

# The ecological interpretation of probabilistic networks

Francis Banville<sup>1,2,3</sup> Tanya Strydom<sup>1,3</sup> Penelope S. A. Blyth<sup>4</sup> Chris Brimacombe<sup>5</sup> Michael Catchen<sup>3,6</sup>  
Gabriel Dansereau<sup>1,3</sup> Dominique Gravel<sup>2,3</sup> Gracielle Higino<sup>2</sup> Thomas Malpas<sup>4</sup> Hana Mayall<sup>4</sup>  
Kari Norman<sup>1</sup> Timothée Poisot<sup>1,3</sup>

<sup>1</sup> Université de Montréal <sup>2</sup> Université de Sherbrooke <sup>3</sup> Quebec Centre for Biodiversity Science <sup>4</sup> University of Sheffield <sup>5</sup> University of Toronto <sup>6</sup> McGill University

## Correspondance to:

Francis Banville — francis.banville@umontreal.ca

The stochastic nature of ecological interactions has led biologists to adopt a probabilistic view of ecological networks. Representing species interactions probabilistically (how likely 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. 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 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 is a substantial challenge.  
5 There are methodological and biological constraints that hinder our ability to observe all interactions, such as  
6 the spatial and temporal uncoupling of species (Jordano (1987)) and the large number of possible interactions in  
7 a community, the vast majority of which are rare (Jordano (2016)). More generally, a handful of conditions  
8 must be satisfied for an interaction to be observed locally. First, both species must have overlapping geographic  
9 ranges, i.e. they must co-occur within the region of interest (Blanchet *et al.* (2020)). Second, they must have  
10 some probability of meeting. Probabilities of interspecific encounters are typically low, especially for rare  
11 species with low relative abundances (Canard *et al.* (2012)). The probability that species meet each other also  
12 depends on their biological characteristics, such as the synchronization of their phenology (Olesen *et al.* (2010),  
13 Singer & McBride (2012)) and their discoverability (e.g., Broom & Ruxton (2005)). Finally, when species do  
14 come into contact, an interaction occurs only if their traits are locally compatible  
15 (Poisot *et al.* (2015)), including but not limited to their body phenotypes (Bolnick *et al.* (2011), Stouffer *et al.*  
16 (2011), Gravel *et al.* (2013)) and behavioral choices (Pulliam (1974), Choh *et al.* (2012)). Interactions may also  
17 be influenced by the presence or prevalence of a third species (e.g., of a more profitable prey species) (Golubski  
18 & Abrams (2011), Sanders & van Veen (2012)). Documenting the location and timing of interactions becomes  
19 even more difficult when accounting for the spatiotemporal variability of ecological interactions (Poisot *et al.*  
20 (2012), Poisot *et al.* (2015)). Environmental factors, such as temperature (Angilletta *et al.* (2004)), drought  
21 (Woodward *et al.* (2012)), climate change (Gilman *et al.* (2010), Woodward *et al.* (2010), Araujo *et al.* (2011)),  
22 and habitat modifications (Tylianakis *et al.* (2007)), contribute to this spatiotemporal variability of interactions  
23 by impacting species abundance and traits. In this context, it is unsurprising that our knowledge of ecological  
24 interactions remains limited (Hortal *et al.* (2015)) despite extensive biodiversity data collection (Schmeller *et*  
25 *al.* (2015)).

26 Knowing the biological capacity of two species to interact is necessary but not sufficient for inferring their  
27 interaction at a specific time and space. The recognition of the intrinsic variability of species interactions has  
28 led ecologists to expand their representation of ecological networks to include a probabilistic view of  
29 interactions (Poisot *et al.* (2016), Dallas *et al.* (2017), Fu *et al.* (2021)). This different perspective allows us to

30 fill in the Eltonian shortfall (Hortal *et al.* (2015)) by modeling the probability of detecting interactions, which  
31 can be an important tool for directing efforts and taking action, especially in places where access and resources  
32 for research are scarce. Representing interactions probabilistically enables us to capture the spatiotemporal  
33 variability of the aforementioned ecological processes and the uncertainties associated with their measurement.  
34 As opposed to binary deterministic networks, in which interactions are regarded as either occurring or not,  
35 probabilistic networks, within a Bayesian framework, express our degree of belief (or confidence) regarding the  
36 occurrence of interactions. Based on the scale at which they are estimated, probabilistic interactions may reflect  
37 our level of confidence in whether interactions will be observed, realized, or biologically feasible. In the  
38 broadest sense, binary networks are also a type of probabilistic network, in which the numerical value of an  
39 interaction is restrained to 0 (non-occurring) or 1 (occurring). In probabilistic networks, only forbidden  
40 interactions (i.e., interactions prohibited by biological traits, Jordano *et al.* (2003), Olesen *et al.* (2010)) have a  
41 probability value of zero, provided that intraspecific trait variability is considered (Gonzalez-Varo & Traveset  
42 (2016)).

43 By accounting for the uncertainty of interactions, probabilistic networks provide a more realistic portrait of  
44 species interactions and network structure (i.e. community-level properties), which is a major driver of the  
45 functioning, dynamics, and resilience of ecosystems worldwide (Proulx *et al.* (2005), McCann (2007), McCann  
46 (2011), Rooney & McCann (2012)). Moreover, the application and development of computational methods in  
47 network ecology, often based on a probabilistic representation of interactions, can alleviate (and guide) the  
48 sampling efforts required to document species interactions (Strydom *et al.* (2021)). For example, statistical  
49 models can be used to estimate the uncertainty of pairwise interactions (Cirtwill *et al.* (2019)) and the  
50 probability of missing (false negatives) and spurious (false positives) interactions (Guimerà & Sales-Pardo  
51 (2009)). Considering the high rate of false negatives in species interaction data due to the difficulty of  
52 witnessing rare interactions (Catchen *et al.* (2023)), these models could inform the identification of priority  
53 sampling locations of ecological networks where data collection would yield the most valuable information,  
54 thereby reducing errors. Optimization models for sampling locations have mostly found applications in  
55 biological systems that are not networks, such as identifying priority sampling sites for disease hotspots  
56 (Andrade-Pacheco *et al.* (2020)), but there is substantial promise in applying them to probabilistic ecological  
57 interactions. Statistical models can also be used to generate network predictions without prior knowledge of  
58 pairwise interactions, for instance using body size (Petchey *et al.* (2008), Gravel *et al.* (2013)), phylogeny  
59 (Elmasri *et al.* (2020), Strydom *et al.* (2022)), or a combination of niche and neutral processes (Bartomeus *et*

60 *al.* (2016), Pomeranz *et al.* (2019)) for inference. Topological null models, which generate probabilistic  
61 networks by preserving chosen characteristics of the binary adjacency matrix while intentionally omitting  
62 others (Bascompte *et al.* (2003), Fortuna & Bascompte (2006)), serve as other examples of common  
63 probabilistic network models. Null models can be used to produce underlying distributions of network measures  
64 for null hypothesis significance testing. Many measures have been developed to describe the structure (Poisot *et*  
65 *al.* (2016)) and diversity (Ohlmann *et al.* (2019), Godsoe *et al.* (2022)) of probabilistic networks. These models  
66 and measures support the use of this approach for the study of a wide range of ecological questions, from  
67 making better predictions of species distribution (Cazelles *et al.* (2016)) to forecasting the impact of climate  
68 change on ecological networks (Gilman *et al.* (2010)).

69 The lack of clear guidelines on the use of probabilistic interaction data is worrisome (Brimacombe *et al.*  
70 (2023)), both for data producers and re-users who generate and manipulate these numbers. Besides  
71 methodological difficulties that may arise when assessing probabilistic interactions, a precise definition of  
72 probabilistic interactions appears to be lacking, making the estimation and use of these data more difficult. We  
73 aim to take a step back by outlining different ways in which probabilistic interactions are defined and used in  
74 network ecology. We distinguish two broad categories of probabilistic networks that necessitate distinct  
75 approaches when applied to key ecological questions: local networks of realized interactions, and regional  
76 networks (metawebs) of potential interactions. We highlight the distinctions in the ecological meaning of these  
77 two representations and show that they yield different statistical outcomes regarding e.g. the spatial and  
78 temporal scaling of interactions and the prediction of binary networks across space. Moreover, there is currently  
79 no metadata standard that could guide the documentation of all types of probabilistic interactions (although see  
80 e.g., Salim *et al.* (2022) who discuss data standards for deterministic mutualistic networks). Well-defined  
81 metadata for probabilistic networks would support more adequate manipulation and integration of interaction  
82 data from different sources and guard against possible misinterpretations arising from ambiguous definitions of  
83 probabilistic networks. These metadata should outline the nature (i.e., local or regional) and type (e.g.,  
84 predatory or pollination) of the interactions, provide information regarding the taxonomic level, identities, and  
85 characteristics (e.g., life stages) of the individuals involved in an interaction, present the mathematical  
86 formulation of probabilities, including clearly identified conditional variables (e.g., spatial and temporal scales),  
87 and describe the methods and contexts (e.g., location, time, environmental conditions) in which interactions  
88 were estimated. Inadequately documented probabilistic interaction data should be used with caution when  
89 analyzing ecological networks. Although our contribution focuses on food webs, our observations and advice

90 can be applied to other types of ecological networks, from plant-pollinator to host-virus networks. Indeed,  
91 excluding networks of indirect interactions such as competition and facilitation networks (Kéfi *et al.* (2015),  
92 Kéfi *et al.* (2016)), most ecological networks describe probabilities of direct interactions, which are  
93 conceptually and mathematically analogous regardless of their biological type (e.g., trophic and mutualistic  
94 interactions).

## 95 **Probabilistic representations of interactions**

96 One of the first aspects to take into consideration when estimating or interpreting probabilities of interactions is  
97 knowing if they describe potential or realized interactions. A potential (regional) interaction is defined as the  
98 biological capacity of two taxa to interact (i.e., the probability that they *can* theoretically interact) whereas a  
99 realized (local) interaction is the materialization or observation of this interaction in a well-defined space and  
100 time (i.e., the probability that they interact locally). Here, we use the terms *metaweb* (Dunne (2006)) to  
101 designate regional networks of potential interactions and *local networks* (Poisot *et al.* (2012)) for those of  
102 realized interactions. Metawebs are the network analogs of the species pool, where local networks originate  
103 from a subset of both species (nodes) and interactions (edges) of the metaweb (Saravia *et al.* (2022)). Without  
104 clear documentation, it can be challenging to know if published probabilistic networks describe local or regional  
105 interactions, or if so-called probabilities are in reality *interaction scores* (i.e., non-probabilistic quantitative  
106 interactions). When probabilistic regional interactions are used and interpreted as local interactions (and  
107 conversely), this may generate misleading findings during data analysis. We believe that a better understanding  
108 of the differences, similarities, and relationships between these two probabilistic representations of ecological  
109 networks would alleviate interpretation errors and facilitate a more adequate utilization of interaction data.

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

111 Local ecological networks and metawebs, like any type of network, are made of nodes and edges that can be  
112 represented at different levels of organization and precision. The basic unit of food webs and other ecological  
113 networks are individuals that interact with each other (e.g., by predation, Elton (2001)), forming  
114 individual-based networks (Melián *et al.* (2011)). The aggregation of these individuals into more or less  
115 homogeneous groups (e.g., populations, species, trophic species, families) allows us to represent nodes at  
116 broader taxonomic scales, which affects our interpretation of the properties of these systems (Guimarães

117 (2020)). Moreover, edges linking these nodes can describe a variety of interaction measures. Ecologists have  
118 traditionally represented interactions as binary objects that were considered realized after observing at least one  
119 individual from group  $i$  interact with at least another individual from group  $j$ . Boolean interactions can be  
120 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  
121 interaction between  $i$  and  $j$  that characterizes our limited knowledge of the system and its intrinsic  
122 spatiotemporal variability. Depending on the type of networks (local or metaweb), the mathematical  
123 formulation and interpretation of stochastic parameters like  $P(i \rightarrow j)$  can be linked to environmental and  
124 biological factors such as species relative abundance, traits, area, and time (tbl. 1), for example using logistic  
125 regression with a logit link function with continuous explanatory variables. In these probabilistic network  
126 representations in which  $P(i \rightarrow j)$  are edge values, the only two possible outcomes are the presence ( $A_{i,j} = 1$ ) or  
127 absence ( $A_{i,j} = 0$ ) of an interaction between each pair of nodes. When considering uncertainties around the  
128 estimation of  $P(i \rightarrow j)$ , a Beta distribution  $\text{Beta}(\alpha, \beta)$  can also be used to encompass all possible probability  
129 values. Observing an interaction between two taxa at a given location and time provides important information  
130 that can be used to update previous estimates of  $P(i \rightarrow j)$ , informing us on the biological capacity of both taxa  
131 to interact and the environmental conditions that enabled them to interact locally.

132 Even though binary networks constitute a highly valuable source of ecological information (Pascual *et al.*  
133 (2006)), they overlook important factors regarding interaction strengths. Represented as quantitative  
134 interactions not confined to the  $[0, 1]$  range, interaction strengths better describe the energy flows, demographic  
135 impacts or frequencies of interactions between nodes (Berlow *et al.* (2004), Borrett & Scharler (2019)), with  
136  $A_{i,j}$  being a natural  $\mathbb{N}$  or real  $\mathbb{R}$  number depending on the measure. For example, they may represent local  
137 interaction rates between pairs of taxa (e.g., the flower-visiting rates of pollinators in a mutualistic network,  
138 Herrera (1989)). When interaction strengths characterize predation pressure on prey taxa in food webs, they can  
139 serve as good estimators of the parameters describing species interactions in a Lotka-Volterra model (e.g.,  
140 Emmerson & Raffaelli (2004)). The extra amount of ecological information in quantitative networks typically  
141 comes at a cost of greater sampling effort and data volume in predictive models (Strydom *et al.* (2021)), which  
142 can lead to relatively high levels of uncertainties when inferring quantitative networks with limited data.

143 Just like binary networks, the uncertainty and spatiotemporal variability of interaction strengths can be  
144 represented probabilistically. However, the need to estimate the probability distribution of all possible values of  
145 interaction strengths can make the inference of probabilities more challenging in quantitative networks  
146 compared to binary networks, 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  $A_{i,j} \sim \text{Poisson}(\lambda_{i \rightarrow j})$  when predicting frequencies of interactions between pairs of nodes, with  $\lambda_{i \rightarrow j}$  being the expected rate at which individuals of taxa  $i$  and  $j$  interact (e.g., the average number of prey  $j$  consumed by all predators  $i$  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 networks due to their typically high sparseness (Jordano (2016)). Because of the methodological difficulties typically encountered when building deterministic quantitative networks, binary networks, which are easier to sample (Jordano (2016)) and predict (Strydom *et al.* (2021)), are documented and modeled more frequently in the literature. Moreover, most published probabilistic networks and methods describe Bernoulli interactions (whether interaction probabilities are regarded as constant or variable, e.g. represented by Beta distributions), which underlines the need for better guidelines regarding the interpretation and manipulation of these types of networks. For these reasons, our primary focus in this contribution will be on addressing the challenges in interpreting and using Bernoulli interactions, in both probabilistic local networks and metawebs.

## Local networks: communities interacting in space and time

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

We define space as the collection of geographic coordinates  $(x, y, z)$ , with  $(x, y)$  representing longitude and latitude coordinates, and  $z$  denoting either altitudes or depths. These point coordinates delineate the spatial boundaries of the system, which may be portrayed as a polyhedron. Ecological interactions may exhibit variations along altitudinal gradients, as evidenced by changes in hummingbird-plant interactions (Weinstein &

176 Graham (2017b) and Weinstein & Graham (2017a)) and mosquito biting rates (e.g., Kulkarni *et al.* (2006)) at  
177 different elevations. In contrast, time is defined as the specific time period within which interactions were either  
178 observed or predicted. With these definitions in mind, space and time can be conceptualized as distinct patches  
179 or time segments. Treating them as discrete dimensions aligns with the common sampling methods of  
180 ecological networks and provides actual probabilities of interactions across space and time. This differs from  
181 the approach of treating them as continuous variables, where edge values represent probability densities (i.e.,  
182 relative likelihoods of interactions occurring at infinitesimal locations and instants in time) rather than discrete  
183 probability values (which can be obtained by integrating probability densities). By employing discrete locations  
184 and time periods, we can quantify both a volume or area  $A$  and a duration  $t$ , which can be readily used in  
185 spatiotemporal analyses of ecological networks. For example, when studying network-area relationships (NAR,  
186 Galiana *et al.* (2018)), we anticipate that local probabilities of interactions scale positively with area and  
187 duration because taxa have more opportunities to interact as these dimensions expand.

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

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

196 Other important factors that can impact interaction probabilities at the local scale are taxa relative abundance  
197 (Canard *et al.* (2012)) and traits (Poisot *et al.* (2015)), as well as environmental factors such as temperature  
198 (Angilletta *et al.* (2004)), precipitation (Woodward *et al.* (2012)), habitat structure (Klecka & Boukal (2014)),  
199 and presence of other interacting taxa in the network (Pilosof *et al.* (2017), Kéfi *et al.* (2012)). Here, we use the  
200 variable  $\Omega$  to describe the biological and ecological context in which interaction probabilities were estimated.  
201 For example, if a research team conducts a mesocosm experiment to estimate interaction probabilities between  
202 predators and prey with and without shelters,  $\Omega$  would represent the presence or absence of these shelters. Like

203 co-occurrence,  $\Omega$  can also be modeled probabilistically when the stochasticity or uncertainty of environmental  
 204 and biological factors is considered. In sum,  $\Omega$  represents all ecological and biological variables that were taken  
 205 into consideration when measuring interaction probabilities and is, therefore, a subset of all factors actually  
 206 impacting ecological interactions.

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

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

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

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

Notation	Type	Description	Reference
$P_M(i \rightarrow j)$	regional	biological feasibility of the interaction	Strydom <i>et al.</i> (2022)

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

## 222 Metawebs: regional catalogs of interactions

223 Metawebs are networks of potential interactions that have been designed for broad spatial, temporal, and  
 224 taxonomic scales (e.g., species food webs at the continental scale). They represent the probability that taxa can  
 225 biologically interact regardless of their co-occurrence and local environmental conditions. Regional interactions  
 226 are by definition context-independent, i.e. they are not measured at a specific location and time. In contrast with  
 227 probabilistic local networks, which represent the stochasticity of interactions occurring in nature, probabilistic  
 228 metawebs measure our degree of belief in the capacity of two taxa to interact (i.e., the probability that their  
 229 traits could support an interaction in the right conditions). Consequently, although *neutrally* forbidden  
 230 interactions (i.e., improbable interactions between rare species, Canard *et al.* (2012)) tend to have low  
 231 probability values in local networks, they may exhibit a higher probability in the metaweb. Potential interactions  
 232 describe the probability that there exists at least one combination of phenotypes of taxa  $i$  and  $j$  that can interact  
 233 with each other if they were to encounter. To reduce any biases in our calculation of this probability, it is crucial  
 234 to ensure that the set of traits sampled or considered accurately reflects the overall trait distribution in both taxa.  
 235 This enhances our confidence in concluding that the taxa cannot interact when no positive observation has been  
 236 made and increases our capacity to detect an interaction when it is biologically feasible. In addition to  
 237 one-on-one interactions, the extent of sampling effort also contributes to shaping our assessment of metaweb  
 238 properties, as sampling a larger number of local networks allows us to capture more regional interactions

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

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

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

241 Starting from a selected set of taxa, which are usually distributed within a broad region of interest, probabilistic  
242 metawebs can be built using different data sources, including literature review, fieldwork, and predictive models  
243 (e.g., the metaweb of trophic interactions between Canadian mammals inferred by Strydom *et al.* (2022)).

244 Every pair of taxa that have confidently been observed to interact at least once can be given a probability of 1  
245 (i.e.,  $P_M(i \rightarrow j) = 1$ ) since we know that they *can* interact. This is not the case in local probabilistic networks,  
246 in which interaction events usually remain stochastic (i.e.,  $P_N(i \rightarrow j) < 1$ ) after empirically observing  
247 interactions because of their intrinsic spatiotemporal variability. Similarly, although rare interactions typically  
248 have low probabilities in local networks, they can have high probabilities in metawebs when the traits of both  
249 taxa are congruent. On the other hand, interactions that were never observed can have low probability values in  
250 both metawebs and local networks, going as low as 0 for forbidden links. However, because of observation  
251 errors due to taxonomic misidentifications and ecological misinterpretations (e.g., due to cryptic species and  
252 interactions, Pringle & Hutchinson (2020)), many observations of interactions are in reality false positives.

253 Likewise, forbidden interactions can be false negatives in metawebs, e.g. if they have been assessed for specific  
254 phenotypes, locations or time. Employing Bayesian models, whether they are mechanistic or phenomenological,  
255 could improve the accuracy of our estimation of interaction probabilities within both local and regional networks  
256 (e.g., Bartomeus *et al.* (2016), Cirtwill *et al.* (2019)). This improvement is achieved in metawebs by leveraging  
257 prior information regarding the feasibility of interactions along with the empirical data on observed interactions.

## 258 Properties of probabilistic networks

259 Probabilistic local networks and metawebs differ in their type of interactions (i.e., realized or potential) and in  
260 the conditional variables upon which interaction values depend. These differences are significant as they  
261 influence the characteristics of probabilistic networks. Neglecting to consider them may result in misleading  
262 results and interpretation errors when analyzing the properties of probabilistic networks, which could be  
263 particularly problematic when addressing crucial ecological questions about networks. Here we compare the

264 characteristics of local networks and metawebs through the presentation of four common applications of  
265 probabilistic interactions. All code and data to reproduce these analyses are available at the Open Science  
266 Framework (TBD).

## 267 Host-parasite network data

268 We use the collection of tripartite host-parasite networks sampled across Europe, created by Kopelke *et al.*  
269 (2017), in most of our case studies. This dataset contains well-resolved binary local interactions between  
270 willows (52 species), willow-galling sawflies (96 species), and their parasitoids (126 species). Given its  
271 replicated networks spanning large spatiotemporal scales, this dataset is well-suited for analyzing a variety of  
272 ecological hypotheses and processes. Out of a total of 374 local networks, we retained those containing at least  
273 5 species, resulting in a set of 233 georeferenced local networks. We built a binary metaweb by aggregating all  
274 local interactions, which gave us a regional network composed of 274 species and 1080 interactions. In the first  
275 two panels of fig. 1, we show how the dissimilarity of interactions between common species ( $\beta_{OS}$ ) and the  
276 dissimilarity in species composition ( $\beta_S$ ) between the metaweb and aggregated local networks (Poisot *et al.*  
277 (2012)) vary with the number of sampled local networks. This shows that networks of local interactions are  
278 highly dissimilar from the metaweb, both in terms of species and interactions, especially when only a limited  
279 number of sites has been sampled.

280 [Figure 1 about here.]

281 We converted these binary networks into probabilistic ones using models based on simple assumptions. Our  
282 models do not aim to precisely estimate the actual values of probabilistic interactions but rather to offer  
283 simplified networks as illustrative examples to underscore the differences between probabilistic local networks  
284 and metawebs. We created two probabilistic metawebs by employing constant false positive and false negative  
285 rates for all regional interactions. In the first metaweb, we set both false positive and false negative rates to zero  
286 to prevent artificially inflating the total number of links, enabling a more accurate comparison with binary  
287 networks. This gave us a probability of regional interaction of 1 when at least one interaction has been observed  
288 and of 0 in the absence of any observed interaction between a given pair of species. In the second metaweb, we  
289 introduced a 5% false positive rate to account for spurious interactions and a 10% false negative rate to capture  
290 the elevated occurrence of false negatives in ecological networks (Catchen *et al.* (2023)). 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 networks, we first recognize that local interactions must initially be biologically feasible before occurring at a specific time and space. A local probability of interaction  $P_N(i \rightarrow j)$  can be expressed as the product of the probability of local interaction given that the two taxa can potentially interact  $P_N(i \rightarrow j|M_{i \rightarrow j} = 1)$ , which we denote as  $p$  for the sake of simplicity, with their probability of regional interaction  $P_M(i \rightarrow j)$ :

$$P_N(i \rightarrow j) = P_N(i \rightarrow j|M_{i \rightarrow j} = 1) \times P_M(i \rightarrow j). \quad (4)$$

We built the probabilistic local networks from the binary ones by using the probabilistic metawebs and a constant value of  $p$  across interactions. Low values of  $p$  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. 4, 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  $S^2$  possible links that are realized, where  $S$  represents species richness) scale with the number of sampled local probabilistic networks, according to different values of  $p$ . When aggregating local probabilistic networks, the constancy of the probability of regional interaction across the entire study area means that any rise in the probability of local interaction is solely attributable to an increase in  $p$ . The probability  $p_{1,2}$  of local interaction among potentially interacting species in an aggregated network  $N_{1,2}$  is obtained by:

$$p_{1,2} = 1 - (1 - p_1) \times (1 - p_2), \quad (5)$$

where  $p_1$  and  $p_2$  are the probabilities of local interaction among two potentially interacting species in the subnetworks  $N_1$  and  $N_2$ , respectively.

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

315 **Taxonomic scaling of interactions**

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

324 There are no inherent differences in the taxonomic scaling between local networks and metawebs, as only the  
325 nodes are defined taxonomically. In other words, the probability values of edges in both local networks (eq. 2)  
326 and metawebs (eq. 3) are not conditional on any taxonomic scale. The phylogenetic scale is tied to the definition  
327 of the event itself (i.e., the interaction between two taxa), not to the conditional variables. In both types of  
328 networks, transitioning to a broader level of organization can be accomplished directly by using probabilities  
329 from finer scales. For example, in a network with  $n_A$  species from genus A and  $n_B$  species from genus B, one  
330 can compute the probability that at least one species from genus A interacts with at least one species from genus  
331 B as follows:

$$P(A \rightarrow B) = 1 - \prod_{i=1}^{n_A} \prod_{j=1}^{n_B} (1 - P(A_i \rightarrow B_j)), \quad (6)$$

332 where  $A_i$  and  $B_j$  are the species of the corresponding genus. If it is known that at least two of these species  
333 interact (i.e.,  $P(A_i \rightarrow B_j) = 1$  for at least one pair of  $i, j$ ), it implies a probability of genus interaction equal to 1.  
334 Canard *et al.* (2012) built a species-based network following a similar approach, by using simulated interactions  
335 between individuals derived from a neutral model (i.e., a model that assumed ecological equivalence among  
336 individuals). In contrast, a more sophisticated approach is necessary when transitioning from a broader to a  
337 finer level of organization. This is because knowledge of an interaction between two genera does not guarantee  
338 that all possible pairwise combinations of their species will also interact. One possible method is to build a  
339 finer-scale network by generating probabilities of interactions through random sampling from a beta  
340 distribution, parameterized by the broader-scale network.

341 Ideally, our biological interpretation of probabilistic interactions should remain consistent across a network  
342 even if it incorporates heterogenous levels of organization (e.g., a network whose nodes are composed of both  
343 species and trophic species). This is common in ecological networks where taxonomic resolution is typically  
344 low (Hemprich-Bennett *et al.* (2021), Vázquez *et al.* (2022)). Interaction probabilities at broader taxonomic  
345 scales should be based on probabilities of interactions between individuals, for both local networks and  
346 metawebs. For instance, in local individual-based food webs, the probability that two individuals interact  
347 reflects our degree of belief that one individual will consume the other. Similarly, in local species-based food  
348 webs, the probability that two species interact represents our degree of belief that at least one individual from  
349 the predator species consumes at least another individual from the prey species. Furthermore, in local  
350 clade-based food webs, the probability that two clades interact represents our degree of belief that at least two  
351 species from these clades interact with each other or, equivalently, that at least two individuals from these clades  
352 interact with each other. Fundamentally, the taxonomic scaling of interactions involves aggregating interactions  
353 between individuals into larger groups, which may exhibit varying degrees of homogeneity based on the  
354 organisms and the study system. In that regard, taxonomic scaling is analogous to the spatial and temporal  
355 scaling of interactions, as they all represent different ways to aggregate individuals into broader groups (either  
356 spatially, temporally, or taxonomically).

## 357 Spatial and temporal scaling of interactions

358 The investigation of network-area relationships (NARs) and interaction accumulation curves (IACs) is an  
359 important area of research in network ecology. First, NARs elucidate the scaling of network properties (such as  
360 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, IACs describe the scaling of the number of observed interactions with  
366 sampling effort (Jordano (2016)), which can also impact various measures of network structure such as  
367 connectance (McLeod *et al.* (2021b)). Apart from sampling effort, the temporal scaling of interactions  
368 elucidates how network structure changes with the duration of the network (Poisot *et al.* (2012)),  
369 acknowledging that distinct interactions take place over time. Given that probabilistic local networks can

370 quantify the spatiotemporal variability of interactions (eq. 2), they serve as valuable tools for developing and  
371 testing equations describing the scaling of network structure with space and time.

372 Metawebs and local networks exhibit distinct relationships with spatial and temporal scales. On one hand,  
373 probabilistic metawebs, being independent of any local context, feature regional interactions that do not scale  
374 with space and time. This is because regional interactions depend solely on the biological capacity of two taxa  
375 to interact, regardless of their co-occurrence and specific environmental conditions. This implies that the  
376 probability of two taxa potentially interacting should theoretically be the same in all metawebs in which they are  
377 present, provided that the data and methods used for estimation are consistent. As a result, if a smaller metaweb  
378  $M_1$  is derived from subsampling a metaweb  $M_0$  to represent potential interactions among a subset of taxa in a  
379 smaller region, their probabilities of interaction should be identical regardless of scale,  
380 i.e.  $P_{M_1}(i \rightarrow j) = P_{M_0}(i \rightarrow j)$ . However, because the number of taxa may be higher in the larger metaweb, it is  
381 expected that the overall number of interactions would be higher in the larger network, despite pairwise  
382 probabilities being identical.

383 On the other hand, local interactions scale both spatially and temporally, given that they have more  
384 opportunities to be realized and observed in larger areas and longer durations. This is attributed to factors such  
385 as a higher number of individuals, greater trait variations, and increased opportunities for encounters, as  
386 highlighted by McLeod *et al.* (2020). For example, if a local probabilistic network  $N_1$  with an area  $A_1$  is  
387 derived from a larger network  $N_0$  with an area  $A_0$ , and  $A_1$  is entirely nested within  $A_0$ , interaction probabilities  
388 should be lower 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  
389 disjoint, interaction probabilities could be higher in the smaller area, contingent upon their environmental and  
390 biological conditions. Likewise, interaction probabilities are expected to be lower in networks with shorter  
391 durations when time intervals are nested. In fig. 2, we show how the expected number of local host-parasite  
392 interactions scales with area, represented as an expanding latitudinal window, in comparison with regional  
393 interactions. Even though we employed local probabilities of interactions equal to regional interactions for the  
394 purpose of comparison (i.e., using  $p = 1$  here), we notice that the total number of regional interactions scales  
395 more rapidly than local interactions. This is because numerous regional interactions involve species that never  
396 co-occur, and as a result, these interactions are not captured in local networks.

397

[Figure 2 about here.]

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

399 Predicting local networks across time and space is a pivotal goal of network ecology (Strydom *et al.* (2021)). In  
400 a context of scarcity of interaction data (Jordano (2016)), ecologists must resort to predictive models for  
401 reconstructing networks at fine spatial and temporal scales. For instance, real-time biomonitoring data coupled  
402 with appropriate numerical models (Bohan *et al.* (2017)) can be employed to reconstruct local ecological  
403 networks, opening avenues for in-depth studies on local ecosystem functioning and dynamics. Apart from their  
404 predictive applications, statistical models can also be crafted for descriptive purposes, elucidating key  
405 parameters of interest such as probabilities of interactions. In such instances, the parameter values themselves  
406 offer valuable ecological insights. Various types of models (e.g., Bayesian and machine learning models) have  
407 been used for both predictive and descriptive purposes in the realm of ecological interactions (Strydom *et al.*  
408 (2021)). The probabilistic representation of interactions acknowledges the inherent uncertainty in these models,  
409 typically expressed through probability distributions. We introduce and develop a simple generative mechanistic  
410 model for probabilistic local interactions that takes into consideration their spatiotemporal variability (i.e. a  
411 spatiotemporally explicit model of local interactions). It is essential to note that our model is not designed for  
412 regional interactions, which are scale-independent. Rather, it could prove valuable for predicting local  
413 interactions across time and space by generating new interaction data following parameter inference.

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

$$P_{i,j}(x, y, z) = P_i(x, y, z)P_j(x, y, z)\gamma. \quad (7)$$

419 When  $\gamma > 1$ , it signifies a positive association in the geographic distributions of both taxa, indicating that the  
420 presence of one taxon enhances the probability of occurrence of the other. In empirical networks,  $\gamma > 1$  holds  
421 true for the majority of species pairs (Catchen *et al.* (2023)). The co-occurrence of both taxa is modeled as the  
422 outcome of a Bernoulli trial

$$C \sim \text{Bernoulli}(P_{i,j}(x, y, z)). \quad (8)$$

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

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

428 which tends toward 1 as  $t_0 \rightarrow \infty$ . It is important to note that the units of  $\lambda$  and  $t_0$  are complementary. For  
 429 instance, if the duration  $t_0$  is measured in months,  $\lambda$  denote the expected number of interactions per month.  
 430 The occurrence of an interaction between  $i$  and  $j$  can be modeled as a Bernoulli trial with a probability of  
 431  $P_N(i \rightarrow j)$ . Consequently, a Bayesian inference model can be built based on the preceding equations to estimate  
 432 the value of the  $\lambda$  and  $\gamma$  parameters and generate novel interaction data:

$$I \sim \text{Bernoulli}(P_N(i \rightarrow j)) \quad (10)$$

433

$$P_N(i \rightarrow j) = P_i(x, y, z)P_j(x, y, z)\gamma(1 - e^{-\lambda t_0}) \quad (11)$$

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

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

434 In fig. 3, we show the variation in the probability of interaction under different parameter values. In the right  
 435 panel, we notice that, irrespective of the interaction rate  $\lambda$ , the probability of interaction converges toward an  
 436 asymptote determined by the co-occurrence  $P_{i,j}(x, y, z)$  (eq. 7). This model can be customized in different ways,  
 437 such as by linking  $\lambda$  with specific environmental variables or explicitly incorporating observation errors (i.e.,  
 438 the probabilities of false negatives and false positives).

440 **Sampling binary networks**

441 The prediction of binary interactions through random draws is an important application of probabilistic  
442 networks. This approach proves beneficial for analyzing the structural characteristics of probabilistic networks,  
443 particularly in the absence of specific analytical measures. By simulating independent Bernoulli trials for each  
444 interaction, a binary network can be generated. A probability distribution of network properties can be obtained  
445 by measuring network structure across multiple randomly generated networks (Poisot *et al.* (2016)). This  
446 method enables the representation of the variability of network structure, albeit with possible biases when  
447 connectance is low (Poisot & Gravel (2014), Chagnon (2015)). Employing this strategy to generate binary  
448 networks under a null model facilitates null hypothesis significance testing, wherein the observed measure is  
449 compared against the simulated distribution (e.g., Bascompte *et al.* (2003)). Additionally, randomly generating  
450 binary networks across spatial and temporal dimensions aids in representing the spatiotemporal variability of  
451 network structure, allowing the testing of ecological hypotheses regarding interactions on large spatial and  
452 temporal scales.

453 There are at least two distinct approaches to sample binary networks from probabilistic webs across space, for  
454 example, when attempting to predict a binary network for each of a number of locations within a given region.

455 The first approach involves performing a singular Bernoulli trial for each pair of taxa based on their regional  
456 probability of interaction. In employing this approach, every pair of taxa predicted to interact in the binary  
457 metaweb will be treated as interacting in all local networks where they co-occur. This will result in local  
458 pairwise interactions without spatial variation. The second approach is to independently sample each of the  
459 local probabilistic networks, which can be achieved by first generating distinct probabilistic networks for each  
460 location. These local probabilistic networks may vary in taxa composition and interaction probabilities.

461 Subsequently, binary networks can be independently sampled for each location, introducing spatial variation in  
462 binary interactions.

463 In fig. 4, we compare the average connectance of binary networks resulting from these two sampling techniques,  
464 where regional and local interactions are drawn from our host-parasite probabilistic networks, generating a  
465 number of binary network realizations for each site in the dataset. These two sampling approaches yield  
466 different outcomes, particularly for lower values of  $p$ , which denote instances where regional interactions do not

467 consistently manifest locally. Small discrepancies are also apparent between these techniques when we equate  
468 the probability of local interaction to the probability of regional interaction (i.e., when using  $p = 1.0$  in eq. 4),  
469 especially when the number of binary network samples for each location is low. As anticipated, we observe that  
470 sampling binary interactions from the metaweb tends to overestimate connectance on average compared to  
471 sampling them from local networks. Furthermore, we observe an increase in the variability of connectance  
472 when employing a single sample, representing what we consider as a more tangible process leading to the  
473 realization of local and regional interactions in nature.

474 [Figure 4 about here.]

475 The choice of a sampling approach can influence the selection of grid cell size when delineating local  
476 communities within a broader region of interest. In the first approach, pairwise interactions remain constant  
477 irrespective of cell size since they are sampled only once from the metaweb. However, in the second approach,  
478 local interaction probabilities are contingent on the network area. For instance, consider networks  $N_1$  and  $N_2$   
479 with an area of  $\frac{1}{2}A_0$ , both nested within  $A_0$  but disjoint from each other, forming  $N_0$ . If we treat  $N_1$  and  $N_2$  as  
480 independent, the probability of interaction between taxa  $i$  and  $j$  in  $N_0$  is given by:

$$P_{N_0}(i \rightarrow j) = 1 - (1 - P_{N_1}(i \rightarrow j)) \times (1 - P_{N_2}(i \rightarrow j)). \quad (14)$$

481 Due to its larger area, the probability that the two taxa interact in  $N_0$  is equal or greater than in  $N_1$  and  $N_2$ .  
482 When sampling binary interactions from local networks, it is crucial to sample at the same spatial scale for  
483 which probabilities were estimated. Otherwise, interaction probabilities must be adjusted to align with the  
484 intended cell size, preventing systematic biases in predictions.

## 485 Prediction of local networks from metawebs

486 Metawebs serve as a valuable source of ecological information for predicting local networks across time and  
487 space. Binary local networks can be reconstructed by selecting a subset of taxa and interactions from the  
488 metaweb (Dunne (2006)). This implies that metawebs consistently contain more interactions than their  
489 corresponding local networks. Determining the list of taxa to select can be achieved empirically or through  
490 methods like range maps or species distribution models. As the species composition of a community is arguably  
491 less difficult to sample or predict than its interactions, the primary challenge lies in deciding which interactions

492 to select from the metaweb, a task that may necessitate advanced statistical models and ecological expertise.  
 493 Inferring the structure of local networks from the metaweb before predicting specific local pairwise interactions  
 494 could hold promise (Strydom *et al.* (2021)), considering that the structure of local networks is constrained by  
 495 the metaweb (Saravia *et al.* (2022)).  
 496 Building probabilistic local networks from a probabilistic metaweb involves a reduction in the value of pairwise  
 497 interaction probabilities. This decrease is attributed to the prerequisite that two taxa must initially possess the  
 498 capacity to interact before engaging in local interactions (eq. 4). Therefore, inferring local networks from their  
 499 metaweb while maintaining identical interaction probability values would introduce systematic biases into the  
 500 predictions. In such cases, these networks would essentially represent smaller-scale metawebs of potential  
 501 interactions, possibly leading to misinterpretations by being perceived as local interactions. As proposed by  
 502 McLeod *et al.* (2021b), although metawebs do not capture the spatiotemporal variability of interactions, they  
 503 establish an upper limit for local interactions. In other words, the probability of two taxa interacting at a specific  
 504 location and time is consistently lower or equal to the probability of their regional interaction:

$$P_N(i \rightarrow j|A, t, C, \Omega) \leq P_M(i \rightarrow j). \quad (15)$$

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

$$\int_{\Omega} \int_A \int_t P_N(i \rightarrow j|A, t, \Omega) dt dA d\Omega \leq P_M(i \rightarrow j). \quad (16)$$

509 Estimating more precisely the probability  $p$  that two taxa interact locally if they can potentially interact allows  
 510 for improved predictions of local networks from a probabilistic metaweb. This task is challenging due to the  
 511 variability of this probability across space and time, as well as its variability across pairwise interactions within  
 512 a network. Using simple models of  $p$ , as demonstrated in our case studies, represents an initial step toward the  
 513 overarching objective of reconstructing local networks from metawebs.

## 514 Conclusion

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

527 It is essential to enhance our comprehension of both regional and local interactions, especially considering the  
528 current scarcity of interaction data. However, while sampling biological communities does decrease the  
529 uncertainty of interactions by accumulating evidence for their feasibility and local realization, there is a limit to  
530 how much we can diminish their inherent randomness. In metawebs, probabilities reflect our limited knowledge  
531 of interactions (i.e., our degree of belief that interactions are feasible), which is expected to improve with a  
532 larger volume of data. We should anticipate that regional interactions will become more definitive (with  
533 probabilities approaching 0 or 1) as we investigate various conditions, including different combinations of  
534 species traits. Conversely, in the case of local networks, which can be seen as random instances of metawebs,  
535 randomness cannot be as reduced. In local interactions, probabilities can be divided into a component  
536 representing uncertainty and another representing spatiotemporal variability. Owing to environmental  
537 heterogeneity, there will invariably be instances in which an interaction occurs and others in which it does not,  
538 across different times and locations, irrespective of the extent to which we can improve our knowledge of its  
539 biological feasibility and the local conditions that facilitate its occurrence. When local networks depict  
540 probabilities of observing interactions rather than just their actual occurrence, we must also consider the  
541 observation variability as an additional source of randomness. Every ecological process is stochastic but there is  
542 also a possibility that a phenomenon goes undetected. Quantifying and partitioning this stochasticity will

543 enable us to make more accurate predictions about ecological interactions at various spatial and temporal  
544 scales. This will prove to be of vital importance as our time to understand nature runs out, especially at the  
545 places where the impacts of climate change and habitat loss hit harder.

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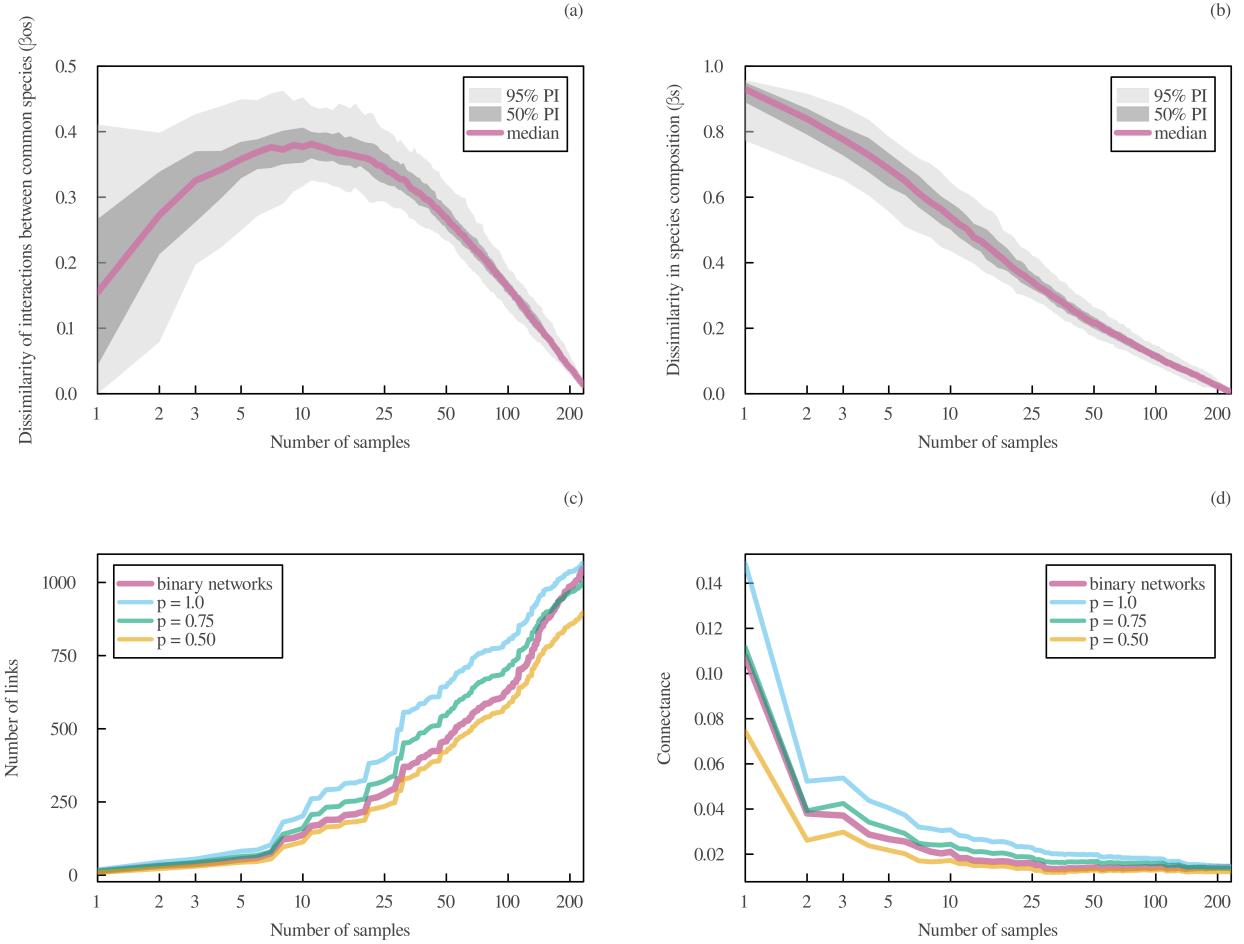
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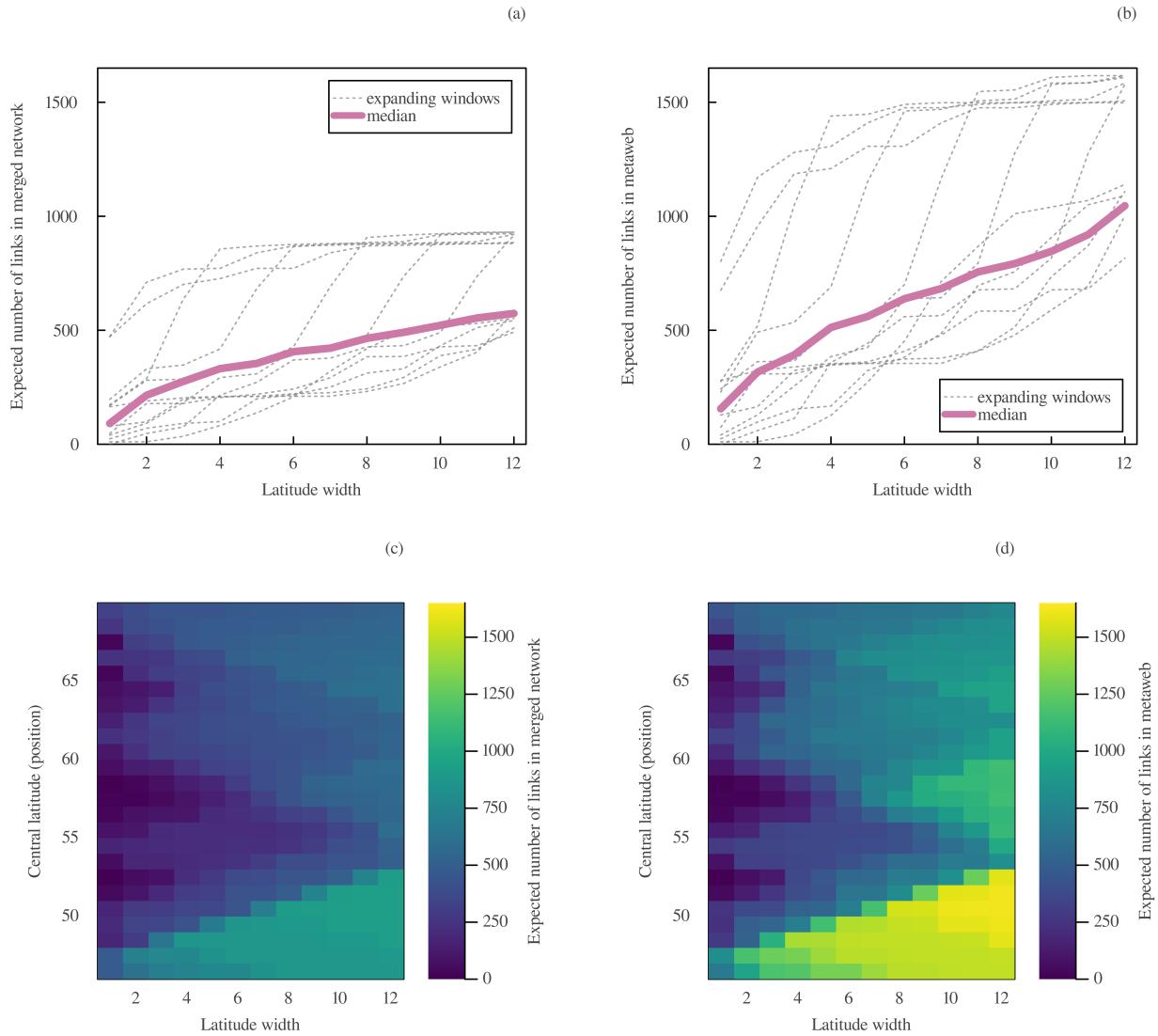
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**Figure 1: Network accumulation curves.** (a) Dissimilarity of interactions between common species and (b) dissimilarity in species composition between aggregated local networks and the binary metaweb of host-parasite interactions. Aggregated local networks were obtained by sequentially and randomly selecting a number of binary local networks 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 networks. For a better comparison with binary networks, local probabilistic networks were derived from the probabilistic metaweb with a false positive and false negative rates of zero. A specific value of  $p$  (the local probability of interaction among potentially interacting species) was used for all local networks within a particular curve. Aggregated probabilistic local networks were obtained by sequentially and randomly selecting a number of probabilistic local networks and aggregating both their species and interactions (with the value of  $p$  adjusting according to eq. 5).



**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  $p$  (the local probability of interaction among potentially interacting species) to 1, ensuring a conservative comparison between aggregated local networks and metawebs. Aggregated local networks were obtained by aggregating both the species and interactions found within a particular latitudinal window, with the values of  $p$  remaining at their maximum value of 1 following eq. 5.

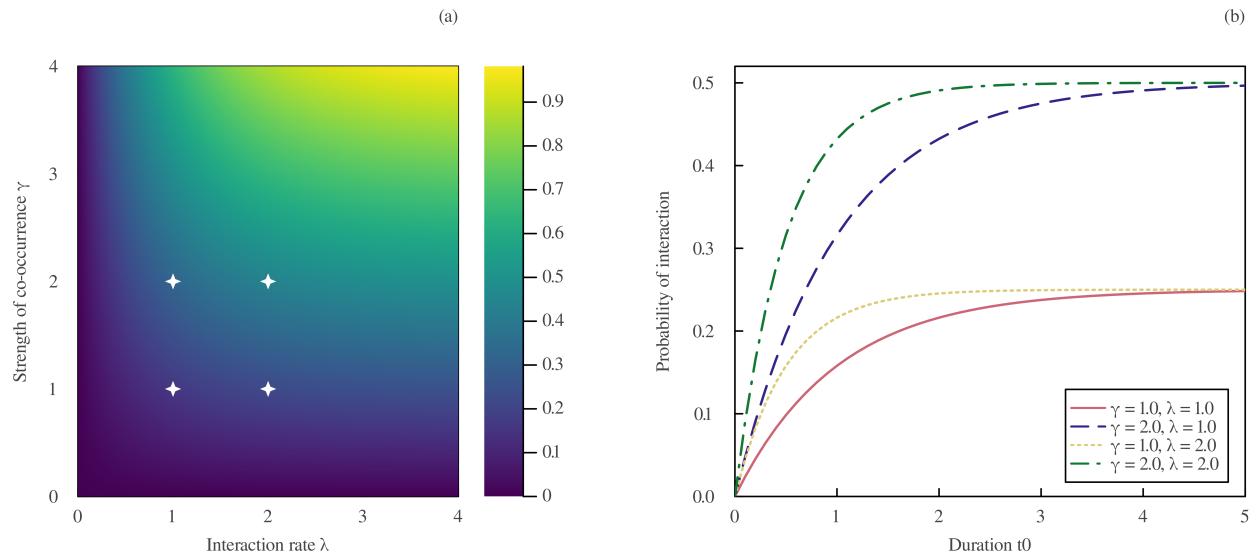
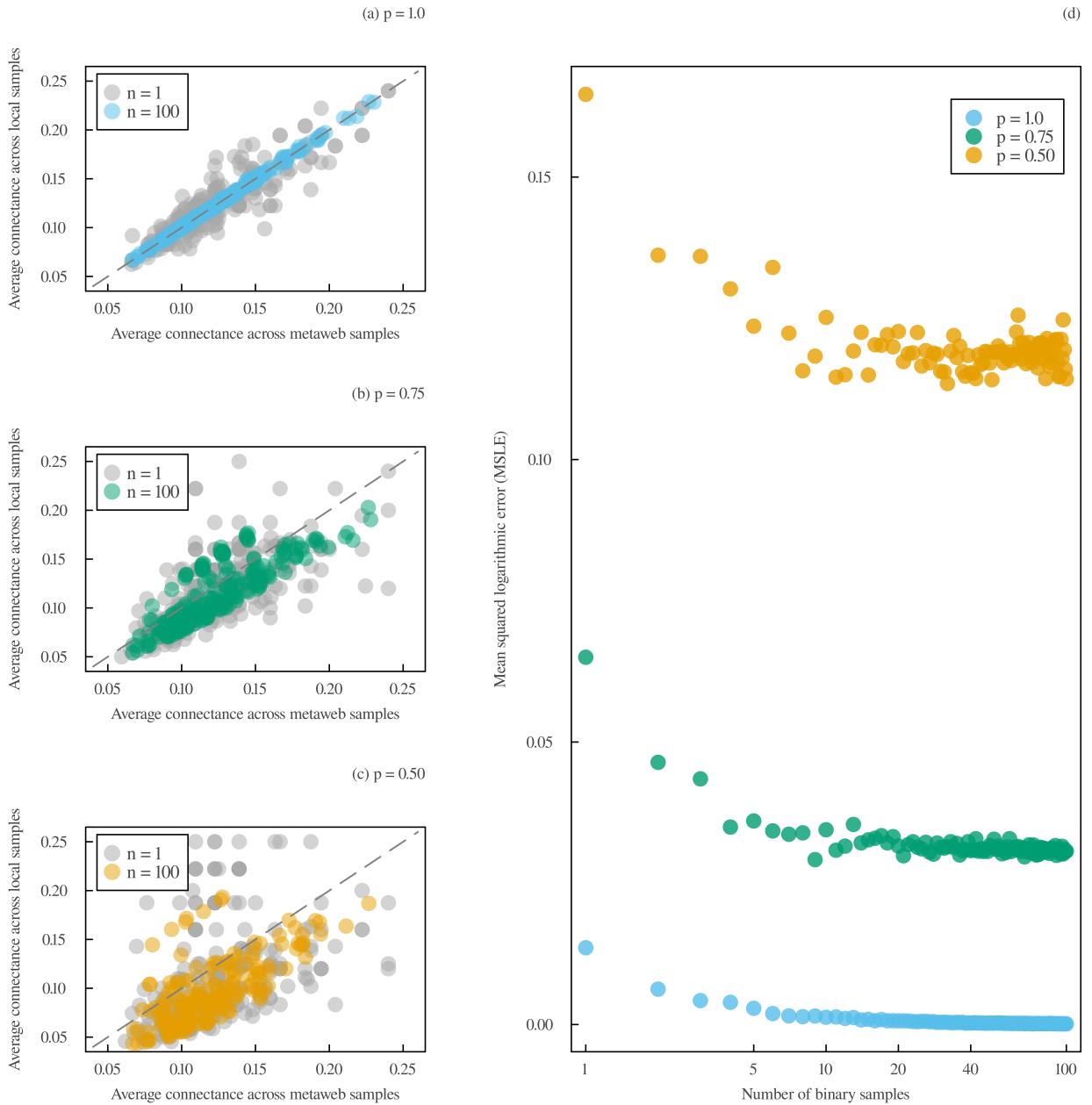


Figure 3: **Parameters of the spatiotemporally explicit model of interactions.** (a) Probability of local interaction given by the process model (eq. 11) under different values of  $\lambda$  and  $\gamma$ , with  $t_0 = 1$ . The parameter values used in the right panel are denoted by the white stars. (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 networks.** Comparison between the average connectance of binary network samples obtained from the probabilistic local networks and metaweb. Each dot corresponds to a different site. The local probability of interaction between potentially interacting species was set to three different values: (a)  $p = 1.0$ , (b)  $p = 0.75$ , and (c)  $p = 0.50$ . 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  $p$  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 networks that include the species potentially engaged in the interactions. Local binary networks were generated by independently sampling binary interactions for each local probabilistic network.