

# 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 they are to occur?) 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 (predatory, herbivory, and parasitic interactions). These definitions are based on the distinction between the realization of an interaction at a specific time and space (local web) and its biological feasibility (metaweb). We show that different network representations have different statistical properties when it comes to common ecological applications. Specifically, we argue that probabilistic local 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 webs from subsets of metawebs. To support our arguments, we develop different case studies using open empirical data on host-parasite interactions in Europe. 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. Comprehensive metadata, providing explicit details on the sources of uncertainty in probabilistic webs, not only supports more rigorous statistical analyses but also broadens the scope of applications of interaction data. This clarity may help with the identification of optimal sampling locations to effectively minimize the uncertainty of trophic interactions.

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## **1 Introduction**

2 As we try to navigate global biodiversity change, filling in knowledge gaps about biodiversity becomes  
3 instrumental to monitoring and mitigating those changes (Gonzalez & Londoño (2022), Abrego *et al.* (2021)).  
4 However, cataloging species, populations and, in particular, ecological interactions (e.g., predation, parasitism,  
5 and pollination) is a substantial challenge (Polis (1991), Pascual *et al.* (2006)). There are methodological and  
6 biological constraints that hinder our ability to observe all ecological interactions, leading to significant  
7 uncertainties in our understanding of these interactions. For example, the spatial and temporal uncoupling of  
8 species (e.g., nocturnal and diurnal species coexisting in the same space without interacting due to differences  
9 in the timing of their daily activities, Jordano (1987)) and the large number of rare and cryptic interactions in a  
10 community contribute to these uncertainties (Jordano (2016)). More generally, a handful of conditions must be  
11 satisfied for an interaction to be observed locally. First, both species must have overlapping geographic ranges,  
12 i.e. they must co-occur within the region of interest (Blanchet *et al.* (2020)). Second, they must have some  
13 probability of meeting. Probabilities of interspecific encounters are typically low, especially for rare species  
14 with low relative abundances (Canard *et al.* (2012)). The probability that species meet each other also depends  
15 on their biological characteristics, such as the synchronization of their phenology (Olesen *et al.* (2010), Singer  
16 & McBride (2012)) and their discoverability (e.g., Broom & Ruxton (2005)). Finally, when species do come  
17 into contact, an interaction occurs only if their traits are locally compatible (Poisot *et al.* (2015)), including but  
18 not limited to their body phenotypes (Bolnick *et al.* (2011), Stouffer *et al.* (2011), Gravel *et al.* (2013)) and  
19 behavioral choices (Pulliam (1974), Choh *et al.* (2012)). Interactions may also be influenced by the presence or  
20 prevalence of a third species (e.g., of a more profitable prey species, Golubski & Abrams (2011), Sanders & van  
21 Veen (2012)). Documenting the location and timing of interactions becomes even more difficult when  
22 accounting for the spatiotemporal variability of ecological interactions (Poisot *et al.* (2012), Poisot *et al.*  
23 (2015)). Environmental factors, such as temperature (Angilletta *et al.* (2004)), drought (Woodward *et al.*  
24 (2012)), climate change (Gilman *et al.* (2010), Woodward *et al.* (2010), Araujo *et al.* (2011)), and habitat  
25 modifications (Tylianakis *et al.* (2007)), contribute to this spatiotemporal variability by impacting species  
26 abundance and traits. Even after satisfying all these conditions, there remains a possibility that the interaction  
27 does not occur locally, either due to the intricate nature of the system or simply by chance. If it does occur, it  
28 might still go unnoticed, particularly if it happens infrequently. In this context, it is unsurprising that our  
29 knowledge of ecological interactions remains limited (Hortal *et al.* (2015)) despite extensive biodiversity data  
30 collection (Schmeller *et al.* (2015)).

31 Knowing the biological capacity of two species to interact directly (via e.g., trophic interactions) is necessary  
32 but not sufficient for inferring their interaction at a specific time and space. The recognition of the intrinsic  
33 variability of species interactions has led ecologists to expand their representation of ecological networks (also  
34 known as ecological webs) to include a probabilistic view of interactions (Poisot *et al.* (2016), Dallas *et al.*  
35 (2017), Fu *et al.* (2021)). This different perspective allows us to fill in the Eltonian shortfall (Hortal *et al.*  
36 (2015)) by modeling the probability of detecting interactions, which can be an important tool for directing  
37 efforts and taking action, especially in places where access and resources for research are scarce. The  
38 probabilistic representation of interactions is thus far limited to direct interactions, which are conceptually and  
39 mathematically analogous regardless of their biological type (e.g., predation and pollination). This is in contrast  
40 with indirect interactions (e.g., interspecific competition), which arise from distinct ecological processes and are  
41 often not directly observable (Kéfi *et al.* (2015), Kéfi *et al.* (2016)). Representing direct interactions  
42 probabilistically enables us to capture the spatiotemporal variability of the aforementioned ecological processes  
43 and the uncertainties associated with their measurement. As opposed to binary deterministic webs, in which  
44 interactions are regarded as either occurring or not, probabilistic webs, within a Bayesian framework, express  
45 our degree of belief (or confidence) regarding the occurrence or observation of interactions. Based on the scale  
46 at which they are estimated, probabilistic interactions may reflect our level of confidence in whether interactions  
47 will be observed, realized locally, or biologically feasible. As an illustration, we could outline a situation in  
48 which there is a 50% certainty that an interaction occurs 50% of the time, or that there is a 50% certainty that it  
49 simply occurs. Our level of confidence should be more definitive (approaching either 0 or 1) as we extend our  
50 sampling to a broader area and over a longer time period, thereby diminishing the uncertainty of the interactions  
51 (but not necessarily the estimation of their variability). In the broadest sense, binary networks are also a type of  
52 probabilistic network, in which the numerical value of an interaction is restrained to 0 (non-occurring) or 1  
53 (occurring). Yet, for the sake of clarity, we omit binary networks from our discussion of probabilistic networks  
54 in this contribution. In probabilistic webs, only forbidden interactions (i.e., interactions prohibited by biological  
55 traits or species absence, Jordano *et al.* (2003), Olesen *et al.* (2010)) have a probability value of zero by default,  
56 provided that intraspecific trait variability is considered (Gonzalez-Varo & Traveset (2016)).

57 By accounting for the uncertainty of interactions, probabilistic webs may provide a more realistic portrait of  
58 species interactions and network structure (i.e. community-level properties), which are major drivers of the  
59 functioning, dynamics, and resilience of ecosystems worldwide (Proulx *et al.* (2005), McCann (2007), McCann  
60 (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 (and guide) 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 webs 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 networks, 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 predictions of ecological webs 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, which generate probabilistic networks by preserving chosen characteristics of the binary adjacency matrix while intentionally omitting others (Bascompte *et al.* (2003), Fortuna & Bascompte (2006)), serve as other examples of common probabilistic network models. Null models can be used to produce underlying distributions of network measures for null hypothesis significance testing. 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 webs. 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 webs (Gilman *et al.* (2010)).

The lack of clear guidelines on the use of probabilistic interaction data is worrisome, both for data producers and re-users who generate and manipulate these numbers. This is concerning because sampling strategies and decisions regarding network construction can affect our understanding of network properties (Brimacombe *et al.* (2023)). Besides methodological difficulties that may arise when assessing probabilistic interactions, a precise definition of probabilistic interactions appears to be lacking, making the estimation and use of these data more difficult. We aim to take a step back by outlining different ways in which probabilistic interactions are defined and used in network ecology. We distinguish two broad categories of probabilistic webs that necessitate distinct approaches when applied to key ecological questions: local webs describing probabilities of realized

91 interactions, and regional webs (metawebs) describing probabilities of potential interactions. We highlight the  
92 distinctions in the ecological meaning of these two representations and examine some of their properties and  
93 relationships (particularly with space, time, and between each other) through empirical case studies. Moreover,  
94 there is currently no metadata standard that could guide the documentation of all types of probabilistic  
95 interactions (although see e.g., Salim *et al.* (2022) who discuss data standards for deterministic mutualistic  
96 webs). Well-defined metadata for probabilistic webs would support more adequate manipulation and integration  
97 of interaction data from different sources and guard against possible misinterpretations arising from ambiguous  
98 definitions of probabilistic networks. These metadata should outline the nature (i.e., local or regional) and type  
99 (e.g., predatory or pollination) of the interactions, provide information regarding the taxonomic level, identities,  
100 and characteristics (e.g., life stages) of the individuals involved in an interaction, present the mathematical  
101 formulation of probabilities, including clearly identified conditional variables (e.g., spatial and temporal scales),  
102 and describe the methods and contexts (e.g., location, time, environmental conditions) in which interactions  
103 were estimated. Inadequately documented probabilistic interaction data should be used with caution when  
104 analyzing ecological webs. Our observations and advice can be applied to most types of ecological networks  
105 representing direct interactions, from food webs to host-virus networks.

## 106 **Probabilistic representations of interactions**

107 One of the first aspects to take into consideration when estimating or interpreting probabilities of interactions is  
108 knowing if they describe potential or realized interactions, as these two types of interactions have distinct  
109 conceptual underpinnings and sources of uncertainty. A potential (regional) interaction is defined as the  
110 biological capacity of two taxa to interact (i.e., the probability that they *can* theoretically interact) whereas a  
111 realized (local) interaction is the materialization or observation of this interaction in a well-defined space and  
112 time (i.e., the probability that they interact locally). Our discussion of local interactions focus on their  
113 occurrence rather than their direct empirical observation, as one of the primary goals of describing them  
114 probabilistically is to characterize our uncertainty regarding their actual manifestation. We use the terms  
115 *metaweb* (Dunne (2006)) to designate regional webs of potential interactions and *local webs* (Poisot *et al.*  
116 (2012)) for those of realized interactions. Metawebs are the network analogs of the species pool, where local  
117 webs originate from a subset of both species (nodes) and interactions (edges) of the regional metaweb (Saravia  
118 *et al.* (2022)). Without clear documentation, it can be challenging to know if published probabilistic webs

119 describe local or regional interactions (tbl. 1 provides examples of studies employing both types of probabilistic  
120 networks), or if so-called probabilities are in reality *interaction scores* (i.e., non-probabilistic quantitative  
121 interactions analogous to interaction strengths). When probabilistic regional interactions are used and  
122 interpreted incorrectly as local interactions (and conversely), this may generate misleading findings during data  
123 analysis. We believe that a better understanding of the differences, similarities, and interconnections between  
124 these two probabilistic representations of ecological webs would alleviate interpretation errors (e.g., when  
125 studying network-area relationships) and facilitate a more adequate utilization of interaction data.

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

127 Local and metawebs, like any type of network, are made of nodes and edges that can be represented at different  
128 levels of organization and precision. The basic units of ecological networks are individuals that interact with  
129 each other (e.g., by predation in food webs, Elton (2001)), forming individual-based networks (Melián *et al.*  
130 (2011)). The aggregation of these individuals into more or less homogeneous groups (e.g., populations, species,  
131 families, feeding guilds) allows us to represent nodes at broader taxonomic scales, which affects our  
132 interpretation of the properties of these systems (Guimarães (2020), Hemprich-Bennett *et al.* (2021)).

133 Edges linking nodes can describe a variety of interaction measures. Ecologists have traditionally represented  
134 interactions as binary objects that were considered realized after observing at least one individual from group  $i$   
135 interact with at least another individual from group  $j$ . In a binary adjacency matrix  $B$ , the presence or absence  
136 of an interaction  $B_{i \rightarrow j}$  between two taxa can be viewed as the result of a Bernoulli process  
137  $B_{i \rightarrow j} \sim \text{Bernoulli}(P(B_{i \rightarrow j}))$ , with  $P(B_{i \rightarrow j})$  being the probability of interaction that characterizes our limited  
138 knowledge of the system and its intrinsic spatiotemporal variability. In probabilistic networks,  $P(B_{i \rightarrow j})$  are edge  
139 values, and the only two possible outcomes are the presence ( $B_{i \rightarrow j} = 1$ ) or absence ( $B_{i \rightarrow j} = 0$ ) of an interaction  
140 between each pair of nodes. Depending on the type of probabilistic network (local or metaweb), the  
141 mathematical formulation and interpretation of stochastic parameters like  $P(B_{i \rightarrow j})$  can be linked to  
142 environmental and biological factors such as species relative abundance, traits, area, and time (tbl. 1), for  
143 example using logistic regression with a logit link function with continuous explanatory variables. Predicting  
144 the number of local webs in which the interaction occurs can be achieved by using a Binomial distribution,  
145 assuming a constant probability of interaction and independence between networks (trials). When considering  
146 uncertainties around the estimation of  $P(B_{i \rightarrow j})$ , a Beta distribution can also be used to encompass all possible  
147 probability values. In that case, a Beta-Binomial distribution can be used to predict the number of networks in

which the interaction occurs. Observing an interaction between two taxa at a given location and time provides important information that can be used to update previous estimates of  $P(B_{i \rightarrow j})$ , informing us on the biological capacity of both taxa to interact and the environmental conditions that enabled them to interact locally.

Even though binary webs constitute a highly valuable source of ecological information (Pascual *et al.* (2006)), they overlook important factors regarding interaction strengths. Represented in a quantitative adjacency matrix  $W$  as numbers not confined to the  $[0, 1]$  range, interaction strengths better describe the energy flows, demographic impacts or frequencies of interactions between nodes (Berlow *et al.* (2004), Borrett & Scharler (2019)), with  $W_{i \rightarrow j}$  being a natural  $\mathbb{N}$  or real  $\mathbb{R}$  number depending on the measure. For example, they may represent local interaction rates between pairs of taxa (e.g., the flower-visiting rates of pollinators in a mutualistic network, Herrera (1989)). When interaction strengths characterize predation pressure on prey taxa in food webs, they can serve as good estimators of the parameters describing species interactions in a Lotka-Volterra model (e.g., Emmerson & Raffaelli (2004)). The extra amount of ecological information in quantitative networks typically comes at a cost of greater sampling effort and data volume in predictive models (Strydom *et al.* (2021)), which can lead to relatively high levels of uncertainties when inferring quantitative webs with limited data.

Just like binary networks, the uncertainty and spatiotemporal variability of interaction strengths can be represented probabilistically. However, the need to estimate the probability distribution of all possible values of interaction strengths can make the inference of probabilities more challenging in quantitative webs compared to binary webs, which require only one probability estimate for each interaction. Interaction strengths can follow various probability distributions depending on the measure used. For instance, they can follow a Poisson distribution  $W_{i \rightarrow j} \sim \text{Poisson}(\lambda_{i \rightarrow j})$  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  $i$  in a given time period). The Poisson distribution can also be 0-inflated after initially modeling non-interacting taxa (e.g., Boulangeat *et al.* (2012) employ a 0-inflated model to analyze species abundance following the modeling of species presence and absence), which constitute the majority of taxa pairs in most local webs due to their typically high sparseness (Jordano (2016)). Because of the methodological difficulties typically encountered when building deterministic quantitative webs (which are only partially mitigated by models such as Ecopath, Plagányi & Butterworth (2004)), binary webs, which are easier to sample (Jordano (2016)) and predict (Strydom *et al.* (2021)), have been more frequently studied and modeled. Moreover, most published probabilistic networks and methods describe probabilistic interactions

178 whose outcome is binary (whether interaction probabilities are regarded as constant or variable, e.g. represented  
179 by a Beta distribution), which underlines the need for better guidelines regarding the interpretation and  
180 manipulation of these types of webs first. For these reasons, our primary focus in this contribution will be on  
181 addressing the challenges in interpreting and using interaction probabilities in Bernoulli distributions, in both  
182 probabilistic local and metawebs.

183 **Local webs: communities interacting in space and time**

184 Probabilistic local webs describe how likely taxa are to interact at a given location and time period (i.e.,  
185 interactions are contingent upon the environmental and biological conditions of the community). In local webs,  
186 edges commonly represent our degree of belief that two taxa interact in nature, but can also represent the  
187 probability of *observing* this interaction (Catchen *et al.* (2023)). For example, Gravel *et al.* (2019) used a  
188 dataset of binary local European food webs of willow-galling sawflies and their natural enemies, all referenced  
189 in space and time and consisting of similar species, to infer the probabilities of locally observing interactions  
190 between co-occurring species. This was achieved by situating local webs within the context of environmental  
191 variables, i.e. by including temperature and precipitation as conditional variables in some of their models.

192 We define space as the collection of geographic coordinates  $(x, y, z)$ , with  $(x, y)$  representing longitude and  
193 latitude coordinates, and  $z$  denoting either altitudes or depths. These point coordinates delineate the spatial  
194 boundaries of the system, which may be portrayed as a polyhedron. Ecological interactions may exhibit  
195 variations along latitudinal and altitudinal gradients, as evidenced by changes in hummingbird-plant  
196 interactions (Weinstein & Graham (2017b), Weinstein & Graham (2017a)) and mosquito biting rates (e.g.,  
197 Kulkarni *et al.* (2006)) at different elevations. In contrast, time is defined as the specific time period within  
198 which interactions were either observed or predicted. Even though space and time are continuous variables that  
199 should yield probability *densities* of interactions (i.e., relative likelihoods of interactions occurring at  
200 infinitesimal locations and instants in time), these definitions enable them to be conceptualised as distinct  
201 patches and time segments. Treating space and time as discrete dimensions aligns with the common sampling  
202 methods of ecological networks and provides actual probabilities of interactions, which can be obtained by  
203 integrating probability densities. Furthermore, we can quantify both an area  $A$  and a duration  $t$ , which can be  
204 readily used in spatiotemporal analyses of ecological networks. For example, when studying network-area  
205 relationships (NAR, Galiana *et al.* (2018)), we anticipate that local probabilities of interactions scale positively  
206 with area and duration because taxa have more opportunities to interact as these dimensions expand.

207 The probability that two taxa  $i$  and  $j$  interact in a local web  $L_{x,y,z,t}$  (spatial and temporal subscripts hereafter  
 208 omitted for clarity) can be conditional on many environmental and biological factors. One of these is their  
 209 co-occurrence  $C_{i,j}$ , which is usually a Boolean describing if the geographic distributions of both taxa overlap  
 210 within the study area. Co-occurrence can be modeled probabilistically, in which case it may conform to a  
 211 Bernoulli distribution  $C_{i,j} \sim \text{Bernoulli}(P(C_{i,j}))$ , where the probability of co-occurrence  $P(C_{i,j})$  can be  
 212 estimated through the application of joint species distribution models (e.g., Pollock *et al.* (2014)). Considering  
 213 that the probability that two non-co-occurring taxa interact locally is zero (i.e.,  $P(L_{i \rightarrow j}|C_{i,j} = 0) = 0$ ), the  
 214 probability of local interaction can be obtained by multiplying the probability of interaction given  
 215 co-occurrence with the probability of co-occurrence:

$$P(L_{i \rightarrow j}) = P(L_{i \rightarrow j}|C_{i,j} = 1) \times P(C_{i,j} = 1). \quad (1)$$

216 Other important factors that can impact interaction probabilities at the local scale are taxa relative abundance  
 217 (Canard *et al.* (2012)) and traits (Poisot *et al.* (2015)), as well as environmental factors such as temperature  
 218 (Angilletta *et al.* (2004)), precipitation (Woodward *et al.* (2012)), habitat structure (Klecka & Boukal (2014)),  
 219 and presence of other interacting taxa in the network (Pilosof *et al.* (2017), Kéfi *et al.* (2012)), as described  
 220 above. Here, we use the variable  $\Omega_{x,y,z,t}$  (hereafter simply  $\Omega$ ) to describe the biological and ecological context  
 221 in which interaction probabilities were estimated. For example, if a research team conducts a mesocosm  
 222 experiment to estimate interaction probabilities between predators and prey with and without shelters (a place  
 223 that offers refuge and protection for prey, shielding them from predators),  $\Omega$  would represent the presence or  
 224 absence of these shelters. Like co-occurrence,  $\Omega$  can also be modeled probabilistically when the stochasticity or  
 225 uncertainty of environmental and biological factors is considered. In sum,  $\Omega$  represents all ecological and  
 226 biological variables that were taken into consideration when measuring interaction probabilities and is,  
 227 therefore, a subset of all factors impacting ecological interactions. It is a vector of random variables whose  
 228 values determine the overall uncertainty of an interaction.

229 The probability that two taxa  $i$  and  $j$  interact in a local web  $L$  can thus be conditional on the area (or volume)  $A$ ,  
 230 the time interval  $t$ , their co-occurrence  $C_{i,j}$  and chosen environmental and biological conditions  $\Omega$ . Although  
 231 these variables are associated with distinct questions or mechanisms related to ecological interactions, they may  
 232 covary with each other, such as the possible dependence of  $C_{i,j}$  and  $\Omega$  on spatial and temporal scales. When  
 233 estimating interaction probabilities using e.g. a generalized linear model with multiple explanatory variables

234 that might not be independent, it may become important to address collinearity. Using variable selection  
 235 techniques, for instance, may be necessary before fitting the model to mitigate this issue. The probability of  
 236 local interaction is described by the following expression when all these conditional variables are included:

$$P(L_{i \rightarrow j} | A, t, C_{i,j}, \Omega) \quad (2)$$

237 The representation of the local context in which probabilities are estimated and the variables that should be  
 238 taken into consideration depend on the study system, the objectives of the study, and the resources available to  
 239 the researchers. In other words, these variables do not systematically need to be accounted for. For example, in  
 240 Gravel *et al.* (2019), for the purpose of model comparison, some models incorporated environmental variables  
 241 as conditional factors to estimate interaction probabilities, while others did not. When accounted for, these  
 242 variables should be clearly described in the documentation of the data (Brimacombe *et al.* (2023)),  
 243 preferentially in mathematical terms to avoid any confusion in their interpretation and to limit manipulation  
 244 errors during their re-use. For instance, ecologists should be explicit about their consideration of co-occurrence  
 245 in their estimation of local interaction probabilities. Indeed, it is important to specify if probability values are  
 246 conditional  $P(L_{i \rightarrow j} | C_{i,j} = 1)$  or not  $P(L_{i \rightarrow j})$  on co-occurrence since this can significantly impact the  
 247 interpretation and analysis of the data. In [tbl. 1](#), we present examples of studies that used these diverse  
 248 formulations of probabilistic interactions and conditional variables.

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

Expression	Type	Outcome	Reference
$P(M_{i \rightarrow j})$	regional	biological feasibility of the interaction	Strydom <i>et al.</i> (2022)
$P(L_{i \rightarrow j})$	local	realization of the interaction	Fortuna & Bascompte (2006) (null model)
$P(L_{i \rightarrow j}   A)$	local	realization of the interaction in a given area or volume	Galiana <i>et al.</i> (2018) *

Expression	Type	Outcome	Reference
$P(L_{i \rightarrow j} t)$	local	realization of the interaction during a given time period	Weinstein & Graham (2017a)
$P(L_{i \rightarrow j} C_{i,j})$	local	realization of the interaction given that the taxa co-occur	Gravel <i>et al.</i> (2019)
$P(L_{i \rightarrow j} \Omega)$	local	realization of the interaction given environmental conditions	Gravel <i>et al.</i> (2019) (temperature and precipitation)
$P(L_{i \rightarrow j} M_{i \rightarrow j})$	local	realization of the interaction given that the taxa can biologically interact	this study

## 249 Metawebs: regional catalogs of interactions

250 Metawebs are networks of potential interactions that have been designed for broad spatial, temporal, and  
 251 taxonomic scales (e.g., species food webs at the continental scale). They represent the probability that taxa can  
 252 biologically interact regardless of their co-occurrence and local environmental conditions. Regional interactions  
 253 are by definition context-independent, i.e. they are not measured at a specific location and time. In contrast with  
 254 probabilistic local webs, which represent the stochasticity of interactions occurring in nature, probabilistic  
 255 metawebs measure our degree of belief in the capacity of two taxa to interact (i.e., the probability that their  
 256 traits could support an interaction in the right conditions). Consequently, although *neutrally* forbidden  
 257 interactions (i.e., improbable interactions between rare species, Canard *et al.* (2012)) tend to have low  
 258 probability values in local webs, they may exhibit a higher probability in the metaweb. Potential interactions  
 259 describe the probability that there exists at least one combination of phenotypes of taxa  $i$  and  $j$  that can interact  
 260 with each other if they were to encounter. For example, a piscivorous species may have the capacity to interact  
 261 with a potential prey species if they share at least one matching combination of body sizes, such as an adult  
 262 predator being able to consume juvenile prey. To reduce any biases in our calculation of this probability, it is  
 263 crucial to ensure that the set of traits sampled or considered accurately reflects the overall trait distribution in  
 264 both taxa. This enhances our confidence in concluding that the taxa cannot interact when no positive  
 265 observation has been made and increases our capacity to detect an interaction when it is biologically feasible. In  
 266 addition to pairwise interactions, the extent of sampling effort also contributes to shaping our assessment of  
 267 metaweb properties, as sampling a larger number of local webs allows us to capture more regional interactions

268 (McLeod *et al.* (2021)). A probability of potential interaction in a metaweb  $M$  can be expressed as

$$P(M_{i \rightarrow j}), \quad (3)$$

269 which, in contrast with local webs, is never conditional on any spatial, temporal, co-occurrence or  
270 environmental variables (tbl. 1).

271 Starting from a selected set of taxa, which are usually distributed within a broad region of interest, metawebs  
272 can be built using different data sources, including literature review (e.g., Maiorano2020Tetraeu), aggregated  
273 local web data (e.g., Gravel *et al.* (2019), Saravia *et al.* (2022)), and predictive models (e.g., Strydom *et al.*  
274 (2022), Shaw *et al.* (2024)). Every pair of taxa that have confidently been observed to interact at least once can  
275 be given a probability of 1 (i.e.,  $P(M_{i \rightarrow j}) = 1$ ) since we know that they *can* interact. This is not the case in local  
276 probabilistic webs, in which interaction events usually remain stochastic (i.e.,  $P(L_{i \rightarrow j}) < 1$ ) after empirically  
277 observing interactions because of their intrinsic spatiotemporal variability. Similarly, although rare interactions  
278 typically have low probabilities in local webs, they can have high probabilities in metawebs when the traits of  
279 both taxa are congruent. On the other hand, interactions that were never observed can have low probability  
280 values in both local and metawebs, going as low as 0 for forbidden links (i.e., interactions forbidden by  
281 biological traits). However, many observations of interactions are in reality false positives because of  
282 observation errors due to taxonomic misidentifications and ecological misinterpretations (e.g., due to cryptic  
283 species and interactions, Pringle & Hutchinson (2020)). Likewise, forbidden interactions can be false negatives  
284 in metawebs, e.g. if they have been assessed for specific phenotypes, locations or time. Employing Bayesian  
285 models, whether they are mechanistic or phenomenological, could improve the accuracy of our estimation of  
286 interaction probabilities within both local and regional webs (e.g., Bartomeus *et al.* (2016), Cirtwill *et al.*  
287 (2019)). This improvement is achieved in metawebs by leveraging prior information regarding the feasibility of  
288 interactions along with the empirical data on observed interactions.

## 289 Properties of probabilistic webs

290 Probabilistic local and metawebs differ in their type of interactions (i.e., realized or potential) and in the  
291 conditional variables upon which interaction values depend. These differences are significant as they influence  
292 the characteristics of probabilistic networks. Neglecting to consider them may result in misleading results and

293 interpretation errors when analyzing the properties of probabilistic webs, which could be particularly  
294 problematic when addressing crucial ecological questions about networks. Here we compare the characteristics  
295 of local and metawebs through the presentation of four applications of probabilistic interactions: (1) describing  
296 their spatial and temporal scaling, (2) describing their taxonomic scaling, (3) sampling for binary webs, and (4)  
297 reconstructing probabilistic local webs from metawebs. All code and data to reproduce these analyses are  
298 available at the Open Science Framework (TBD).

## 299 Host-parasite network data

300 We use the collection of tripartite host-parasite networks sampled across Europe, created by Kopelke *et al.*  
301 (2017), in the following case studies. This dataset contains well-resolved binary local interactions between  
302 willows (52 species), willow-galling sawflies (96 species), and their parasitoids (126 species). Given its  
303 replicated webs spanning large spatiotemporal scales, this dataset is well-suited for analyzing a variety of  
304 ecological hypotheses and processes. Out of a total of 374 local webs, we retained those containing at least 5  
305 species, resulting in a set of 233 georeferenced local webs (networks sampled within areas of 0.1 to 0.3 km<sup>2</sup>  
306 during June and/or July spanning 29 years). We built a binary metaweb by aggregating all local interactions,  
307 which gave us a regional web composed of 274 species and 1080 interactions. In the first two panels of fig. 1,  
308 we show how the dissimilarity of interactions between common species ( $\beta_{OS}$ ) and the dissimilarity in species  
309 composition ( $\beta_S$ ) between the metaweb and aggregated local webs (Poisot *et al.* (2012)) vary with the number  
310 of sampled local webs. This shows that networks of local interactions are highly dissimilar from the metaweb,  
311 both in terms of species and interactions, especially when only a limited number of sites has been sampled.  
312 Both dissimilarity indices were calculated based on the number of items shared by the two webs ( $c_{LM}$ ) and the  
313 number of items unique to the metaweb ( $u_M$ ) and to the aggregated local web ( $u_L$ ). The  $\beta_S$  dissimilarity index  
314 uses species (nodes) as items being compared, while the  $\beta_{OS}$  index assesses dissimilarity based on interactions  
315 between shared species (Poisot *et al.* (2012)). Both indices were calculated following the  $\beta_W$  index of  
316 Whittaker (1960):

$$\beta_W = \frac{c_{LM} + u_L + u_M}{(2c_{LM} + u_L + u_M)/2} - 1. \quad (4)$$

317 [Figure 1 about here.]

318 We converted these binary networks into probabilistic ones using models based on simple assumptions. Our

models are not designed to estimate the exact values of probabilistic interactions. Instead, their purpose is to create plausible networks that serve as illustrative examples to highlight distinctions between probabilistic local and metawebs. We created two probabilistic metawebs by employing constant false positive and false negative rates for all regional interactions. In the first metaweb, we set both false positive and false negative rates to zero to prevent artificially inflating the total number of links, enabling a more accurate comparison with binary webs. This gave us a probability of regional interaction of 1 when at least one interaction has been observed and of 0 in the absence of any observed interaction between a given pair of species. In the second metaweb, we introduced a 5% false positive rate to account for spurious interactions and a 10% false negative rate to address the elevated occurrence of missing interactions in ecological networks (Catchen *et al.* (2023)). We believe these rates represent reasonable estimates of missing and spurious potential interactions, but confirming their accuracy is challenging due to the unavailability of data on the actual feasibility of interaction. Observed interactions were thus given a probability of regional interaction of 95%, whereas unobserved ones were assigned a probability of 10%.

To build probabilistic local webs, we first recognize that local interactions must initially be biologically feasible before occurring at a specific time and space. A local probability of interaction  $P(L_{i \rightarrow j})$  can be expressed as the product of the probability of local interaction given that the two taxa can potentially interact  $P(L_{i \rightarrow j}|M_{i \rightarrow j} = 1)$ , which we denote as  $P(L|M)$  for the sake of simplicity, with their probability of regional interaction  $P(M_{i \rightarrow j})$ :

$$P(L_{i \rightarrow j}) = P(L_{i \rightarrow j}|M_{i \rightarrow j} = 1) \times P(M_{i \rightarrow j} = 1). \quad (5)$$

We built the probabilistic local webs from the binary ones by using the probabilistic metawebs and a constant value of  $P(L|M)$  across interactions. Low values of  $P(L|M)$  indicate that feasible interactions rarely occur locally, intermediate values around 50% suggest considerable spatiotemporal variability, while high values indicate that regional interactions are nearly always realized locally. Following eq. 5, the local probability of interaction between a given pair of taxa consistently remained equal to or below their probability of regional interaction.

In the last two panels of fig. 1, we show how the aggregated number of links and connectance (i.e., the proportion of all of the non-forbidden links that are realized) scale with the number of sampled local probabilistic webs, according to different values of  $P(L|M)$ . When aggregating local probabilistic webs, the constancy of the probability of regional interaction across the entire study area means that any rise in the

346 probability of local interaction is solely attributable to an increase in  $P(L|M)$ . The probability  $P(L_{1,2}|M)$  of  
347 local interaction among potentially interacting species in an aggregated web  $L_{1,2}$  is obtained by:

$$P(L_{1,2}|M) = 1 - (1 - P(L_1|M)) \times (1 - P(L_2|M)), \quad (6)$$

348 where  $P(L_1|M)$  and  $P(L_2|M)$  are the probabilities of local interaction among two potentially interacting species  
349 in the subnetworks  $L_1$  and  $L_2$ , respectively. This equation provides the probability that the interaction is realized  
350 in either (1) exclusively the local web  $L_1$ , (2) exclusively the local web  $L_2$  or (3) both local webs, given that the  
351 two taxa have the biological capacity to interact.

352 By comparing the scaling relationships observed in binary and probabilistic webs, fig. 1 illustrates that high  
353 values of  $P(L|M)$  lead to systematic overestimations in the number of links and connectance, especially when  
354  $P(L|M) = 1$  (corresponding to the scenario where local probabilities of interactions are equivalent to the  
355 probabilities of regional interactions). However, these biases tend to diminish as the number of sampled webs  
356 increases.

## 357 Spatial and temporal scaling of interactions

358 The investigation of network-area relationships and interaction accumulation curves is an important area of  
359 research in network ecology. First, network-area relationships elucidate the scaling of network properties (such  
360 as modularity and trophic chain lengths) with spatial scale (e.g., Wood *et al.* (2015), Galiana *et al.* (2018)). The  
361 variations in network structure across spatial scales may stem from the scaling of species richness (species-area  
362 relationships, SARs) and the number of interactions (Brose *et al.* (2004)) with the sampled area. Additionally,  
363 ecological processes unfolding at distinct spatial scales, such as the spatial variability in local community  
364 composition resulting from different sequences of extinction and colonization events, can also contribute to this  
365 variation (Galiana *et al.* (2018)). Next, interaction accumulation curves describe the scaling of the number of  
366 observed interactions with sampling effort (Jordano (2016)). Sampling effort, which may correspond to the  
367 duration of the sampling period used to construct the network, can impact connectance (Bersier *et al.* (1999))  
368 and various measures of network structure (Banašek-Richter *et al.* (2004), McLeod *et al.* (2021)). Apart from  
369 sampling effort, the temporal scaling of interactions also elucidates how network structure changes with the  
370 temporal resolution of the network (Poisot *et al.* (2012)), acknowledging that distinct interactions take place  
371 over time, ranging from short-term fluctuations of interactions to long-term trends. As probabilistic local webs

372 may explicitly account for the spatiotemporal variability of interactions, they offer a distinct approach to  
373 investigating the scaling of network structure with space and time, in contrast to binary and quantitative webs,  
374 by making the stochasticity of interactions the focal point of the modeling process.

375 Local and metawebs exhibit distinct relationships with spatial and temporal scales. On one hand, probabilistic  
376 metawebs, being independent of any local context, feature regional interactions that do not scale with space and  
377 time. This is because regional interactions depend solely on the biological capacity of two taxa to interact,  
378 regardless of their co-occurrence and specific environmental conditions. However, probabilities of potential  
379 interactions may change (tending to become more definitive) upon updating previous estimates with increased  
380 sampling effort, even though they do not vary in a specific direction with the spatial and temporal extent  
381 (boundaries) of the network. The probability of two taxa potentially interacting should theoretically be the same  
382 in all metawebs in which they are present, provided that the data and methods used for estimation are consistent.  
383 For example, if a smaller metaweb  $M_1$  is derived from a larger metaweb  $M_0$  by selecting the subset of taxa  
384 present in the region described by  $M_1$  and retaining all their interactions, their probabilities of interaction  
385 should be identical regardless of scale, i.e.  $P(M_{1,i \rightarrow j}) = P(M_{0,i \rightarrow j})$ . With a larger or equal number of taxa in  $M_0$   
386 as compared to  $M_1$ , the total number of interactions is expected to be higher or at least equal in the larger web,  
387 even though pairwise probabilities remain identical.

388 On the other hand, local interactions scale both spatially and temporally, given that they have more  
389 opportunities to be realized and observed in larger areas and longer durations. This is attributed to factors such  
390 as a higher number of individuals, greater trait variations, and increased opportunities for encounters, as  
391 highlighted by McLeod *et al.* (2020). For example, if a local probabilistic web  $L_1$  with an area  $A_1$  is derived  
392 from a larger web  $L_0$  with an area  $A_0$ , and  $A_1$  is entirely nested within  $A_0$ , interaction probabilities should be  
393 lower in the smaller web, i.e.  $P(L_{1,i \rightarrow j}|A_1 < A_0) \leq P(L_{0,i \rightarrow j}|A_0)$ . However, if  $A_1$  and  $A_0$  are disjoint, interaction  
394 probabilities could be higher in the smaller area, contingent upon their environmental and biological conditions.  
395 Likewise, interaction probabilities are expected to be lower in webs with shorter durations when time intervals  
396 are nested. In fig. 2, we show how the expected number of local host-parasite interactions scales with area,  
397 represented as an expanding latitudinal window, in comparison with regional interactions. Even though we  
398 employed local probabilities of interactions equal to regional interactions for the purpose of comparison (i.e.,  
399 using  $P(L|M) = 1$  here), we notice that the total number of regional interactions scales more rapidly than local  
400 interactions. This is because numerous regional interactions involve species that never co-occur, and as a result,  
401 these interactions are not captured in local webs.

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

404 Predicting local webs across time and space is a pivotal goal of network ecology, especially given the scarcity of  
 405 interaction data (Strydom *et al.* (2021)). Ecologists may resort to predictive models (e.g., generative Bayesian  
 406 and machine learning models) to reconstruct networks at fine spatial and temporal scales with limited  
 407 interaction data. For instance, real-time biomonitoring data coupled with appropriate numerical models (Bohan  
 408 *et al.* (2017)) can be employed to reconstruct local ecological webs, opening avenues for in-depth studies on  
 409 local ecosystem functioning and dynamics. The probabilistic representation of interactions acknowledges the  
 410 inherent uncertainty in these models, typically expressed through probability distributions. We introduce and  
 411 develop a simple generative mechanistic model for probabilistic local interactions that takes into consideration  
 412 their spatiotemporal variability (i.e. a spatiotemporally explicit model of local interactions). It is essential to  
 413 note that our model is not designed for regional interactions, which are scale-independent. Rather, it could  
 414 prove valuable for predicting local interactions across time and space by generating new interaction data  
 415 following parameter inference.

416 As indicated by eq. 1, the probability that two taxa  $i$  and  $j$  interact at a specific location  $(x, y, z)$  may be  
 417 determined by the product of their probability of interaction given co-occurrence and their probability of  
 418 co-occurrence. First, their co-occurrence probability can be calculated using their individual occurrence  
 419 probabilities  $P(X_i)$  and  $P(X_j)$ , along with the strength of association  $\gamma$  between their occurrences and  
 420 co-occurrence (Cazelles *et al.* (2016)):

$$P(C_{i,j}) = P(X_i, X_j) = P(X_i)P(X_j)\gamma. \quad (7)$$

421 When  $\gamma > 1$ , it signifies a positive association in the geographic distributions of both taxa, indicating that the  
 422 presence of one taxon enhances the probability of occurrence of the other. Attractions may be the result of  
 423 positive interactions (e.g., mutualism) or positive/negative interactions (e.g., antagonism between predators and  
 424 prey, Cazelles *et al.* (2016)). In empirical webs,  $\gamma > 1$  holds true for the majority of species pairs (Catchen *et*  
 425 *al.* (2023)). In contrast, repulsions ( $\gamma < 1$ ) may be caused by strong interspecific competition (Cazelles *et al.*  
 426 (2016)). We model the co-occurrence of both taxa as the outcome of a Bernoulli trial

$$C_{i,j} \sim \text{Bernoulli}(P(X_i, X_j)). \quad (8)$$

427 Next, the probability of interaction given co-occurrence can be made temporally explicit by modeling it as a  
 428 Poisson process with rate parameter  $\lambda$ . This parameter represents the expected frequency of interaction between  
 429 the taxa within a defined time interval and can be estimated using prior data on interaction strengths, when  
 430 accessible. The probability that two co-occurring taxa engage in an interaction during a time period  $t_0$  is given  
 431 by:

$$P(L_{i \rightarrow j} | C_{i,j} = 1) = 1 - e^{-\lambda t_0}, \quad (9)$$

432 which tends toward 1 as  $t_0 \rightarrow \infty$  if  $\lambda > 0$ . In other words, two co-occurring taxa with a nonzero rate of  
 433 interaction will inevitably do so in a sufficiently long observation period. It is important to note that the units of  
 434  $\lambda$  and  $t_0$  are complementary. For instance, if the duration  $t_0$  is measured in months,  $\lambda$  denote the expected  
 435 number of interactions per month.

436 The occurrence of an interaction between  $i$  and  $j$  can be modeled as a Bernoulli trial with a probability of  
 437  $P(L_{i \rightarrow j})$ . Consequently, a Bayesian inference model can be built based on the preceding equations to estimate  
 438 the value of the  $\lambda$  and  $\gamma$  parameters and generate novel interaction data:

$$L_{i \rightarrow j} \sim \text{Bernoulli}(P(L_{i \rightarrow j})) \quad (10)$$

$$P(L_{i \rightarrow j}) = P(X_i)P(X_j)\gamma(1 - e^{-\lambda t_0}) \quad (11)$$

$$\gamma \sim \text{Gamma}(2, 0.5) \quad (12)$$

$$\lambda \sim \text{Exponential}(2) \quad (13)$$

439 In fig. 3, we show the variation in the probability of interaction under different parameter values. In the right  
 440 panel, we notice that, irrespective of the interaction rate  $\lambda$ , the probability of interaction converges toward an

441 asymptote determined by the co-occurrence  $P(C_{i,j})$  (eq. 7). This model can be customized in different ways,  
442 such as by linking  $\lambda$  with specific environmental variables or explicitly incorporating observation errors (i.e.,  
443 the probabilities of false negatives and false positives).

444 [Figure 3 about here.]

#### 445 Taxonomic scaling of interactions

446 Probabilistic webs offer a versatile approach to tackle a broad array of ecological questions, depending on their  
447 level of organization. For instance, the assemblage of interactions across ecological scales can be explored  
448 through species-based networks, while clade-based networks provide insights into macroevolutionary processes  
449 (e.g., Gomez *et al.* (2010)). Given that our interpretation of the properties and dynamics of ecological webs  
450 depends on their taxonomic scale (Guimarães (2020)), investigating the phylogenetic scaling of network  
451 structure emerges as a promising research avenue. Examining the same system at various taxonomic scales can  
452 yield meaningful and complementary ecological information, and, in our perspective, employing probabilistic  
453 webs is an effective approach for such analyses.

454 There are no inherent differences in the taxonomic scaling between local and metawebs, as only the nodes are  
455 defined taxonomically. In other words, the probability values of edges in both local (eq. 2) and metawebs (eq. 3)  
456 are not conditional on any taxonomic scale. The phylogenetic scale is tied to the definition of the event itself  
457 (i.e., the interaction between two taxa, defined at the desired taxonomical scale), not to the variables on which  
458 interaction probabilities are conditional. In both types of webs, transitioning to a broader level of organization  
459 (e.g., from a species-level web  $S$  to a genus-level web  $G$ ) can be accomplished directly by using probabilities  
460 from finer scales. For example, in a network with  $n_1$  species from genus  $g_1$  and  $n_2$  species from genus  $g_2$ , one  
461 can compute the probability that at least one species from genus  $g_1$  interacts with at least one species from  
462 genus  $g_2$  as follows:

$$P(G_{g_1 \rightarrow g_2}) = 1 - \prod_{i=1}^{n_1} \prod_{j=1}^{n_2} (1 - P(S_{g_{1i} \rightarrow g_{2j}})), \quad (14)$$

463 where  $g_{1i}$  and  $g_{2j}$  are the species of the corresponding genus. If it is known that at least two of these species  
464 interact (i.e.,  $P(S_{g_{1i} \rightarrow g_{2j}}) = 1$  for at least one pair of  $(g_{1i}, g_{2j})$ ), it implies a probability of genus interaction  
465 equal to 1. Canard *et al.* (2012) built a species-based network following a similar approach, by using simulated

466 interactions between individuals derived from a neutral model (i.e., a model that assumed ecological  
467 equivalence among individuals). In contrast, a more sophisticated approach is necessary when transitioning  
468 from a broader to a finer level of organization. This is because knowledge of an interaction between two genera  
469 does not guarantee that all possible pairwise combinations of their species will also interact. One possible  
470 method is to build a finer-scale network by generating probabilities of interactions through random sampling  
471 from a beta distribution, parameterized by the broader-scale network.

472 Ideally, our biological interpretation of probabilistic interactions should remain consistent across a network  
473 even if it incorporates heterogeneous levels of organization, such as a network whose nodes represent both  
474 species and trophic species (groups of species sharing similar predators and prey). This is common in  
475 ecological webs where taxonomic resolution is typically low (Hemprich-Bennett *et al.* (2021), Vázquez§ *et al.*  
476 (2022)). Interaction probabilities at broader taxonomic scales should be based on probabilities of interactions  
477 between individuals, for both local and metawebs. For instance, in local individual-based food webs, the  
478 probability that two individuals interact reflects our degree of belief that one individual will consume the other.  
479 Similarly, in local species-based food webs, the probability that two species interact represents our degree of  
480 belief that at least one individual from the predator species consumes at least another individual from the prey  
481 species. Furthermore, in local clade-based food webs, the probability that two clades interact represents our  
482 degree of belief that at least two species from these clades interact with each other or, equivalently, that at least  
483 two individuals from these clades interact with each other. Fundamentally, the taxonomic scaling of interactions  
484 involves aggregating interactions between individuals into larger groups, which may exhibit varying degrees of  
485 homogeneity based on the organisms and the study system. In that regard, taxonomic scaling is analogous to the  
486 spatial and temporal scaling of interactions, as they all represent different ways to aggregate individuals into  
487 broader groups (either spatially, temporally, or taxonomically).

## 488 Sampling for binary webs

489 The prediction of binary interactions through Bernoulli trials is an important application of probabilistic webs.  
490 This approach proves beneficial for analyzing the structural characteristics of probabilistic webs, particularly in  
491 the absence of specific analytical measures. By performing independent Bernoulli trials for each interaction in a  
492 probabilistic web, a binary network may be generated. A probability distribution of network properties can be  
493 obtained by measuring network structure across multiple randomly generated networks (Poisot *et al.* (2016)).  
494 This method enables the representation of the variability of network structure, albeit with possible biases when

495 connectance is low (Poisot & Gravel (2014), Chagnon (2015)). Employing this strategy to generate binary  
496 networks under a null model facilitates null hypothesis significance testing, wherein the observed measure is  
497 compared against the simulated distribution (e.g., Bascompte *et al.* (2003)). Additionally, the random  
498 generation of binary networks, from a probabilistic web that accounts for the spatiotemporal variability of  
499 interactions, may effectively capture network structure across space and time. This facilitates the investigation  
500 of ecological hypotheses about interactions at broad spatial and temporal scales.

501 There are at least two distinct approaches to sample binary networks from probabilistic webs across space, for  
502 example, when attempting to predict a binary network for each of a number of locations within a given region.  
503 The first approach involves performing a singular Bernoulli trial for each pair of taxa based on their regional  
504 probability of interaction. In employing this approach, every pair of taxa predicted to interact in the binary  
505 metaweb will be treated as interacting in all local webs where they co-occur. This will result in local pairwise  
506 interactions without spatial variation. The second approach is to independently sample each of the local  
507 probabilistic webs, which can be achieved by first generating distinct probabilistic networks for each location.  
508 These local probabilistic webs may vary in taxa composition and interaction probabilities. Subsequently, binary  
509 networks can be independently sampled for each location, introducing spatial variation in binary interactions.  
510 In fig. 4, we compare the average connectance of binary networks resulting from these two sampling techniques,  
511 where regional and local interactions are drawn from our host-parasite probabilistic networks, generating a  
512 number of binary web realizations for each site in the dataset. These two sampling approaches yield different  
513 outcomes, particularly for lower values of  $P(L|M)$ , which denote instances where regional interactions do not  
514 consistently manifest locally. Small discrepancies are also apparent between these techniques when we equate  
515 the probability of local interaction to the probability of regional interaction (i.e., when using  $P(L|M) = 1.0$  in  
516 eq. 5), especially when the number of binary network samples for each location is low. As anticipated, we  
517 observe that sampling binary interactions from the metaweb tends to overestimate connectance on average  
518 compared to sampling them from local webs. Furthermore, we observe an increase in the variability of  
519 connectance when employing a single sample, representing what we consider as a more tangible process  
520 leading to the realization of local and regional interactions in nature.

521 [Figure 4 about here.]

522 The choice of a sampling approach can influence the selection of grid cell size when delineating local  
523 communities within a broader region of interest. In the first approach, pairwise interactions remain constant

524 irrespective of cell size since they are sampled only once from the metaweb. However, in the second approach,  
525 local interaction probabilities are contingent on the network area. For instance, consider the local webs  $L_1$  and  
526  $L_2$  with an area of  $\frac{1}{2}A_0$ , both nested within  $A_0$  but disjoint from each other, forming  $L_0$ . If we treat  $L_1$  and  $L_2$  as  
527 independent, the probability of interaction between taxa  $i$  and  $j$  in  $L_0$  is given by:

$$P(L_{0,i \rightarrow j}) = 1 - (1 - P(L_{1,i \rightarrow j}) \times P(L_{2,i \rightarrow j})). \quad (15)$$

528 Due to its larger area, the probability that the two taxa interact in  $L_0$  is equal or greater than in  $L_1$  and  $L_2$ . When  
529 sampling binary interactions from local webs, it is crucial to sample at the same spatial scale for which  
530 probabilities were estimated. Otherwise, interaction probabilities must be adjusted to align with the intended  
531 cell size, preventing systematic biases in predictions.

## 532 Prediction of local webs from metawebs

533 Metawebs serve as a valuable source of ecological information for predicting local webs across time and space.  
534 Binary local webs can be reconstructed by selecting a subset of taxa and interactions from the metaweb (Dunne  
535 (2006)). This implies that metawebs consistently contain more interactions than their corresponding local webs.  
536 Determining the list of taxa to select can be achieved empirically or through methods like range maps or species  
537 distribution models. As the species composition of a community is arguably less difficult to sample or predict  
538 than its interactions, the primary challenge lies in deciding which interactions to select from the metaweb, a task  
539 that may necessitate advanced statistical models and ecological expertise. Inferring the structure of local webs  
540 from the metaweb before predicting specific local pairwise interactions could hold promise (Strydom *et al.*  
541 (2021)), considering that the structure of local webs is constrained by the metaweb (Saravia *et al.* (2022)).

542 Building probabilistic local webs from a probabilistic metaweb involves a reduction in the value of pairwise  
543 interaction probabilities. This decrease is attributed to the prerequisite that two taxa must initially possess the  
544 capacity to interact before engaging in local interactions (eq. 5). Therefore, inferring local webs from their  
545 metaweb while maintaining identical interaction probability values would introduce systematic biases into the  
546 predictions. In such cases, these networks would essentially represent smaller-scale metawebs of potential  
547 interactions, possibly leading to misinterpretations by being perceived as local interactions. As proposed by  
548 McLeod *et al.* (2021), although metawebs do not capture the spatiotemporal variability of interactions, they  
549 establish an upper limit for local interactions. In other words, the probability of two taxa interacting at a specific

550 location and time is consistently lower or equal to the probability of their regional interaction:

$$P(L_{i \rightarrow j}|A, t, C, \Omega) \leq P(M_{i \rightarrow j}). \quad (16)$$

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

$$\int_{\Omega} \int_A \int_t P(L_{i \rightarrow j}|A, t, \Omega) dt dA d\Omega \leq P(M_{i \rightarrow j}). \quad (17)$$

555 Estimating more precisely the probability  $P(L|M)$  that two taxa interact locally if they can potentially interact  
556 allows for improved predictions of local webs from a probabilistic metaweb. This task is challenging due to the  
557 variability of this probability across space and time, as well as its variability across pairwise interactions within  
558 a network. Using simple models of  $P(L|M)$ , as demonstrated in our case studies, represents an initial step  
559 toward the overarching objective of reconstructing local webs from metawebs.

## 560 Conclusion

561 In this contribution, we underline the importance of network metadata for adequately interpreting and  
562 manipulating probabilistic interaction data. The mathematical representation of probabilities and their statistical  
563 properties depend on the type of interactions (local or regional) and the conditions under which these  
564 interactions were evaluated. We showed that probabilistic local and metawebs differ in their relationship to  
565 spatial and temporal scales, with regional interactions remaining consistent across scales. In contrast with  
566 metawebs, local interactions are measured in a specific context (e.g., in a given area, time, and biological and  
567 environmental conditions) and depend on taxa co-occurrence. These important conceptual differences bring to  
568 light the need to use probabilistic data with caution, for instance when generating binary network realizations  
569 across space and predicting local webs from metawebs. Clear metadata describing the type of interaction and  
570 the variables used in their estimation are required to ensure adequate data manipulation. Better data practices  
571 and foundations for probabilistic thinking in network ecology could enable more reliable assessments of the  
572 spatiotemporal variability and uncertainty of biotic interactions.

573 It is essential to enhance our comprehension of both regional and local interactions, especially considering the  
574 current scarcity of interaction data. However, while sampling biological communities does decrease the  
575 uncertainty of interactions by accumulating evidence for their feasibility and local realization, there is a limit to  
576 how much we can diminish their inherent randomness. In metawebs, probabilities reflect our limited knowledge  
577 of interactions (i.e., our degree of belief that interactions are feasible), which is expected to improve with a  
578 larger volume of data. We should anticipate that regional interactions will become more definitive (with  
579 probabilities approaching 0 or 1) as we investigate various conditions, including different combinations of  
580 species traits. Conversely, in the case of local webs, which can be seen as random instances of metawebs,  
581 randomness cannot be as reduced. In local interactions, probabilities can be divided into a component  
582 representing uncertainty and another representing spatiotemporal variability. Owing to environmental  
583 heterogeneity, there will invariably be instances in which an interaction occurs and others in which it does not,  
584 across different times and locations, irrespective of the extent to which we can improve our knowledge of its  
585 biological feasibility and the local conditions that facilitate its occurrence. When local webs depict probabilities  
586 of observing interactions rather than just their actual occurrence, we must also consider the observation  
587 variability as an additional source of randomness. Every ecological process is stochastic but there is also a  
588 possibility that a phenomenon goes undetected. Quantifying and partitioning this stochasticity will enable us to  
589 make more accurate predictions about ecological interactions at various spatial and temporal scales. This will  
590 prove to be of vital importance as our time to understand nature runs out, especially at the places where the  
591 impacts of climate change and habitat loss hit harder.

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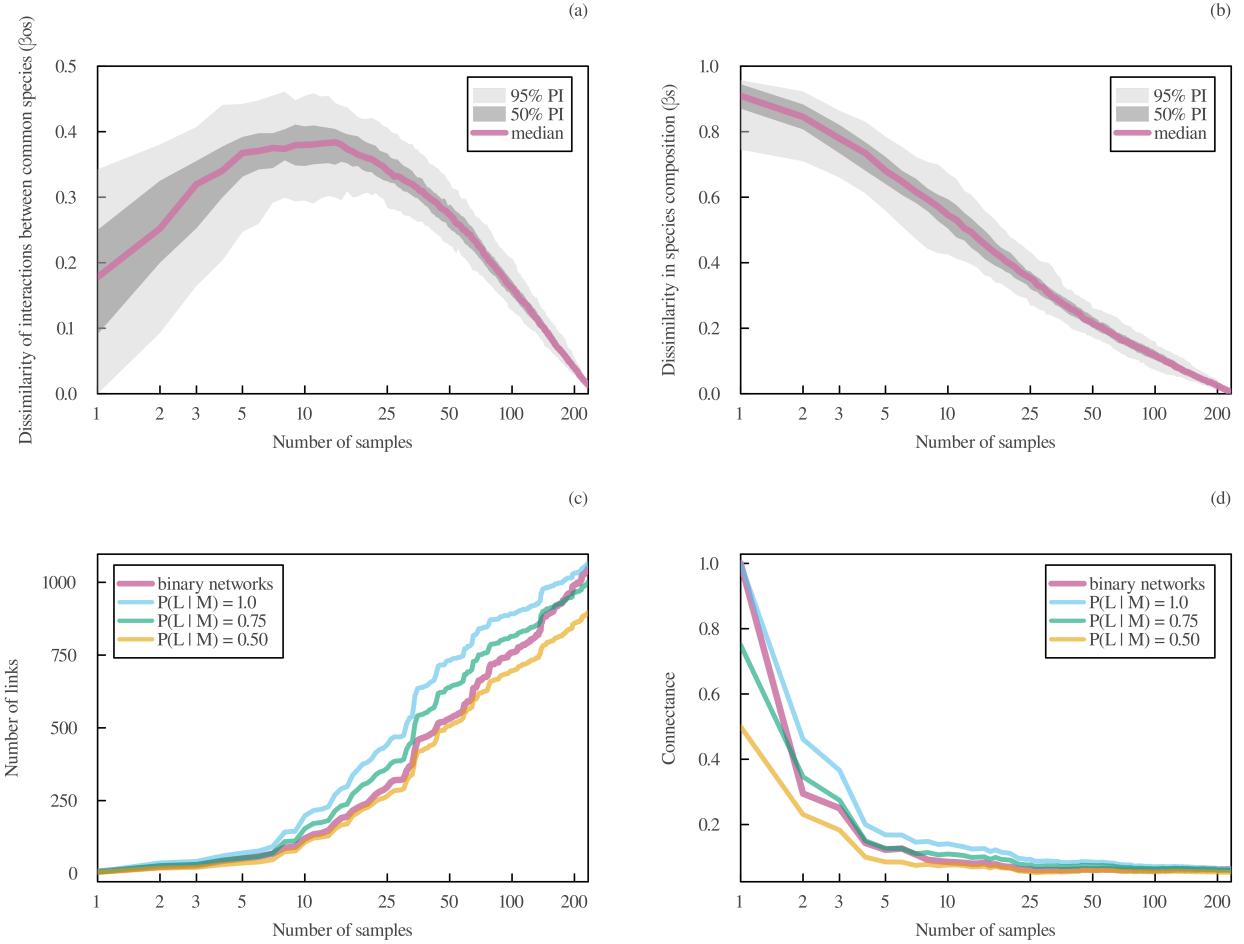
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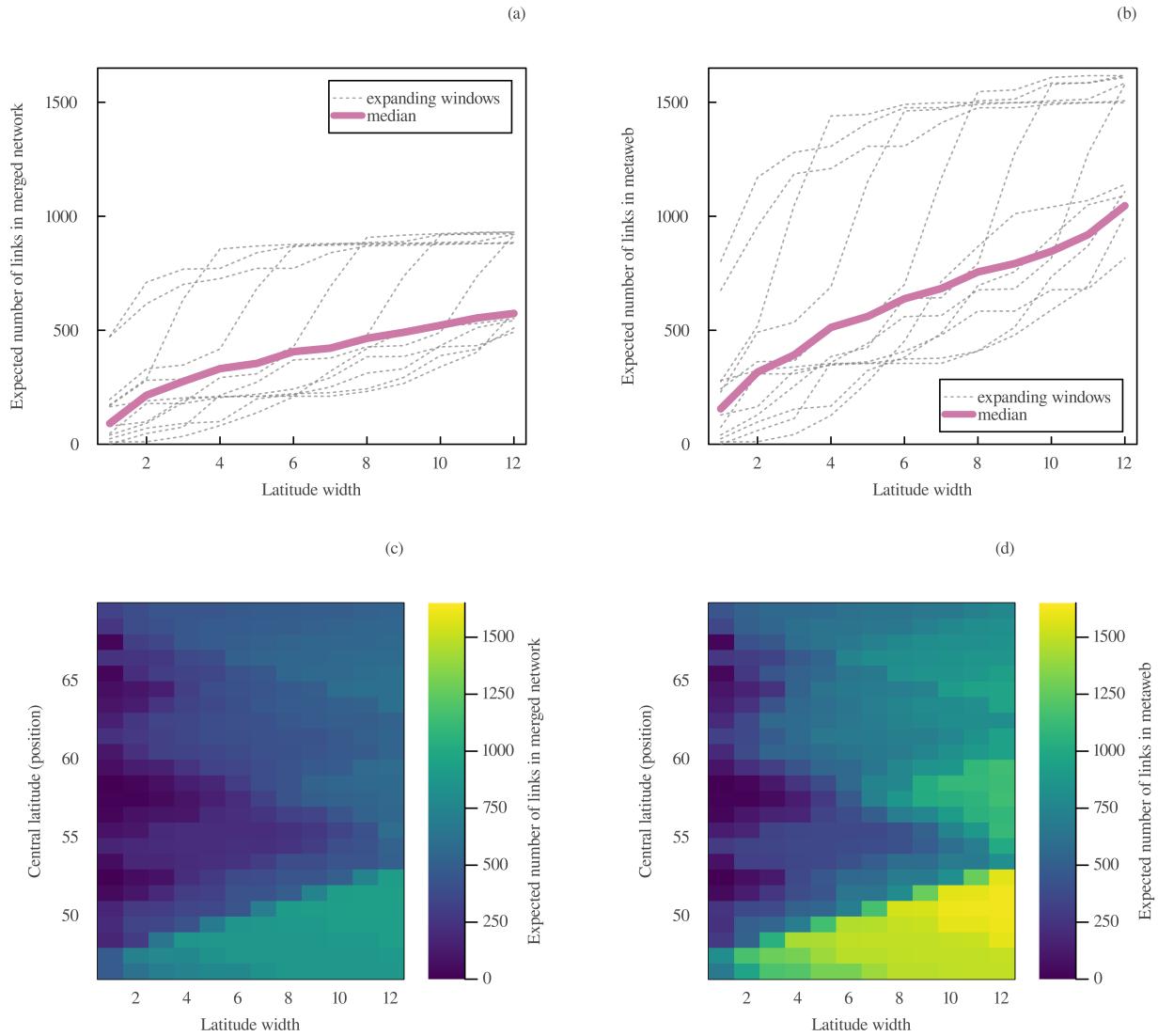
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**Figure 1: Network accumulation curves.** (a) Dissimilarity of interactions between common species and (b) dissimilarity in species composition between aggregated local webs and the binary metaweb of host-parasite interactions. Aggregated local webs were obtained by sequentially and randomly selecting a number of binary local webs and aggregating both their species and interactions. In both panels, the colored line represents the median dissimilarity across simulations and the grey areas cover the 50% and 95% percentile intervals. (c) Scaling of the number of links and (d) scaling of connectance with the number of sampled binary and probabilistic local webs. For a better comparison with binary webs, local probabilistic webs were derived from the probabilistic metaweb with a false positive and false negative rate of zero. A specific value of  $P(L|M)$  (the local probability of interaction among potentially interacting species) was used for all local webs within a particular curve. Aggregated probabilistic local webs were obtained by sequentially and randomly selecting a number of probabilistic local webs and aggregating both their species and interactions (with the value of  $P(L|M)$  adjusting according to eq. 6).



**Figure 2: Spatial scaling of interactions.** Expected number of host-parasite interactions in a network aggregating all probabilistic (a) local and (b) regional interactions within a latitudinal window of a given length. Every dashed curve corresponds to a different expanding window characterized by a different central latitude, with the colored solid line representing the median number of interactions. Heatmaps of the expected number of (c) local and (d) regional interactions found in windows of specified length and central latitudes. Probabilities of regional interactions were obtained with a false positive rate of 5% and a false negative rate of 10%. Local probabilistic interactions were derived from the probabilistic metaweb by setting the value of  $P(L|M)$  (the local probability of interaction among potentially interacting species) to 1, ensuring a conservative comparison between aggregated local webs and metawebs. Aggregated local webs were obtained by aggregating both the species and interactions found within a particular latitudinal window, with the values of  $P(L|M)$  remaining at their maximum value of 1 following eq. 6.

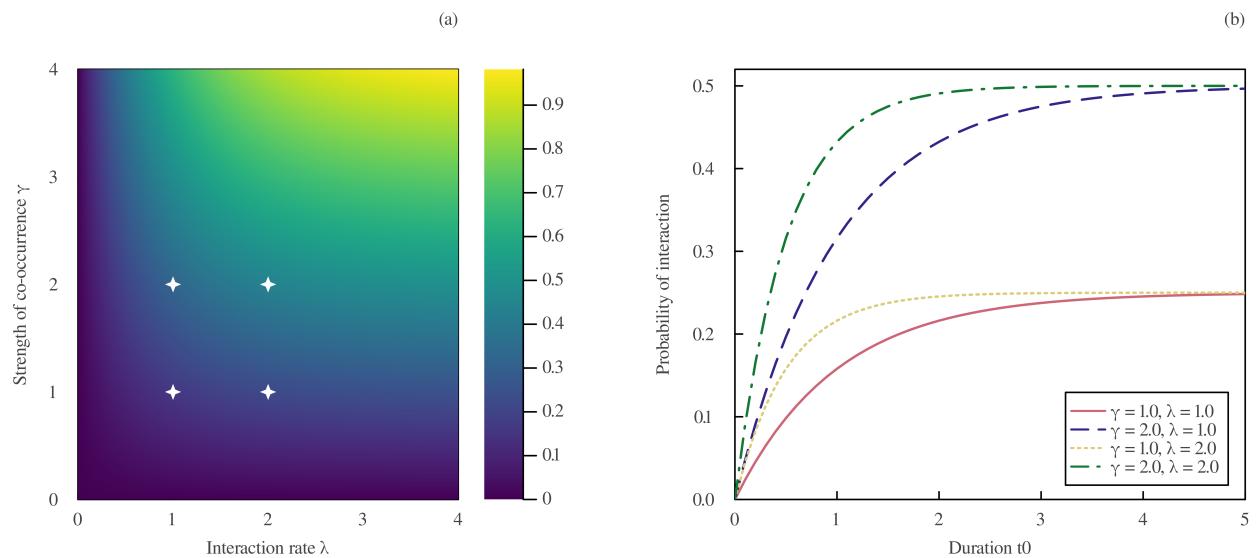
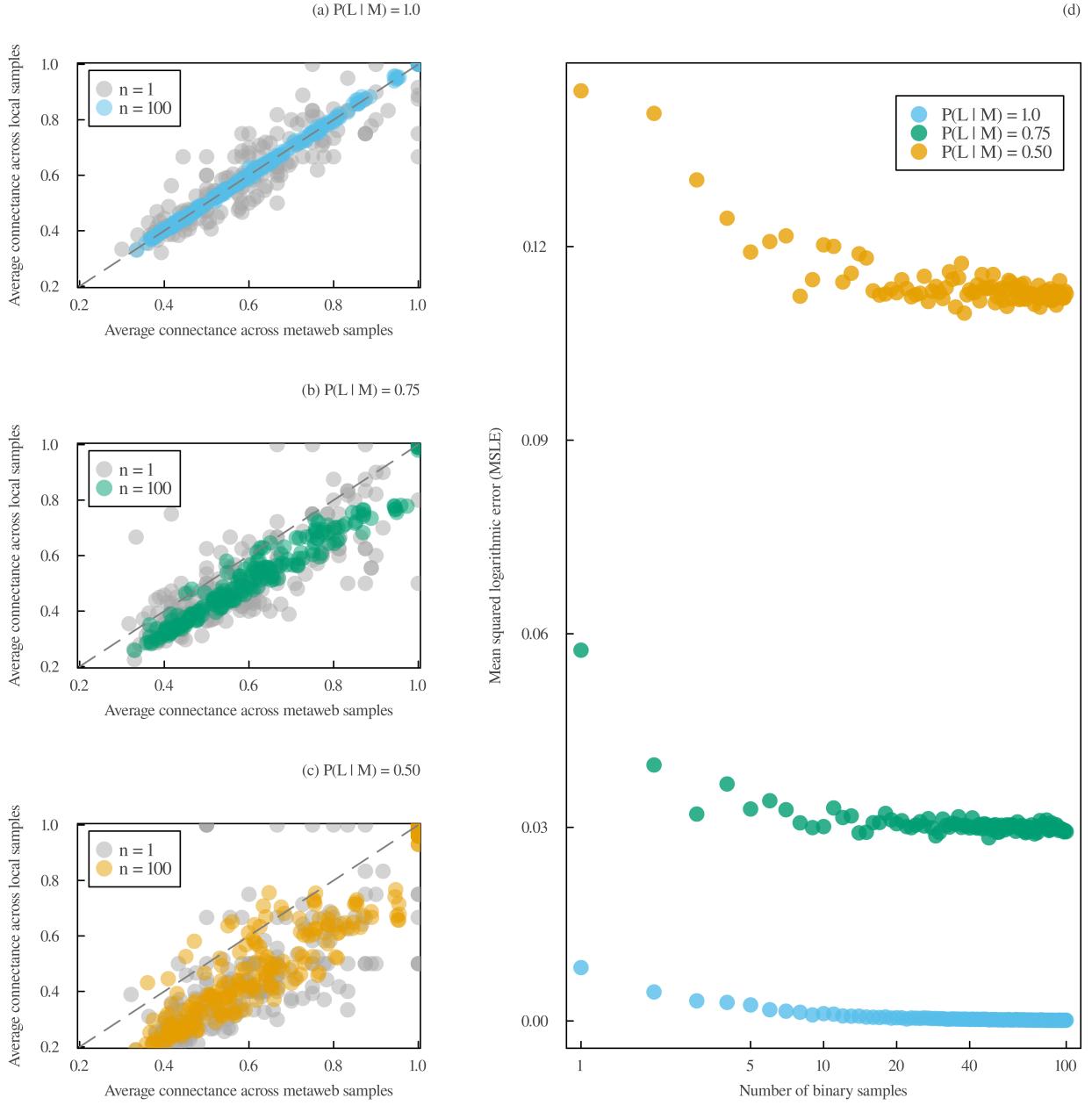


Figure 3: **Parameters of the spatiotemporally explicit model of interactions.** (a) Probability of local interaction given by the process model (eq. 11) under different values of  $\lambda$  and  $\gamma$ , with  $t_0 = 1$ . The parameter values used in the right panel are denoted by the white stars. (b) Scaling of the probability of interaction with the duration parameter  $t_0$  in eq. 11, for different values of  $\lambda$  and  $\gamma$ . In both panels, the individual probabilities of occurrence  $P_i(x, y, z)$  and  $P_j(x, y, z)$  are set to a constant value of 0.5.



**Figure 4: Connectance of sampled binary webs.** Comparison between the average connectance of binary network samples obtained from the probabilistic local and metawebs. Each dot corresponds to a different site. The local probability of interaction between potentially interacting species was set to three different values: (a)  $P(L|M) = 1.0$ , (b)  $P(L|M) = 0.75$ , and (c)  $P(L|M) = 0.50$ . Grey dots represent the outcome of a single trial, while colored dots represent the average connectance of each network across 100 trials. (d) Reduction in the mean squared logarithmic error between the average connectance of binary networks obtained from these two sampling methods as the number of trials increases, for the same values of  $P(L|M)$  used in panels a-c. Probabilities of regional interactions were obtained with a false positive rate of 5% and a false negative rate of 10%. Metaweb samples were obtained by randomly sampling binary interactions from the probabilistic metaweb, and then propagating this result to all local webs that include the species potentially engaged in the interactions. Local binary webs were generated by independently sampling binary interactions for each local probabilistic web.