

# The ecological interpretation of probabilistic networks

Francis Banville<sup>1,2,3,‡</sup> Tanya Strydom<sup>1,3,‡</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>‡</sup> Equal contributions

## 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 interpretations of probabilistic  
73 networks. These metadata should outline the nature (i.e., potential or local) and type (e.g., predatory or  
74 pollination) of the interactions, provide information regarding the taxonomic level, identities, and characteristics  
75 (e.g., life stages) of the individuals involved in an interaction, present the mathematical formulation of  
76 probabilities, including clearly identified conditional variables, and describe the methods and contexts (e.g.,  
77 location, environmental conditions) in which interactions were estimated. Inadequately documented  
78 probabilistic interaction data should be used with caution when analyzing ecological networks. Although our  
79 contribution focuses on food webs, our observations and advice can be applied to other types of ecological  
80 networks, from plant-pollinator to host-virus networks. Indeed, excluding networks of indirect interactions such  
81 as competition and facilitation networks (Kéfi *et al.* (2015), Kéfi *et al.* (2016)), most ecological networks  
82 describe probabilities of direct interactions, which are conceptually and mathematically analogous regardless of  
83 their biological type (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

88 interaction refers to the materialization or observation of this interaction in a well-defined space and time (i.e.,  
89 the probability that they interact locally). Here, we use the terms *metaweb* (Dunne (2006)) to designate  
90 networks of potential interactions and *local networks* (Poisot *et al.* (2012)) for those of realized interactions.  
91 Metawebs are the network analogues of the species pool, where local networks originate from a subset of both  
92 species (nodes) and interactions (edges) of the regional metaweb (Saravia *et al.* (2022)). It can be challenging to  
93 know when published probabilistic networks describe potential or realized interactions, or when so-called  
94 probabilities are in reality *interaction scores* (i.e., non-probabilistic quantitative interactions). Moreover,  
95 probabilistic potential interactions are often used and interpreted as realized interactions (and conversely),  
96 which may generate misleading findings when analyzing these data. We believe that a better understanding of  
97 the differences, similarities, and relationships between these two probabilistic representations of ecological  
98 networks would alleviate interpretation errors and facilitate a more adequate utilization of interaction data.

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

100 Local ecological networks and metawebs, like any type of network, are made of nodes and edges that can be  
101 represented at different levels of organization and precision. The basic unit of food webs and other ecological  
102 networks are individuals that interact with each other (e.g., by predation, Elton (2001)), forming  
103 individual-based networks (Melián *et al.* (2011)). The aggregation of these individuals into more or less  
104 homogeneous groups (e.g., populations, species, trophic species, families) allows us to represent nodes at  
105 broader taxonomic scales, which affects our interpretation of the properties of these systems (Guimarães  
106 (2020)). Moreover, edges linking these nodes can describe a variety of interaction measures. Ecologists have  
107 traditionally represented interactions as binary objects that were considered realized after observing at least one  
108 individual from group  $i$  interact with at least another individual from group  $j$ . Boolean interactions can be  
109 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  
110 interaction between  $i$  and  $j$  that characterizes our limited knowledge of the system and its intrinsic  
111 spatiotemporal variability. Depending on the type of networks (local or metaweb), the mathematical  
112 formulation and interpretation of stochastic parameters like  $P(i \rightarrow j)$  can be linked to environmental and  
113 biological factors such as species relative abundance, traits, area, and time (tbl. 1). In these probabilistic  
114 network representations in which  $P(i \rightarrow j)$  are edge values, the only two possible outcomes are the presence  
115 ( $A_{i,j} = 1$ ) or absence ( $A_{i,j} = 0$ ) of an interaction between each pair of nodes. Observing an interaction between  
116 two taxa at a given location and time provides important information that can be used to update previous

estimates of  $P(i \rightarrow j)$ , informing us on the biological capacity of both taxa to interact and the environmental conditions that enabled them to interact locally.

Even though binary networks constitute a highly valuable source of ecological information (Pascual *et al.* (2006)), they overlook important factors regarding interaction strengths. These are represented using quantitative interactions, which better describe the energy flows, demographic impacts or frequencies of interactions between nodes (Berlow *et al.* (2004), Borrett & Scharler (2019)), with  $A_{i,j}$  being a natural number  $\mathbb{N}$  or a real number  $\mathbb{R}$  depending on the measure. For example, they can represent the average number of prey individuals consumed by a predator in a given time period (e.g., the average number of fish in the stomach of a piscivorous species). Because quantitative interactions can describe predation pressure on prey taxa, they can be good estimators of the parameters describing species interactions in a Lotka-Volterra model (e.g., Emmerson & Raffaelli (2004)). However, this extra amount of ecological information typically comes at a cost of greater sampling effort or data volume in predictive models (Strydom *et al.* (2021)), which can lead to relatively high levels of uncertainties when inferring quantitative networks with limited data. Just like binary networks, the uncertainty and spatiotemporal variability of quantitative interactions can be represented probabilistically, with the difference that quantitative interactions can follow various probability distributions depending on the measure used, the event's outcome being the value of interaction strength. For instance, quantitative interactions can follow a Poisson distribution  $A_{i,j} \sim \text{Poisson}(\lambda_{i \rightarrow j})$  when predicting frequencies of interactions between pairs of nodes, with  $\lambda_{i \rightarrow j}$  being the expected rate at which individuals of taxa  $i$  and  $j$  interact (e.g., the average number of prey  $j$  consumed by all predators  $i$ ). The Poisson distribution can also be 0-inflated when considering non-interacting taxa, which constitute the majority of taxa pairs in most local networks due to their typically high sparseness (Jordano (2016)). Because of the methodological difficulties typically encountered when building deterministic quantitative networks, binary networks, which are easier to sample (Jordano (2016)) and predict (Strydom *et al.* (2021)), are much more documented and modeled in the literature. Moreover, most published probabilistic networks and methods describe Bernoulli interactions, which underlines the need for better guidelines regarding the interpretation and manipulation of these types of networks. For these reasons, our primary focus in this contribution will be on addressing the challenges in estimating and using Bernoulli interactions, in both probabilistic local networks and metawebs.

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

145 Probabilistic local networks describe how likely taxa are to interact at a given location and time period (i.e., they  
146 are context-dependent). In local networks, edges commonly represent our degree of belief that two taxa interact  
147 in nature, but can also document the probability of *observing* this interaction (Catchen *et al.* (2023)). For  
148 example, Kopelke *et al.* (2017) assembled a dataset of binary local European food webs of willow-galling  
149 sawflies and their natural enemies, clearly referencing each food web in space and time. Because of its large  
150 number of replicated samples, this dataset can be used to infer the probability of locally observing an interaction  
151 between any pair of taxa by measuring the proportion of sites where an interaction was observed (Gravel *et al.*  
152 (2019)). More generally, we define space as the geographic coordinates ( $x, y$ ) of the spatial boundaries  
153 delineating the system (sampled or targeted) and time as the time interval during which interactions were  
154 sampled or for which they were predicted. Given that space and time are in reality continuous variables, the  
155 probability that an interaction occurs within a particular spatial and temporal setting is given by the integral of  
156 the probability density function describing the relative likelihood that this interaction is realized at any specific  
157 and infinitely small location and time. Therefore, the edge value could represent a probability density or a  
158 probability mass depending on how space and time are measured. For simplicity reasons, we will consider  
159 space and time as discrete dimensions that provide actual probabilities of interactions, which is conform to how  
160 ecological interactions are usually sampled. Using space and time intervals allows us to measure an area  $A$  and  
161 duration  $t$ , which can be directly used in spatiotemporal analyses of ecological networks. For example, when  
162 studying network-area relationships (NAR, Galiana *et al.* (2018)), we should expect local probabilities of  
163 interactions to scale positively with area and duration because taxa have more opportunities to interact.

164 The probability that two taxa  $i$  and  $j$  interact locally can also be conditional on many environmental and  
165 biological factors. One of these is their co-occurrence  $C_{i,j}$ , which is usually a Boolean describing if the  
166 geographic distribution of both taxa overlaps within the study area. In local networks, the probability that the  
167 interaction is realized must be 0 when taxa do not co-occur, i.e.  $P_N(i \rightarrow j | C = 0) = 0$ . Co-occurrence can also  
168 be modeled probabilistically. In that case, it follows a Bernoulli distribution  $C_{i,j} \sim \text{Bernoulli}(P_{i,j}(x, y))$ , where  
169 the probability of co-occurrence  $P_{i,j}(x, y)$  can be estimated using joint species distribution models (e.g., Pollock  
170 *et al.* (2014)). More generally, the probability that two taxa interact locally can be obtained by the product of  
171 their probability of interaction given co-occurrence with their probability of co-occurrence:

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

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

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

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

186 The local context in which probabilities are estimated and the variables that should be taken into consideration  
 187 depend on the study system, the objective of the study, and the resources available to the researchers. In other  
 188 words, these variables do not systematically need to be accounted for. However, when they are, they should be  
 189 specified in the documentation of the data (Brimacombe *et al.* (2023)), preferentially in mathematical terms to  
 190 avoid any confusion in their interpretation and to limit manipulation errors during their re-use. For example,  
 191 ecologists should be explicit about their consideration of co-occurrence in their estimation of local interaction  
 192 probabilities. Indeed, it is important to specify if probability values are conditional  $P_N(i \rightarrow j|C = 1)$  or not  
 193  $P_N(i \rightarrow j)$  on co-occurrence since this can significantly impact the interpretation and analysis of the data. In  
 194 [tbl. 1](#), we present a handful of studies of probabilistic ecological networks and their formulation of probabilistic  
 195 interactions. This table illustrates the variety of definitions of probabilistic interactions found in the literature  
 196 and emphasizes the need to carefully describe interaction data before integrating and analyzing them.

Table 1: Interaction probabilities are interpreted differently in metawebs ( $M$ ) and local networks ( $N$ ). Each formula includes different conditional variables and is described in plain text. A non-exhaustive list of studies using these formulas is included, with the variables used specified in parentheses.

Formula	Description	Studies
$P_M(i \rightarrow j)$	probability that the interaction is biologically feasible	
$P_N(i \rightarrow j)$	probability that the interaction is realized locally	
$P_N(i \rightarrow j A)$	probability that the interaction is realized locally given network area	
$P_N(i \rightarrow j t)$	probability that the interaction is realized locally given duration	
$P_N(i \rightarrow j C)$	probability that the interaction is realized locally given co-occurrence	
$P_N(i \rightarrow j \Omega)$	probability that the interaction is realized locally given chosen environmental and biological factors	
$P_N(i \rightarrow j A, t, C, \Omega)$	probability that the interaction is realized locally given many conditional factors	

## 197 Metawebs: regional catalogs of interactions

198 Metawebs are networks of potential interactions that have been designed for broad spatial, temporal, and  
 199 taxonomic scales (e.g., species food webs at the continental scale). They represent the probability that two taxa  
 200 can biologically interact regardless of their co-occurrence and local environmental conditions. Potential  
 201 interactions are by definition context-independent, i.e. they are not measured at a specific location and time. In  
 202 contrast with probabilistic local networks, which represent the stochasticity of interactions occurring in nature,  
 203 probabilistic metawebs measure our degree of belief in the capacity of two taxa to interact (i.e., the probability  
 204 that their traits could support an interaction in the right conditions). In other words, potential interactions  
 205 describe the probability that there exists at least one combination of phenotypes of taxa  $i$  and  $j$  that can interact  
 206 with each other if they were to encounter. This probability of interaction, in a metaweb  $M$ , can be expressed as

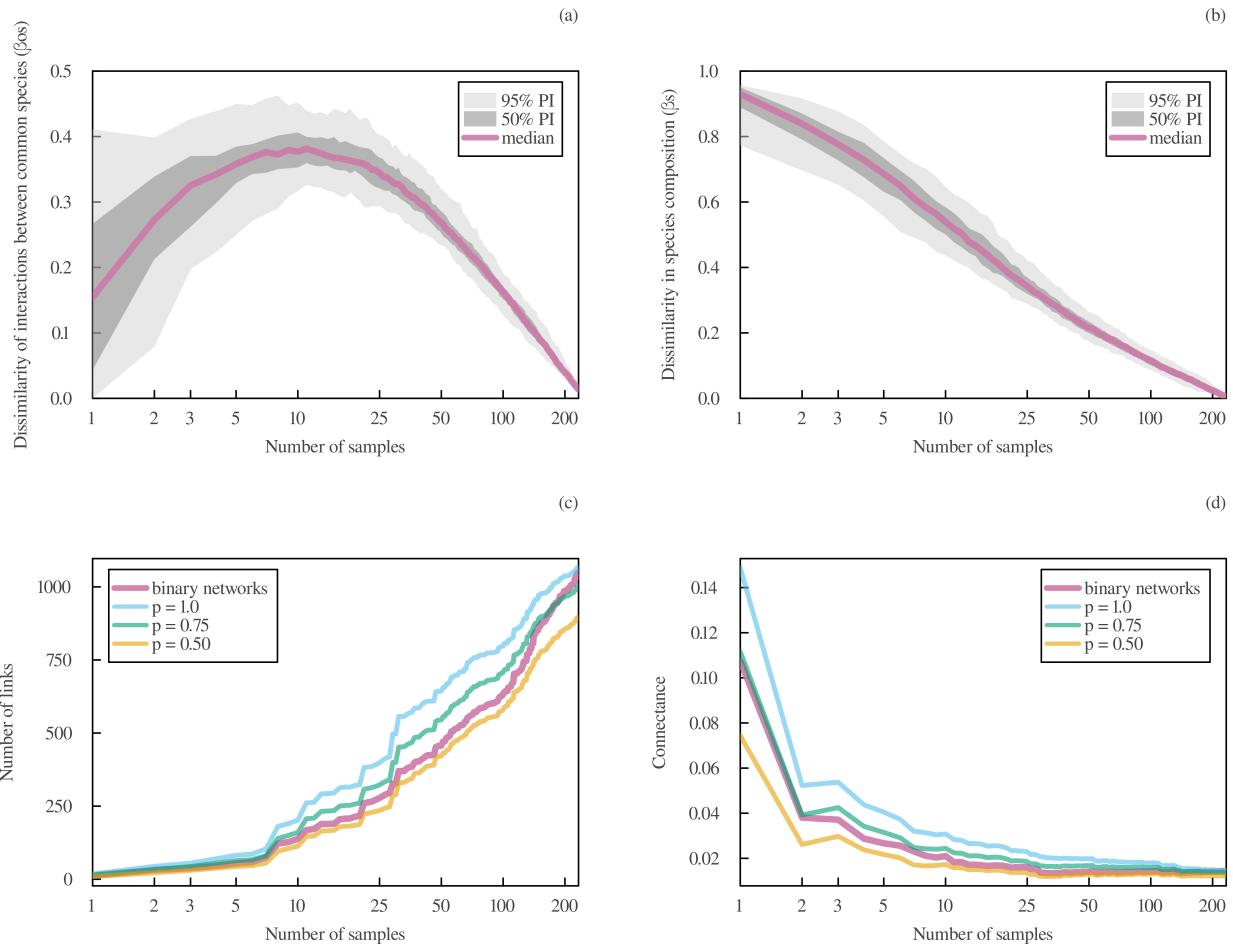
$$P_M(i \rightarrow j), \quad (3)$$

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

208 Starting from a selected set of taxa, which are usually distributed within a broad region of interest, metawebs  
209 can be built using different data sources, including literature review, fieldwork, and predictive models (e.g., the  
210 metaweb of trophic interactions between Canadian mammals inferred by Strydom *et al.* (2022)). Every pair of  
211 taxa that have confidently been observed to interact at least once can be given a probability of 1 (i.e.,  
212  $P_M(i \rightarrow j) = 1$ ) since we know that they *can* interact. This is usually not the case in local probabilistic networks,  
213 in which probabilities usually remain stochastic (i.e.,  $P_N(i \rightarrow j) < 1$ ) after empirically observing interactions  
214 because of their intrinsic spatiotemporal variability. Similarly, although rare interactions typically have low  
215 probabilities in local networks, they can have high probabilities in metawebs if the traits of both taxa match. On  
216 the other hand, interactions that were never observed can have low probability values in both metawebs and  
217 local networks, going as low as 0 for forbidden links. However, because of observation errors due to taxonomic  
218 misidentifications and ecological misinterpretations (e.g., due to cryptic species and interactions, Pringle &  
219 Hutchinson (2020)), many observations of interactions are only false positives. Similarly, forbidden interactions  
220 can be false negatives in metawebs, e.g. if they have been assessed for specific phenotypes, locations or time.  
221 Implementing a Bayesian framework, which updates prior probabilities with empirical data (e.g., Bartomeus *et*  
222 *al.* (2016), Cirtwill *et al.* (2019)), could improve our estimation of interaction probabilities in both systems.

## 223 Probabilistic networks in action

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



229

## 230 Taxonomic scaling of interactions

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

239 There is no qualitative difference in the taxonomic scaling of local networks compared to metawebs because  
 240 only the nodes are defined taxonomically. In other words, the edge probability values of local networks (eq. 2)  
 241 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.

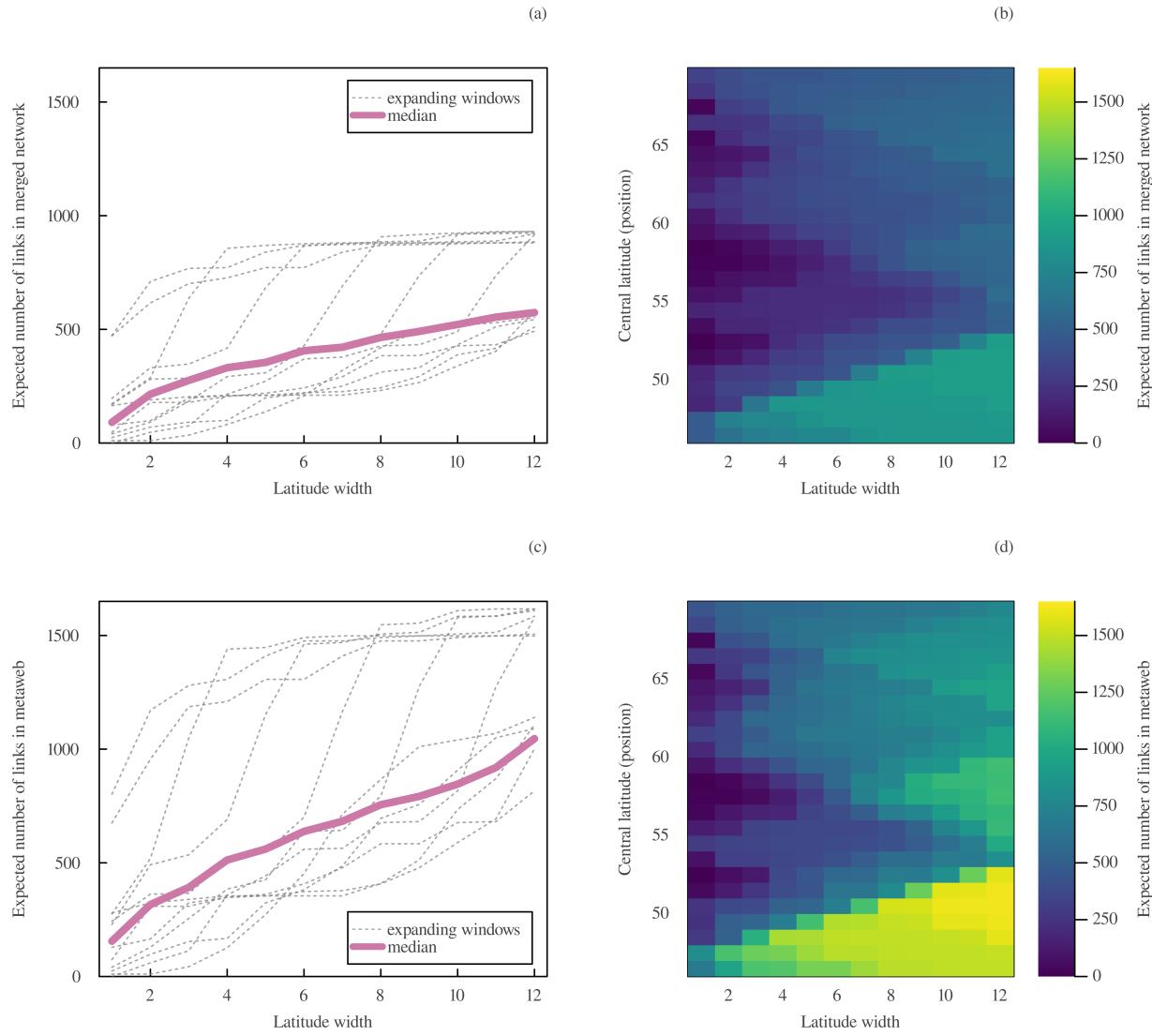
Ideally, the biological interpretation of probabilistic interactions should not differ across a network even if it has heterogenous levels of organization, i.e. if different nodes are represented at different taxonomic scales (e.g., a network composed of species and trophic species). This is frequent 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.

269 **Spatial and temporal scaling of interactions**

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

283 Metawebs and local networks intrinsically differ in their relationship to spatial and temporal scales. On one  
284 hand, because probabilistic metawebs are context-independent, potential interactions do not scale with space  
285 and time since they depend solely on the biological capacity of the two taxa to interact, regardless of any  
286 particular environmental conditions. This suggests that the probability that two taxa can potentially interact  
287 should theoretically be the same in all metawebs in which they are present, provided that the data and methods  
288 used to estimate them are the same. As a result, if a potential network  $M_1$  is subsampled from a regional  
289 metaweb  $M_0$  to represent the potential interactions between a subset of taxa found in a smaller region, their  
290 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  
291 hand, local ecological networks scale both spatially and temporally since interactions have more opportunities to  
292 be realized and observed in a larger area and duration (e.g., more individuals, more trait variations, more chance  
293 of an encounter, McLeod *et al.* (2020)). For example, if a local probabilistic network  $N_1$  of area  $A_1$  is obtained  
294 from a larger network  $N_0$  of area  $A_0$ , with  $A_1$  being completely nested within  $A_0$ , interaction probabilities should  
295 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,  
296 interaction probabilities could be incidentally higher in the smaller area depending on their environmental and  
297 biological conditions. Similarly, interaction probabilities should be smaller in networks of shorter durations if  
298 time intervals are nested. Statistical models, such as network-area relationships and interaction accumulation

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



300

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

302 Predicting local networks across time and space is an important goal of network ecology (Strydom *et al.*  
303 (2021)). Indeed, in a context of scarcity of interaction data (Jordano (2016)), ecologists must rely on predictive  
304 models to reconstruct networks at fine spatial and temporal scales. For example, local ecological networks  
305 could be reconstructed using real-time biomonitoring data and adequate numerical models (Bohan *et al.*  
306 (2017)), which could pave the way for fine-scale studies of ecosystem functioning and dynamics. Besides  
307 predictive models, statistical models can also be built to describe parameters of interest, such as probabilities of  
308 interactions. In that case, parameter values provide valuable ecological information in their own rights.

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

316 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  
 317 of their probability of interaction given co-occurrence and their probability of co-occurrence. First, their  
 318 probability of co-occurrence is given by their respective probabilities of occurrence  $P_i(x, y)$  and  $P_j(x, y)$  and the  
 319 strength of association  $\gamma$  between their occurrence and co-occurrence (Cazelles *et al.* (2016)):

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

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

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

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

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

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

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

330 and generate new interaction data:

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

331

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

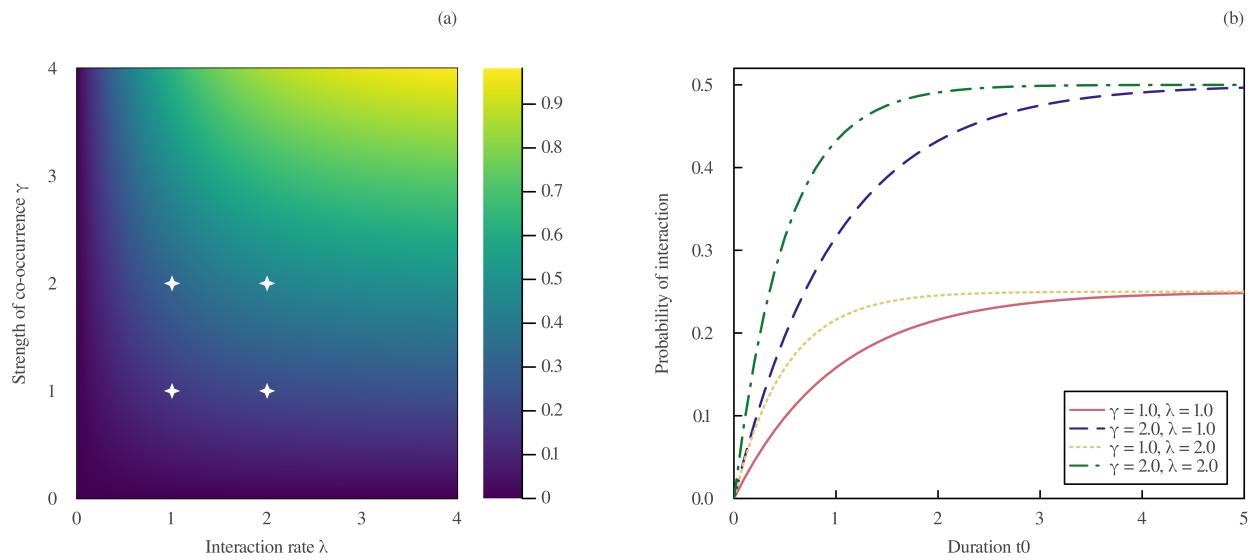
332

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

333

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

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



336

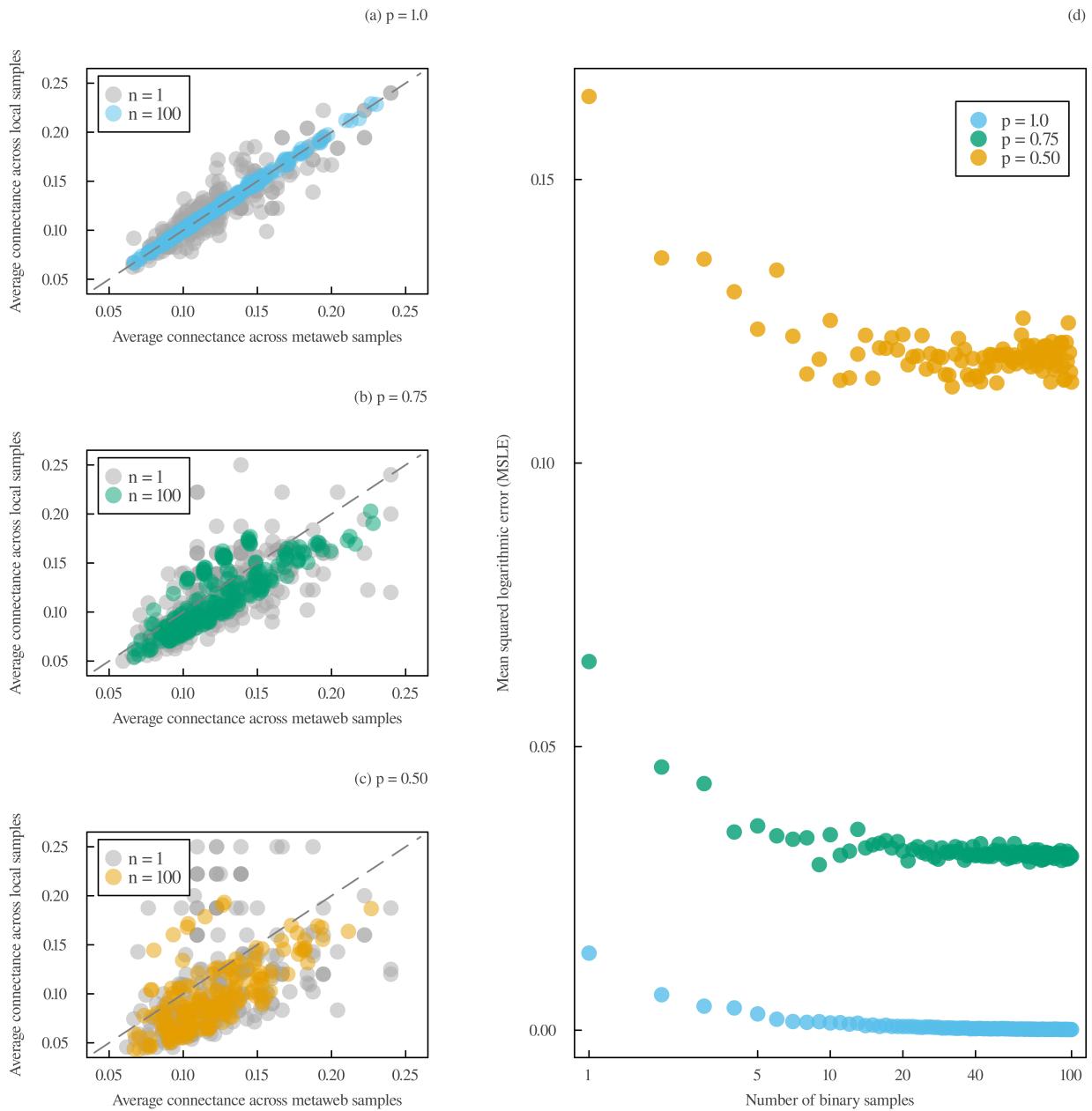
### 337 Sampling binary networks

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

345 observed measure is compared to a null distribution (e.g., Bascompte *et al.* (2003)). Furthermore, randomly  
346 generating binary networks across space and time can help us visualize the spatiotemporal variability of  
347 network structure and test ecological hypotheses on interactions across large spatial and temporal scales.  
  
348 There are at least two different approaches when sampling binary networks from probabilistic webs across  
349 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  
350 single Bernoulli trial for each pair of taxa found in the region of interest based on their regional probability of  
351 interaction. As a result, each pair of taxa that are predicted to interact in the regional network realization will  
352 interact in all of the  $n^2$  networks in which they co-occur. This sampling technique is best used with potential  
353 interactions that have no spatial variation. The second approach is to independently sample each of the  $n^2$   
354 networks. In practice, this can be done by generating a different probabilistic network for each grid cell.  
355 Depending on how they were obtained, these networks can differ in their taxa composition (nodes) and/or  
356 interaction probabilities (edges). Then, binary networks can be independently sampled for each grid cell.  
357 Because this method generates spatial variation in binary interactions, it is best used with local interactions.  
  
358 The choice of sampling approach has an impact on the selection of grid cell size. In the first approach,  
359 interactions will be the same regardless of cell size because interactions are sampled only once from the  
360 regional network. However, in the second approach, local interaction probabilities depend on the network area.  
361 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  
362 contiguous cells that form  $N_0$ . If  $N_1$  and  $N_2$  are independent (which is rarely the case in reality because of  
363 spatial auto-correlation), the probability that two taxa  $i$  and  $j$  interact in  $N_0$  is given by:

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

364 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  
365 sampling binary interactions from local networks, it is thus important to sample at the same spatial scale as the  
366 one for which probabilities were estimated. Otherwise, interaction probabilities must be adjusted to correspond  
367 to the targeted cell size and avoid systematic biases in prediction.



368

### 369 Prediction of local networks from metawebs

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

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

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

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

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

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

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

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

## 392 Conclusion

393 In this contribution, we underlined the importance of network metadata for adequately interpreting and  
394 manipulating probabilistic interaction data. Indeed, the mathematical representation of probabilities and their

395 statistical properties depend on the type of interactions (local or potential) and the conditions in which they  
396 were estimated. We showed that probabilistic local networks and metawebs differ in their relationship to spatial  
397 and temporal scales, with potential interactions being scale-independent. In contrast, local interactions are  
398 measured in a specific context (e.g., in a given area, time, and biological and environmental conditions) and are  
399 conditional on taxa co-occurrence. These important conceptual differences bring to light the need to use  
400 probabilistic data with caution, for instance when generating binary network realizations across space and  
401 predicting local networks from metawebs. Clear metadata describing the type of interaction and the variables  
402 used in their estimation are required to ensure adequate data manipulation. Better data practices and rigorous  
403 foundations for probabilistic thinking in network ecology could enable more reliable assessments of the  
404 spatiotemporal variability and measurement uncertainty of biotic interactions.

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