

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

Consider a scenario where a species of avian predator has just established itself in a northern habitat home to a small rodent species. Suppose these species have never co-occurred before, and as a result, their interaction has not been previously observed. What is the probability that the rodent is part of the diet of the avian predator, or put differently, what is the probability that they interact? Answering this question requires some clarification, as there are multiple ways to interpret and calculate interaction probabilities. We may calculate the probability that the traits of these species match, i.e. that the avian predator possesses the biological attributes to capture and

119 consume the rodent. We may also calculate the probability that their traits support an interaction under the
120 typical environmental conditions of the new habitat. For example, because avian predators hunt by sight,
121 predation could be possible in the absence of snow but highly improbable when snow is present, as rodents may
122 use it as a shelter to hide from predators. Finally, we may calculate the probability that the avian predator will
123 consume the rodent at *that* particular location, for which the spatial and temporal boundaries need to be
124 specified. The estimation of interaction probabilities, whether through predictive models or prior distributions,
125 hinges on our comprehension of these probabilities and the specific ecological processes we aim to capture.

126 One of the first aspects to take into consideration when estimating or interpreting probabilities of interactions is
127 knowing if they describe potential or realized interactions, as these two types of interactions have distinct
128 conceptual underpinnings and sources of uncertainty. A potential (regional) interaction is defined as the
129 biological capacity of two taxa to interact (i.e., the probability that they interact if they were to encounter each
130 other and given sufficient time) whereas a realized (local) interaction is the occurrence or observation of this
131 interaction in a well-defined space and time (i.e., the probability that they interact locally). For two co-occurring
132 taxa and over infinite time, the probability of local interaction is equivalent to the probability of regional
133 (potential) interaction. Our discussion of local interactions focuses on their occurrence rather than their direct
134 empirical observation, as one of the primary goals of describing them probabilistically is to characterize our
135 uncertainty regarding their actual realization. We use the terms *metaweb* (Dunne (2006)) to designate regional
136 webs of potential interactions and *local webs* (Poisot *et al.* (2012)) for those of realized interactions. Metawebs
137 are the network analogs of the species pool, where local webs originate from a subset of both species (nodes)
138 and interactions (edges) of the regional metaweb (Saravia *et al.* (2022)). Without clear documentation, it can be
139 challenging to know if published probabilistic interaction webs describe local or regional interactions (tbl. 1
140 provides examples of studies employing both types of probabilistic interaction networks), or if so-called
141 probabilities are in reality *interaction scores* (i.e., non-probabilistic quantitative interactions analogous to
142 interaction strengths). When probabilistic regional interactions are used and interpreted incorrectly as local
143 interactions (and conversely), this may generate misleading findings during data analysis. We believe that a
144 better understanding of the differences, similarities, and interconnections between these two probabilistic
145 representations of ecological interactions would alleviate interpretation errors (e.g., when studying network-area
146 relationships) and facilitate a more adequate utilization of interaction data.

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

148 Local and metawebs, like any type of network, are made of nodes and edges that may be represented at different
149 levels of organization and precision. The basic units of ecological networks are individuals that interact with
150 each other (e.g., by predation in food webs, Elton (2001)), forming individual-based networks (Melián *et al.*
151 (2011)). The aggregation of these individuals into more or less homogeneous groups (e.g., populations, species,
152 families, feeding guilds) allows us to represent nodes at broader taxonomic scales, which affects our
153 interpretation of the properties of these systems (Guimarães (2020), Hemprich-Bennett *et al.* (2021)).

154 Edges linking nodes may describe a variety of interaction measures. Ecologists have traditionally represented
155 interactions as binary objects that were considered realized after observing at least one individual from group i
156 interact with at least another individual from group j . In an adjacency matrix B of binary interactions, the
157 presence or absence of an interaction $B_{i \rightarrow j}$ between two taxa can be viewed as the result of a Bernoulli trial
158 $B_{i \rightarrow j} \sim \text{Bernoulli}(P(B_{i \rightarrow j}))$, with $P(B_{i \rightarrow j})$ being the probability of interaction that characterizes our limited
159 knowledge of the system and/or its intrinsic spatiotemporal variability. In networks of probabilistic interactions,
160 $P(B_{i \rightarrow j})$ are edge values, and the only two possible outcomes are the presence ($B_{i \rightarrow j} = 1$) or absence ($B_{i \rightarrow j} = 0$)
161 of an interaction between each pair of nodes. Depending on the type of probabilistic interaction network (local
162 or metaweb), the mathematical formulation and interpretation of stochastic parameters like $P(B_{i \rightarrow j})$ can be
163 linked to environmental and biological factors such as species abundance, traits, area, and time (tbl. 1), for
164 example using logistic regression with continuous explanatory variables. Predicting the number of local webs in
165 which the interaction between two given taxa occurs can be achieved by using a Binomial distribution,
166 assuming a constant probability of interaction and independence between networks (trials). When considering
167 uncertainties around the estimation of $P(B_{i \rightarrow j})$, a Beta distribution can also be used to encompass all possible
168 probability values. In that case, a Beta-Binomial distribution can be used to predict the number of networks in
169 which the interaction occurs. Empirically observing an interaction between two taxa at a given location and
170 time provides important information that can be used to update previous estimates of $P(B_{i \rightarrow j})$, informing us on
171 the biological capacity of both taxa to interact and the environmental conditions that enabled them to interact
172 locally.

173 Even though binary interaction webs constitute a highly valuable source of ecological information (Pascual *et*
174 *al.* (2006)), they overlook important factors regarding interaction strengths. Represented in a quantitative
175 adjacency matrix W as numbers not confined to the $[0, 1]$ range, interaction strengths better describe the energy

flows, demographic impacts or frequencies of interactions between nodes (Berlow *et al.* (2004), Borrett & Scharler (2019)), with $W_{i \rightarrow j}$ being a natural \mathbb{N} or real \mathbb{R} number depending on the measure. For example, they may represent local interaction rates between pairs of taxa (e.g., the flower-visiting rates of pollinators in a mutualistic network, Herrera (1989)). When interaction strengths characterize predation pressure on prey taxa in food webs, they can serve as good estimators of the parameters describing species interactions in a Lotka-Volterra model (e.g., Emmerson & Raffaelli (2004)). The extra amount of ecological information in quantitative networks typically comes at a cost of greater sampling effort and data volume in predictive models (Strydom *et al.* (2021)), which can lead to relatively high levels of uncertainties when inferring quantitative webs with limited data.

Just like binary interaction networks, the uncertainty and spatiotemporal variability of interaction strengths can be represented probabilistically. However, the need to estimate the probability distribution of all possible values of interaction strengths can make the inference of probabilities more challenging in quantitative webs compared to binary interaction webs, which require only one probability estimate for each interaction. Interaction strengths can follow various probability distributions depending on the measure used. For instance, they can follow a Poisson distribution $W_{i \rightarrow j} \sim \text{Poisson}(\lambda_{i \rightarrow j})$ when predicting frequencies of interactions between pairs of nodes, with $\lambda_{i \rightarrow j}$ being the expected rate at which individuals of taxa i and j interact (e.g., the average number of prey j consumed by all predators i in a given time period). The Poisson distribution can also be 0-inflated after initially modeling non-interacting taxa (e.g., Boulangeat *et al.* (2012) employ a 0-inflated model to analyze species abundance following the modeling of species presence and absence), which constitute the majority of taxa pairs in most local webs due to their typically high sparseness (Jordano (2016)). Because of the methodological difficulties typically encountered when building deterministic quantitative webs (which are only partially mitigated by models such as Ecopath, Plagányi & Butterworth (2004)), binary interaction webs, which are easier to sample (Jordano (2016)) and predict (Strydom *et al.* (2021)), have been more frequently studied and modeled. Moreover, most published networks of probabilistic interactions and methods describe probabilistic interactions whose outcome is binary (whether interaction probabilities are regarded as constant or variable, e.g. represented by a Beta distribution), which underlines the need for better guidelines regarding the interpretation and manipulation of these types of webs first. For these reasons, our primary focus in this contribution will be on addressing the challenges in interpreting and using interaction probabilities in Bernoulli distributions, in both local and metawebs.

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

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

214 We define space as the collection of geographic coordinates (x, y, z) , with (x, y) representing longitude and
215 latitude coordinates, and z denoting either altitudes or depths. These point coordinates delineate the spatial
216 boundaries of the system, which may be portrayed as a polyhedron. Ecological interactions may exhibit
217 variations along latitudinal and altitudinal gradients, as evidenced by changes in hummingbird-plant interactions
218 (Weinstein & Graham (2017b), Weinstein & Graham (2017a)) and mosquito biting rates (e.g., Kulkarni *et al.*
219 (2006)) at different elevations. In contrast, time is defined as the specific time period within which interactions
220 were either observed or predicted. Even though space and time are continuous variables that should yield
221 probability *densities* of interactions (i.e., relative likelihoods of interactions occurring at infinitesimal locations
222 and instants in time), these definitions enable them to be conceptualized as distinct patches and time segments.

223 Treating space and time as discrete dimensions aligns with the common sampling methods of ecological
224 networks and provides actual probabilities of interactions, which can be obtained by integrating probability
225 densities over space and time. Furthermore, we can quantify both an area A and a duration t , which can be
226 readily used in spatiotemporal analyses of ecological networks. For example, when studying network-area
227 relationships (NAR, Galiana *et al.* (2018)), we anticipate that local probabilities of interactions scale positively
228 with area and duration because taxa have more opportunities to interact as these dimensions expand.

229 The probability that two taxa i and j interact in a local web $L_{x,y,z,t}$ (spatial and temporal subscripts hereafter
230 omitted or replaced by the shorter subscript l for clarity) can be conditioned on many environmental and
231 biological factors. In addition to network area (or volume) and duration, they may be conditioned on taxa
232 co-occurrence $X_{i,j,l}$, which is usually a Boolean describing if the geographic distributions of both taxa overlap
233 within the study area. Co-occurrence may be modeled probabilistically, in which case it may conform to a

234 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 /
 235 absence) of both taxa. The probability of co-occurrence $P(X_{i,l}, X_{j,l})$ can be estimated through the application of
 236 joint species distribution models (e.g., Pollock *et al.* (2014)), potentially taking into account biotic interactions
 237 (Staniczenko *et al.* (2017)). Given that the probability that two non-co-occurring taxa interact locally is zero
 238 (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
 239 of interaction given co-occurrence with the probability of co-occurrence:

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

240 Other important factors that can impact interaction probabilities at the local scale are taxa local abundances $N_{i,l}$,
 241 and $N_{j,l}$, which affect encounter probabilities (Canard *et al.* (2012)), and local traits distributions $T_{i,l}$ and $T_{j,l}$
 242 (e.g., body mass, presence of given anatomical features, host resistance), which determine the ability of
 243 individuals to interact after encountering each other (Poisot *et al.* (2015)). Moreover, local interactions may be
 244 conditional on local environmental factors such as temperature (Angilletta *et al.* (2004)), precipitation
 245 (Woodward *et al.* (2012)), habitat structure (Klecka & Boukal (2014)), and presence of other taxa in the
 246 network (Pilosof *et al.* (2017), Kéfi *et al.* (2012)), as described above. Here, we use the variable E_l to describe
 247 the local ecological context in which interaction probabilities were estimated. For example, if a research team
 248 conducts a mesocosm experiment to estimate interaction probabilities between predators and prey with and
 249 without shelters (a place that offers refuge and protection for prey, shielding them from predators), E_l would
 250 represent the presence or absence of these shelters. Like co-occurrence, E_l can also be modeled probabilistically
 251 when the stochasticity or uncertainty of environmental factors is considered. In sum, E_l represents all
 252 ecological variables that were taken into consideration when measuring interaction probabilities and is,
 253 therefore, a subset of all environmental factors impacting ecological interactions. Finally, local interaction
 254 probabilities may be conditioned on higher-level properties of the network, which we denote by $f(L)$. Many
 255 topological null models (i.e., statistical models that randomize interactions by retaining certain properties of the
 256 network while excluding others) provides interaction probabilities from selected measures of network structure,
 257 such as connectance (Fortuna & Bascompte (2006)) and the degree distribution (Bascompte *et al.* (2003)).

258 The probability that two taxa i and j interact in a local web L can thus be conditioned on their co-occurrence
 259 $X_{i,j,l}$ (or more explicitly on their occurrences $X_{i,l}$ and $X_{j,l}$), local abundances $N_{i,l}$ and $N_{j,l}$, local traits
 260 distributions $T_{i,l}$ and $T_{j,l}$, local environmental conditions E_l , network area (or volume) A , time interval t , and

network properties $f(L)$. Although these variables correspond to distinct ecological inquiries or mechanisms related to ecological interactions, they may covary with each other, such as the possible dependence of $X_{i,j,l}$ and E_l on spatial and temporal scales. When estimating interaction probabilities using e.g. a generalized linear model with multiple explanatory variables that might not be independent, it may become important to address collinearity. In such case, to mitigate this issue, it may be necessary to use variable selection techniques before fitting the model to data. The probability that a local interaction is realized is described by the following expression when all these conditional variables are included:

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

The representation of the local context in which probabilities are estimated and the variables that should be taken into consideration depend on the study system, the objectives of the study, and the resources available to the researchers. In other words, these variables do not systematically need to be accounted for. For example, in Gravel *et al.* (2019), for the purpose of model comparison, some models incorporated environmental variables as conditions of interaction probabilities, while others did not. When accounted for, these variables should be 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		Reference
			sources		
$P(L_{i \rightarrow j} X_{i,l}, X_{j,l}, \dots)$	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		(temperature and
		conditions			precipitation)
$P(L_{i \rightarrow j} A, \dots)$	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	temporal models	Weinstein & Graham (2017a)	
		during a given time period			
$P(L_{i \rightarrow j} f(L), \dots)$	local	realization of the interaction	topological null	Fortuna & Bascompte (2006) (connectance)	
		given network structure	models		
$P(L_{i \rightarrow j} M_{i \rightarrow j}, \dots)$	local	realization of the interaction	spatiotemporal	this study	
		given that the taxa can			
		biologically interact	variability		
$P(O_{i \rightarrow j} L_{i \rightarrow j}, \dots)$	local	observation of the interaction	sampling model	Catchen <i>et al.</i> (2023)	
		given that it is realized locally			

Expression	Type	Outcome	Uncertainty	
			sources	Reference
$P(M_{i \rightarrow j} T_i, T_j)$	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

282 Metawebs: regional catalogs of interactions

283 Metawebs are networks of potential interactions that have been designed for broad spatial, temporal, and
 284 taxonomic scales (e.g., species food webs at the continental scale). Potential interactions describe the biological
 285 capacity of taxa to interact, which is typically assessed at the regional scale. Metawebs of probabilistic
 286 interactions are particularly useful in situations where there is high uncertainty in the ability of taxa to interact if
 287 they were to encounter each other. This uncertainty frequently arises due to insufficient interaction data,
 288 especially for taxa that have not yet been observed to co-occur, and uncertainties in trait-matching models. As
 289 data accumulates, interactions in metawebs should tend towards binarity, approaching probability values of 0
 290 (repeatedly failing to observe an interaction between two co-occurring taxa) and 1 (observing an interaction at
 291 least once). The extent of sampling effort thus influences our evaluation of probabilities of potential
 292 interactions, as sampling over a larger area or for a longer duration enables us to capture a greater number of
 293 regional interactions (McLeod *et al.* (2021)). However, in contrast with local webs of probabilistic interactions,
 294 which describe interaction stochasticity in local natural settings, regional interactions are not evaluated for any
 295 particular local context. Although *neutrally* forbidden interactions (i.e., improbable interactions between rare
 296 species, Canard *et al.* (2012)) tend to have low probability values in local webs, they may have higher
 297 probabilities in the metaweb (i.e., when species' biological traits can support an interaction if they were to
 298 encounter each other). Likewise, non-co-occurring taxa may have a non-zero probability of interaction in the
 299 metaweb.
 300 Potential interactions describe what we refer to as the *biological* feasibility of interactions, which is based solely

301 on the regional traits distributions T_i and T_j of taxa i and j , respectively. A probability of potential interaction in
302 a metaweb M describing the biological feasibility of interactions may be expressed as:

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

303 which, in contrast with local webs, is not conditioned on any spatial, temporal, co-occurrence or environmental
304 variables (tbl. 1). Regional traits may differ from local traits $T_{i,l}$ and $T_{j,l}$, which may vary spatially and
305 temporally due to phenotypic plasticity (Berg & Ellers (2010)). The biological feasibility of interactions
306 expresses our degree of belief that there exists at least one combination of phenotypes that could support an
307 interaction if they were to encounter each other, assuming they had infinite time to interact. Evaluating this
308 probability is conducted without incorporating the environmental conditions under which they encounter each
309 other into the model. It is the complement of the probability $P(F_{i \rightarrow j} | T_i, T_j)$ of forbidden interactions based
310 uniquely on biological traits (i.e., the probability that their traits do not support an interaction):

$$P(M_{i \rightarrow j} | T_i, T_j) = 1 - P(F_{i \rightarrow j} | T_i, T_j). \quad (4)$$

311 For example, let i be a western diamondback rattlesnake (*Crotalus atrox*) and j , a wood lemming (*Myopus*
312 *schisticolor*). These two taxa never co-occur, the rattlesnake being adapted to warm regions of North America
313 (Castoe *et al.* (2007)) and the lemming, to northern habitats of Eurasia (Fedorov *et al.* (2008)). As we lack
314 direct observations of an interaction between these two species, we have to rely on expert knowledge or
315 trait-matching models to estimate their probability of potential interaction. To accurately estimate this
316 probability using trait-matching models, it is crucial to ensure that the set of traits considered reflects the overall
317 traits distributions of both taxa. We could for instance consider their average body mass and the average
318 phylogenetic proximity of lemmings to rattlesnakes' prey. Doing so, we might find a high probability of
319 potential interaction based on these traits.

320 The biological feasibility of interactions should not be confused with what we refer to as the *ecological*
321 feasibility of interactions. A probability of potential interaction in a metaweb M^* describing ecological
322 feasibility of interactions may be expressed as:

$$P(M_{i \rightarrow j}^* | T_i, T_j, E), \quad (5)$$

323 where E is the environmental conditions under which potential interactions are evaluated (tbl. 1). Unlike E_l ,
 324 these environmental conditions do not represent conditions occurring at specific locations. Ecological
 325 feasibility represents the probability that two taxa interact if they were to encounter each other under given
 326 environmental conditions, assuming they had infinite time to interact. Incorporating environmental conditions
 327 into a trait-matching model may be important when there is high covariation between the environment and
 328 biological traits. For instance, in our example involving rattlesnakes and lemmings, the probability of potential
 329 interaction between these two species may be low in most environmental conditions. Western diamondback
 330 rattlesnakes may be unactive under low temperatures (Kissner *et al.* (1997)), whereas wood lemmings may have
 331 low tolerance to high temperatures (Kausrud *et al.* (2008)). The probability that an interaction is ecologically
 332 feasible is always lower than the probability that it is biologically feasible, even across all environmental
 333 conditions:

$$\int_E P(M_{i \rightarrow j}^* | T_i, T_j, E) dE \leq P(M_{i \rightarrow j} | T_i, T_j). \quad (6)$$

334 This is because the biological feasibility of an interaction is a prerequisite for its ecological feasibility.
 335 Biological feasibility is necessary but not sufficient for an interaction to be ecologically feasible. Our discussion
 336 of metawebs will focus on the biological feasibility of interactions since most methods developed for inferring
 337 probabilities of regional interactions do not explicitly take into account environmental conditions (e.g., Strydom
 338 *et al.* (2022)).

339 Starting from a selected set of taxa, which are usually distributed within a broad region of interest, metawebs
 340 can be built using different data sources, including literature review (e.g., Maiorano2020Tetraeu), aggregated
 341 local web data (e.g., Gravel *et al.* (2019), Saravia *et al.* (2022)), trait-matching models (e.g., Strydom *et al.*
 342 (2022), Shaw *et al.* (2024)), and expert knowledge. Every pair of taxa that has confidently been observed to
 343 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.
 344 This differs from local webs of probabilistic interactions, where interaction events may remain stochastic (i.e.,
 345 $P(L_{i \rightarrow j}) < 1$) even after empirically observing interactions due to their spatiotemporal variability. Interactions
 346 that were never observed may have low probability values in local webs and low to high values in metawebs,
 347 going as low as 0 for forbidden links. However, many observations of interactions are in reality false positives
 348 because of observation errors due to taxonomic misidentifications and ecological misinterpretations (e.g., due to
 349 cryptic species and interactions, Pringle & Hutchinson (2020)). Likewise, forbidden interactions may be false

350 negatives, e.g. if they have been evaluated based on unrepresentative or incomplete traits distributions.
351 Employing Bayesian models could prove valuable when estimating interaction probabilities in metawebs (e.g.,
352 Bartomeus *et al.* (2016), Cirtwill *et al.* (2019)). This improvement is achieved by updating prior information
353 regarding the feasibility of interactions (e.g., experts' prior assessments of interaction probabilities) with
354 empirical data on interactions and traits.

355 Properties of probabilistic interaction webs

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

365 Host-parasite network data

366 We use the collection of tripartite host-parasite networks sampled across Europe, created by Kopelke *et al.*
367 (2017), in the following case studies. This dataset contains well-resolved binary local interactions between
368 willows (52 species), willow-galling sawflies (96 species), and their parasitoids (126 species). Given its
369 replicated webs spanning large spatiotemporal scales, this dataset is well-suited for analyzing a variety of
370 ecological hypotheses and processes. Out of a total of 374 local webs, we retained those containing at least 5
371 species, resulting in a set of 233 georeferenced local webs (networks sampled within areas of 0.1 to 0.3 km²
372 during June and/or July spanning 29 years). We built a metaweb of binary interactions by aggregating all local
373 interactions, which gave us a regional web composed of 274 species and 1080 interactions. In the first two
374 panels of fig. 1, we show how the dissimilarity of interactions between common species (β_{OS}) and the
375 dissimilarity in species composition (β_S) between the metaweb and aggregated local webs (Poisot *et al.* (2012))
376 vary with the number of sampled local webs. This shows that networks of local interactions are highly

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

$$\beta_W = \frac{c_{LM} + u_L + u_M}{(2c_{LM} + u_L + u_M)/2} - 1. \quad (7)$$

383 [Figure 1 about here.]

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

398 To build local webs of probabilistic interactions, we first recognize that local interactions must initially be
399 biologically feasible before occurring at a specific time and space. A local probability of interaction $P(L_{i \rightarrow j})$
400 can be expressed as the product of the probability of local interaction given that the two taxa can potentially
401 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
402 regional interaction $P(M_{i \rightarrow j})$:

$$P(L_{i \rightarrow j}) = P(L_{i \rightarrow j} | M_{i \rightarrow j} = 1) \times P(M_{i \rightarrow j} = 1). \quad (8)$$

403 We built local webs of probabilistic interactions using the taxa found in the empirical local networks and
 404 attributing pairwise interaction probabilities based on the metawebs of probabilistic interactions and a constant
 405 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
 406 occur locally, intermediate values around 50 suggest considerable spatiotemporal variability, while high values
 407 indicate that regional interactions are nearly always realized locally. Following eq. 8, the local probability of
 408 interaction between a given pair of taxa consistently remained equal to or below their probability of regional
 409 interaction.

410 In the last two panels of fig. 1, we show how the aggregated number of links and connectance (i.e., the
 411 proportion of all of the non-forbidden links that are realized) scale with the number of sampled local webs,
 412 according to different values of $P(L_{i \rightarrow j} | M_{i \rightarrow j})$. When aggregating local webs of probabilistic interactions, the
 413 constancy of the probability of regional interaction across the entire study area means that any rise in the
 414 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
 415 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
 416 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
 417 these taxa interact in the aggregated web $L_{1,2}$ is obtained by:

$$P(L_{1,2,i \rightarrow j} | M_{i \rightarrow j}) = 1 - (1 - P(L_{1,i \rightarrow j} | M_{i \rightarrow j})) \times (1 - P(L_{2,i \rightarrow j} | M_{i \rightarrow j})), \quad (9)$$

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

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

426 **Spatial and temporal scaling of interactions**

427 The investigation of network-area relationships and interaction accumulation curves is an important area of
428 research in network ecology. First, network-area relationships elucidate the scaling of network properties (such
429 as modularity and trophic chain lengths) with spatial scale (e.g., Wood *et al.* (2015), Galiana *et al.* (2018)). The
430 variations in network structure across spatial scales may stem from the scaling of species richness (species-area
431 relationships, SARs), the number of interactions (Brose *et al.* (2004)), and many other higher-level properties of
432 the system (e.g., environmental heterogeneity, Thompson & Townsend (2005)) with the sampled area.

433 Additionally, ecological processes occurring at distinct spatial scales, such as the spatial variability in local
434 community composition resulting from different sequences of extinction and colonization events, can also
435 contribute to this variation (Galiana *et al.* (2018)). Next, interaction accumulation curves describe the scaling of
436 the number of observed interactions with sampling effort (Jordano (2016)). Sampling effort, which may
437 correspond to the duration of the sampling period used to construct the network, can impact connectance
438 (Bersier *et al.* (1999)) and various measures of network structure (Banašek-Richter *et al.* (2004), McLeod *et al.*
439 (2021)). Apart from sampling effort, the temporal scaling of interactions also elucidates how network structure
440 changes with the temporal resolution of the network (Poisot *et al.* (2012)), acknowledging that distinct
441 interactions take place over time, ranging from short-term fluctuations of interactions to long-term trends. As
442 local webs of probabilistic interactions may explicitly account for the spatiotemporal variability of interactions,
443 they offer a distinct approach to investigating the scaling of network structure with space and time, in contrast to
444 webs of binary and quantitative interactions, by making the stochasticity of interactions the focal point of the
445 modeling process.

446 Local and metawebs exhibit distinct relationships with spatial and temporal scales. On one hand, metawebs of
447 probabilistic interactions, representing biological feasibility, feature regional interactions that do not scale with
448 space and time. This is because regional interactions depend solely on the biological capacity of two taxa to
449 interact, regardless of their co-occurrence and local environmental conditions. However, probabilities of
450 potential interactions may change (tending to become more definitive) upon updating previous estimates with
451 increased sampling effort, even though they do not vary in a specific direction with the spatial and temporal
452 extent (boundaries) of the network. The probability of two taxa potentially interacting should theoretically be
453 the same in all metawebs in which they are present, provided that the data and methods used for estimation are
454 consistent. For example, if a smaller metaweb M_1 is derived from a larger metaweb M_0 by selecting the subset
455 of taxa present in the region described by M_1 and retaining all their interactions, their probabilities of

456 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
457 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
458 larger web, even though pairwise probabilities remain identical.

459 On the other hand, local interactions scale both spatially and temporally, given that they have more
460 opportunities to be realized and observed in larger areas and longer durations. This is attributed to factors such
461 as a higher number of individuals, greater trait variations, and increased opportunities for encounters, as
462 highlighted by McLeod *et al.* (2020). For example, if a local web of probabilistic interactions L_1 with an area
463 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
464 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,
465 interaction probabilities could be higher in the smaller area, contingent upon their environmental and biological
466 conditions. Likewise, interaction probabilities are expected to be lower in webs with shorter durations when
467 time intervals are nested. In fig. 2, we show how the expected number of local host-parasite interactions scales
468 with area, represented as an expanding latitudinal window, in comparison with regional interactions. Even
469 though we employed local probabilities of interactions equal to regional interactions for the purpose of
470 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
471 more rapidly than local interactions. This is because numerous regional interactions involve species that never
472 co-occur, and as a result, these interactions are not captured in any local web.

473 [Figure 2 about here.]

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

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

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

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

$$P(X_{i,l}, X_{j,l}) = P(X_{i,l}|X_{j,l})P(X_{j,l}) = P(X_{i,l})P(X_{j,l})\gamma. \quad (10)$$

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

$$X_{i,j,l} \sim \text{Bernoulli}(P(X_{i,l}, X_{j,l})). \quad (11)$$

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

$$P(L_{i \rightarrow j}|X_{i,j,l} = 1) = 1 - e^{-\lambda_l t_0}, \quad (12)$$

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

510 The occurrence of an interaction between i and j can be modeled as a Bernoulli trial with a probability of
 511 $P(L_{i \rightarrow j})$. Consequently, a Bayesian inference model can be built based on the preceding equations to estimate
 512 the value of the λ_l and γ parameters and generate novel interaction data:

$$L_{i \rightarrow j} \sim \text{Bernoulli}(P(L_{i \rightarrow j})) \quad (13)$$

$$P(L_{i \rightarrow j}) = P(X_{i,l})P(X_{j,l})\gamma(1 - e^{-\lambda_l t_0}) \quad (14)$$

$$\gamma \sim \text{Gamma}(2, 0.5) \quad (15)$$

$$\lambda_l \sim \text{Exponential}(2) \quad (16)$$

513 In fig. 3, we show the variation in the probability of interaction under different parameter values. In the right
 514 panel, we notice that, irrespective of the interaction rate λ_l , the probability of interaction converges toward an
 515 asymptote determined by the probability of co-occurrence $P(X_{i,j,l})$ (eq. 10). This model can be customized in
 516 different ways, such as by linking λ_l with specific environmental variables or explicitly incorporating
 517 observation errors (i.e., the probabilities of false negatives and false positives).

518 [Figure 3 about here.]

519 Taxonomic scaling of interactions

520 Probabilistic interaction networks offer a versatile approach to tackle a broad array of ecological questions,
 521 depending on their level of organization. For instance, the assemblage of interactions across ecological scales
 522 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:

$$P(G_{g_1 \rightarrow g_2} = 1) = 1 - \prod_{i=1}^{n_1} \prod_{j=1}^{n_2} (1 - P(S_{g_{1i} \rightarrow g_{2j}} = 1)), \quad (17)$$

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

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

Sampling for binary interaction webs

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

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

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

595 In fig. 4, we compare the average connectance of binary interaction networks resulting from these two sampling
596 techniques, where regional and local interactions are drawn from our host-parasite networks of probabilistic
597 interactions, generating a number of binary interaction web realizations for each site in the dataset. These two
598 sampling approaches yield different outcomes, particularly for lower values of $P(L_{i \rightarrow j} | M_{i \rightarrow j})$, which represent
599 instances where regional interactions do not consistently manifest locally. Small discrepancies are also apparent
600 between these techniques when we equate the probability of local interaction to the probability of regional
601 interaction (i.e., when using $P(L_{i \rightarrow j} | M_{i \rightarrow j}) = 1.0$ in eq. 8), especially when the number of samples of binary
602 interaction networks for each location is low. As anticipated, we observe that sampling binary interactions from
603 the metaweb tends to overestimate connectance on average compared to sampling them from local webs.
604 Furthermore, we observe an increase in the variability of connectance when employing a single sample,
605 representing what we consider as a more tangible process leading to the realization of local and regional
606 interactions in nature.

607

[Figure 4 about here.]

608 The choice of a sampling approach can influence the selection of grid cell size when delineating local
609 communities within a broader region of interest. In the first approach, pairwise interactions remain constant
610 irrespective of cell size since they are sampled only once from the metaweb. However, in the second approach,
611 local interaction probabilities are contingent on the network area. For instance, consider the local webs L_1 and
612 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
613 independent, the probability of interaction between taxa i and j in L_0 is given by:

$$P(L_{0,i \rightarrow j}) = 1 - (1 - P(L_{1,i \rightarrow j}) \times P(L_{2,i \rightarrow j})). \quad (18)$$

614 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
615 sampling binary interactions from local webs, it is crucial to sample at the same spatial scale for which
616 probabilities were estimated. Otherwise, interaction probabilities must be adjusted to align with the intended
617 cell size, preventing systematic biases in predictions.

618 Prediction of local webs from metawebs

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

630 Building local webs of probabilistic interactions from a metaweb of probabilistic interactions involves a
631 reduction in the value of pairwise interaction probabilities. This decrease is attributed to the prerequisite that
632 two taxa must initially possess the capacity to interact before engaging in local interactions (eq. 8). Therefore,
633 inferring local webs from their metaweb while maintaining identical interaction probability values would

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

$$P(L_{i \rightarrow j} | X_{i,l}, X_{j,l}, N_{i,l}, N_{j,l}, T_{i,l}, T_{j,l}, E_l, A, t, f(L)) \leq P(M_{i \rightarrow j} | T_i, T_j). \quad (19)$$

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

$$\int_{E_l} \int_A \int_t P(L_{i \rightarrow j} | E_l, A, t) dt dA dE_l \leq P(M_{i \rightarrow j} | T_i, T_j). \quad (20)$$

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

649 Conclusion

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

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

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

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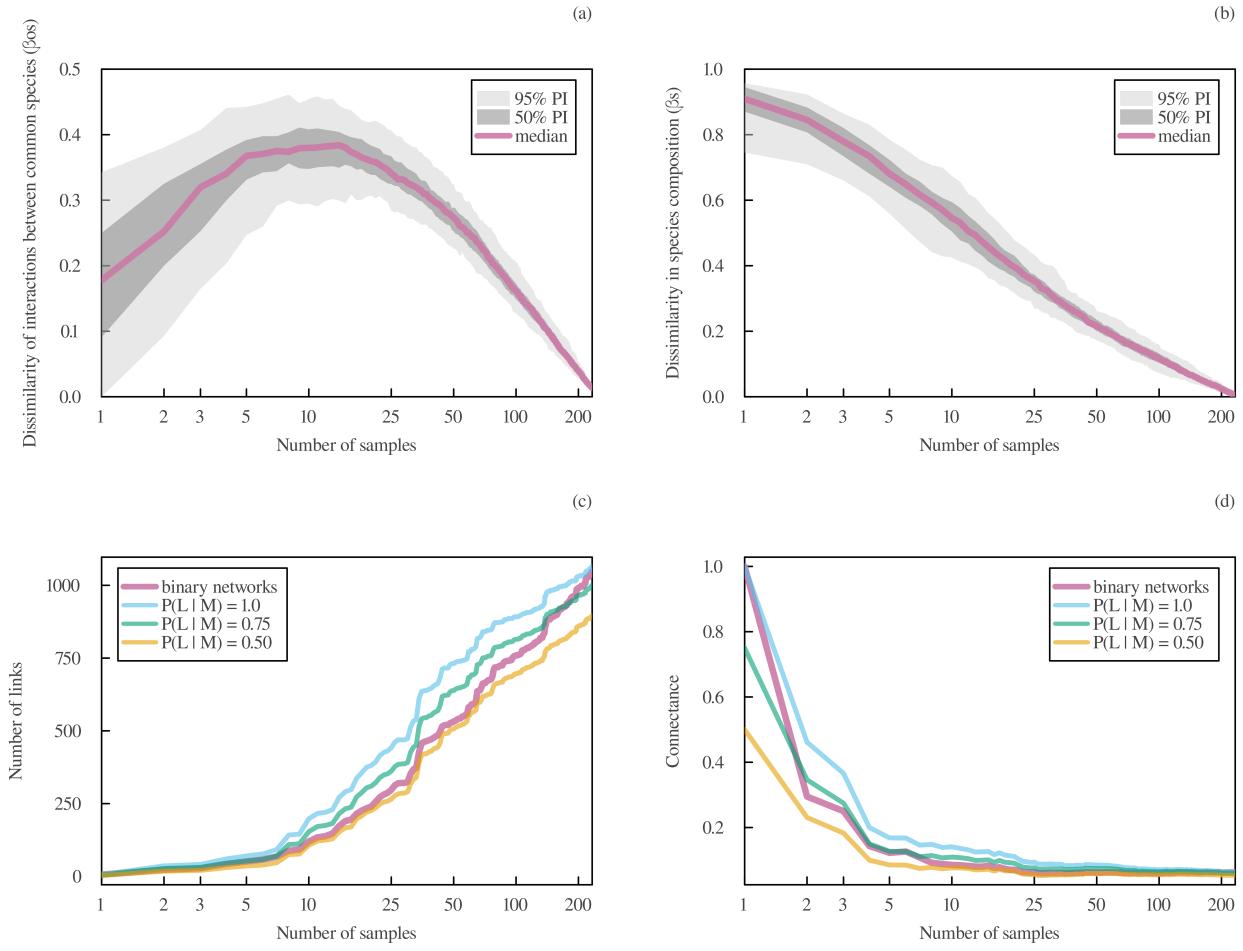


Figure 1: Network accumulation curves. (a) Dissimilarity of interactions between common species and (b) dissimilarity in species composition between aggregated local webs and the metaweb of binary host-parasite interactions. Aggregated local webs were obtained by sequentially and randomly selecting a 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. 9).

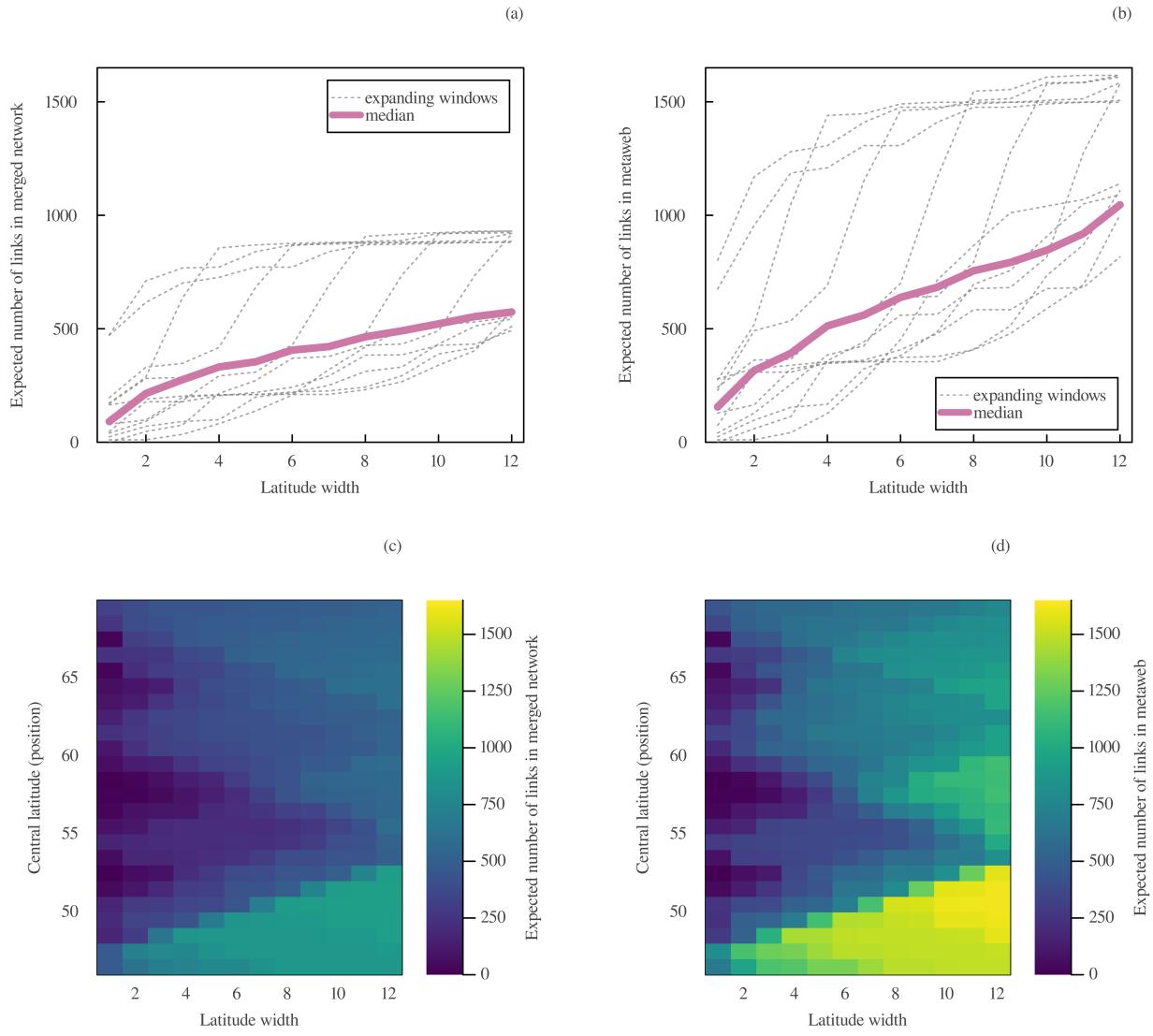


Figure 2: Spatial scaling of interactions. Expected number of host-parasite interactions in a network aggregating all (a) local and (b) regional probabilistic interactions within a latitudinal window of a given length. Every dashed curve corresponds to a different expanding window characterized by a 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. 9.

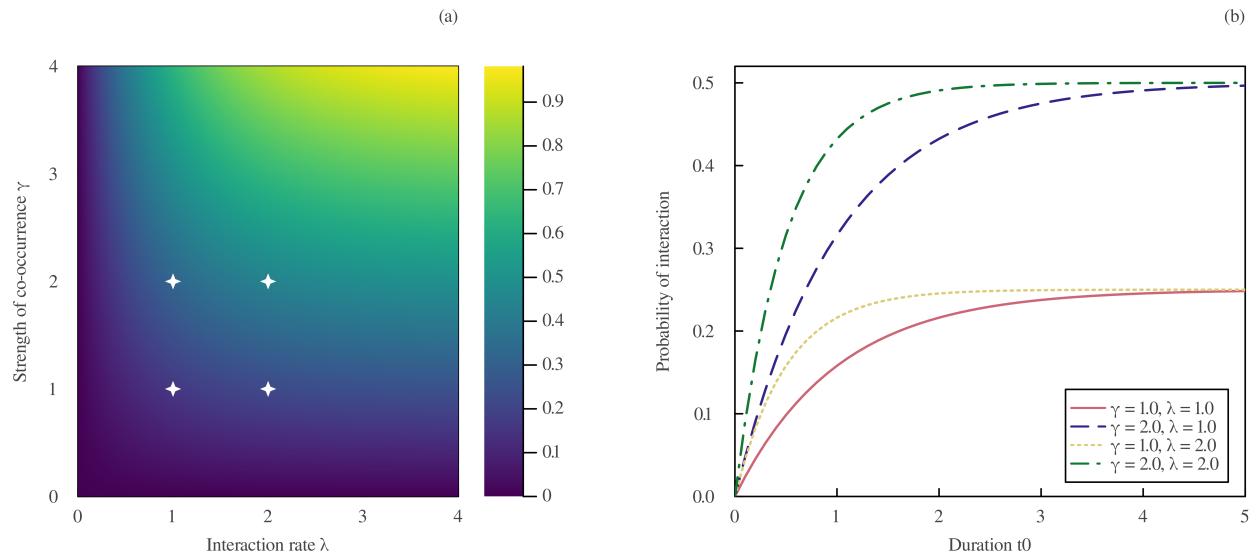


Figure 3: **Parameters of the spatiotemporally explicit model of interactions.** (a) Probability of local interaction given by the process model (eq. 14) under different values of λ_l and γ , with $t_0 = 1$. The parameter values used in the right panel are denoted by the white stars. (b) Scaling of the probability of interaction with the duration parameter t_0 in eq. 14, 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.

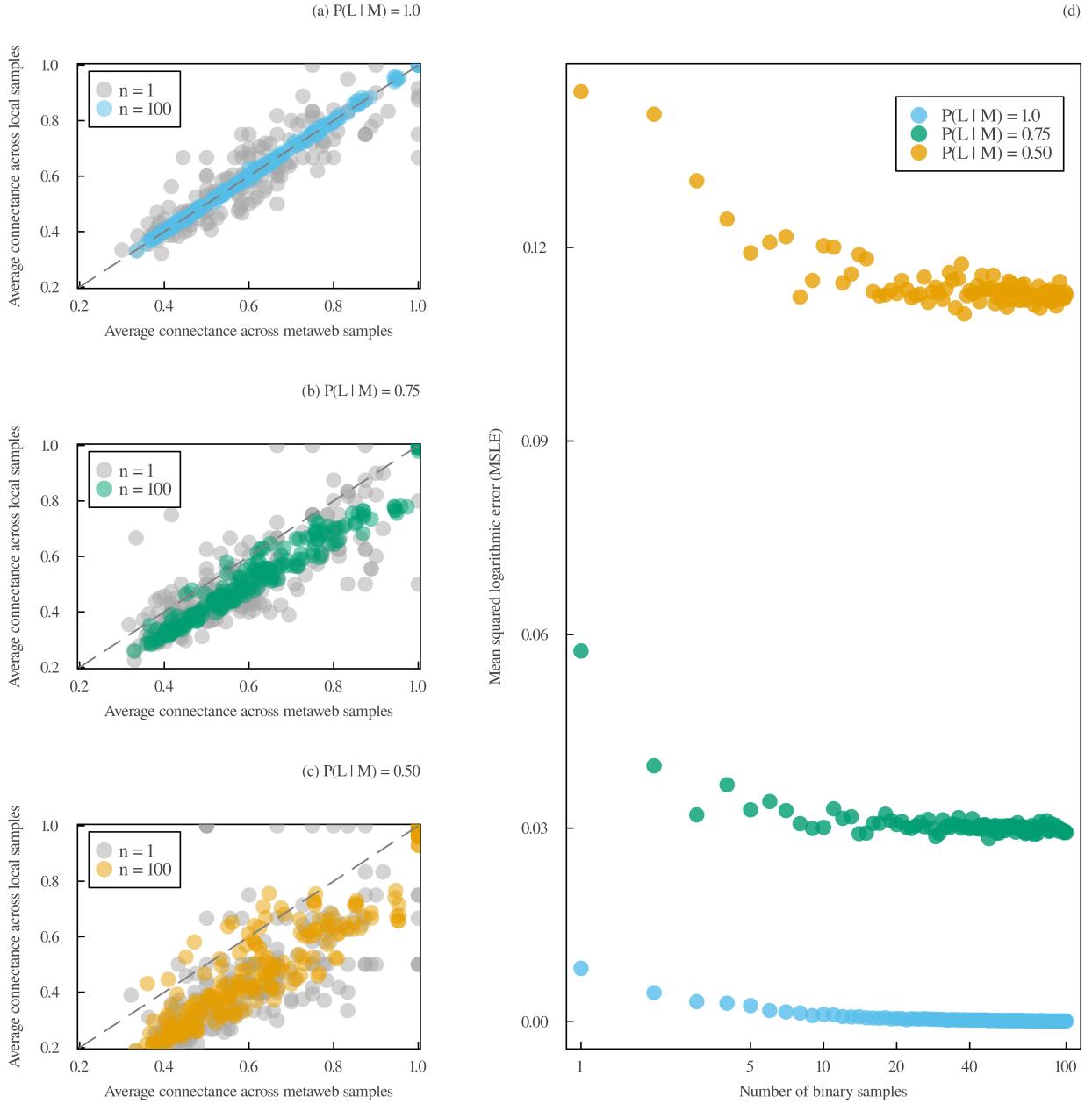


Figure 4: Connectance of sampled binary interaction webs. Comparison between the average connectance of binary interaction network samples obtained from the local and metawebs of probabilistic interactions. Each dot corresponds to a different site. The local probability of interaction between potentially 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.