

The ecological interpretation of probabilistic networks

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

171 The probability that two taxa i and j interact locally can also be conditional on many environmental and
172 biological factors. One of these is their co-occurrence $C_{i,j}$, which is usually a Boolean describing if the
173 geographic distribution of both taxa overlaps within the study area. In local networks, the probability that the
174 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
175 be modeled probabilistically. In that case, it follows a Bernoulli distribution $C_{i,j} \sim \text{Bernoulli}(P_{i,j}(x, y))$, where

176 the probability of co-occurrence $P_{i,j}(x,y)$ can be estimated using joint species distribution models (e.g., Pollock
177 *et al.* (2014)). More generally, the probability that two taxa interact locally can be obtained by the product of
178 their probability of interaction given co-occurrence with their probability of co-occurrence:

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

179 Other important factors that can impact our estimation of interaction probabilities at the local scale are taxa
180 relative abundance (Canard *et al.* (2012)) and traits (Poisot *et al.* (2015)), as well as environmental factors such
181 as temperature (Angilletta *et al.* (2004)), precipitation (Woodward *et al.* (2012)), habitat structure (Klecka &
182 Boukal (2014)), and presence of other interacting taxa in the network (Pilosof *et al.* (2017), Kéfi *et al.* (2012)).

183 Here, we will use the variable Ω to describe the biological and ecological context in which interaction
184 probabilities were estimated. For example, if a research team conducts a mesocosm experiment to estimate
185 interaction probabilities between predators and prey with and without shelters, Ω would represent the presence
186 or absence of these shelters. Like co-occurrence, Ω can also be modeled probabilistically when the stochasticity
187 or uncertainty of environmental and biological factors is considered. In sum, Ω represents all ecological and
188 biological variables that were taken into consideration when measuring interaction probabilities and is,
189 therefore, a subset of all factors actually impacting ecological interactions.

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

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

193 The local context in which probabilities are estimated and the variables that should be taken into consideration
194 depend on the study system, the objective of the study, and the resources available to the researchers. In other
195 words, these variables do not systematically need to be accounted for. However, when they are, they should be
196 specified in the documentation of the data (Brimacombe *et al.* (2023)), preferentially in mathematical terms to
197 avoid any confusion in their interpretation and to limit manipulation errors during their re-use. For example,
198 ecologists should be explicit about their consideration of co-occurrence in their estimation of local interaction
199 probabilities. Indeed, it is important to specify if probability values are conditional $P_N(i \rightarrow j|C = 1)$ or not

200 $P_N(i \rightarrow j)$ on co-occurrence since this can significantly impact the interpretation and analysis of the data. In
 201 tbl. 1, we present a handful of studies of probabilistic ecological networks and their formulation of probabilistic
 202 interactions. This table illustrates the variety of definitions of probabilistic interactions found in the literature
 203 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	

204 **Metawebs: regional catalogs of interactions**

205 Metawebs are networks of potential interactions that have been designed for broad spatial, temporal, and
 206 taxonomic scales (e.g., species food webs at the continental scale). They represent the probability that two taxa
 207 can biologically interact regardless of their co-occurrence and local environmental conditions. Potential
 208 interactions are by definition context-independent, i.e. they are not measured at a specific location and time. In
 209 contrast with probabilistic local networks, which represent the stochasticity of interactions occurring in nature,
 210 probabilistic metawebs measure our degree of belief in the capacity of two taxa to interact (i.e., the probability
 211 that their traits could support an interaction in the right conditions). In other words, potential interactions

212 describe the probability that there exists at least one combination of phenotypes of taxa i and j that can interact
213 with each other if they were to encounter. This probability of interaction, in a metaweb M , can be expressed as

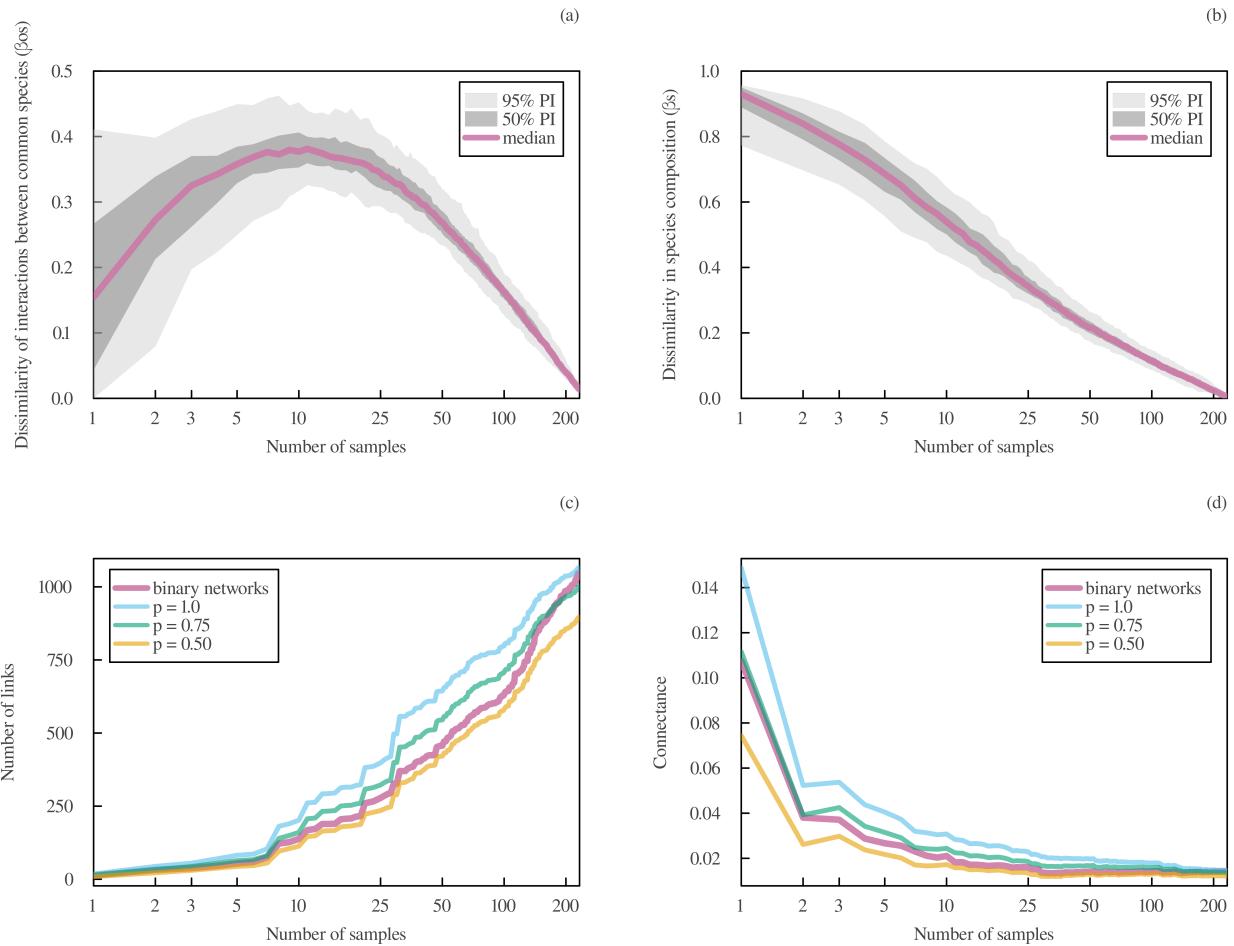
$$P_M(i \rightarrow j), \quad (3)$$

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

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

230 Probabilistic networks in action

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



236

237 Taxonomic scaling of interactions

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

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

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

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

253 where A_i and B_j are the species of the corresponding genus. Knowing that two species interact (i.e.,
254 $P(A_i \rightarrow B_j) = 1$) gives a probability of genus interaction of 1. Canard *et al.* (2012) built a species-based
255 network from neutrally simulated interactions between individuals using a similar approach. In contrast, more
256 sophisticated models need to be built when shifting to a finer level of organization. Indeed, knowing that two
257 genera interact does not imply that all of their pairwise species combinations can also interact. One could, for
258 example, build a finer-scale network by generating probabilities of species interactions by randomly sampling
259 them from a beta distribution parametrized by the broader-scale network.

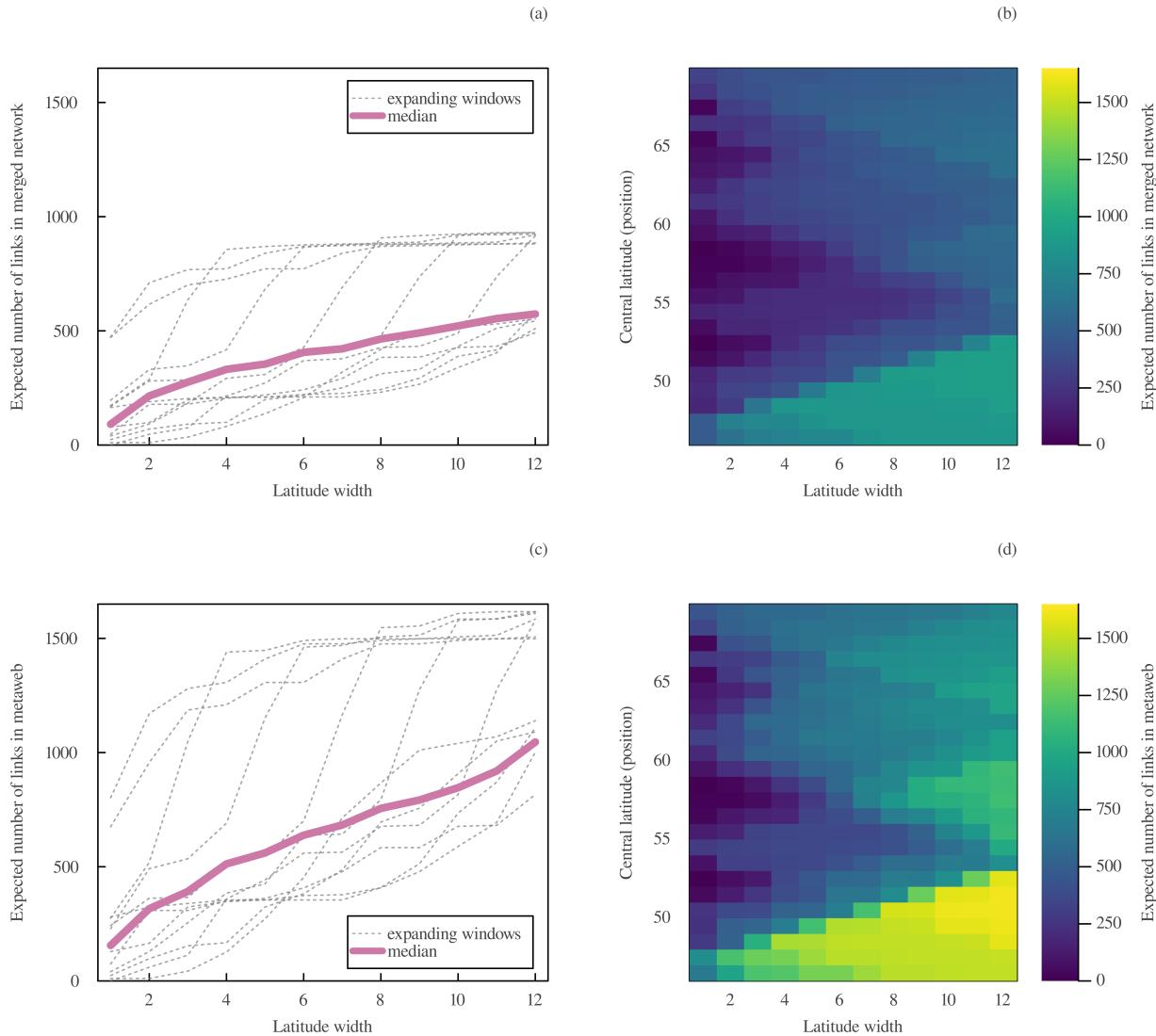
260 Ideally, the biological interpretation of probabilistic interactions should not differ across a network even if it has
261 heterogenous levels of organization, i.e. if different nodes are represented at different taxonomic scales (e.g., a
262 network composed of species and trophic species). This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

276 **Spatial and temporal scaling of interactions**

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

290 Metawebs and local networks intrinsically differ in their relationship to spatial and temporal scales. On one
291 hand, because probabilistic metawebs are context-independent, potential interactions do not scale with space
292 and time since they depend solely on the biological capacity of the two taxa to interact, regardless of any
293 particular environmental conditions. This suggests that the probability that two taxa can potentially interact
294 should theoretically be the same in all metawebs in which they are present, provided that the data and methods
295 used to estimate them are the same. As a result, if a potential network M_1 is subsampled from a regional
296 metaweb M_0 to represent the potential interactions between a subset of taxa found in a smaller region, their
297 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
298 hand, local ecological networks scale both spatially and temporally since interactions have more opportunities to
299 be realized and observed in a larger area and duration (e.g., more individuals, more trait variations, more chance
300 of an encounter, McLeod *et al.* (2020)). For example, if a local probabilistic network N_1 of area A_1 is obtained
301 from a larger network N_0 of area A_0 , with A_1 being completely nested within A_0 , interaction probabilities should
302 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,
303 interaction probabilities could be incidentally higher in the smaller area depending on their environmental and
304 biological conditions. Similarly, interaction probabilities should be smaller in networks of shorter durations if
305 time intervals are nested. Statistical models, such as network-area relationships and interaction accumulation

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



307

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

309 Predicting local networks across time and space is an important goal of network ecology (Strydom *et al.*
310 (2021)). Indeed, in a context of scarcity of interaction data (Jordano (2016)), ecologists must rely on predictive
311 models to reconstruct networks at fine spatial and temporal scales. For example, local ecological networks
312 could be reconstructed using real-time biomonitoring data and adequate numerical models (Bohan *et al.*
313 (2017)), which could pave the way for fine-scale studies of ecosystem functioning and dynamics. Besides
314 predictive models, statistical models can also be built to describe parameters of interest, such as probabilities of
315 interactions. In that case, parameter values provide valuable ecological information in their own rights.

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

323 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
 324 of their probability of interaction given co-occurrence and their probability of co-occurrence. First, their
 325 probability of co-occurrence is given by their respective probabilities of occurrence $P_i(x, y)$ and $P_j(x, y)$ and the
 326 strength of association γ between their occurrence and co-occurrence (Cazelles *et al.* (2016)):

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

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

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

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

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

334 which approaches 1 when $t_0 \rightarrow \infty$.
 335 The realization of the interaction between i and j is the result of a Bernoulli trial with probability $P_N(i \rightarrow j)$. A
 336 Bayesian inference model can thus be built from the previous equations to estimate the value of the λ parameter

337 and generate new interaction data:

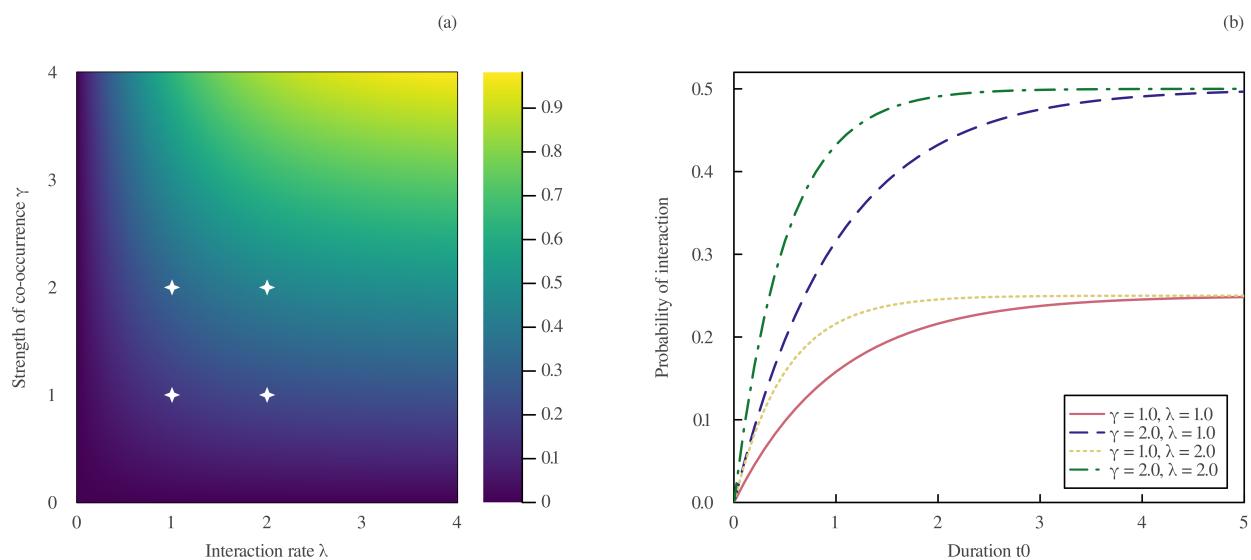
$$I \sim \text{Bernoulli}(P_N(i \rightarrow j)) \quad (8)$$

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

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

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

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



343

344 Sampling binary networks

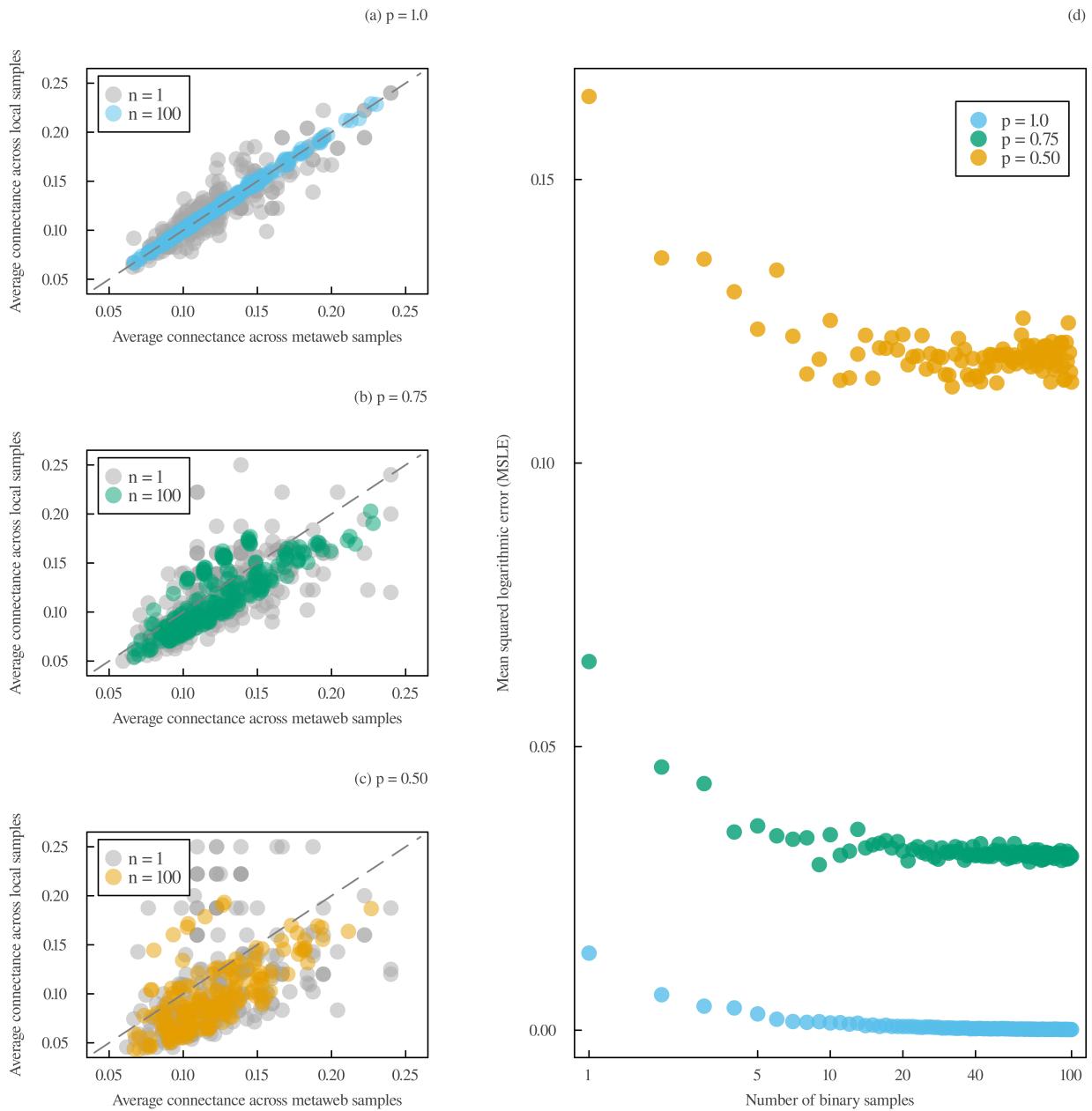
345 Probabilistic networks can be used to predict binary interactions through random draws. This can be useful
 346 when analyzing the structure of a probabilistic network when analytical probabilistic measures are lacking. A
 347 binary network can be generated from independent Bernoulli trials for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

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

355 There are at least two different approaches when sampling binary networks from probabilistic webs across
356 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
357 single Bernoulli trial for each pair of taxa found in the region of interest based on their regional probability of
358 interaction. As a result, each pair of taxa that are predicted to interact in the regional network realization will
359 interact in all of the n^2 networks in which they co-occur. This sampling technique is best used with potential
360 interactions that have no spatial variation. The second approach is to independently sample each of the n^2
361 networks. In practice, this can be done by generating a different probabilistic network for each grid cell.
362 Depending on how they were obtained, these networks can differ in their taxa composition (nodes) and/or
363 interaction probabilities (edges). Then, binary networks can be independently sampled for each grid cell.
364 Because this method generates spatial variation in binary interactions, it is best used with local interactions.
365 The choice of sampling approach has an impact on the selection of grid cell size. In the first approach,
366 interactions will be the same regardless of cell size because interactions are sampled only once from the
367 regional network. However, in the second approach, local interaction probabilities depend on the network area.
368 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
369 contiguous cells that form N_0 . If N_1 and N_2 are independent (which is rarely the case in reality because of
370 spatial auto-correlation), the probability that two taxa i and j interact in N_0 is given by:

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

371 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
372 sampling binary interactions from local networks, it is thus important to sample at the same spatial scale as the
373 one for which probabilities were estimated. Otherwise, interaction probabilities must be adjusted to correspond
374 to the targeted cell size and avoid systematic biases in prediction.



375

376 Prediction of local networks from metawebs

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

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

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

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

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

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

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

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

399 Conclusion

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

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

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