Poulin, R. (2007). [Species](#)  
710 [abundance and asymmetric interaction strength in ecological networks.](#) *Oikos*, 116, 1120–1127.
- 711 Wagenmakers, E.-J. & Farrell, S. (2004). [AIC model selection using Akaike weights.](#) *Psychonomic Bulletin &*  
712 *Review*, 11, 192–196.
- 713 Weinstein, B.G. & Graham, C.H. (2017a). [On comparing traits and abundance for predicting species](#)  
714 [interactions with imperfect detection.](#) *Food Webs*, 11, 17–25.
- 715 Weinstein, B.G. & Graham, C.H. (2017b). [Persistent bill and corolla matching despite shifting temporal](#)  
716 [resources in tropical hummingbird-plant interactions.](#) *Ecology Letters*, 20, 326–335.
- 717 Woodward, G., Benstead, J.P., Beveridge, O.S., Blanchard, J., Brey, T., Brown, L.E., *et al.* (2010). [Chapter 2 -](#)  
718 [Ecological Networks in a Changing Climate.](#) In: *Advances in Ecological Research*, Ecological Networks

- 719 (ed. Woodward, G.). Academic Press, pp. 71–138.
- 720 Woodward, G., Brown, L.E., Edwards, F.K., Hudson, L.N., Milner, A.M., Reuman, D.C., *et al.* (2012). [Climate](#)  
721 [change impacts in multispecies systems: Drought alters food web size structure in a field experiment.](#)
- 722 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 2990–2997.
- 723 Young, J.-G., Valdovinos, F.S. & Newman, M.E.J. (2021). [Reconstruction of plant–pollinator networks from](#)  
724 [observational data](#). *Nature Communications*, 12, 3911.