

# The ecological interpretation of probabilistic networks

Francis Banville<sup>1,2,3</sup> Tanya Strydom<sup>1,3</sup> Chris Brimacombe<sup>4</sup> Michael Catchen<sup>3,5</sup> Dominique Gravel<sup>2,3</sup>

Gracielle Higino<sup>2</sup> Kari Norman<sup>1</sup> Timothée Poisot<sup>1,3</sup>

<sup>1</sup> Université de Montréal <sup>2</sup> Université de Sherbrooke <sup>3</sup> Quebec Centre for Biodiversity Science <sup>4</sup> University of Toronto <sup>5</sup> McGill University

## Correspondance to:

Francis Banville — francis.banville@umontreal.ca

The stochastic nature of ecological interactions has led biologists to adopt a probabilistic view of ecological networks. Representing species interactions probabilistically (how likely are they occurring?) as opposed to deterministically (are they occurring?) allows a better assessment of their spatiotemporal variability and accounts for inherent uncertainties in both observations and predictions. However, despite this growing interest in probabilistic networks, guidelines for the estimation and documentation of probabilistic interaction data are still lacking. This is concerning given that our biological understanding of probabilistic interactions and their appropriate analyses depend on the often elusive methods and variables used for their estimation. We review how probabilistic interactions are defined at different spatial scales, from local interactions to regional networks (metawebs), with a strong emphasis on trophic interactions. These definitions are based on the distinction between the observation of an interaction at a specific time and space and its biological feasibility. We show that different network representations have different statistical properties when it comes to common ecological applications. Specifically, we argue that local probabilistic networks and metawebs differ in their spatial and temporal scaling of interactions, with potential interactions in metawebs remaining constant across spatial and temporal scales. This is in contrast with the taxonomic scaling of interactions, which does not qualitatively differ between both types of networks. We suggest two approaches to inferring deterministic networks from probabilistic webs that account for these differences and argue that systematic biases arise when directly inferring local networks from subsets of metawebs. To support our arguments, we build a spatiotemporally explicit model of probabilistic interactions and develop different case studies using empirical data on host-parasite interactions in Europe. Overall, our results underscore the importance of clear metadata for

probabilistic ecological networks, both at the local and regional scales, to inform the appropriate reuse of interaction data.

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## **1 Introduction**

2 Cataloging ecological interactions is a substantial challenge. There are methodological and biological  
3 constraints that hinder our ability to observe all interactions, such as the spatial and temporal uncoupling of  
4 species (Jordano (1987)) and the large number of possible interactions in a community, of which the vast  
5 majority are rare (Jordano (2016)). Documenting the location and timing of interactions becomes even more  
6 difficult when accounting for the spatiotemporal variability of ecological networks (Poisot *et al.* (2012), Poisot  
7 *et al.* (2015)). Indeed, knowing the biological capacity of two species to interact is necessary but not sufficient  
8 for inferring their interaction at a specific time and space. For example, Golubski & Abrams (2011) presented  
9 many cases where trophic interactions in food webs depend on the presence or abundance of a third species  
10 (e.g., of a more profitable prey species). More generally, a handful of conditions must be satisfied for an  
11 interaction to be observed locally. First, both species must have overlapping geographic ranges, i.e. they must  
12 co-occur within the region of interest (Blanchet *et al.* (2020)). Then, they must encounter locally. Probabilities  
13 of interspecific encounters are typically low, especially for rare species with low relative abundances (Canard *et*  
14 *al.* (2012)). Finally, their traits must be locally compatible (Poisot *et al.* (2015)). This includes their phenology  
15 (Olesen *et al.* (2010), Singer & McBride (2012)), behavioral choices (Pulliam (1974), Choh *et al.* (2012)) and  
16 phenotypes (Bolnick *et al.* (2011), Stouffer *et al.* (2011), Gravel *et al.* (2013)). Environmental factors, such as  
17 temperature (Angilletta *et al.* (2004)), drought (Woodward *et al.* (2012)), climate change (Gilman *et al.* (2010),  
18 Woodward *et al.* (2010), Araujo *et al.* (2011)), and habitat modifications (Tylianakis *et al.* (2007)), contribute  
19 to this spatiotemporal variability of interactions by impacting species abundance and traits. In this context, it is  
20 unsurprising that our knowledge of ecological interactions remains limited (Hortal *et al.* (2015)) despite  
21 extensive biodiversity data collection (Schmeller *et al.* (2015)).

22 The recognition of the intrinsic variability of species interactions has led ecologists to expand their  
23 representation of ecological networks to include a probabilistic view of interactions (Poisot *et al.* (2016)). As  
24 opposed to binary deterministic networks, in which interactions are regarded as either occurring or not,  
25 probabilistic networks represent our degree of belief about the realization or feasibility of pairwise interactions  
26 at the local or regional scale, respectively. In other words, representing interactions probabilistically takes into  
27 account inherent uncertainties and variability associated with ecological data. In the broadest sense, binary  
28 networks are also a type of probabilistic network, in which the numerical value of an interaction is restrained to  
29 0 (non-occurring) or 1 (occurring). In probabilistic networks, only forbidden interactions (i.e., interactions

prohibited by biological traits, Jordano *et al.* (2003), Olesen *et al.* (2010)) have a probability value of zero, provided that intraspecific trait variability is considered (Gonzalez-Varo & Traveset (2016)). However, *neutrally* forbidden interactions (i.e., improbable interactions between rare species, Canard *et al.* (2012)) could have low probability values in local networks but high probability in a regional network (metaweb) describing the biological capacity of species to interact.

By accounting for the uncertainty of interactions, probabilistic networks provide a more realistic portrait of species interactions and network structure (i.e. community-level properties), which is a major driver of the functioning, dynamics, and resilience of ecosystems worldwide (Proulx *et al.* (2005), McCann (2007), McCann (2011), Rooney & McCann (2012)). Moreover, the application and development of computational methods in network ecology, often based on a probabilistic representation of interactions, can alleviate the sampling efforts required to document species interactions (Strydom *et al.* (2021)). For example, statistical models can be used to estimate the uncertainty of pairwise interactions (Cirtwill *et al.* (2019)) and the probability of missing (false negatives) and spurious (false positives) interactions (Guimerà & Sales-Pardo (2009)). Considering the high rate of false negatives in species interaction data due to the difficulty of witnessing rare interactions (Catchen *et al.* (2023)), these models could inform the identification of priority sampling locations of ecological networks where data collection would yield the most valuable information, thereby reducing errors. Optimization models for sampling locations have mostly found applications in biological systems that are not networked, such as identifying priority sampling sites for disease hotspots (Andrade-Pacheco *et al.* (2020)), but there is substantial promise in applying them to probabilistic ecological interactions. Statistical models can also be used to generate network predictions without prior knowledge of pairwise interactions, for instance using body size (Petchey *et al.* (2008), Gravel *et al.* (2013)), phylogeny (Elmasri *et al.* (2020), Strydom *et al.* (2022)), or a combination of niche and neutral processes (Bartomeus *et al.* (2016), Pomeranz *et al.* (2019)) for inference. Topological null models (e.g., Bascompte *et al.* (2003), Fortuna & Bascompte (2006)), which can be used to generate underlying distributions of network measures for null hypothesis significance testing, are other examples of common probabilistic network models. Many measures have been developed to describe the structure (Poisot *et al.* (2016)) and diversity (Ohlmann *et al.* (2019), Godsoe *et al.* (2022)) of probabilistic networks. These models and measures support the use of this approach for the study of a wide range of ecological questions, from making better predictions of species distribution (Cazelles *et al.* (2016)) to forecasting the impact of climate change on ecological networks (Gilman *et al.* (2010)).

The lack of clear guidelines on the use of probabilistic interaction data is worrisome (Brimacombe *et al.*

60 (2023)), both for data producers and re-users who generate and manipulate these numbers. Besides  
61 methodological difficulties that may arise when assessing probabilistic interactions, a precise definition of  
62 probabilistic interactions appears to be lacking, making the estimation and use of these data more difficult. We  
63 aim to take a step back by outlining different ways in which probabilistic interactions are defined and used in  
64 network ecology. We distinguish two broad categories of probabilistic networks that necessitate distinct  
65 approaches when applied to key ecological questions: local networks of realized interactions, and regional  
66 networks (metawebs) of potential interactions. We highlight the distinctions in the ecological meaning of these  
67 two representations and show that they yield different statistical outcomes regarding e.g. the spatial and  
68 temporal scaling of interactions and the prediction of binary networks across space. Moreover, there is currently  
69 no metadata standard that could guide the documentation of all types of probabilistic interactions (Salim *et al.*  
70 (2022) discuss data standards for deterministic mutualistic networks). Well-defined metadata for probabilistic  
71 networks would support more adequate manipulation and integration of interaction data from different sources  
72 and guard against the potential misinterpretations arising from ambiguous definitions of probabilistic networks.  
73 These metadata should outline the nature (i.e., potential or local) and type (e.g., predatory or pollination) of the  
74 interactions, provide information regarding the taxonomic level, identities, and characteristics (e.g., life stages)  
75 of the individuals involved in an interaction, present the mathematical formulation of probabilities, including  
76 clearly identified conditional variables, and describe the methods and contexts (e.g., location, time,  
77 environmental conditions) in which interactions were estimated. Inadequately documented probabilistic  
78 interaction data should be used with caution when analyzing ecological networks. Although our contribution  
79 focuses on food webs, our observations and advice can be applied to other types of ecological networks, from  
80 plant-pollinator to host-virus networks. Indeed, excluding networks of indirect interactions such as competition  
81 and facilitation networks (Kéfi *et al.* (2015), Kéfi *et al.* (2016)), most ecological networks describe probabilities  
82 of direct interactions, which are conceptually and mathematically analogous regardless of their biological type  
83 (e.g., trophic and mutualistic interactions).

## 84 **Probabilistic representations of interactions**

85 One of the first aspects to take into consideration when estimating or interpreting probabilities of interactions is  
86 knowing if they describe potential or realized interactions. A potential interaction is defined as the biological  
87 capacity of two taxa to interact (i.e., the probability that they *can* theoretically interact) whereas a realized

interaction is the materialization or observation of this interaction in a well-defined space and time (i.e., the probability that they interact locally). Here, we use the terms *metaweb* (Dunne (2006)) to designate networks of potential interactions and *local networks* (Poisot *et al.* (2012)) for those of realized interactions. Metawebs are the network analogues of the species pool, where local networks originate from a subset of both species (nodes) and interactions (edges) of the regional metaweb (Saravia *et al.* (2022)). Without clear documentation, it can be challenging to know if published probabilistic networks describe potential or realized interactions, or if so-called probabilities are in reality *interaction scores* (i.e., non-probabilistic quantitative interactions). When probabilistic potential interactions are used and interpreted as local interactions (and conversely), this may generate misleading findings during data analysis. We believe that a better understanding of the differences, similarities, and relationships between these two probabilistic representations of ecological networks would alleviate interpretation errors and facilitate a more adequate utilization of interaction data.

## 99 Pairwise interactions: the building blocks of ecological networks

Local ecological networks and metawebs, like any type of network, are made of nodes and edges that can be represented at different levels of organization and precision. The basic unit of food webs and other ecological networks are individuals that interact with each other (e.g., by predation, Elton (2001)), forming individual-based networks (Melián *et al.* (2011)). The aggregation of these individuals into more or less homogeneous groups (e.g., populations, species, trophic species, families) allows us to represent nodes at broader taxonomic scales, which affects our interpretation of the properties of these systems (Guimarães (2020)). Moreover, edges linking these nodes can describe a variety of interaction measures. Ecologists have traditionally represented interactions as binary objects that were considered realized after observing at least one individual from group  $i$  interact with at least another individual from group  $j$ . Boolean interactions can be viewed as the result of a Bernoulli process  $A_{i,j} \sim \text{Bernoulli}(P(i \rightarrow j))$ , with  $P(i \rightarrow j)$  being the probability of interaction between  $i$  and  $j$  that characterizes our limited knowledge of the system and its intrinsic spatiotemporal variability. Depending on the type of networks (local or metaweb), the mathematical formulation and interpretation of stochastic parameters like  $P(i \rightarrow j)$  can be linked to environmental and biological factors such as species relative abundance, traits, area, and time (tbl. 1), for example using logistic regression with a logit link function with continuous explanatory variables. In these probabilistic network representations in which  $P(i \rightarrow j)$  are edge values, the only two possible outcomes are the presence ( $A_{i,j} = 1$ ) or absence ( $A_{i,j} = 0$ ) of an interaction between each pair of nodes. When considering uncertainties around the

117 estimation of  $P(i \rightarrow j)$ , a Beta distribution  $\text{Beta}(\alpha, \beta)$  can also be used to encompass all possible probability  
118 values. Observing an interaction between two taxa at a given location and time provides important information  
119 that can be used to update previous estimates of  $P(i \rightarrow j)$ , informing us on the biological capacity of both taxa  
120 to interact and the environmental conditions that enabled them to interact locally.

121 Even though binary networks constitute a highly valuable source of ecological information (Pascual *et al.*  
122 (2006)), they overlook important factors regarding interaction strengths. These are represented using  
123 quantitative interactions, which better describe the energy flows, demographic impacts or frequencies of  
124 interactions between nodes (Berlow *et al.* (2004), Borrett & Scharler (2019)), with  $A_{i,j}$  being a natural number  
125  $\mathbb{N}$  or a real number  $\mathbb{R}$  depending on the measure. For example, they may represent local interaction rates  
126 between pairs of taxa (e.g., the flower visiting rates of pollinators in a mutualistic network, Herrera (1989)).  
127 Because quantitative interactions can also describe predation pressure on prey taxa in food webs, they can be  
128 good estimators of the parameters describing species interactions in a Lotka-Volterra model (e.g., Emmerson &  
129 Raffaelli (2004)). The extra amount of ecological information in quantitative networks typically comes at a cost  
130 of greater sampling effort and data volume in predictive models (Strydom *et al.* (2021)), which can lead to  
131 relatively high levels of uncertainties when inferring quantitative networks with limited data. Just like binary  
132 networks, the uncertainty and spatiotemporal variability of quantitative interactions can be represented  
133 probabilistically. However, the need to estimate the probability distribution of all possible value of interaction  
134 strengths can make the inference of probabilities more challenging in quantitative networks compared to binary  
135 networks, which require only one probability estimate for each interaction. Quantitative interactions can follow  
136 various probability distributions depending on the measure used, the event's outcome being the value of  
137 interaction strength. For instance, quantitative interactions can follow a Poisson distribution  
138  $A_{i,j} \sim \text{Poisson}(\lambda_{i \rightarrow j})$  when predicting frequencies of interactions between pairs of nodes, with  $\lambda_{i \rightarrow j}$  being the  
139 expected rate at which individuals of taxa  $i$  and  $j$  interact (e.g., the average number of prey  $j$  consumed by all  
140 predators  $i$  in a given time period). The Poisson distribution can also be 0-inflated after initially modeling  
141 non-interacting taxa (e.g., Boulangeat *et al.* (2012) employ a 0-inflated model to analyze species abundance  
142 following the modeling of species presence and absence), which constitute the majority of taxa pairs in most  
143 local networks due to their typically high sparseness (Jordano (2016)). Because of the methodological  
144 difficulties typically encountered when building deterministic quantitative networks, binary networks, which are  
145 easier to sample (Jordano (2016)) and predict (Strydom *et al.* (2021)), are much more documented and modeled  
146 in the literature. Moreover, most published probabilistic networks and methods describe Bernoulli interactions

147 (whether interaction probabilities are regarded as constant or variable, e.g. represented by Beta distributions),  
148 which underlines the need for better guidelines regarding the interpretation and manipulation of these types of  
149 networks. For these reasons, our primary focus in this contribution will be on addressing the challenges in  
150 interpreting and using Bernoulli interactions, in both probabilistic local networks and metawebs.

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

152 Probabilistic local networks describe how likely taxa are to interact at a given location and time period (i.e.,  
153 interactions are contingent upon the environmental and biological conditions of the community). In local  
154 networks, edges commonly represent our degree of belief that two taxa interact in nature, but can also represent  
155 the probability of *observing* this interaction (Catchen *et al.* (2023)). For example, Kopelke *et al.* (2017)  
156 assembled a dataset of binary local European food webs of willow-galling sawflies and their natural enemies,  
157 clearly referencing each food web in space and time. Gravel *et al.* (2019) used this dataset to infer the  
158 probabilities of locally observing interactions between co-occurring species, with the added aspect of situating  
159 local networks within the context of environmental variables. This was achieved by including temperature and  
160 precipitation as conditional variables in some of their models.

161 We define space as the set of geographic coordinates ( $x, y, z$ ) of the spatial boundaries delineating the system,  
162 whether sampled or targeted. Ecological interactions may exhibit variations spatially and along altitudinal  
163 gradients, as evidenced by changes in hummingbird-plant interactions (Weinstein & Graham (2017b) and  
164 Weinstein & Graham (2017a)) and mosquitoes biting rates (e.g., Kulkarni *et al.* (2006)) at different elevations.

165 In contrast, time is defined as the specific time period within which interactions were either observed or  
166 predicted. With these definitions in mind, space and time can be conceptualized as distinct patches or time  
167 segments. Treating them as discrete dimensions aligns with the common sampling methods of ecological  
168 networks and provides actual probabilities of interactions across space and time. This differs from the approach  
169 of treating them as continuous variables, where edge values represent probability densities (i.e., relative  
170 likelihoods of interactions occurring at infinitesimal locations and instants in time) rather than discrete  
171 probability values (which can be obtained by integrating probability densities). By employing discrete locations  
172 and time periods, we can quantify both an area  $A$  and a duration  $t$ , which can be readily used in spatiotemporal  
173 analyses of ecological networks. For example, when studying network-area relationships (NAR, Galiana *et al.*  
174 (2018)), we anticipate that local probabilities of interactions scale positively with area and duration because  
175 taxa have more opportunities to interact as these dimensions expand.

176 The probability that two taxa  $i$  and  $j$  interact locally can be conditional on many environmental and biological  
 177 factors. One of these is their co-occurrence  $C_{i,j}$ , which is usually a Boolean describing if the geographic  
 178 distributions of both taxa overlap within the study area. Co-occurrence can be modeled probabilistically, in  
 179 which case it may conform to a Bernoulli distribution  $C_{i,j} \sim \text{Bernoulli}(P_{i,j}(x, y, z))$ , where the probability of  
 180 co-occurrence  $P_{i,j}(x, y, z)$  can be estimated through the application of joint species distribution models (e.g.,  
 181 Pollock *et al.* (2014)). Considering that the probability that two non co-occurring taxa interact locally is zero  
 182 (i.e.,  $P_N(i \rightarrow j|C = 0) = 0$ ), the probability of local interaction can be obtained by multiplying the probability of  
 183 interaction given co-occurrence with the probability of co-occurrence:

$$P_N(i \rightarrow j) = P_N(i \rightarrow j|C = 1) \times P_{i,j}(x, y, z). \quad (1)$$

184 Other important factors that can impact our estimation of interaction probabilities at the local scale are taxa  
 185 relative abundance (Canard *et al.* (2012)) and traits (Poisot *et al.* (2015)), as well as environmental factors such  
 186 as temperature (Angilletta *et al.* (2004)), precipitation (Woodward *et al.* (2012)), habitat structure (Klecka &  
 187 Boukal (2014)), and presence of other interacting taxa in the network (Pilosof *et al.* (2017), Kéfi *et al.* (2012)).  
 188 Here, we use the variable  $\Omega$  to describe the biological and ecological context in which interaction probabilities  
 189 were estimated. For example, if a research team conducts a mesocosm experiment to estimate interaction  
 190 probabilities between predators and prey with and without shelters,  $\Omega$  would represent the presence or absence  
 191 of these shelters. Like co-occurrence,  $\Omega$  can also be modeled probabilistically when the stochasticity or  
 192 uncertainty of environmental and biological factors is considered. In sum,  $\Omega$  represents all ecological and  
 193 biological variables that were taken into consideration when measuring interaction probabilities and is,  
 194 therefore, a subset of all factors actually impacting ecological interactions.

195 The probability that two taxa  $i$  and  $j$  interact in a local network  $N$  can thus be conditional on the area  $A$ , the time  
 196 interval  $t$ , their co-occurrence  $C$  and chosen environmental and biological conditions  $\Omega$ . This gives us the  
 197 following equation when all of these conditions are included in the estimation of interaction probabilities:

$$P_N(i \rightarrow j|A, t, C, \Omega). \quad (2)$$

198 The representation of the local context in which probabilities are estimated and the variables that should be  
 199 taken into consideration depend on the study system, the objectives of the study, and the resources available to

the researchers. In other words, these variables do not systematically need to be accounted for. For example, in Gravel *et al.* (2019), for the purpose of model comparison, some models incorporated environmental variables as conditional factors to estimate interaction probabilities, while others did not. When accounted for, these variables should be clearly described in the documentation of the data (Brimacombe *et al.* (2023)), preferentially in mathematical terms to avoid any confusion in their interpretation and to limit manipulation errors during their re-use. For instance, ecologists should be explicit about their consideration of co-occurrence in their estimation of local interaction probabilities. Indeed, it is important to specify if probability values are conditional  $P_N(i \rightarrow j|C = 1)$  or not  $P_N(i \rightarrow j)$  on co-occurrence since this can significantly impact the interpretation and analysis of the data. In [tbl. 1](#), we present examples of studies that used these diverse formulations of probabilistic interactions and conditional variables.

**Table 1: Notation of probabilistic interactions.** The probability of interaction between two taxa  $i$  and  $j$  is interpreted differently in a metaweb  $M$  of potential interactions and a local network  $N$  of realized interactions. Each notation includes a different conditional variable, when applicable. An example of a study employing each of these notations and conditional variables is provided, with the specific variables used indicated in parentheses. The study marked with an asterisk has been carried out on binary networks. Note that interaction probabilities can be contingent upon multiple conditional variables, or none at all. Additionally, local interaction probabilities might represent the probability of observing an interaction, not necessarily its actual occurrence.

Notation	Type	Description	Reference
$P_M(i \rightarrow j)$	potential	biological feasibility of the interaction	Strydom <i>et al.</i> (2022)
$P_N(i \rightarrow j)$	local	realization of the interaction	Fortuna & Bascompte (2006) (null model)
$P_N(i \rightarrow j A)$	local	realization of the interaction in a given area	Galiana <i>et al.</i> (2018) *
$P_N(i \rightarrow j t)$	local	realization of the interaction during a given time period	Weinstein & Graham (2017a)
$P_N(i \rightarrow j C)$	local	realization of the interaction given that the taxa co-occur	Gravel <i>et al.</i> (2019)
$P_N(i \rightarrow j \Omega)$	local	realization of the interaction given environmental conditions	Gravel <i>et al.</i> (2019) (temperature and precipitation)

210 **Metawebs: regional catalogs of interactions**

211 Metawebs are networks of potential interactions that have been designed for broad spatial, temporal, and  
212 taxonomic scales (e.g., species food webs at the continental scale). They represent the probability that taxa can  
213 biologically interact regardless of their co-occurrence and local environmental conditions. Potential interactions  
214 are by definition context-independent, i.e. they are not measured at a specific location and time. In contrast with  
215 probabilistic local networks, which represent the stochasticity of interactions occurring in nature, probabilistic  
216 metawebs measure our degree of belief in the capacity of two taxa to interact (i.e., the probability that their  
217 traits could support an interaction in the right conditions). In other words, potential interactions describe the  
218 probability that there exists at least one combination of phenotypes of taxa  $i$  and  $j$  that can interact with each  
219 other if they were to encounter. To reduce any biases in our calculation of this probability, it is crucial to ensure  
220 that the set of traits sampled or considered accurately reflects the overall trait distribution in both taxa. This  
221 enhances our confidence in concluding that the taxa cannot interact when no positive observation has been  
222 made and increases our capacity to detect an interaction when it is biologically feasible. In addition to  
223 one-on-one interactions, the extent of sampling effort also contributes to shaping our assessment of metaweb  
224 properties, as sampling a larger number of local networks allows us to capture more potential interactions  
225 (McLeod *et al.* (2021a)). A probability of potential interaction in a metaweb  $M$  can be expressed as

$$P_M(i \rightarrow j), \quad (3)$$

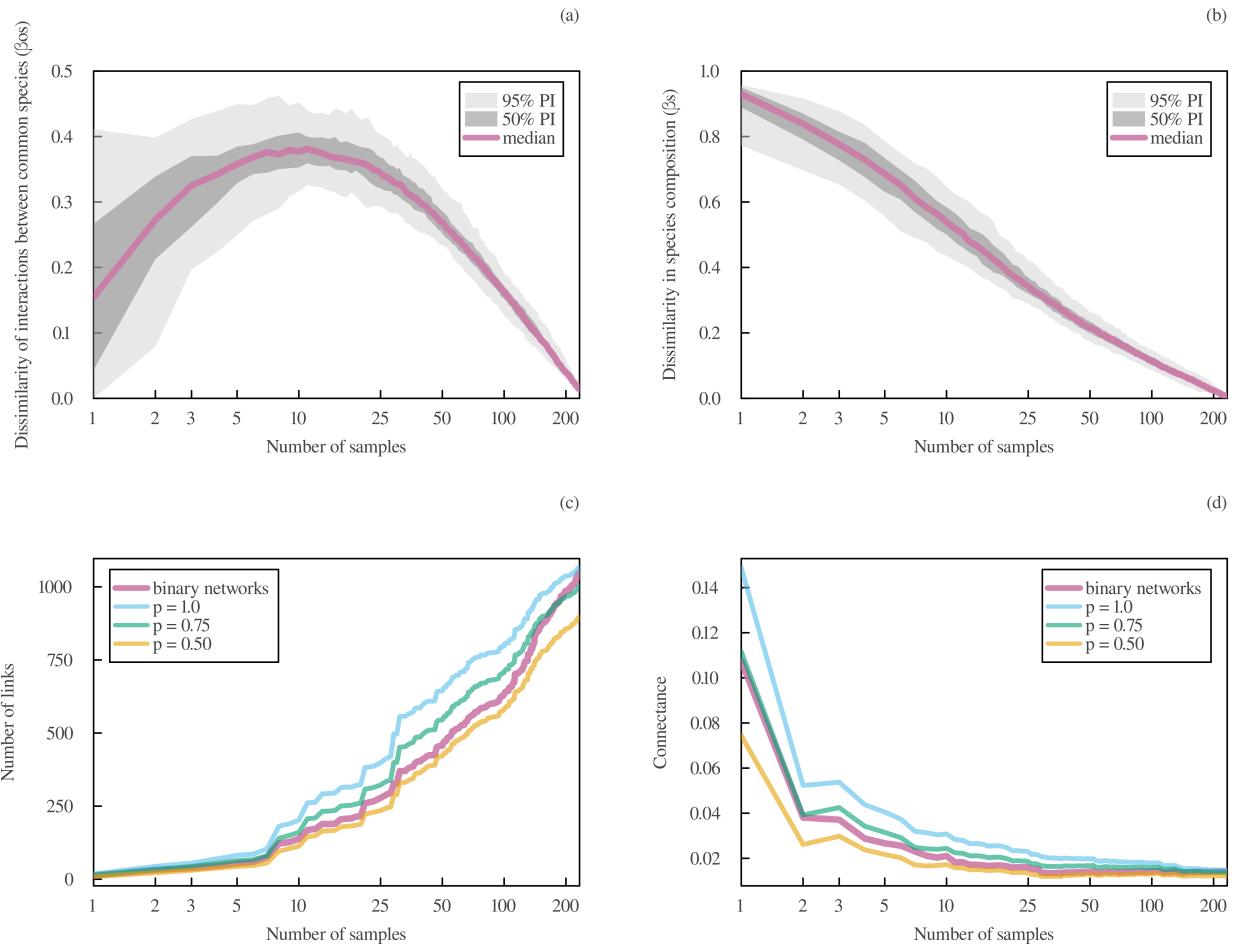
226 which, in contrast with eq. 2, is not conditional on any spatial, temporal, or environmental variables (tbl. 1).

227 Starting from a selected set of taxa, which are usually distributed within a broad region of interest, probabilistic  
228 metawebs can be built using different data sources, including literature review, fieldwork, and predictive models  
229 (e.g., the metaweb of trophic interactions between Canadian mammals inferred by Strydom *et al.* (2022)).  
230 Every pair of taxa that have confidently been observed to interact at least once can be given a probability of 1  
231 (i.e.,  $P_M(i \rightarrow j) = 1$ ) since we know that they *can* interact. This is not the case in local probabilistic networks,  
232 in which interaction events usually remain stochastic (i.e.,  $P_N(i \rightarrow j) < 1$ ) after empirically observing  
233 interactions because of their intrinsic spatiotemporal variability. Similarly, although rare interactions typically  
234 have low probabilities in local networks, they can have high probabilities in metawebs when the traits of both  
235 taxa are congruent. On the other hand, interactions that were never observed can have low probability values in  
236 both metawebs and local networks, going as low as 0 for forbidden links. However, because of observation

237 errors due to taxonomic misidentifications and ecological misinterpretations (e.g., due to cryptic species and  
238 interactions, Pringle & Hutchinson (2020)), many observations of interactions are in reality false positives.  
239 Likewise, forbidden interactions can be false negatives in metawebs, e.g. if they have been assessed for specific  
240 phenotypes, locations or time. Employing Bayesian models, whether they are mechanistic or  
241 phenomenological, has the potential to enhance the accuracy of our estimation of interaction probabilities  
242 within both local and potential networks (e.g., Bartomeus *et al.* (2016), Cirtwill *et al.* (2019)). This  
243 improvement is achieved in potential networks by leveraging prior information regarding the feasibility of  
244 interactions along with the empirical data on observed interactions.

## 245 **Properties of probabilistic networks**

246 The differences in the mathematical formulations of local and potential interactions can affect their statistical  
247 properties when applied to key ecological questions. These disparities must therefore be taken into account  
248 when analyzing probabilistic interaction data to prevent misleading results and minimize interpretation errors.  
249 Here we show four common applications of probabilistic interactions and compare the characteristics of local  
250 networks and metawebs using simulated and empirical data.



251

## 252 Taxonomic scaling of interactions

253 Probabilistic networks can be used to address a wide range of ecological questions based on their level of  
 254 organization. For example, the assemblage of interactions across ecological scales can be studied using  
 255 species-based networks, whereas clade-based networks can be used to study macroevolutionary processes (e.g.,  
 256 Gomez *et al.* (2010)). Because our interpretation of the properties and dynamics of ecological networks  
 257 depends on their taxonomic scale (Guimarães (2020)), examining the phylogenetic scaling of network structure  
 258 is also a promising research avenue. Analyzing the same system at different taxonomic scales can thus provide  
 259 meaningful and complementary ecological information and is, in our perspective, best conducted using  
 260 probabilistic networks.

261 There is no qualitative difference in the taxonomic scaling of local networks compared to metawebs because  
 262 only the nodes are defined taxonomically. In other words, the edge probability values of local networks (eq. 2)  
 263 and metawebs (eq. 3) are not conditional on any taxonomic scale. It is the definition of the event itself (i.e., the

interaction of the two taxa) that has a given phylogenetic scale, not their conditional variables. In both types of networks, shifting to a broader level of organization can be directly done using probabilities at finer scales. For example, if we have a network of  $n_A$  species from genus A and  $n_B$  species from genus B, we can calculate the probability that at least one species from genus A interact with at least one species from genus B as follows:

$$P(A \rightarrow B) = 1 - \prod_{i=1}^{n_A} \prod_{j=1}^{n_B} (1 - P(A_i \rightarrow B_j)), \quad (4)$$

where  $A_i$  and  $B_j$  are the species of the corresponding genus. Knowing that two species interact (i.e.,  $P(A_i \rightarrow B_j) = 1$ ) gives a probability of genus interaction of 1. Canard *et al.* (2012) built a species-based network from neutrally simulated interactions between individuals using a similar approach. In contrast, more sophisticated models need to be built when shifting to a finer level of organization. Indeed, knowing that two genera interact does not imply that all of their pairwise species combinations can also interact. One could, for example, build a finer-scale network by generating probabilities of species interactions by randomly sampling them from a beta distribution parametrized by the broader-scale network.

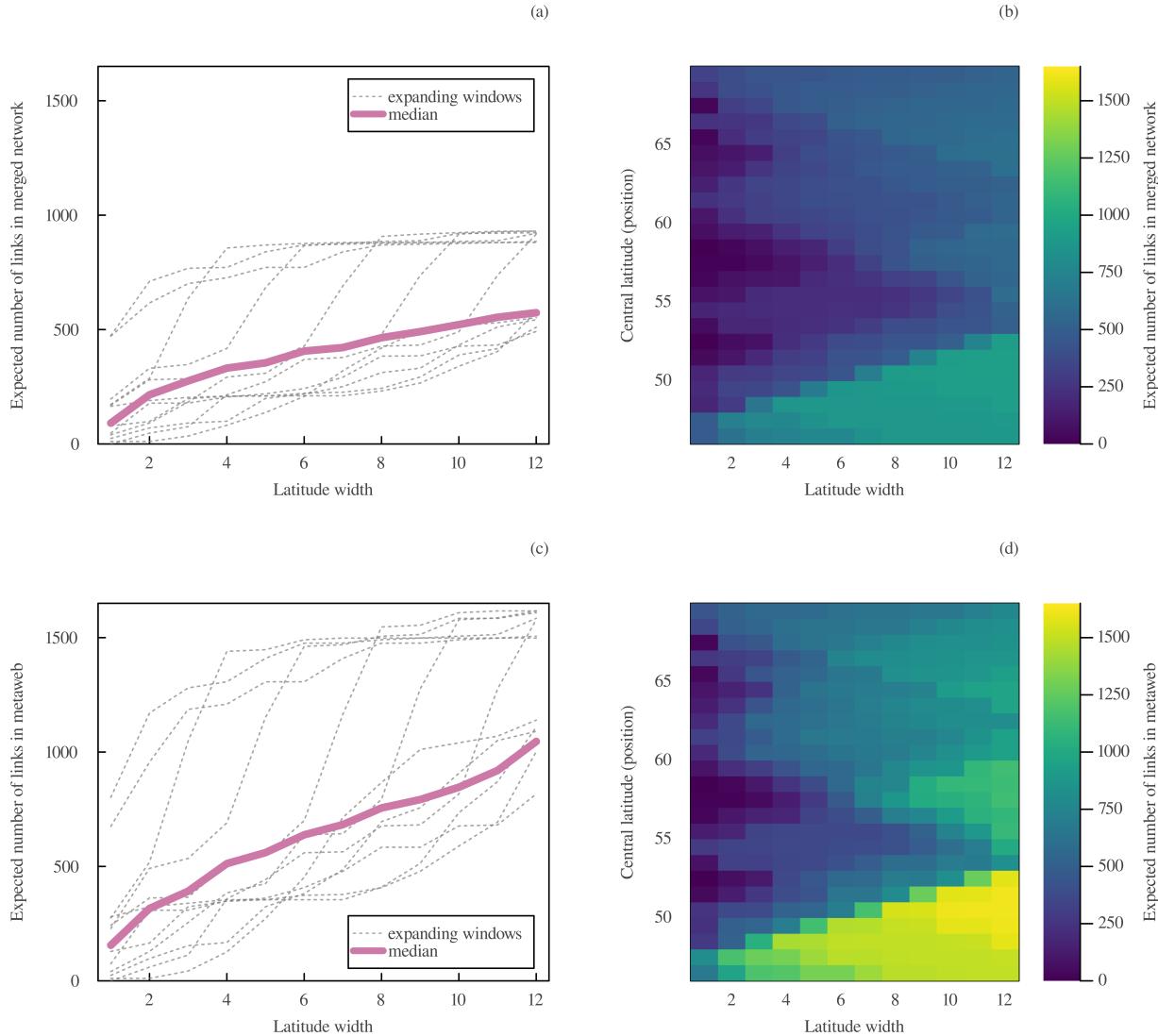
Ideally, the biological interpretation of probabilistic interactions should not differ across a network even if it has heterogenous levels of organization, i.e. if different nodes are represented at different taxonomic scales (e.g., a network composed of species and trophic species). This is frequent in ecological networks where taxonomic resolution is typically low (Hemprich-Bennett *et al.* (2021), Vázquez *et al.* (2022)). Broader-scale interactions should be based on probabilities of interactions between individuals, either at the local or regional scale. For example, in local individual-based food webs, the probability that two individuals interact represents the degree of belief that one individual will actually consume the other. Similarly, in local species-based food webs, the probability that two species interact represents the degree of belief that at least one individual from the predator species consumes at least another individual from the prey species. Moreover, in local clade-based food webs, the probability that two clades interact represents the degree of belief that at least two species from these clades interact with each other or, equivalently, that at least two individuals from these clades interact with each other. Fundamentally, the taxonomic scaling of interactions is an aggregation of interactions between individuals into larger groups, which could be more or less homogeneous depending on the organisms and the study system. This type of scaling is analogous to the spatial and temporal scaling of interactions to the extent that they represent different ways to aggregate individuals into broader groups, either spatially, temporally, or taxonomically.

291 **Spatial and temporal scaling of interactions**

292 The study of network-area relationships (NARs) and interaction accumulation curves (IACs) are important  
293 realms of research in network ecology. Firstly, NARs describe the scaling of network properties (such as  
294 modularity and trophic chain lengths) with spatial scale (e.g., Wood *et al.* (2015), Galiana *et al.* (2018)). The  
295 variation of network structure across spatial scales can be the result of the scaling of species richness  
296 (species-area relationships, SARs) and the number of interactions (Brose *et al.* (2004)) with the area sampled,  
297 but can also be due to ecological processes (e.g., spatial variability in community composition and extinction  
298 and colonization events) occurring at different scales (Galiana *et al.* (2018)). Secondly, IACs describe the  
299 scaling of the number of interactions observed with sampling effort (Jordano (2016)), which can impact many  
300 measures of network structure such as connectance (McLeod *et al.* (2021b)). Beyond sampling effort, the  
301 temporal scaling of interactions describes how network structure changes with the duration of the network  
302 (Poisot *et al.* (2012)) given that different interactions are occurring through time. Because probabilistic local  
303 networks can assess the spatiotemporal variability of interactions (eq. 2), they are useful tools to develop and  
304 test different equations of the scaling of network structure with space and time.

305 Metawebs and local networks intrinsically differ in their relationship to spatial and temporal scales. On one  
306 hand, because probabilistic metawebs are context-independent, potential interactions do not scale with space  
307 and time since they depend solely on the biological capacity of the two taxa to interact, regardless of any  
308 particular environmental conditions. This suggests that the probability that two taxa can potentially interact  
309 should theoretically be the same in all metawebs in which they are present, provided that the data and methods  
310 used to estimate them are the same. As a result, if a potential network  $M_1$  is subsampled from a regional  
311 metaweb  $M_0$  to represent the potential interactions between a subset of taxa found in a smaller region, their  
312 probabilities of interaction should be identical regardless of scale, i.e.  $P_{M_1}(i \rightarrow j) = P_{M_0}(i \rightarrow j)$ . On the other  
313 hand, local ecological networks scale both spatially and temporally since interactions have more opportunities to  
314 be realized and observed in a larger area and duration (e.g., more individuals, more trait variations, more chance  
315 of an encounter, McLeod *et al.* (2020)). For example, if a local probabilistic network  $N_1$  of area  $A_1$  is obtained  
316 from a larger network  $N_0$  of area  $A_0$ , with  $A_1$  being completely nested within  $A_0$ , interaction probabilities should  
317 be smaller in the smaller network, i.e.  $P_{N_1}(i \rightarrow j|A_1 < A_0) \leq P_{N_0}(i \rightarrow j|A_0)$ . However, if  $A_1$  and  $A_0$  are disjoint,  
318 interaction probabilities could be incidentally higher in the smaller area depending on their environmental and  
319 biological conditions. Similarly, interaction probabilities should be smaller in networks of shorter durations if  
320 time intervals are nested. Statistical models, such as network-area relationships and interaction accumulation

321 curves, can be used to generate estimates of local probabilities of interactions across spatial and temporal scales.



322

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

324 Predicting local networks across time and space is an important goal of network ecology (Strydom *et al.*  
325 (2021)). Indeed, in a context of scarcity of interaction data (Jordano (2016)), ecologists must rely on predictive  
326 models to reconstruct networks at fine spatial and temporal scales. For example, local ecological networks  
327 could be reconstructed using real-time biomonitoring data and adequate numerical models (Bohan *et al.*  
328 (2017)), which could pave the way for fine-scale studies of ecosystem functioning and dynamics. Besides  
329 predictive models, statistical models can also be built to describe parameters of interest, such as probabilities of  
330 interactions. In that case, parameter values provide valuable ecological information in their own rights.

331 Different types of models (e.g., Bayesian and machine learning models) of ecological interactions have been  
 332 built for predictive and descriptive purposes (Strydom *et al.* (2021)). Representing interactions probabilistically  
 333 reflects the uncertainty of these models, which is usually represented in terms of probability distributions. Here  
 334 we show how to build a simple generative mechanistic model of probabilistic interactions that takes into account  
 335 their inherent spatiotemporal variability, i.e. a spatiotemporally-explicit model. Our model is not suitable for  
 336 potential interactions, which are scale-independent. Rather, it could prove useful for predicting local  
 337 interactions across time and space by generating new interaction data after parameter inference.

338 As stated by eq. 1, the probability that two taxa  $i$  and  $j$  interact at a given location  $(x, y)$  is given by the product  
 339 of their probability of interaction given co-occurrence and their probability of co-occurrence. First, their  
 340 probability of co-occurrence is given by their respective probabilities of occurrence  $P_i(x, y)$  and  $P_j(x, y)$  and the  
 341 strength of association  $\gamma$  between their occurrence and co-occurrence (Cazelles *et al.* (2016)):

$$P_{i,j}(x, y) = P_i(x, y)P_j(x, y)\gamma. \quad (5)$$

342 When  $\gamma > 1$ , the geographic distributions of both taxa are positively associated, which implies that the  
 343 occurrence of one taxon increases the probability of occurrence of the other. In empirical networks,  $\gamma > 1$  for  
 344 most species pairs (Catchen *et al.* (2023)). The co-occurrence of both taxa is the result of a Bernoulli trial

$$C \sim \text{Bernoulli}(P_{i,j}(x, y)). \quad (6)$$

345 Second, the probability of interaction given co-occurrence can be made temporally explicit by modeling it as a  
 346 Poisson process with rate  $\lambda$ . This parameter corresponds to the expected frequency of interaction between both  
 347 taxa in a given time period and its value can be estimated using prior data on interaction strengths, if available.  
 348 Specifically, the probability that two co-occurring taxa interact during a time period  $t_0$  is:

$$P_N(i \rightarrow j|C = 1) = 1 - e^{-\lambda t_0}, \quad (7)$$

349 which approaches 1 when  $t_0 \rightarrow \infty$ .

350 The realization of the interaction between  $i$  and  $j$  is the result of a Bernoulli trial with probability  $P_N(i \rightarrow j)$ . A  
 351 Bayesian inference model can thus be built from the previous equations to estimate the value of the  $\lambda$  parameter

352 and generate new interaction data:

$$I \sim \text{Bernoulli}(P_N(i \rightarrow j)) \quad (8)$$

353

$$P_N(i \rightarrow j) = P_i(x, y)P_j(x, y)\gamma(1 - e^{-\lambda t_0}) \quad (9)$$

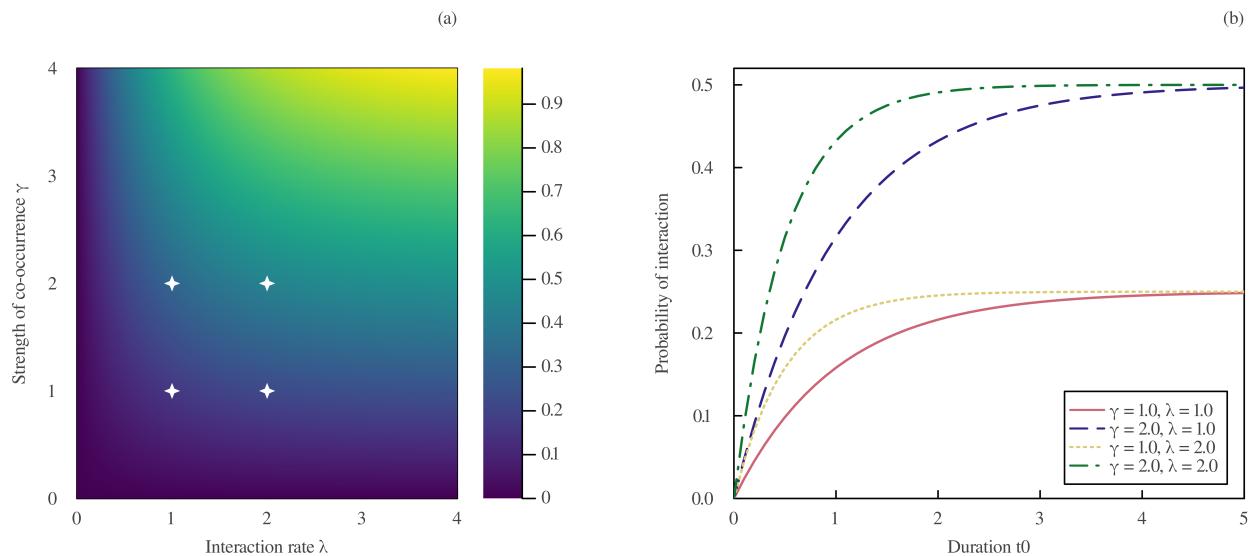
354

$$\gamma \sim \text{Gamma}(2, 0.5) \quad (10)$$

355

$$\lambda \sim \text{Exponential}(2) \quad (11)$$

356 This simple model can be customized in many ways, e.g. by linking  $\lambda$  with given environmental variables or by  
 357 explicitly modeling observation errors (i.e., the probability of false negatives and false positives).



358

## 359 Sampling binary networks

360 Probabilistic networks can be used to predict binary interactions through random draws. This can be useful  
 361 when analyzing the structure of a probabilistic network when analytical probabilistic measures are lacking. A  
 362 binary network can be generated from independent Bernoulli trials for each interaction. The distribution of a  
 363 network's property can then be obtained after measuring the structure of all randomly generated networks  
 364 (Poisot *et al.* (2016)). Doing so allows us to represent the variability of network structure, although possibly  
 365 with biases when connectance is low (Poisot & Gravel (2014), Chagnon (2015)). When binary networks are  
 366 generated under a null model, this method can be used for null hypothesis significance testing, in which case the

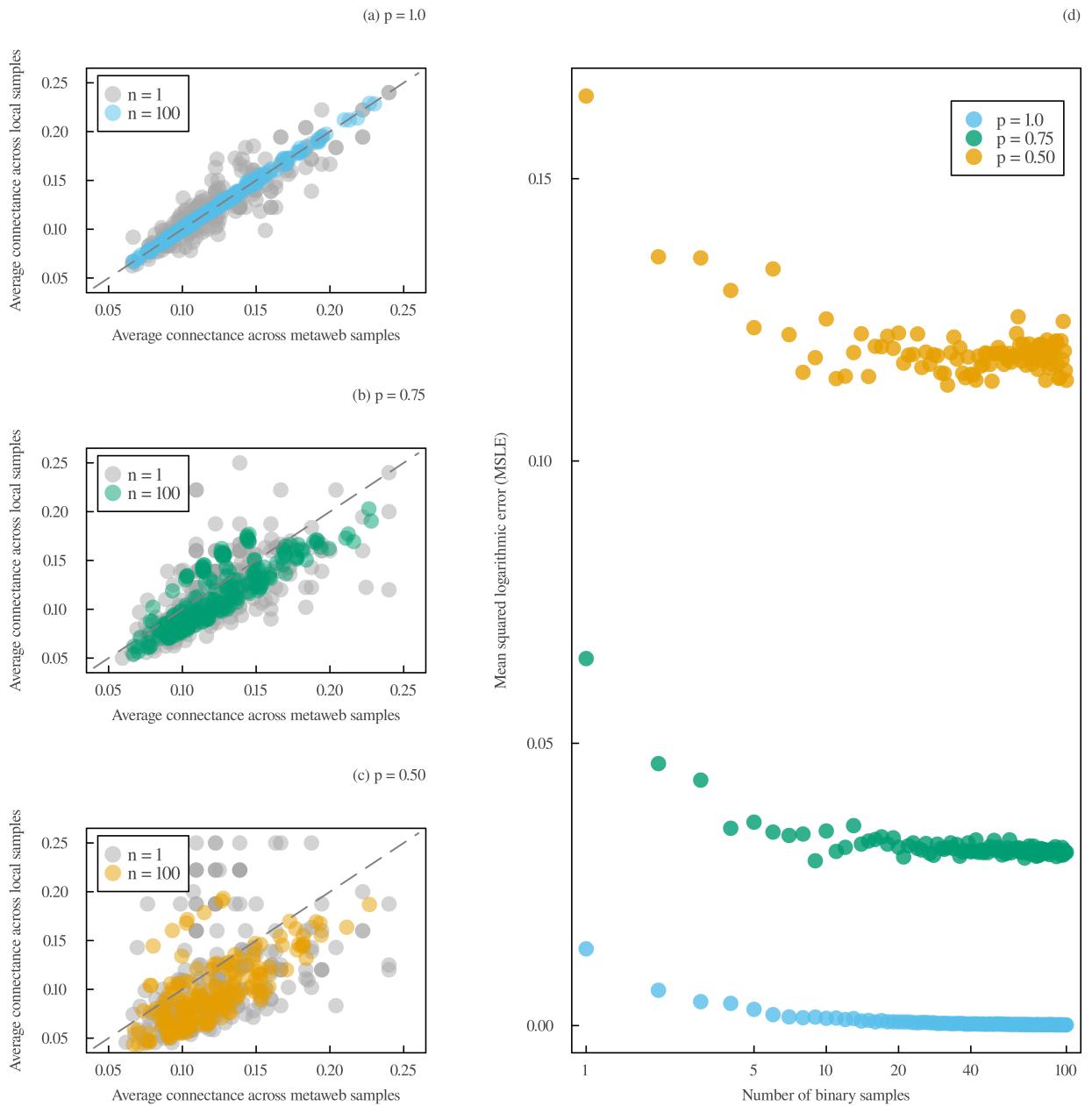
367 observed measure is compared to a null distribution (e.g., Bascompte *et al.* (2003)). Furthermore, randomly  
368 generating binary networks across space and time can help us visualize the spatiotemporal variability of  
369 network structure and test ecological hypotheses on interactions across large spatial and temporal scales.

370 There are at least two different approaches when sampling binary networks from probabilistic webs across  
371 space, e.g. if we want to predict a binary network for each of  $n \times n$  grid cells. The first approach is to conduct a  
372 single Bernoulli trial for each pair of taxa found in the region of interest based on their regional probability of  
373 interaction. As a result, each pair of taxa that are predicted to interact in the regional network realization will  
374 interact in all of the  $n^2$  networks in which they co-occur. This sampling technique is best used with potential  
375 interactions that have no spatial variation. The second approach is to independently sample each of the  $n^2$   
376 networks. In practice, this can be done by generating a different probabilistic network for each grid cell.  
377 Depending on how they were obtained, these networks can differ in their taxa composition (nodes) and/or  
378 interaction probabilities (edges). Then, binary networks can be independently sampled for each grid cell.  
379 Because this method generates spatial variation in binary interactions, it is best used with local interactions.

380 The choice of sampling approach has an impact on the selection of grid cell size. In the first approach,  
381 interactions will be the same regardless of cell size because interactions are sampled only once from the  
382 regional network. However, in the second approach, local interaction probabilities depend on the network area.  
383 For example, let  $N_1$  and  $N_2$  be networks of area  $\frac{1}{2}A_0$  nested within  $A_0$  and disjoint from each other, i.e. two  
384 contiguous cells that form  $N_0$ . If  $N_1$  and  $N_2$  are independent (which is rarely the case in reality because of  
385 spatial auto-correlation), the probability that two taxa  $i$  and  $j$  interact in  $N_0$  is given by:

$$P_{N_0}(i \rightarrow j) = 1 - (1 - P_{N_1}(i \rightarrow j)) \times (1 - P_{N_2}(i \rightarrow j)). \quad (12)$$

386 Because of its larger area, the probability that the two taxa interact in  $N_0$  is higher than in  $N_1$  and  $N_2$ . When  
387 sampling binary interactions from local networks, it is thus important to sample at the same spatial scale as the  
388 one for which probabilities were estimated. Otherwise, interaction probabilities must be adjusted to correspond  
389 to the targeted cell size and avoid systematic biases in prediction.



390

### 391 Prediction of local networks from metawebs

392 Metawebs are an important source of ecological information that can be leveraged for predicting local networks.  
 393 Indeed, binary local networks can be reconstructed by selecting a subset of both taxa and interactions from the  
 394 metaweb (Dunne (2006)). This implies that there are always more interactions in a metaweb compared to its  
 395 corresponding local networks. In practice, because a community's composition is arguably easier to sample or  
 396 predict than its interactions, the list of taxa to select can be known empirically or obtained using range maps or

397 species distribution models. The challenge is rather to choose which interactions to select from the metaweb,  
398 which could require more sophisticated statistical models and ecological knowledge. Because the structure of  
399 local networks is constrained by the one of the metaweb (Saravia *et al.* (2022)), inferring their structure from  
400 the metaweb before predicting local pairwise interactions could prove promising (Strydom *et al.* (2021)).

401 When building probabilistic local networks from a probabilistic metaweb, interaction probabilities decrease.  
402 This is because two taxa must first have the capacity to interact (i.e.,  $M_{i,j}^* = 1$  in the binary metaweb  $M^*$ ) before  
403 interacting locally:

$$P_N(i \rightarrow j) = P_M(i \rightarrow j) \times P_N(i \rightarrow j | M_{i,j}^* = 1).$$

404 Therefore, inferring local networks from their metaweb keeping the same values of interaction probability  
405 would generate systematic biases in the prediction. In that case, these networks would instead represent  
406 smaller-scale metawebs of potential interactions, which could be misinterpreted as local interactions. As  
407 suggested by McLeod *et al.* (2021b), even though metawebs do not capture the spatiotemporal variability of  
408 interactions, they set the upper limit of local interactions. In other words, the probability that two taxa interact at  
409 a given location and time is always lower or equal to the probability of their potential interaction:

$$P_N(i \rightarrow j | A, t, C, \Omega) \leq P_M(i \rightarrow j). \quad (13)$$

410 Moreover, the probability that two taxa have the biological capacity to interact must be higher than the  
411 probability that they will ever interact because they might never co-occur or encounter locally. More precisely,  
412 the accumulated probability of realized interactions across all spatial, temporal, and environmental conditions  
413 must be lower than the probability of potential interaction, i.e.

$$\int_{\Omega} \int_A \int_t P_N(i \rightarrow j | A, t, \Omega) dt dA d\Omega \leq P_M(i \rightarrow j). \quad (14)$$

## 414 Conclusion

415 In this contribution, we underline the importance of network metadata for adequately interpreting and  
416 manipulating probabilistic interaction data. The mathematical representation of probabilities and their statistical

417 properties depend on the type of interactions (local or potential) and the conditions in which they were  
418 estimated. We showed that probabilistic local networks and metawebs differ in their relationship to spatial and  
419 temporal scales, with potential interactions remaining consistent across scales. In contrast with metawebs, local  
420 interactions are measured in a specific context (e.g., in a given area, time, and biological and environmental  
421 conditions) and depend on taxa co-occurrence. These important conceptual differences bring to light the need  
422 to use probabilistic data with caution, for instance when generating binary network realizations across space and  
423 predicting local networks from metawebs. Clear metadata describing the type of interaction and the variables  
424 used in their estimation are required to ensure adequate data manipulation. Better data practices and  
425 foundations for probabilistic thinking in network ecology could enable more reliable assessments of the  
426 spatiotemporal variability and uncertainty of biotic interactions.

427 It is essential to enhance our comprehension of both potential and local interactions, especially considering the  
428 current scarcity of interaction data. However, while sampling biological communities does decrease the  
429 uncertainty of interactions by accumulating evidence for their feasibility and local realization, there is a limit to  
430 how much we can diminish their inherent randomness. In metawebs, probabilities reflect our limited knowledge  
431 of interactions (i.e., our degree of belief that interactions are feasible), which is expected to improve with a  
432 larger volume of data. We should anticipate that potential interactions will become more definitive (with  
433 probabilities approaching 0 or 1) as we investigate various conditions, including different combinations of  
434 species traits. Conversely, in the case of local networks, which can be seen as random instances of metawebs,  
435 randomness cannot be as reduced. In local interactions, probabilities can be divided into a component  
436 representing uncertainty and another representing spatiotemporal variability. Owing to environmental  
437 heterogeneity, there will invariably be instances in which an interaction occurs and others in which it does not,  
438 across different times and locations, irrespective of the extent to which we can improve our knowledge of its  
439 biological feasibility and the local conditions that facilitate its occurrence. When local networks depict  
440 probabilities of observing interactions rather than just their actual occurrence, we must also consider the  
441 observation variability as an additional source of randomness. Every ecological process is stochastic but there is  
442 also a possibility that a phenomenon goes undetected. Quantifying and partitioning this stochasticity will enable  
443 us to make more accurate predictions about ecological interactions at various spatial and temporal scales.

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## 452 References

- 453 Andrade-Pacheco, R., Rerolle, F., Lemoine, J., Hernandez, L., Meïté, A., Juziwelo, L., *et al.* (2020). [Finding](#)  
454 [hotspots: Development of an adaptive spatial sampling approach](#). *Scientific Reports*, 10, 10939.
- 455 Angilletta, M.J., Jr., Steury, T.D. & Sears, M.W. (2004). [Temperature, Growth Rate, and Body Size in](#)  
456 [Ectotherms: Fitting Pieces of a Life-History Puzzle1](#). *Integrative and Comparative Biology*, 44, 498–509.
- 457 Araujo, M.B., Rozenfeld, A., Rahbek, C. & Marquet, P.A. (2011). [Using species co-occurrence networks to](#)  
458 [assess the impacts of climate change](#). *Ecography*, 34, 897–908.
- 459 Bartomeus, I., Gravel, D., Tylianakis, J.M., Aizen, M.A., Dickie, I.A. & Bernard-Verdier, M. (2016). [A](#)  
460 [common framework for identifying linkage rules across different types of interactions](#). *Functional Ecology*,  
461 30, 1894–1903.
- 462 Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003). [The nested assembly of plantanimal mutualistic](#)  
463 [networks](#). *Proceedings of the National Academy of Sciences*, 100, 9383–9387.
- 464 Berlow, E.L., Neutel, A.-M., Cohen, J.E., De Ruiter, P.C., Ebenman, B., Emmerson, M., *et al.* (2004).  
465 [Interaction strengths in food webs: Issues and opportunities](#). *Journal of Animal Ecology*, 73, 585–598.
- 466 Blanchet, F.G., Cazelles, K. & Gravel, D. (2020). [Co-occurrence is not evidence of ecological interactions](#).  
467 *Ecology Letters*, 23, 1050–1063.
- 468 Bohan, D.A., Vacher, C., Tamaddoni-Nezhad, A., Raybould, A., Dumbrell, A.J. & Woodward, G. (2017).  
469 [Next-Generation Global Biomonitoring: Large-scale, Automated Reconstruction of Ecological Networks](#).

- 470      *Trends in Ecology & Evolution*, 32, 477–487.
- 471      Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., *et al.* (2011). Why  
472      intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26, 183–192.
- 473      Borrett, S.R. & Scharler, U.M. (2019). Walk partitions of flow in Ecological Network Analysis: Review and  
474      synthesis of methods and indicators. *Ecological Indicators*, 106, 105451.
- 475      Boulangeat, I., Gravel, D. & Thuiller, W. (2012). Accounting for dispersal and biotic interactions to disentangle  
476      the drivers of species distributions and their abundances. *Ecology Letters*, 15, 584–593.
- 477      Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T. & Fortin, M.-J. (2023). Shortcomings of reusing  
478      species interaction networks created by different sets of researchers. *PLOS Biology*, 21, e3002068.
- 479      Brose, U., Ostling, A., Harrison, K. & Martinez, N.D. (2004). Unified spatial scaling of species and their  
480      trophic interactions. *Nature*, 428, 167–171.
- 481      Canard, E., Mouquet, N., Marescot, L., Gaston, K.J., Gravel, D. & Mouillot, D. (2012). Emergence of  
482      Structural Patterns in Neutral Trophic Networks. *PLOS ONE*, 7, e38295.
- 483      Catchen, M.D., Poisot, T., Pollock, L.J. & Gonzalez, A. (2023). The missing link: Discerning true from false  
484      negatives when sampling species interaction networks.
- 485      Cazelles, K., Araujo, M.B., Mouquet, N. & Gravel, D. (2016). A theory for species co-occurrence in interaction  
486      networks. *Theoretical Ecology*, 9, 39–48.
- 487      Chagnon, P.-L. (2015). Characterizing topology of ecological networks along gradients: The limits of metrics'  
488      standardization. *Ecological Complexity*, 22, 36–39.
- 489      Choh, Y., Ignacio, M., Sabelis, M.W. & Janssen, A. (2012). Predator-prey role reversals, juvenile experience  
490      and adult antipredator behaviour. *Scientific Reports*, 2, 728.
- 491      Cirtwill, A.R., Eklöf, A., Roslin, T., Wootton, K. & Gravel, D. (2019). A quantitative framework for  
492      investigating the reliability of empirical network construction. *Methods in Ecology and Evolution*, 10,  
493      902–911.
- 494      Dunne, J.A. (2006). The Network Structure of Food Webs. In: *Ecological networks: Linking structure and*  
495      *dynamics* (eds. Dunne, J.A. & Pascual, M.). Oxford University Press, pp. 27–86.

- 496 Elmasri, M., Farrell, M.J., Davies, T.J. & Stephens, D.A. (2020). **A hierarchical Bayesian model for predicting**  
497 **ecological interactions using scaled evolutionary relationships.** *The Annals of Applied Statistics*, 14,  
498 221–240.
- 499 Elton, C.S. (2001). *Animal Ecology*. University of Chicago Press, Chicago, IL.
- 500 Emmerson, M.C. & Raffaelli, D. (2004). **Predatorprey body size, interaction strength and the stability of a real**  
501 **food web.** *Journal of Animal Ecology*, 73, 399–409.
- 502 Fortuna, M.A. & Bascompte, J. (2006). **Habitat loss and the structure of plantanimal mutualistic networks.**  
503 *Ecology Letters*, 9, 281–286.
- 504 Galiana, N., Lurgi, M., Claramunt-López, B., Fortin, M.-J., Leroux, S., Cazelles, K., et al. (2018). **The spatial**  
505 **scaling of species interaction networks.** *Nature Ecology & Evolution*, 2, 782–790.
- 506 Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010). **A framework for community**  
507 **interactions under climate change.** *Trends in Ecology & Evolution*, 25, 325–331.
- 508 Godsoe, W., Murray, R. & Iritani, R. (2022). **Species interactions and diversity: A unified framework using Hill**  
509 **numbers.** *Oikos*, n/a, e09282.
- 510 Golubski, A.J. & Abrams, P.A. (2011). **Modifying modifiers: What happens when interspecific interactions**  
511 **interact?** *Journal of Animal Ecology*, 80, 1097–1108.
- 512 Gomez, J.M., Verdu, M. & Perfectti, F. (2010). **Ecological interactions are evolutionarily conserved across the**  
513 **entire tree of life.** *Nature*, 465, 918–U6.
- 514 Gonzalez-Varo, J.P. & Traveset, A. (2016). **The Labile Limits of Forbidden Interactions.** *Trends in Ecology &*  
515 *Evolution*, 31, 700–710.
- 516 Gravel, D., Baiser, B., Dunne, J.A., Kopelke, J.-P., Martinez, N.D., Nyman, T., et al. (2019). **Bringing Elton**  
517 **and Grinnell together: A quantitative framework to represent the biogeography of ecological interaction**  
518 **networks.** *EcoGraphy*, 42, 401–415.
- 519 Gravel, D., Poisot, T., Albouy, C., Velez, L. & Mouillot, D. (2013). **Inferring food web structure from**  
520 **predatorprey body size relationships.** *Methods in Ecology and Evolution*, 4, 1083–1090.
- 521 Guimarães, P.R. (2020). **The Structure of Ecological Networks Across Levels of Organization.** *Annual Review*  
522 *of Ecology, Evolution, and Systematics*, 51, 433–460.

- 523 Guimerà, R. & Sales-Pardo, M. (2009). [Missing and spurious interactions and the reconstruction of complex](#)  
524 [networks](#). *Proceedings of the National Academy of Sciences*, 106, 22073–22078.
- 525 Hemprich-Bennett, D.R., Oliveira, H.F.M., Le Comber, S.C., Rossiter, S.J. & Clare, E.L. (2021). [Assessing the](#)  
526 [impact of taxon resolution on network structure](#). *Ecology*, 102, e03256.
- 527 Herrera, C.M. (1989). [Pollinator abundance, morphology, and flower visitation rate: Analysis of the “quantity”](#)  
528 [component in a plant-pollinator system](#). *Oecologia*, 80, 241–248.
- 529 Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M. & Ladle, R.J. (2015). [Seven Shortfalls](#)  
530 [that Beset Large-Scale Knowledge of Biodiversity](#). *Annual Review of Ecology, Evolution, and Systematics*,  
531 46, 523–549.
- 532 Jordano, P. (1987). [Patterns of Mutualistic Interactions in Pollination and Seed Dispersal: Connectance,](#)  
533 [Dependence Asymmetries, and Coevolution](#). *The American Naturalist*, 129, 657–677.
- 534 Jordano, P. (2016). [Sampling networks of ecological interactions](#). *Functional Ecology*, 30, 1883–1893.
- 535 Jordano, P., Bascompte, J. & Olesen, J.M. (2003). [Invariant properties in coevolutionary networks of](#)  
536 [plantanimal interactions](#). *Ecology Letters*, 6, 69–81.
- 537 Kéfi, S., Berlow, E.L., Wieters, E.A., Joppa, L.N., Wood, S.A., Brose, U., *et al.* (2015). [Network structure](#)  
538 [beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky shores](#). *Ecology*, 96,  
539 291–303.
- 540 Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., *et al.* (2012). [More than a](#)  
541 [meal... integrating non-feeding interactions into food webs](#). *Ecology Letters*, 15, 291–300.
- 542 Kéfi, S., Miele, V., Wieters, E.A., Navarrete, S.A. & Berlow, E.L. (2016). [How Structured Is the Entangled](#)  
543 [Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks Leads to Increased](#)  
544 [Persistence and Resilience](#). *PLOS Biology*, 14, e1002527.
- 545 Klecka, J. & Boukal, D.S. (2014). [The effect of habitat structure on prey mortality depends on predator and](#)  
546 [prey microhabitat use](#). *Oecologia*, 176, 183–191.
- 547 Kopelke, J.-P., Nyman, T., Cazelles, K., Gravel, D., Vissault, S. & Roslin, T. (2017). [Food-web structure of](#)  
548 [willow-galling sawflies and their natural enemies across Europe](#). *Ecology*, 98, 1730–1730.
- 549 Kulkarni, M.A., Kweka, E., Nyale, E., Lyatuu, E., Mosha, F.W., Chandramohan, D., *et al.* (2006).  
550 [Entomological Evaluation of Malaria Vectors at Different Altitudes in Hai District, Northeastern Tanzania](#).

- 551      *Journal of Medical Entomology*, 43, 580–588.
- 552      McCann, K. (2007). Protecting biostructure. *Nature*, 446, 29–29.
- 553      McCann, K.S. (2011). Food webs (MPB-50). In: *Food Webs (MPB-50)*. Princeton University Press.
- 554      McLeod, A., Leroux, S.J., Gravel, D., Chu, C., Cirtwill, A.R., Fortin, M.-J., *et al.* (2021a). [Sampling and asymptotic network properties of spatial multi-trophic networks](#). *Oikos*, 130, 2250–2259.
- 555
- 556      McLeod, A., Leroux, S.J., Gravel, D., Chu, C., Cirtwill, A.R., Fortin, M.-J., *et al.* (2021b). [Sampling and asymptotic network properties of spatial multi-trophic networks](#). *Oikos*, n/a.
- 557
- 558      McLeod, A.M., Leroux, S.J. & Chu, C. (2020). [Effects of species traits, motif profiles, and environment on spatial variation in multi-trophic antagonistic networks](#). *Ecosphere*, 11, e03018.
- 559
- 560      Melián, C.J., Vilas, C., Baldó, F., González-Ortegón, E., Drake, P. & Williams, R.J. (2011). [Eco-evolutionary Dynamics of Individual-Based Food Webs](#). In: *Advances in Ecological Research*, The Role of Body Size in Multispecies Systems (ed. Belgrano, A.). Academic Press, pp. 225–268.
- 561
- 562
- 563      Ohlmann, M., Miele, V., Dray, S., Chalmandrier, L., O'Connor, L. & Thuiller, W. (2019). [Diversity indices for ecological networks: A unifying framework using Hill numbers](#). *Ecology Letters*, 22, 737–747.
- 564
- 565      Olesen, J.M., Bascompte, J., Dupont, Y.L., Elberling, H., Rasmussen, C. & Jordano, P. (2010). [Missing and forbidden links in mutualistic networks](#). *Proceedings of the Royal Society B: Biological Sciences*, 278, 725–732.
- 566
- 567
- 568      Pascual, M., Dunne, J.A. & Dunne, J.A. (2006). *Ecological Networks: Linking Structure to Dynamics in Food Webs*. Oxford University Press, USA.
- 569
- 570      Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2008). [Size, foraging, and food web structure](#). *Proceedings of the National Academy of Sciences*, 105, 4191–4196.
- 571
- 572      Pilosof, S., Porter, M.A., Pascual, M. & Kéfi, S. (2017). [The multilayer nature of ecological networks](#). *Nature Ecology & Evolution*, 1, 1–9.
- 573
- 574      Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D. (2012). [The dissimilarity of species interaction networks](#). *Ecology Letters*, 15, 1353–1361.
- 575
- 576      Poisot, T., Cirtwill, A.R., Cazelles, K., Gravel, D., Fortin, M.-J. & Stouffer, D.B. (2016). [The structure of probabilistic networks](#). *Methods in Ecology and Evolution*, 7, 303–312.
- 577

- 578 Poisot, T. & Gravel, D. (2014). When is an ecological network complex? Connectance drives degree  
579 distribution and emerging network properties. *PeerJ*, 2, e251.
- 580 Poisot, T., Stouffer, D.B. & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary  
581 through space and time. *Oikos*, 124, 243–251.
- 582 Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O’Hara, R.B., Parris, K.M., et al. (2014). Understanding  
583 co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM).  
584 *Methods in Ecology and Evolution*, 5, 397–406.
- 585 Pomeranz, J.P.F., Thompson, R.M., Poisot, T. & Harding, J.S. (2019). Inferring predator-prey interactions in  
586 food webs. *Methods in Ecology and Evolution*, 10, 356–367.
- 587 Pringle, R.M. & Hutchinson, M.C. (2020). Resolving Food-Web Structure. *Annual Review of Ecology,*  
588 *Evolution, and Systematics*, 51, 55–80.
- 589 Proulx, S.R., Promislow, D.E.L. & Phillips, P.C. (2005). Network thinking in ecology and evolution. *Trends in*  
590 *Ecology & Evolution*, SPECIAL ISSUE: BUMPER BOOK REVIEW, 20, 345–353.
- 591 Pulliam, H.R. (1974). On the Theory of Optimal Diets. *The American Naturalist*, 108, 59–74.
- 592 Rooney, N. & McCann, K.S. (2012). Integrating food web diversity, structure and stability. *Trends in Ecology*  
593 *& Evolution*, 27, 40–46.
- 594 Salim, J.A., Saraiva, A.M., Zermoglio, P.F., Agostini, K., Wolowski, M., Drucker, D.P., et al. (2022). Data  
595 standardization of plant-pollinator interactions. *GigaScience*, 11, giac043.
- 596 Saravia, L.A., Marina, T.I., Kristensen, N.P., De Troch, M. & Momo, F.R. (2022). Ecological network  
597 assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, 91, 630–642.
- 598 Schmeller, D.S., Julliard, R., Bellingham, P.J., Böhm, M., Brummitt, N., Chiarucci, A., et al. (2015). Towards a  
599 global terrestrial species monitoring program. *Journal for Nature Conservation*, 25, 51–57.
- 600 Singer, M.C. & McBride, C.S. (2012). Geographic mosaics of species’ association: A definition and an  
601 example driven by plant-insect phenological synchrony. *Ecology*, 93, 2658–2673.
- 602 Stouffer, D.B., Rezende, E.L. & Amaral, L.A.N. (2011). The role of body mass in diet contiguity and food-web  
603 structure. *Journal of Animal Ecology*, 80, 632–639.

- 604 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M.J., *et al.* (2022). [Food web](#)  
605 [reconstruction through phylogenetic transfer of low-rank network representation](#). *Methods in Ecology and*  
606 *Evolution*, 13.
- 607 Strydom, T., Catchen, M.D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., *et al.* (2021). [A](#)  
608 [roadmap towards predicting species interaction networks \(across space and time\)](#). *Philosophical*  
609 *Transactions of the Royal Society B-Biological Sciences*, 376, 20210063.
- 610 Tylianakis, J.M., Tscharntke, T. & Lewis, O.T. (2007). [Habitat modification alters the structure of tropical](#)  
611 [hostparasitoid food webs](#). *Nature*, 445, 202–205.
- 612 Vázquez, D.P., Peralta, G., Cagnolo, L., Santos, M. & Igual, E. autores contribuyeron por. (2022). [Ecological](#)  
613 [interaction networks. What we know, what we don't, and why it matters](#). *Ecología Austral*, 32, 670–697.
- 614 Weinstein, B.G. & Graham, C.H. (2017a). [On comparing traits and abundance for predicting species](#)  
615 [interactions with imperfect detection](#). *Food Webs*, 11, 17–25.
- 616 Weinstein, B.G. & Graham, C.H. (2017b). [Persistent bill and corolla matching despite shifting temporal](#)  
617 [resources in tropical hummingbird-plant interactions](#). *Ecology Letters*, 20, 326–335.
- 618 Wood, S.A., Russell, R., Hanson, D., Williams, R.J. & Dunne, J.A. (2015). [Effects of spatial scale of sampling](#)  
619 [on food web structure](#). *Ecology and Evolution*, 5, 3769–3782.
- 620 Woodward, G., Benstead, J.P., Beveridge, O.S., Blanchard, J., Brey, T., Brown, L.E., *et al.* (2010). [Chapter 2 -](#)  
621 [Ecological Networks in a Changing Climate](#). In: *Advances in Ecological Research*, Ecological Networks  
622 (ed. Woodward, G.). Academic Press, pp. 71–138.
- 623 Woodward, G., Brown, L.E., Edwards, F.K., Hudson, L.N., Milner, A.M., Reuman, D.C., *et al.* (2012). [Climate](#)  
624 [change impacts in multispecies systems: Drought alters food web size structure in a field experiment](#).  
625 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 2990–2997.