

Deciphering ecological networks of probabilistic interactions

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The stochastic nature of ecological interactions has led biologists to adopt a probabilistic view of ecological networks. Representing species interactions probabilistically (how likely are they to occur?) as opposed to deterministically (are they occurring?) highlights uncertainties in our knowledge of interactions. The origin of the uncertainty captured by interaction probabilities differs depending on the method used to evaluate them. It may consist of the uncertainty of predictive models, the subjective assessment of experts, or even the empirical evaluation of interaction spatiotemporal variability. Despite this growing interest in probabilistic interactions, guidelines for the estimation and documentation of probabilistic interaction data are still lacking. This is concerning because our biological understanding of interaction probabilities and the decisions made during data analysis rely heavily on the often elusive definition of the probabilistic event. 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) and its biological feasibility (regional). Through case studies using open data on host-parasite interactions in Europe, we show that these two network representations have different statistical properties when it comes to common ecological applications. Specifically, we found that local and metawebs differ in their spatial and temporal scaling of probabilistic interactions, but not in their taxonomic scaling. We suggest two approaches to inferring binary interactions from probabilistic ones that account for these differences and show that systematic biases arise when directly inferring local webs from subsets of metawebs. Our results underscore the importance of clear metadata for networks of probabilistic interactions that describe the type of interaction (local or regional)

and uncertainty sources. Comprehensive metadata are particularly useful for the identification of optimal sampling locations where data collection may provide the greatest amount of new information on interactions and minimize their uncertainty.

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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 abundances. While species' absolute abundances may impact interaction frequencies (Vázquez *et al.*
15 (2007)), encounter probabilities are determined by their relative abundances (Canard *et al.* (2012), Canard *et al.*
16 (2012)). The probability that species meet each other also depends on their biological characteristics, such as
17 the synchronization of their phenology (Olesen *et al.* (2010), Singer & McBride (2012)) and their
18 discoverability (e.g., Broom & Ruxton (2005)). Finally, when species do come into contact, an interaction
19 occurs only if their traits are locally compatible (Poisot *et al.* (2015)), including but not limited to their body
20 phenotypes (Bolnick *et al.* (2011), Stouffer *et al.* (2011), Gravel *et al.* (2013)) and behavioral choices (Pulliam
21 (1974), Choh *et al.* (2012)). Interactions may also be influenced by the presence or prevalence of a third species
22 (e.g., of a more profitable prey species, Golubski & Abrams (2011), Sanders & van Veen (2012)). Documenting
23 the location and timing of interactions becomes even more difficult when accounting for the spatiotemporal
24 variability of ecological interactions (Poisot *et al.* (2012), Poisot *et al.* (2015)). Environmental factors, such as
25 temperature (Angilletta *et al.* (2004)), drought (Woodward *et al.* (2012)), climate change (Gilman *et al.* (2010),
26 Woodward *et al.* (2010), Araujo *et al.* (2011)), and habitat modifications (Tylianakis *et al.* (2007)), contribute
27 to this spatiotemporal variability by impacting species abundance and traits. Even after satisfying all these
28 conditions, there remains a possibility that the interaction does not occur locally, either due to the intricate
29 nature of the system or simply by chance. If it does occur, it might still go unnoticed, particularly if it happens
30 infrequently. In this context, it is unsurprising that our knowledge of ecological interactions remains limited

31 (Hortal *et al.* (2015)) despite extensive biodiversity data collection (Schmeller *et al.* (2015)).

32 Knowing the biological capacity of two species to interact directly (via e.g., trophic interactions) is necessary

33 but not sufficient for inferring their interaction at a specific time and space. The recognition of the intrinsic

34 variability of species interactions has led ecologists to expand their representation of ecological networks (also

35 known as ecological webs) to include a probabilistic view of interactions (Poisot *et al.* (2016), Dallas *et al.*

36 (2017), Fu *et al.* (2021)). This different perspective allows us to fill in the Eltonian shortfall (Hortal *et al.*

37 (2015)) by modeling the probability of occurrence of interactions, which can be an important tool for directing

38 efforts and taking action, especially in places where access and resources for research are scarce. The

39 probabilistic representation of interactions is thus far limited to direct interactions, which are conceptually and

40 mathematically analogous regardless of their biological type (e.g., predation and pollination). This is in contrast

41 with indirect interactions (e.g., interspecific competition), which arise from distinct ecological processes and are

42 often not directly observable (Kéfi *et al.* (2015), Kéfi *et al.* (2016)). Representing direct interactions

43 probabilistically enables us to capture the spatiotemporal variability of the aforementioned ecological processes

44 and the uncertainties associated with their occurrence. As opposed to webs of binary deterministic interactions,

45 in which interactions are regarded as either occurring or not, webs of probabilistic interactions, within a

46 Bayesian framework, express our degree of belief (or confidence) regarding the occurrence or observation of

47 interactions. Based on the scale at which they are estimated, probabilistic interactions may reflect our level of

48 confidence in whether interactions will be observed, realized locally, or biologically feasible. As an illustration,

49 we could outline a situation in which there is a 50% certainty that an interaction occurs 50% of the time, or that

50 there is a 50% certainty that it simply occurs. Our level of confidence should be more definitive (approaching

51 either 0 or 1) as we extend our sampling to a broader area and over a longer time period, thereby diminishing the

52 uncertainty of the interactions (but not necessarily the estimation of their variability). In the broadest sense,

53 binary interactions are also a type of probabilistic interaction, in which the numerical value of an interaction is

54 restrained to 0 (non-occurring) or 1 (occurring). Yet, for the sake of clarity, we omit binary interactions from

55 our discussion of probabilistic interactions in this contribution. In networks of probabilistic interactions, only

56 forbidden interactions (i.e., interactions prohibited by biological traits or species absence, Jordano *et al.* (2003),

57 Olesen *et al.* (2010)) have a probability value of zero, provided that intraspecific trait variability is considered

58 (Gonzalez-Varo & Traveset (2016)).

59 By accounting for the uncertainty of interactions, networks of probabilistic interactions may provide a more

60 realistic portrait of species interactions. However, how the uncertainty of pairwise interactions propagates to

network structure (i.e., community-level properties driving the functioning, dynamics, and resilience of ecosystems, Proulx *et al.* (2005), McCann (2007), McCann (2011), Rooney & McCann (2012)) remains to be elucidated. 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 networks of probabilistic interactions by preserving chosen characteristics of the adjacency matrix of binary interactions while intentionally omitting others (Bascompte *et al.* (2003), Fortuna & Bascompte (2006)), serve as other examples of common probabilistic interaction 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 interaction 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 interaction networks that necessitate distinct approaches when applied to key ecological questions: local webs describing probabilities of realized interactions, and regional webs (metawebs) describing probabilities of potential interactions. We highlight the distinctions in the ecological meaning of these two representations and examine some of their properties and relationships (particularly with space, time, and between each other) through empirical case studies. Moreover, there is currently no metadata standard that could guide the documentation of all types of probabilistic interactions (although see e.g., Salim *et al.* (2022) who discuss data standards for deterministic mutualistic webs). Well-defined metadata for probabilistic interactions would support more adequate manipulation and integration of interaction data from different sources and guard against possible misinterpretations arising from ambiguous definitions of probabilistic interaction networks. These metadata should outline the nature (i.e., local or regional) and type (e.g., predatory or pollination) of the interactions, provide information regarding the taxonomic level, identities, and characteristics (e.g., life stages) of the individuals involved in an interaction, present the mathematical formulation of probabilities, including clearly identified conditional variables (e.g., spatial and temporal scales), and describe the methods and contexts (e.g., location, time, environmental conditions) in which interactions were estimated. Inadequately documented probabilistic interaction data should be used with caution when analyzing ecological webs. Our observations and advice can be applied to most types of ecological networks representing direct interactions, from food webs to host-virus networks. Even though the measurement of interaction probabilities may differ between network types (e.g., estimations often based on frequencies of interactions in plant-pollinator networks), the broad principles underlying our findings remain relevant and applicable across diverse ecological contexts.

Probabilistic representations of interactions

One of the first aspects to take into consideration when estimating or interpreting probabilities of interactions is knowing if they describe potential or realized interactions, as these two types of interactions have distinct conceptual underpinnings and sources of uncertainty. A potential (regional) interaction is defined as the biological capacity of two taxa to interact (i.e., the probability that they interact if they were to encounter each other and given sufficient time) whereas a realized (local) interaction is the occurrence or observation of this interaction in a well-defined space and time (i.e., the probability that they interact locally). For two co-occurring

119 taxa and over infinite time, the probability of local interaction is equivalent to the probability of regional
120 (potential) interaction. Our discussion of local interactions focuses on their occurrence rather than their direct
121 empirical observation, as one of the primary goals of describing them probabilistically is to characterize our
122 uncertainty regarding their actual realization. We use the terms *metaweb* (Dunne (2006)) to designate regional
123 webs of potential interactions and *local webs* (Poisot *et al.* (2012)) for those of realized interactions. Metawebs
124 are the network analogs of the species pool, where local webs originate from a subset of both species (nodes)
125 and interactions (edges) of the regional metaweb (Saravia *et al.* (2022)). Without clear documentation, it can be
126 challenging to know if published probabilistic interaction webs describe local or regional interactions (tbl. 1
127 provides examples of studies employing both types of probabilistic interaction networks), or if so-called
128 probabilities are in reality *interaction scores* (i.e., non-probabilistic quantitative interactions analogous to
129 interaction strengths). When probabilistic regional interactions are used and interpreted incorrectly as local
130 interactions (and conversely), this may generate misleading findings during data analysis. We believe that a
131 better understanding of the differences, similarities, and interconnections between these two probabilistic
132 representations of ecological interactions would alleviate interpretation errors (e.g., when studying network-area
133 relationships) and facilitate a more adequate utilization of interaction data.

134 **Pairwise interactions: the building blocks of ecological networks**

135 Local and metawebs, like any type of network, are made of nodes and edges that may be represented at different
136 levels of organization and precision. The basic units of ecological networks are individuals that interact with
137 each other (e.g., by predation in food webs, Elton (2001)), forming individual-based networks (Melián *et al.*
138 (2011)). The aggregation of these individuals into more or less homogeneous groups (e.g., populations, species,
139 families, feeding guilds) allows us to represent nodes at broader taxonomic scales, which affects our
140 interpretation of the properties of these systems (Guimarães (2020), Hemprich-Bennett *et al.* (2021)).

141 Edges linking nodes may describe a variety of interaction measures. Ecologists have traditionally represented
142 interactions as binary objects that were considered realized after observing at least one individual from group i
143 interact with at least another individual from group j . In an adjacency matrix B of binary interactions, the
144 presence or absence of an interaction $B_{i \rightarrow j}$ between two taxa can be viewed as the result of a Bernoulli trial
145 $B_{i \rightarrow j} \sim \text{Bernoulli}(P(B_{i \rightarrow j}))$, with $P(B_{i \rightarrow j})$ being the probability of interaction that characterizes our limited
146 knowledge of the system and/or its intrinsic spatiotemporal variability. In networks of probabilistic interactions,
147 $P(B_{i \rightarrow j})$ are edge values, and the only two possible outcomes are the presence ($B_{i \rightarrow j} = 1$) or absence ($B_{i \rightarrow j} = 0$)

148 of an interaction between each pair of nodes. Depending on the type of probabilistic interaction network (local
149 or metaweb), the mathematical formulation and interpretation of stochastic parameters like $P(B_{i \rightarrow j})$ can be
150 linked to environmental and biological factors such as species abundance, traits, area, and time (tbl. 1), for
151 example using logistic regression with continuous explanatory variables. Predicting the number of local webs in
152 which the interaction between two given taxa occurs can be achieved by using a Binomial distribution,
153 assuming a constant probability of interaction and independence between networks (trials). When considering
154 uncertainties around the estimation of $P(B_{i \rightarrow j})$, a Beta distribution can also be used to encompass all possible
155 probability values. In that case, a Beta-Binomial distribution can be used to predict the number of networks in
156 which the interaction occurs. Empirically observing an interaction between two taxa at a given location and
157 time provides important information that can be used to update previous estimates of $P(B_{i \rightarrow j})$, informing us on
158 the biological capacity of both taxa to interact and the environmental conditions that enabled them to interact
159 locally.

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

172 Just like binary interaction networks, the uncertainty and spatiotemporal variability of interaction strengths can
173 be represented probabilistically. However, the need to estimate the probability distribution of all possible values
174 of interaction strengths can make the inference of probabilities more challenging in quantitative webs compared
175 to binary interaction webs, which require only one probability estimate for each interaction. Interaction
176 strengths can follow various probability distributions depending on the measure used. For instance, they can
177 follow a Poisson distribution $W_{i \rightarrow j} \sim \text{Poisson}(\lambda_{i \rightarrow j})$ when predicting frequencies of interactions between pairs

178 of nodes, with $\lambda_{i \rightarrow j}$ being the expected rate at which individuals of taxa i and j interact (e.g., the average
179 number of prey j consumed by all predators i in a given time period). The Poisson distribution can also be
180 0-inflated after initially modeling non-interacting taxa (e.g., Boulangeat *et al.* (2012) employ a 0-inflated model
181 to analyze species abundance following the modeling of species presence and absence), which constitute the
182 majority of taxa pairs in most local webs due to their typically high sparseness (Jordano (2016)). Because of the
183 methodological difficulties typically encountered when building deterministic quantitative webs (which are only
184 partially mitigated by models such as Ecopath, Plagányi & Butterworth (2004)), binary interaction webs, which
185 are easier to sample (Jordano (2016)) and predict (Strydom *et al.* (2021)), have been more frequently studied
186 and modeled. Moreover, most published networks of probabilistic interactions and methods describe
187 probabilistic interactions whose outcome is binary (whether interaction probabilities are regarded as constant or
188 variable, e.g. represented by a Beta distribution), which underlines the need for better guidelines regarding the
189 interpretation and manipulation of these types of webs first. For these reasons, our primary focus in this
190 contribution will be on addressing the challenges in interpreting and using interaction probabilities in Bernoulli
191 distributions, in both local and metawebs.

192 Local webs: communities interacting in space and time

193 Local webs of probabilistic interactions describe how likely taxa are to interact at a given location and time
194 period (i.e., interactions are contingent upon the environmental and biological conditions of the community). In
195 local webs, edges commonly represent our degree of belief that two taxa interact in nature, but can also
196 represent the probability of *observing* this interaction (Catchen *et al.* (2023)). For example, Gravel *et al.* (2019)
197 analyzed local European trophic webs of willow-galling sawflies and their natural enemies depicting binary
198 interactions, all referenced in space and time, to infer the probabilities of locally observing interactions between
199 co-occurring species. This was achieved by situating local webs within the context of environmental variables,
200 i.e. by including temperature and precipitation as conditional variables in some of their models.

201 We define space as the collection of geographic coordinates (x, y, z) , with (x, y) representing longitude and
202 latitude coordinates, and z denoting either altitudes or depths. These point coordinates delineate the spatial
203 boundaries of the system, which may be portrayed as a polyhedron. Ecological interactions may exhibit
204 variations along latitudinal and altitudinal gradients, as evidenced by changes in hummingbird-plant interactions
205 (Weinstein & Graham (2017b), Weinstein & Graham (2017a)) and mosquito biting rates (e.g., Kulkarni *et al.*
206 (2006)) at different elevations. In contrast, time is defined as the specific time period within which interactions

were either observed or predicted. Even though space and time are continuous variables that should yield probability *densities* of interactions (i.e., relative likelihoods of interactions occurring at infinitesimal locations and instants in time), these definitions enable them to be conceptualized as distinct patches and time segments. Treating space and time as discrete dimensions aligns with the common sampling methods of ecological networks and provides actual probabilities of interactions, which can be obtained by integrating probability densities over space and time. Furthermore, we can quantify both an area A and a duration t , which can be readily used in spatiotemporal analyses of ecological networks. For example, when studying network-area relationships (NAR, Galiana *et al.* (2018)), we anticipate that local probabilities of interactions scale positively with area and duration because taxa have more opportunities to interact as these dimensions expand.

The probability that two taxa i and j interact in a local web $L_{x,y,z,t}$ (spatial and temporal subscripts hereafter omitted or replaced by the shorter subscript l for clarity) can be conditioned on many environmental and biological factors. In addition to network area (or volume) and duration, they may be conditioned on taxa co-occurrence $X_{i,j,l}$, which is usually a Boolean describing if the geographic distributions of both taxa overlap within the study area. Co-occurrence may be modeled probabilistically, in which case it may conform to a Bernoulli distribution $X_{i,j,l} \sim \text{Bernoulli}(P(X_{i,l}, X_{j,l}))$, where $X_{i,l}$ and $X_{j,l}$ are the local occurrences (presence / absence) of both taxa. The probability of co-occurrence $P(X_{i,l}, X_{j,l})$ can be estimated through the application of joint species distribution models (e.g., Pollock *et al.* (2014)), potentially taking into account biotic interactions (Staniczenko *et al.* (2017)). Given that the probability that two non-co-occurring taxa interact locally is zero (i.e., $P(L_{i \rightarrow j}|X_{i,j,l} = 0) = 0$), the probability of local interaction can be obtained by multiplying the probability of interaction given co-occurrence with the probability of co-occurrence:

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

Other important factors that can impact interaction probabilities at the local scale are taxa local abundances $N_{i,l}$ and $N_{j,l}$, which affect encounter probabilities (Canard *et al.* (2012)), and local traits distributions $T_{i,l}$ and $T_{j,l}$ (e.g., body mass, presence of given anatomical features, host resistance), which determine the ability of individuals to interact after encountering each other (Poisot *et al.* (2015)). Moreover, local interactions may be conditional on local environmental factors such as temperature (Angilletta *et al.* (2004)), precipitation (Woodward *et al.* (2012)), habitat structure (Klecka & Boukal (2014)), and presence of other taxa in the network (Pilosof *et al.* (2017), Kéfi *et al.* (2012)), as described above. Here, we use the variable E_l to describe

234 the local ecological context in which interaction probabilities were estimated. For example, if a research team
235 conducts a mesocosm experiment to estimate interaction probabilities between predators and prey with and
236 without shelters (a place that offers refuge and protection for prey, shielding them from predators), E_l would
237 represent the presence or absence of these shelters. Like co-occurrence, E_l can also be modeled probabilistically
238 when the stochasticity or uncertainty of environmental factors is considered. In sum, E_l represents all
239 ecological variables that were taken into consideration when measuring interaction probabilities and is,
240 therefore, a subset of all environmental factors impacting ecological interactions. Finally, local interaction
241 probabilities may be conditioned on higher-level properties of the network, which we denote by $f(L)$. Many
242 topological null models (i.e., statistical models that randomize interactions by retaining certain properties of the
243 network while excluding others) provides interaction probabilities from selected measures of network structure,
244 such as connectance (Fortuna & Bascompte (2006)) and the degree distribution (Bascompte *et al.* (2003)).

245 The probability that two taxa i and j interact in a local web L can thus be conditioned on their co-occurrence
246 $X_{i,j,l}$ (or more explicitly on their occurrences $X_{i,l}$ and $X_{j,l}$), local abundances $N_{i,l}$ and $N_{j,l}$, local traits
247 distributions $T_{i,l}$ and $T_{j,l}$, local environmental conditions E_l , network area (or volume) A , time interval t , and
248 network properties $f(L)$. Although these variables correspond to distinct ecological inquiries or mechanisms
249 related to ecological interactions, they may covary with each other, such as the possible dependence of $X_{i,j,l}$ and
250 E_l on spatial and temporal scales. When estimating interaction probabilities using e.g. a generalized linear
251 model with multiple explanatory variables that might not be independent, it may become important to address
252 collinearity. In such case, to mitigate this issue, it may be necessary to use variable selection techniques before
253 fitting the model to data. The probability that a local interaction is realized is described by the following
254 expression when all these conditional variables are included:

$$P(L_{i \rightarrow j} | X_{i,l}, X_{j,l}, N_{i,l}, N_{j,l}, T_{i,l}, T_{j,l}, E_l, A, t, f(L)) \quad (2)$$

255 The representation of the local context in which probabilities are estimated and the variables that should be
256 taken into consideration depend on the study system, the objectives of the study, and the resources available to
257 the researchers. In other words, these variables do not systematically need to be accounted for. For example, in
258 Gravel *et al.* (2019), for the purpose of model comparison, some models incorporated environmental variables
259 as conditions of interaction probabilities, while others did not. When accounted for, these variables should be
260 clearly described in the documentation of the data (Brimacombe *et al.* (2023)), preferentially in mathematical

terms to avoid any confusion in their interpretation and to limit manipulation errors during their re-use. For instance, ecologists should be explicit about their consideration of co-occurrence in their estimation of local interaction probabilities. Indeed, it is important to specify if probability values are conditional $P(L_{i \rightarrow j}|X_{i,j,l} = 1)$ or not $P(L_{i \rightarrow j})$ on co-occurrence since this can significantly impact the interpretation and analysis of the data. In tbl. 1, we present examples of studies that used these different formulations of probabilistic interactions and conditional variables. We have included the probability of empirically observing an interaction that is realized locally $P(O_{i \rightarrow j}|L_{i \rightarrow j})$ to underscore the distinction between local observations and actual realizations of interactions, even though the focus of this manuscript is not on the observation of interactions.

Table 1: Mathematical expressions of probabilistic interactions. The probability of interaction between two taxa i and j is interpreted differently in a metaweb M of potential interactions (representing the *biological* feasibility of interactions), a metaweb M^* of potential interactions (representing the *ecological* feasibility of interactions), a local web L of realized interactions and a local web O of observed interactions. Each expression emphasizes a different conditional variable, the three dots serving as a placeholder for other variables not explicitly stated in the expression. The outcome of each of these probabilistic events, along with common uncertainty sources (often stemming from the model used for estimation), is presented alongside examples of studies that employed them (with specific variables indicated in parentheses, when applicable). The study marked with an asterisk has been conducted on binary interaction webs.

Expression	Type	Outcome	Uncertainty	
			sources	Reference
$P(L_{i \rightarrow j} X_{i,l}, X_{j,l}, \dots)$	local	realization of the interaction	spatiotemporal	Gravel <i>et al.</i> (2019)
		given taxa co-occurrence	variability	
$P(L_{i \rightarrow j} N_{i,l}, N_{j,l}, \dots)$	local	realization of the interaction	neutral models	Canard <i>et al.</i> (2014)
		given taxa abundances		
$P(L_{i \rightarrow j} T_{i,l}, T_{j,l}, \dots)$	local	realization of the interaction	trait matching	Gravel <i>et al.</i> (2016)
		given local traits	models	
$P(L_{i \rightarrow j} E_l, \dots)$	local	realization of the interaction	environmental-	Gravel <i>et al.</i> (2019)
		given local environmental	based models	
		conditions		
$P(L_{i \rightarrow j} A, \dots)$	local	realization of the interaction in	spatial models	Galiana <i>et al.</i> (2018)
		a given area or volume		
$P(L_{i \rightarrow j} t, \dots)$	local	realization of the interaction during a given time period	temporal models	Weinstein & Graham (2017a)

Expression	Type	Outcome	Uncertainty	
			sources	Reference
$P(L_{i \rightarrow j} f(L), \dots)$	local	realization of the interaction given network structure	topological null models	Fortuna & Bascompte (2006) (connectance)
$P(L_{i \rightarrow j} M_{i \rightarrow j}, \dots)$	local	realization of the interaction given that the taxa can biologically interact	spatiotemporal variability	this study
$P(O_{i \rightarrow j} L_{i \rightarrow j}, \dots)$	local	observation of the interaction given that it is realized locally	sampling model	Catchen <i>et al.</i> (2023)
$P(M_{i \rightarrow j} T_i, T_j)$	regional	biological feasibility of the interaction given regional traits (non-forbiddenness)	trait matching models	Strydom <i>et al.</i> (2022)
$P(M_{i \rightarrow j}^* T_i, T_j, E)$	regional	ecological feasibility of the interaction given regional traits and environmental conditions	trait matching and environmental-based models	this study

269 Metawebs: regional catalogs of interactions

270 Metawebs are networks of potential interactions that have been designed for broad spatial, temporal, and
 271 taxonomic scales (e.g., species food webs at the continental scale). They represent the probability that taxa can
 272 biologically interact regardless of their co-occurrence and local environmental conditions. Metawebs of
 273 probabilistic interactions are particularly valuable when interaction data is limited, i.e. when the uncertainty of
 274 potential interactions is high. As data accumulates, interactions in metawebs should tend towards binarity,
 275 approaching probability values of 0 (repeatedly failing to observe an interaction) and 1 (observing an
 276 interaction at least once).

277 Regional interactions are not evaluated for a particular local context. In contrast with local webs of probabilistic
 278 interactions, which represent the stochasticity of interactions occurring in nature, metawebs of probabilistic
 279 interactions measure our degree of belief in the capacity of two taxa to interact (i.e., the probability that their
 280 traits could support an interaction in the right conditions). Consequently, although *neutrally* forbidden

interactions (i.e., improbable interactions between rare species, Canard *et al.* (2012)) tend to have low probability values in local webs, they may exhibit a higher probability in the metaweb. Potential interactions describe the probability that there exists at least one combination of phenotypes of taxa i and j that can interact with each other if they were to encounter. For example, a piscivorous species may have the capacity to interact with a potential prey species if they share at least one matching combination of body sizes, such as an adult predator being able to consume juvenile prey. To reduce any biases in our calculation of this probability, it is crucial to ensure that the set of traits sampled or considered accurately reflects the overall trait distribution in both taxa. This enhances our confidence in concluding that the taxa cannot interact when no positive observation has been made and increases our capacity to detect an interaction when it is biologically feasible. In addition to pairwise interactions, the extent of sampling effort also contributes to shaping our assessment of metaweb properties, as sampling a larger number of local webs allows us to capture more regional interactions (McLeod *et al.* (2021)). A probability of potential interaction in a metaweb M can be expressed as

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

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

Starting from a selected set of taxa, which are usually distributed within a broad region of interest, metawebs can be built using different data sources, including literature review (e.g., Maiorano2020Tetraeuia), aggregated local web data (e.g., Gravel *et al.* (2019), Saravia *et al.* (2022)), and predictive models (e.g., Strydom *et al.* (2022), Shaw *et al.* (2024)). Every pair of taxa that have confidently been observed to interact at least once can 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 webs of probabilistic interactions, in which interaction events could remain stochastic (i.e., $P(L_{i \rightarrow j}) < 1$) after empirically observing interactions because of their intrinsic spatiotemporal variability. Similarly, although rare interactions typically have low probabilities in local webs, they can have high probabilities in metawebs when the traits of both taxa are congruent. On the other hand, interactions that were never observed can have low probability values in both local and metawebs, going as low as 0 for forbidden links (i.e., interactions forbidden by biological traits). However, many observations of interactions are in reality false positives because of observation errors due to taxonomic misidentifications and ecological misinterpretations (e.g., due to cryptic species and interactions, Pringle & Hutchinson (2020)). Likewise, forbidden interactions can be false negatives

308 in metawebs, e.g. if they have been assessed for specific phenotypes, locations or time. Employing Bayesian
309 models, whether they are mechanistic or phenomenological, could improve the accuracy of our estimation of
310 interaction probabilities within both local and regional webs (e.g., Bartomeus *et al.* (2016), Cirtwill *et al.*
311 (2019)). This improvement is achieved in metawebs by leveraging prior information regarding the feasibility of
312 interactions along with the empirical data on observed interactions.

313 Properties of probabilistic interaction webs

314 Local and metawebs of probabilistic interactions differ in their type of interactions (i.e., realized or potential)
315 and in the conditional variables upon which interaction values depend. These differences are significant as they
316 influence the characteristics of probabilistic interaction networks. Neglecting to consider them may result in
317 misleading results and interpretation errors when analyzing the properties of probabilistic interaction webs,
318 which could be particularly problematic when addressing crucial ecological questions about networks. Here we
319 compare the characteristics of local and metawebs through the presentation of four applications of probabilistic
320 interactions: (1) describing their spatial and temporal scaling, (2) describing their taxonomic scaling, (3)
321 sampling for binary interaction webs, and (4) reconstructing local webs of probabilistic interactions from
322 metawebs. All code and data to reproduce these analyses are available at the Open Science Framework (TBD).

323 Host-parasite network data

324 We use the collection of tripartite host-parasite networks sampled across Europe, created by Kopelke *et al.*
325 (2017), in the following case studies. This dataset contains well-resolved binary local interactions between
326 willows (52 species), willow-galling sawflies (96 species), and their parasitoids (126 species). Given its
327 replicated webs spanning large spatiotemporal scales, this dataset is well-suited for analyzing a variety of
328 ecological hypotheses and processes. Out of a total of 374 local webs, we retained those containing at least 5
329 species, resulting in a set of 233 georeferenced local webs (networks sampled within areas of 0.1 to 0.3 km²
330 during June and/or July spanning 29 years). We built a metaweb of binary interactions by aggregating all local
331 interactions, which gave us a regional web composed of 274 species and 1080 interactions. In the first two
332 panels of fig. 1, we show how the dissimilarity of interactions between common species (β_{OS}) and the
333 dissimilarity in species composition (β_S) between the metaweb and aggregated local webs (Poisot *et al.* (2012))
334 vary with the number of sampled local webs. This shows that networks of local interactions are highly

335 dissimilar from the metaweb, both in terms of species and interactions, especially when only a limited number
 336 of sites has been sampled. Both dissimilarity indices were calculated based on the number of items shared by
 337 the two webs (c_{LM}) and the number of items unique to the metaweb (u_M) and to the aggregated local web (u_L).
 338 The β_S dissimilarity index uses species (nodes) as items being compared, while the β_{OS} index assesses
 339 dissimilarity based on interactions between shared species (Poisot *et al.* (2012)). Both indices were calculated
 340 following the β_W index of Whittaker (1960):

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

341 [Figure 1 about here.]

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

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

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

361 We built local webs of probabilistic interactions using the taxa found in the empirical local networks and
 362 attributing pairwise interaction probabilities based on the metawebs of probabilistic interactions and a constant
 363 value of $P(L_{i \rightarrow j} | M_{i \rightarrow j})$ across interactions. Low values of $P(L_{i \rightarrow j} | M_{i \rightarrow j})$ indicate that feasible interactions rarely
 364 occur locally, intermediate values around 50 suggest considerable spatiotemporal variability, while high values
 365 indicate that regional interactions are nearly always realized locally. Following eq. 5, the local probability of
 366 interaction between a given pair of taxa consistently remained equal to or below their probability of regional
 367 interaction.

368 In the last two panels of fig. 1, we show how the aggregated number of links and connectance (i.e., the
 369 proportion of all of the non-forbidden links that are realized) scale with the number of sampled local webs,
 370 according to different values of $P(L_{i \rightarrow j} | M_{i \rightarrow j})$. When aggregating local webs of probabilistic interactions, the
 371 constancy of the probability of regional interaction across the entire study area means that any rise in the
 372 probability of local interaction is solely attributable to an increase in $P(L_{i \rightarrow j} | M_{i \rightarrow j})$. For example, let L_1 and L_2
 373 be two local networks and $L_{1,2}$ the aggregated web. If $P(L_{1,i \rightarrow j} | M_{i \rightarrow j})$ and $P(L_{2,i \rightarrow j} | M_{i \rightarrow j})$ are the probabilities
 374 that two potentially interacting taxa interact respectively in L_1 and L_2 , the probability $P(L_{1,2,i \rightarrow j} | M_{i \rightarrow j})$ that
 375 these taxa interact in the aggregated web $L_{1,2}$ is obtained by:

$$P(L_{1,2,i \rightarrow j} | M_{i \rightarrow j}) = 1 - (1 - P(L_{1,i \rightarrow j} | M_{i \rightarrow j})) \times (1 - P(L_{2,i \rightarrow j} | M_{i \rightarrow j})), \quad (6)$$

376 assuming independence between the interactions of two taxa in different networks. This equation represents the
 377 probability that the interaction is realized in either (1) exclusively the local web L_1 , (2) exclusively the local web
 378 L_2 or (3) both local webs, given that the two taxa have the biological capacity to interact.

379 By comparing the scaling relationships observed in webs of binary and probabilistic interactions, fig. 1
 380 illustrates that high values of $P(L_{i \rightarrow j} | M_{i \rightarrow j})$ lead to systematic overestimations in the number of links and
 381 connectance, especially when $P(L_{i \rightarrow j} | M_{i \rightarrow j}) = 1$ (corresponding to the scenario where local probabilities of
 382 interactions are equivalent to the probabilities of regional interactions). However, these biases tend to diminish
 383 as the number of sampled webs increases.

384 **Spatial and temporal scaling of interactions**

385 The investigation of network-area relationships and interaction accumulation curves is an important area of
386 research in network ecology. First, network-area relationships elucidate the scaling of network properties (such
387 as modularity and trophic chain lengths) with spatial scale (e.g., Wood *et al.* (2015), Galiana *et al.* (2018)). The
388 variations in network structure across spatial scales may stem from the scaling of species richness (species-area
389 relationships, SARs), the number of interactions (Brose *et al.* (2004)), and many other higher-level properties of
390 the system (e.g., environmental heterogeneity, Thompson & Townsend (2005)) with the sampled area.
391 Additionally, ecological processes occurring at distinct spatial scales, such as the spatial variability in local
392 community composition resulting from different sequences of extinction and colonization events, can also
393 contribute to this variation (Galiana *et al.* (2018)). Next, interaction accumulation curves describe the scaling of
394 the number of observed interactions with sampling effort (Jordano (2016)). Sampling effort, which may
395 correspond to the duration of the sampling period used to construct the network, can impact connectance
396 (Bersier *et al.* (1999)) and various measures of network structure (Banašek-Richter *et al.* (2004), McLeod *et al.*
397 (2021)). Apart from sampling effort, the temporal scaling of interactions also elucidates how network structure
398 changes with the temporal resolution of the network (Poisot *et al.* (2012)), acknowledging that distinct
399 interactions take place over time, ranging from short-term fluctuations of interactions to long-term trends. As
400 local webs of probabilistic interactions may explicitly account for the spatiotemporal variability of interactions,
401 they offer a distinct approach to investigating the scaling of network structure with space and time, in contrast to
402 webs of binary and quantitative interactions, by making the stochasticity of interactions the focal point of the
403 modeling process.
404 Local and metawebs exhibit distinct relationships with spatial and temporal scales. On one hand, metawebs of
405 probabilistic interactions, representing biological feasibility, feature regional interactions that do not scale with
406 space and time. This is because regional interactions depend solely on the biological capacity of two taxa to
407 interact, regardless of their co-occurrence and local environmental conditions. However, probabilities of
408 potential interactions may change (tending to become more definitive) upon updating previous estimates with
409 increased sampling effort, even though they do not vary in a specific direction with the spatial and temporal
410 extent (boundaries) of the network. The probability of two taxa potentially interacting should theoretically be
411 the same in all metawebs in which they are present, provided that the data and methods used for estimation are
412 consistent. For example, if a smaller metaweb M_1 is derived from a larger metaweb M_0 by selecting the subset
413 of taxa present in the region described by M_1 and retaining all their interactions, their probabilities of

interaction 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 as compared to M_1 , the total number of interactions is expected to be higher or at least equal in the larger web, even though pairwise probabilities remain identical.

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

[Figure 2 about here.]

Box 1: A spatiotemporally explicit model of interactions

Predicting local webs across time and space is a pivotal goal of network ecology, especially given the scarcity of interaction data (Strydom *et al.* (2021)). Ecologists may resort to predictive models (e.g., generative Bayesian and machine learning models) to reconstruct networks at fine spatial and temporal scales with limited interaction data. For instance, real-time biomonitoring data coupled with appropriate numerical models (Bohan *et al.* (2017)) can be employed to reconstruct local ecological webs, opening avenues for in-depth studies on local ecosystem functioning and dynamics. The probabilistic representation of interactions describes the inherent uncertainty in these models, typically expressed through probability distributions. We introduce and develop a simple generative mechanistic model for probabilistic local interactions that takes into consideration their spatiotemporal variability (i.e., a spatiotemporally explicit model of local interactions). It is essential to

442 note that our model is not designed for regional interactions, which are scale-independent. Rather, it could
 443 prove valuable for predicting local interactions across time and space by generating new interaction data
 444 following parameter inference.

445 As indicated by eq. 1, the probability that two taxa i and j interact at a specific location and time l may be
 446 determined by the product of their probability of interaction given co-occurrence and their probability of
 447 co-occurrence. First, their co-occurrence probability can be calculated using their individual (marginal)
 448 occurrence probabilities $P(X_{i,l})$ and $P(X_{j,l})$. Given that taxa occurrences are not independent of each other, the
 449 joint probability of both taxa occurring together can be calculated by multiplying the probability of one taxon
 450 being present by the conditional probability of the other occurring when the first one is present. Alternatively,
 451 the joint occurrence probability can be obtained by multiplying the marginal probabilities by the strength of
 452 association γ between the occurrences of both taxa (Cazelles *et al.* (2016)):

$$P(X_{i,l}, X_{j,l}) = P(X_{i,l}|X_{j,l})P(X_{j,l}) = P(X_{i,l})P(X_{j,l})\gamma. \quad (7)$$

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

$$X_{i,j,l} \sim \text{Bernoulli}(P(X_{i,l}, X_{j,l})). \quad (8)$$

459 Next, the probability of interaction given co-occurrence can be made temporally explicit by modeling it as a
 460 Poisson process with rate parameter λ_l . This parameter represents the local expected frequency of interaction
 461 between the taxa within a defined time interval and can be estimated using prior data on interaction strengths,
 462 when accessible. The probability that two co-occurring taxa engage in an interaction during a time period t_0 is
 463 given by:

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

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

468 The occurrence of an interaction between i and j can be modeled as a Bernoulli trial with a probability of
469 $P(L_{i \rightarrow j})$. Consequently, a Bayesian inference model can be built based on the preceding equations to estimate
470 the value of the λ_l and γ parameters and generate novel interaction data:

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

$$P(L_{i \rightarrow j}) = P(X_{i,l})P(X_{j,l})\gamma(1 - e^{-\lambda_l t_0}) \quad (11)$$

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

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

471 In fig. 3, we show the variation in the probability of interaction under different parameter values. In the right
472 panel, we notice that, irrespective of the interaction rate λ_l , the probability of interaction converges toward an
473 asymptote determined by the probability of co-occurrence $P(X_{i,j,l})$ (eq. 7). This model can be customized in
474 different ways, such as by linking λ_l with specific environmental variables or explicitly incorporating
475 observation errors (i.e., the probabilities of false negatives and false positives).

476 [Figure 3 about here.]

477 Taxonomic scaling of interactions

478 Probabilistic interaction networks offer a versatile approach to tackle a broad array of ecological questions,
479 depending on their level of organization. For instance, the assemblage of interactions across ecological scales
480 can be explored through species-based networks, while clade-based networks provide insights into

macroevolutionary processes (e.g., Gomez *et al.* (2010)). Given that our interpretation of the properties and dynamics of ecological webs depends on their taxonomic level (Guimarães (2020)), investigating the taxonomic scaling of interactions (i.e., how interaction probabilities change with taxonomic level) emerges as a promising research avenue. Examining the same system at various taxonomic scales can yield meaningful and complementary ecological information, and, in our perspective, employing webs of probabilistic interactions is an effective approach for such analyses.

There are no inherent differences in the taxonomic scaling between local and metawebs, as only the nodes are defined taxonomically. In other words, the probability values of edges in both local (eq. 2) and metawebs (eq. 3) are not conditional on any taxonomic level. The taxonomic scale is tied to the definition of the event itself (i.e., the interaction between two taxa, defined at the desired taxonomical scale), not to the variables on which interaction probabilities are conditional. In both types of webs, transitioning to a broader level of organization (e.g., from a species-level web S to a genus-level web G) can be accomplished directly by using probabilities 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 can compute the probability that at least one species from genus g_1 interacts with at least one species from genus g_2 (i.e., that there is a non-zero number of species-level interactions or, equivalently, that the genus-level interaction occurs) as follows:

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

where $g_{1,i}$ and $g_{2,j}$ are the species of the corresponding genus and assuming independence between species-level interactions. If it is known that at least two of these species interact (i.e., $P(S_{g_{1,i} \rightarrow g_{2,j}} = 1)$ for at least one pair of $(g_{1,i}, g_{2,j})$), it implies a probability of genus interaction equal to 1. Canard *et al.* (2012) built a species-based network following a similar approach, by using simulated interactions between individuals derived from a neutral model (i.e., a model that assumed ecological equivalence among individuals). In contrast, a more sophisticated approach is necessary when transitioning from a broader to a finer level of organization. This is because knowledge of an interaction between two genera does not guarantee that all possible pairwise combinations of their species will also interact. One possible method is to build a finer-scale network by generating probabilities of interactions through random sampling from a beta distribution, parameterized by the broader-scale network.

Ideally, our biological interpretation of probabilistic interactions should remain consistent across a network

508 even if it incorporates heterogeneous levels of organization, such as a network whose nodes represent both
509 species and trophic species (groups of species sharing similar predators and prey). This is common in
510 ecological webs where taxonomic resolution is typically low (Hemprich-Bennett *et al.* (2021), Vázquez§ *et al.*
511 (2022)). Interaction probabilities at broader taxonomic scales should be based on probabilities of interactions
512 between individuals, for both local and metawebs. For instance, in local individual-based food webs, the
513 probability that two individuals interact reflects our degree of belief that one individual will consume the other.
514 Similarly, in local species-based food webs, the probability that two species interact represents our degree of
515 belief that at least one individual from the predator species consumes at least another individual from the prey
516 species. Furthermore, in local clade-based food webs, the probability that two clades interact represents our
517 degree of belief that at least two species from these clades interact with each other or, equivalently, that at least
518 two individuals from these clades interact with each other. Fundamentally, the taxonomic scaling of interactions
519 involves aggregating interactions between individuals into larger groups, which may exhibit varying degrees of
520 homogeneity based on the organisms and the study system. In that regard, taxonomic scaling is analogous to the
521 spatial and temporal scaling of interactions, as they all represent different ways to aggregate individuals into
522 broader groups (either spatially, temporally, or taxonomically).

523 Sampling for binary interaction webs

524 The prediction of binary interactions through Bernoulli trials is an important application of probabilistic
525 interaction webs. This approach proves beneficial for analyzing the structural characteristics of probabilistic
526 interaction webs, particularly in the absence of specific analytical measures. By performing independent
527 Bernoulli trials for each interaction, a network of binary interactions may be generated. A probability
528 distribution of network properties can be obtained by measuring network structure across multiple randomly
529 generated networks (Poisot *et al.* (2016)). This method enables the representation of the variability of network
530 structure, albeit with possible biases when connectance is low (Poisot & Gravel (2014), Chagnon (2015)).
531 Employing this strategy to generate binary interaction networks under a null model facilitates null hypothesis
532 significance testing, wherein the observed measure is compared against the simulated distribution (e.g.,
533 Bascompte *et al.* (2003)). Additionally, the random generation of binary interaction networks, from a
534 probabilistic interaction web that accounts for the spatiotemporal variability of interactions, may effectively
535 capture network structure across space and time. This facilitates the investigation of ecological hypotheses
536 about interactions at broad spatial and temporal scales. Yet, inferring network structure through sampling for

537 binary interactions assumes independence among interactions, which might not accurately represent reality.
538 Covariation among interactions could exist even if we do not explicitly condition interactions on others. For
539 example, an interaction between two taxa could be more probable when another interaction occurs. The
540 consequences of this assumption of independence on the prediction of network structure have yet to be
541 empirically examined.

542 There are at least two distinct approaches to sample binary interaction networks from probabilistic interaction
543 webs across space, for example, when attempting to predict a binary interaction network for each of a number of
544 locations within a given region. Both approaches assume independence between interactions. The first
545 approach involves performing a singular Bernoulli trial for each pair of taxa based on their regional probability
546 of interaction. In employing this approach, every pair of taxa predicted to interact in the metaweb of binary
547 interactions will be treated as interacting in all local webs where they co-occur. This will result in local pairwise
548 interactions without spatial variation. The second approach is to independently sample each of the local webs of
549 probabilistic interactions, which can be achieved by first generating distinct probabilistic interaction networks
550 for each location. These local webs of probabilistic interactions may vary in taxa composition and interaction
551 probabilities. Subsequently, binary interaction networks can be independently sampled for each location,
552 introducing spatial variation in binary interactions.

553 In fig. 4, we compare the average connectance of binary interaction networks resulting from these two sampling
554 techniques, where regional and local interactions are drawn from our host-parasite networks of probabilistic
555 interactions, generating a number of binary interaction web realizations for each site in the dataset. These two
556 sampling approaches yield different outcomes, particularly for lower values of $P(L_{i \rightarrow j} | M_{i \rightarrow j})$, which represent
557 instances where regional interactions do not consistently manifest locally. Small discrepancies are also apparent
558 between these techniques when we equate the probability of local interaction to the probability of regional
559 interaction (i.e., when using $P(L_{i \rightarrow j} | M_{i \rightarrow j}) = 1.0$ in eq. 5), especially when the number of samples of binary
560 interaction networks for each location is low. As anticipated, we observe that sampling binary interactions from
561 the metaweb tends to overestimate connectance on average compared to sampling them from local webs.
562 Furthermore, we observe an increase in the variability of connectance when employing a single sample,
563 representing what we consider as a more tangible process leading to the realization of local and regional
564 interactions in nature.

565

[Figure 4 about here.]

566 The choice of a sampling approach can influence the selection of grid cell size when delineating local
567 communities within a broader region of interest. In the first approach, pairwise interactions remain constant
568 irrespective of cell size since they are sampled only once from the metaweb. However, in the second approach,
569 local interaction probabilities are contingent on the network area. For instance, consider the local webs L_1 and
570 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
571 independent, the probability of interaction between taxa i and j in L_0 is given by:

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

572 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
573 sampling binary interactions from local webs, it is crucial to sample at the same spatial scale for which
574 probabilities were estimated. Otherwise, interaction probabilities must be adjusted to align with the intended
575 cell size, preventing systematic biases in predictions.

576 Prediction of local webs from metawebs

577 Metawebs serve as a valuable source of ecological information for predicting local webs across time and space.
578 Local webs of binary interactions can be reconstructed by selecting a subset of taxa and interactions from the
579 metaweb (Dunne (2006)). This implies that metawebs consistently contain more interactions than their
580 corresponding local webs, even though their connectance is usually much smaller than the ones of local webs
581 (Gravel *et al.* (2011)). Determining the list of taxa to select can be achieved empirically or through numerical
582 methods like range maps or species distribution models. As species composition is arguably less difficult to
583 sample or predict than pairwise interactions, the primary challenge lies in deciding which interactions to select
584 from the metaweb, a task that may necessitate advanced statistical models and ecological expertise. Inferring
585 the structure of local webs from the metaweb before predicting specific local pairwise interactions could hold
586 promise (Strydom *et al.* (2021)), considering that the structure of local webs is constrained by the metaweb
587 (Saravia *et al.* (2022)).

588 Building local webs of probabilistic interactions from a metaweb of probabilistic interactions involves a
589 reduction in the value of pairwise interaction probabilities. This decrease is attributed to the prerequisite that
590 two taxa must initially possess the capacity to interact before engaging in local interactions (eq. 5). Therefore,
591 inferring local webs from their metaweb while maintaining identical interaction probability values would

592 introduce systematic biases into the predictions. In such cases, these networks would essentially represent
 593 smaller-scale metawebs of potential interactions, possibly leading to misinterpretations by being perceived as
 594 local interactions. As proposed by McLeod *et al.* (2021), although metawebs do not capture the spatiotemporal
 595 variability of interactions, they establish an upper limit for local interactions. In other words, the probability of
 596 two taxa interacting at a specific location and time is consistently lower or equal to the probability of their
 597 regional interaction:

$$P(L_{i \rightarrow j} | X_{i,l}, X_{j,l}, N_{i,l}, N_{j,l}, T_{i,l}, T_{j,l}, E_l, A, t, f(L)) \leq P(M_{i \rightarrow j} | T_i, T_j). \quad (16)$$

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

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

602 Estimating more precisely the probability $P(L_{i \rightarrow j} | M_{i \rightarrow j})$ that two taxa interact locally if they can potentially
 603 interact allows for improved predictions of local webs from the metaweb of probabilistic interactions. This task
 604 is challenging due to the variability of this probability across space and time, as well as its variability across
 605 pairwise interactions within a network. Using simple models of $P(L_{i \rightarrow j} | M_{i \rightarrow j})$, as demonstrated in our case
 606 studies, represents an initial step toward the overarching objective of reconstructing local webs from metawebs.

607 Conclusion

608 In this contribution, we underline the importance of network metadata for adequately interpreting and
 609 manipulating probabilistic interaction data. The mathematical representation of probabilities and their statistical
 610 properties depend on the type of interactions (local or regional) and the conditions under which these
 611 interactions were evaluated. We showed that local and metawebs of probabilistic interactions differ in their
 612 relationship to spatial and temporal scales, with regional interactions remaining consistent across scales. In
 613 contrast with metawebs, local interactions are measured in a specific context (e.g., in a given area, time, and
 614 biological and environmental conditions) and depend on taxa co-occurrence. These conceptual differences

615 bring to light the need to use probabilistic data with caution, for instance when generating network realizations
616 of binary interactions across space and predicting local webs from metawebs. Clear metadata describing the
617 type of interaction and the variables used in their estimation are required to ensure adequate data manipulation.
618 Better data practices and foundations for probabilistic thinking in network ecology could enable more reliable
619 assessments of the spatiotemporal variability and uncertainty of biotic interactions.

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

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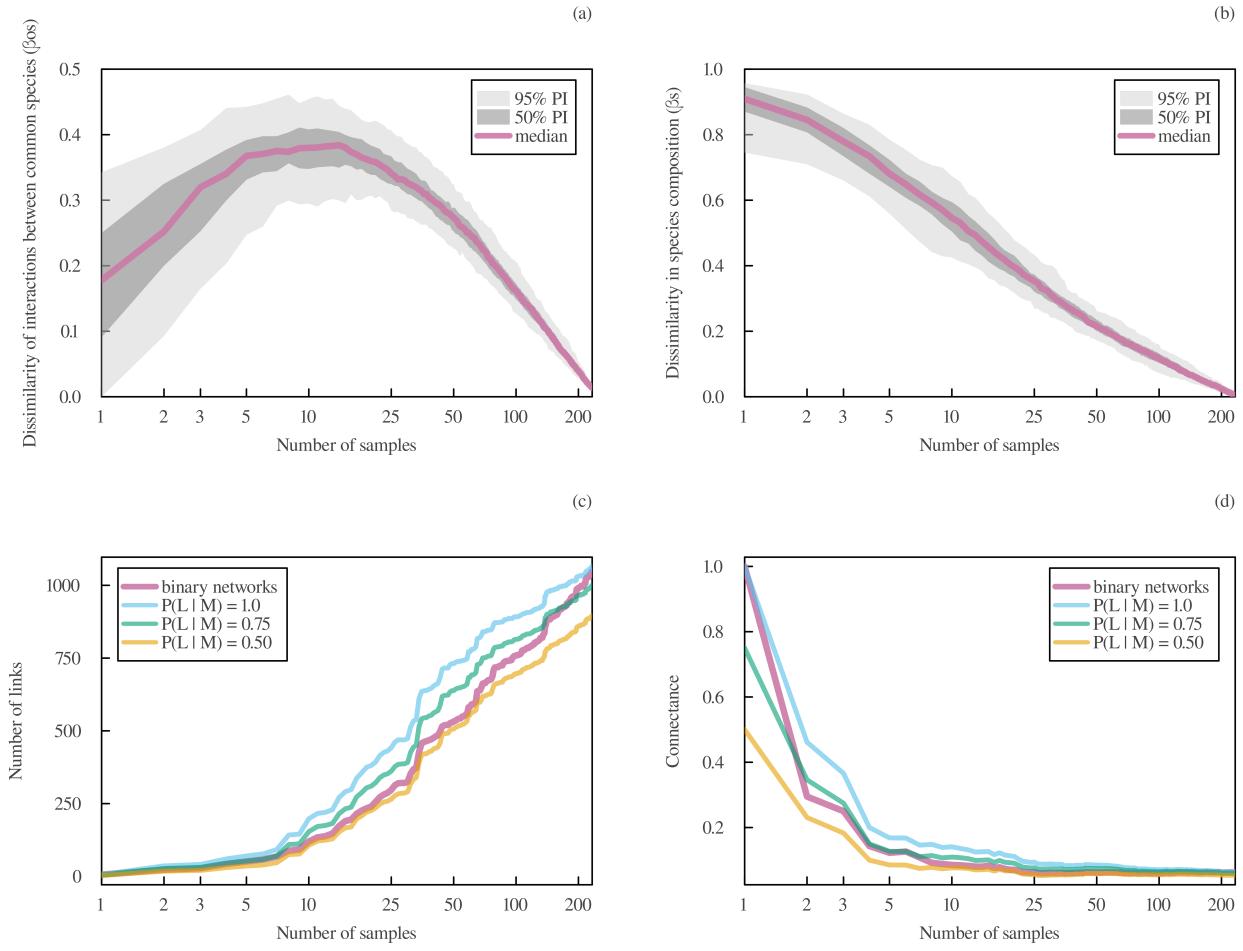


Figure 1: Network accumulation curves. (a) Dissimilarity of interactions between common species and (b) dissimilarity in species composition between aggregated local webs and the metaweb of binary host-parasite interactions. Aggregated local webs were obtained by sequentially and randomly selecting a number of local webs of binary interactions 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 interaction webs. For a better comparison with binary interactions, local webs of probabilistic interactions were derived from the metaweb of probabilistic interactions with a false positive and false negative rate of zero. A specific value of $P(L_{i \rightarrow j} \mid M_{i \rightarrow j})$ (the local probability of interaction among potentially interacting species, indices omitted in the figure for simplicity) was used for all local webs within a particular curve. Aggregated local webs of probabilistic interactions were obtained by sequentially and randomly selecting a number of local webs and aggregating both their species and interactions (with the value of $P(L_{i \rightarrow j} \mid M_{i \rightarrow j})$ adjusting according to eq. 6).

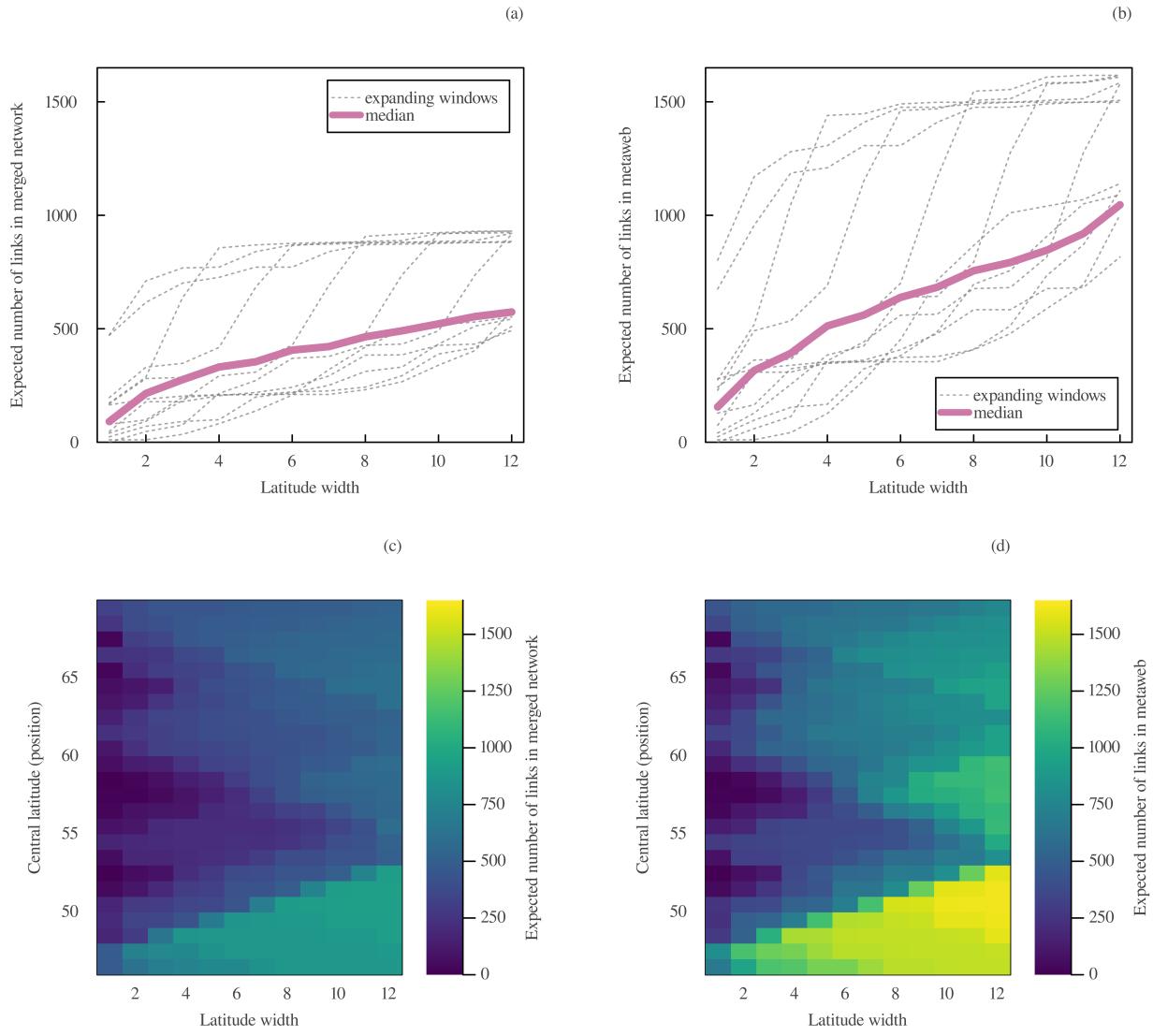


Figure 2: Spatial scaling of interactions. Expected number of host-parasite interactions in a network aggregating all (a) local and (b) regional probabilistic interactions within a latitudinal window of a given length. Every dashed curve corresponds to a different expanding window characterized by a 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 probabilistic regional interactions by setting the value of $P(L_{i \rightarrow j} | M_{i \rightarrow j})$ (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 $P(L_{i \rightarrow j} | M_{i \rightarrow j})$ remaining at their maximum value of 1 following eq. 6.

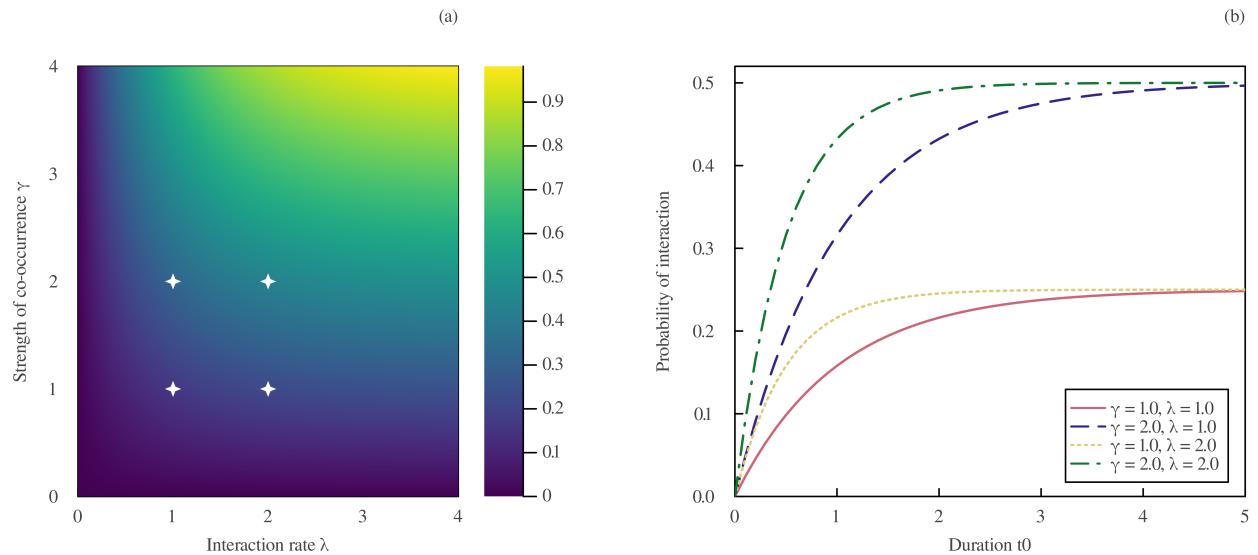


Figure 3: **Parameters of the spatiotemporally explicit model of interactions.** (a) Probability of local interaction given by the process model (eq. 11) under different values of λ_l and γ , with $t_0 = 1$. The parameter values used in the right panel are denoted by the white stars. (b) Scaling of the probability of interaction with the duration parameter t_0 in eq. 11, for different values of λ_l and γ . In both panels, the marginal probabilities of occurrence $P(X_{i,l})$ and $P(X_{j,l})$ are set to a constant value of 0.5.

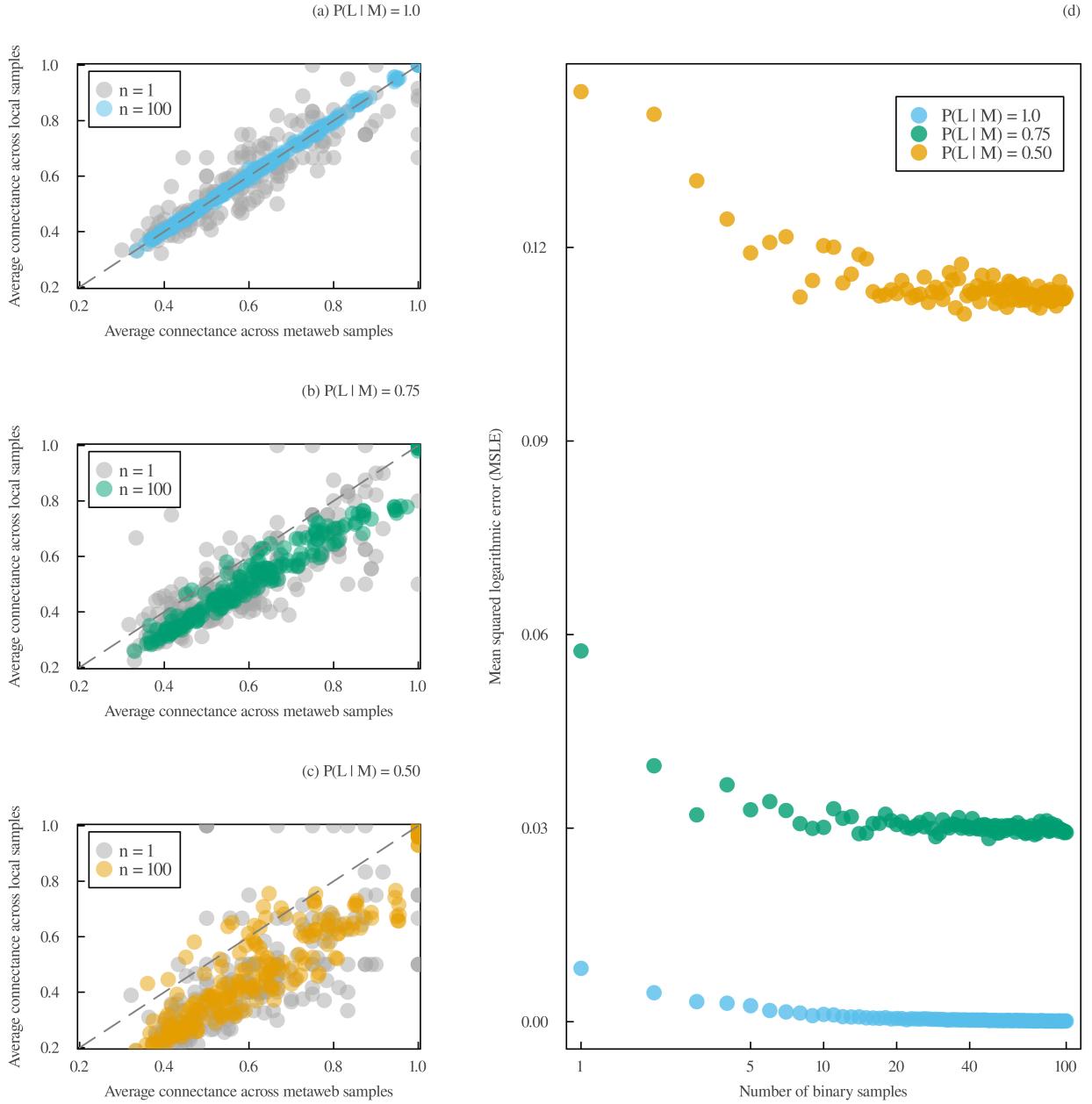


Figure 4: Connectance of sampled binary interaction webs. Comparison between the average connectance of binary interaction network samples obtained from the local and metawebs of probabilistic interactions. Each dot corresponds to a different site. The local probability of interaction between potentially interacting species was set to three different values: (a) $P(L_{i \rightarrow j} \mid M_{i \rightarrow j}) = 1.0$, (b) $P(L_{i \rightarrow j} \mid M_{i \rightarrow j}) = 0.75$, and (c) $P(L_{i \rightarrow j} \mid M_{i \rightarrow j}) = 0.50$. 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 interaction networks obtained from these two sampling methods as the number of trials increases, for the same values of $P(L_{i \rightarrow j} \mid M_{i \rightarrow j})$ 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 interaction metaweb, and then propagating this result to all local webs that include the species potentially engaged in the interactions. Local binary interaction webs were generated by independently sampling binary interactions for each local web of probabilistic interactions.