

Deciphering probabilistic species interaction networks

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Representing species interactions probabilistically (how likely are they to occur?) as opposed to deterministically (are they occurring?) expresses uncertainties in our knowledge of interactions. The sources of uncertainty captured by interaction probabilities depend on the method used to evaluate them: uncertainty of predictive models, subjective assessment of experts, or empirical measurement of interaction spatiotemporal variability. However, guidelines for the estimation and documentation of probabilistic interaction data are still lacking. This is concerning because our understanding and analysis of interaction probabilities depend on their sometimes elusive definition and uncertainty sources. We review how probabilistic interactions are defined at different spatial scales, from local interactions to regional networks (metawebs), with a strong emphasis on host-parasite and trophic (predatory and herbivory) 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 host-parasite interactions in Europe, we illustrate how these two network representations differ in their statistical properties, specifically: how local networks and metawebs differ in their spatial and temporal scaling of probabilistic interactions, but not in their taxonomic scaling. We present two approaches to inferring binary interactions from probabilistic ones that account for these differences and show that systematic biases arise when directly inferring local networks from metawebs. Our results underscore the importance of more rigorous descriptions of probabilistic species interaction networks that specify their type of interaction (local or regional) and uncertainty sources.

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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 (Abrego *et al.* 2021; Gonzalez & Londoño 2022;
4 Hortal *et al.* 2015). However, cataloging species, populations and, in particular, ecological interactions (e.g.,
5 predation, parasitism, and pollination) is a substantial challenge (Pascual *et al.* 2006; Polis 1991). There are
6 methodological and biological constraints that hinder our ability to document species interactions, inevitably
7 leading to uncertainty in our knowledge of interactions. For example, the spatial and temporal uncoupling of
8 species (e.g., nocturnal and diurnal species coexisting in the same space with different daily activity timings,
9 Jordano 1987) and the large number of rare and cryptic interactions in a community, contribute to these
10 knowledge gaps (Jordano 2016).

11 More generally, several conditions must be satisfied for an interaction to be observed locally. First, both species
12 must have overlapping geographic ranges, i.e. they must co-occur within the region of interest (Cazelles *et al.*
13 2016; Morales-Castilla *et al.* 2015). Second, they must have some probability of meeting (Poisot *et al.* 2015).
14 Probabilities of interspecific encounters are typically low, especially for rare species with low abundances.
15 While species' absolute abundances may impact interaction frequencies (Vázquez *et al.* 2007), encounter
16 probabilities are determined by their relative abundances (Canard *et al.* 2012). The probability that species
17 meet also depends on their biology, such as their phenology (Olesen *et al.* 2010; Singer & McBride 2012) and
18 discoverability (Broom & Ruxton 2005). Finally, when species do come into contact, an interaction occurs only
19 if their traits are locally compatible (Poisot *et al.* 2015), including their phenotypes (Bolnick *et al.* 2011; Gravel
20 *et al.* 2013; Stouffer *et al.* 2011) and behavior (Choh *et al.* 2012; Pulliam 1974). Interactions may also be
21 influenced by a third species (e.g., a more profitable prey species, Golubski & Abrams 2011; Sanders & van
22 Veen 2012). Documenting the location and timing of interactions becomes even more difficult when accounting
23 for the spatiotemporal variability of ecological interactions (Poisot *et al.* 2012, 2015). Environmental factors,
24 such as temperature (Angilletta *et al.* 2004), drought (Woodward *et al.* 2012), climate change (Araujo *et al.*
25 2011; Gilman *et al.* 2010; Woodward *et al.* 2010), and habitat modifications (Tylianakis *et al.* 2007), contribute
26 to this spatiotemporal variability by impacting species abundance and traits. Even under favorable
27 circumstances, there remains a possibility that the interaction does not occur locally, either due to the intricate
28 nature of the system or simply by chance. If it does occur, it might go undetected, particularly if it happens
29 infrequently. In this context, it is unsurprising that our knowledge of ecological interactions remains limited

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

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

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

33 variability of species interactions has led ecologists to expand their representation of ecological networks to

34 include a probabilistic view of interactions (Dallas *et al.* 2017; Fu *et al.* 2021; Poisot *et al.* 2016). This allows

35 filling in the Eltonian shortfall (Hortal *et al.* 2015) by modeling the probability of occurrence of interactions

36 (e.g., Gravel *et al.* 2019), which can be an important tool for directing efforts and taking action (Carlson *et al.*

37 2021), especially in places where access and resources for research are scarce. The probabilistic representation

38 of interactions has been applied to direct interactions, which are conceptually and mathematically analogous

39 regardless of their biological type (e.g., predation and pollination). This is in contrast with indirect interactions

40 (e.g., interspecific competition), which arise from distinct ecological processes and are often not directly

41 observable (Kéfi *et al.* 2015, 2016).

42 Representing direct interactions probabilistically can capture the spatiotemporal variability of the

43 aforementioned ecological processes and the uncertainty in our knowledge of interactions. Networks of

44 probabilistic interactions, within a Bayesian perspective, express our degree of belief (or confidence) regarding

45 the occurrence or observation of interactions. In contrast, interactions are simply regarded as either occurring or

46 not in networks of deterministic binary interactions. Based on the scale at which they are estimated, interaction

47 probabilities may reflect our level of confidence in whether interactions will be observed, realized locally, or

48 biologically feasible. As an illustration, we could outline a situation in which there is a 50% certainty that an

49 interaction occurs 50% of the time. Our level of confidence should be more definitive (approaching either 0 or

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

51 uncertainty of our knowledge of interactions (but not necessarily the estimation of their variability). In the

52 broadest sense, binary interactions are also a type of probabilistic interaction, in which the numerical value of

53 an interaction is restrained to 0 (non-occurring) or 1 (occurring). In networks of probabilistic interactions, only

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

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

56 (Gonzalez-Varo & Traveset 2016).

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

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

59 network structure (i.e., community-level properties driving the functioning, dynamics, and resilience of

60 ecosystems, McCann 2007; McCann 2011; Proulx *et al.* 2005; Rooney & McCann 2012) remains to be
61 elucidated. The application and development of computational methods in network ecology, often based on a
62 probabilistic representation of interactions, can alleviate (and guide) the sampling efforts required to document
63 species interactions (Strydom *et al.* 2021). For example, statistical models can be used to estimate the
64 uncertainty of pairwise interactions (Cirtwill *et al.* 2019) and the probability of missing (false negatives) and
65 spurious (false positives) interactions (Guimerà & Sales-Pardo 2009). Statistical models can generate
66 predictions of ecological networks without prior knowledge of pairwise interactions. They may do so using
67 body size (Gravel *et al.* 2013; Petchey *et al.* 2008), phylogeny (Elmasri *et al.* 2020; Strydom *et al.* 2022), or a
68 combination of niche and neutral processes (Bartomeus *et al.* 2016; Pomeranz *et al.* 2019) for inference.
69 Topological null models, which generate networks of probabilistic interactions by preserving chosen
70 characteristics of the adjacency matrix of binary interactions while intentionally omitting others (Bascompte *et*
71 *al.* 2003; Fortuna & Bascompte 2006), are examples of common probabilistic interaction models. Null models
72 can be used to produce underlying distributions of network measures for null hypothesis significance testing.
73 Many measures have been developed to describe the structure (Poisot *et al.* 2016) and diversity (Godsoe *et al.*
74 2022; Ohlmann *et al.* 2019) of probabilistic interaction networks. These models and measures support the use
75 of this approach for the study of a wide range of ecological questions, from making better predictions of species
76 distribution (Cazelles *et al.* 2016) to forecasting the impact of climate change on ecological networks (Gilman
77 *et al.* 2010).
78 Yet, a precise definition of probabilistic interactions appears to be lacking, making the estimation and use of
79 these data more difficult. In this manuscript, we aim to take a step back by outlining different ways in which
80 probabilistic interactions are defined and used in network ecology. We distinguish two broad categories of
81 probabilistic interaction networks that necessitate distinct approaches: local networks describing probabilities
82 of realized interactions, and regional networks (metawebs) describing probabilities of potential interactions. We
83 highlight the distinctions in the ecological meaning of these two representations and examine some of their
84 properties and relationships (particularly with space, time, and between each other) through empirical case
85 studies. Moreover, the lack of clear guidelines on the use of probabilistic interaction data is worrisome, as it
86 affects both data producers and re-users who generate and manipulate these numbers. This is concerning
87 because sampling strategies and decisions regarding network construction can affect our understanding of
88 network properties (Brimacombe *et al.* 2023). There is currently no reporting standard that could guide the
89 documentation of all types of probabilistic interactions (although see e.g., Salim *et al.* 2022 who discuss data

90 standards for deterministic mutualistic networks). Well-defined reporting standards for probabilistic interactions
91 would support more adequate manipulation and integration of interaction data from different sources and guard
92 against possible misinterpretations arising from ambiguous definitions of probabilistic interaction networks.
93 This documentation should outline the nature (i.e., local or regional) and type (e.g., predatory or pollination) of
94 the interactions, provide information regarding the taxonomic level, identities, and characteristics (e.g., life
95 stages) of the individuals involved in an interaction, present the mathematical formulation of probabilities,
96 including clearly identified conditional variables (e.g., spatial and temporal scales), and describe the methods
97 and contexts (e.g., location, time, environmental conditions) in which interactions were estimated. Inadequately
98 documented probabilistic interaction data should be used with caution when analyzing ecological networks.
99 The broad principles underlying our findings remain relevant and applicable across diverse ecological contexts.

100 **Probabilistic representations of interactions**

101 Consider a scenario where an avian predator has just established itself in a northern habitat home to a small
102 rodent. Suppose these species have never co-occurred before, and as a result, their interaction has not been
103 previously observed. What is the probability that the rodent is part of the diet of the avian predator, or put
104 differently, what is the probability that they interact? Answering this question requires some clarification, as
105 there are multiple ways to interpret and calculate interaction probabilities. We could calculate the probability
106 that the traits of these species match, i.e. that the avian predator possesses the biological attributes to capture
107 and consume the rodent. We could also calculate the probability that their traits support an interaction under the
108 typical environmental conditions of the new habitat. For example, because avian predators hunt by sight,
109 predation could be possible in the absence of snow but highly improbable when snow is present, as rodents may
110 use it as a shelter to hide from predators. Finally, we could calculate the probability that the avian predator will
111 consume the rodent at *that* particular location, for which the spatial and temporal boundaries need to be
112 specified. The estimation of interaction probabilities, whether through predictive models or prior distributions,
113 hinges on our understanding of these probabilities and the specific ecological processes we aim to capture.

114 An important aspect to consider when using probabilities of interactions is knowing if they describe potential or
115 realized interactions, as these two types of interactions have distinct conceptual underpinnings and sources of
116 uncertainty. A potential (regional) interaction is defined as the biological capacity of two taxa to interact (i.e.,
117 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 taxa and over infinite time, the probability of local interaction is equivalent to the probability of regional (potential) interaction. We use the terms *metaweb* (Dunne 2006) to designate regional networks of potential interactions and *local networks* (Poisot *et al.* 2012) for those of realized interactions. Metawebs are the network analogs of the species pool, where local networks originate from a subset of both species (nodes) and interactions (edges) of the regional metaweb (Saravia *et al.* 2022). Without clear documentation, it can be challenging to know if published probabilistic interaction networks describe local or regional interactions (Tbl. 1 provides examples of studies employing both types of probabilistic interaction networks), or if so-called probabilities are in reality a form of interaction score. When probabilistic regional interactions are used and interpreted incorrectly as local interactions (and conversely), this may generate misleading findings during data analysis. We believe that a better understanding of probabilistic local and regional interactions would prevent interpretation errors (e.g., when studying network-area relationships with metawebs or local networks) and facilitate a more adequate use of interaction data. In the following sections, we delve into these distinctions as we scale up from pairwise interactions to higher-level representations of ecological networks, i.e. local networks and metawebs.

Pairwise interactions: the building blocks of ecological networks

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

Ecologists have traditionally represented interactions (edges) as binary objects that were considered realized after observing at least one individual from group i interact with at least another individual from group j . In an adjacency matrix B of binary interactions, the presence or absence of an interaction $B_{i \rightarrow j}$ between two taxa can be viewed as the result of a Bernoulli trial $B_{i \rightarrow j} \sim \text{Bernoulli}(P(B_{i \rightarrow j}))$, with $P(B_{i \rightarrow j})$ being the probability of interaction. This interaction probability characterizes our limited ecological knowledge and/or the intrinsic spatiotemporal variability of interactions. It may be estimated through predictive models (e.g., those based on

146 biological traits and species abundances) or expert (prior) knowledge about the interaction. In networks of
147 probabilistic interactions, the edge values $P(B_{i \rightarrow j})$ are probabilistic events whose only two possible outcomes
148 are the presence ($B_{i \rightarrow j} = 1$) or absence ($B_{i \rightarrow j} = 0$) of an interaction between each pair of nodes. Depending on
149 the type of probabilistic interaction network (local or metaweb), the mathematical formulation and interpretation
150 of stochastic parameters like $P(B_{i \rightarrow j})$ can be linked to environmental and biological factors such as species
151 abundance, traits, area, and time, for example using logistic regression with continuous explanatory variables.

152 Predicting the number of local networks in which the interaction between two given taxa occurs can be achieved
153 by using a Binomial distribution, assuming a constant interaction probability and independence between
154 networks (trials). When considering uncertainties around the estimation of $P(B_{i \rightarrow j})$ or its spatiotemporal
155 variability, a Beta distribution may be used to represent the relative likelihood of different probability values.
156 For example, when calculating the probability of interaction between two taxa based on their local abundances,
157 any spatiotemporal fluctuations in their abundances would introduce variability in the interaction probability at
158 the local scale. If we take into account the stochasticity of the interaction probability, a Beta-Binomial
159 distribution can be used to predict the number of networks in which the interaction occurs. Empirically
160 observing an interaction between two taxa at a given location and time provides important information that can
161 be used to update previous estimates of $P(B_{i \rightarrow j})$, informing us on the biological capacity of both taxa to interact
162 and the environmental conditions that enabled them to interact locally.

163 Even though binary interaction networks constitute a highly valuable source of ecological information (Pascual
164 *et al.* 2006), they overlook interaction strengths. Represented in a quantitative adjacency matrix W , interaction
165 strengths better describe the energy flows, demographic impacts or frequencies of interactions between nodes
166 (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
167 measure. For example, they may represent local interaction rates between pairs of taxa (e.g., the flower-visiting
168 rates of pollinators in a mutualistic network, Herrera 1989). When interaction strengths characterize predation
169 pressure on prey, they can serve as parameters in a Lotka-Volterra model (e.g., Emmerson & Raffaelli 2004).
170 The extra amount of ecological information in quantitative networks typically comes at a cost of greater
171 sampling effort and data volume in predictive models (Strydom *et al.* 2021), which can lead to relatively high
172 levels of uncertainties when inferring quantitative networks with limited data.

173 As for binary interaction networks, the uncertainty and variability of interaction strengths can be represented
174 probabilistically. However, the need to estimate the probability distribution of interaction strengths makes the
175 inference of probabilities more challenging in quantitative networks compared to binary interaction networks.

176 Interaction strengths can follow many probability distributions depending on the method. For instance, they can
177 follow a Poisson distribution $W_{i \rightarrow j} \sim \text{Poisson}(\lambda_{i \rightarrow j})$ when predicting the number 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 networks due to their typically high sparseness (Jordano 2016). Because of
183 the methodological difficulties typically encountered when building deterministic quantitative networks (which
184 are only partially mitigated by models such as Ecopath, Plagányi & Butterworth 2004), binary interaction
185 networks, which are easier to sample (Jordano 2016) and predict (Strydom *et al.* 2021), have been more
186 frequently studied and modeled. Moreover, most published probabilistic interaction networks and methods
187 describe 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 networks first. For these reasons, our primary focus is
190 interpreting and using interaction probabilities in Bernoulli distributions, in both local networks and metawebs.

191 Local networks: communities interacting in space and time

192 Local networks of probabilistic interactions describe how likely taxa are to interact at a given location and time
193 period. Local interactions are contingent upon the environmental conditions of the community and the matching
194 of taxa biological traits. In local networks, edges commonly represent our degree of belief that two taxa interact
195 in nature, but can also represent the probability of empirically *observing* this interaction (Catchen *et al.* 2023).
196 We define space as the collection of geographic coordinates (x, y, z) , with (x, y) representing longitude and
197 latitude coordinates, and z denoting either altitudes or depths. These point coordinates delineate the spatial
198 boundaries of the system, which may be portrayed as a polyhedron. Ecological interactions may exhibit
199 variations along latitudinal and altitudinal gradients, as evidenced by changes in hummingbird-plant
200 interactions (Weinstein & Graham 2017a, b) and mosquito biting rates (e.g., Kulkarni *et al.* 2006) at different
201 elevations. In contrast, time is defined as the specific time period within which interactions were either observed
202 or predicted. Even though space and time are continuous variables that should yield probability *densities* of
203 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 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. 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 network $L_{x,y,z,t}$ (spatial and temporal subscripts hereafter omitted or replaced by the shorter subscript k 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 $X_{i,j,k}$, which is usually a Boolean describing if the geographic distributions of both taxa overlap within the study area. As illustrated in Box 1, co-occurrence may be modeled probabilistically, in which case it may conform to a Bernoulli distribution $X_{i,j,k} \sim \text{Bernoulli}(P(X_{i,k}, X_{j,k}))$, where $X_{i,k}$ and $X_{j,k}$ are the local occurrences of both taxa. The probability of co-occurrence $P(X_{i,k}, X_{j,k})$ 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., $P(L_{i \rightarrow j}|X_{i,j,k} = 0) = 0$), the probability of local interaction can be obtained by multiplying the probability of interaction given co-occurrence with the probability of co-occurrence:

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

Other important factors that can impact interaction probabilities at the local scale are taxa local abundances $N_{i,k}$ and $N_{j,k}$, which affect encounter probabilities (Canard *et al.* 2012), and local traits distributions $T_{i,k}$ and $T_{j,k}$ (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 (Kéfi *et al.* 2012; Pilosof *et al.* 2017), as described above. Here, we use the variable E_k to describe the local environmental context in which interaction probabilities were estimated. For example, in a mesocosm experiment estimating interaction probabilities between predators and prey with and without shelters, E_k would

231 represent the presence or absence of these shelters. Like co-occurrence, E_k can also be modeled
232 probabilistically when the stochasticity or uncertainty of environmental factors is considered. E_k represents all
233 environmental variables that were taken into consideration when measuring interaction probabilities; it is a
234 subset of all environmental factors acting on ecological interactions. Finally, local interaction probabilities may
235 be conditioned on higher-level properties of the network, which we denote by $f(L)$. Many topological null
236 models (i.e., statistical models that randomize interactions by retaining certain properties of the network while
237 excluding others) provide interaction probabilities from selected measures of network structure, such as
238 connectance (Fortuna & Bascompte 2006) and the degree distribution (Bascompte *et al.* 2003).

239 Local interactions must be biologically feasible before occurring at a specific time and space. A local
240 probability of interaction $P(L_{i \rightarrow j})$ can be expressed as the product of the probability of local interaction given
241 that the two taxa can potentially interact $P(L_{i \rightarrow j}|M_{i \rightarrow j} = 1)$, which we sometimes denote as $P(L_{i \rightarrow j}|M_{i \rightarrow j})$ for the
242 sake of simplicity, with their probability of regional interaction $P(M_{i \rightarrow j})$:

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

243 Low values of $P(L_{i \rightarrow j}|M_{i \rightarrow j})$ indicate that feasible interactions rarely occur locally, intermediate values around
244 50% suggest considerable spatiotemporal variability, while high values indicate that regional interactions are
245 nearly always realized locally. The local probability of interaction between a given pair of taxa is always equal
246 to or below their probability of regional interaction.

247 The probability that two taxa i and j interact in a local network L can thus be conditioned on their co-occurrence
248 $X_{i,j,k}$ (or more explicitly on their occurrences $X_{i,k}$ and $X_{j,k}$), local abundances $N_{i,k}$ and $N_{j,k}$, local traits
249 distributions $T_{i,k}$ and $T_{j,k}$, local environmental conditions E_k , network area (or volume) A , time interval t ,
250 network properties $f(L)$ and biological (or regional) feasibility $P(M_{i \rightarrow j})$.

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

$$P(L_{i \rightarrow j} | X_{i,k}, X_{j,k}, N_{i,k}, N_{j,k}, T_{i,k}, T_{j,k}, E_k, A, t, f(L), M_{i \rightarrow j}) \quad (3)$$

258 The representation of the local context in which probabilities are estimated and the variables that should be
 259 taken into consideration depend on the study system, the objectives of the study, and the resources available to
 260 the researchers. In other words, these variables do not systematically need to be accounted for. For example,
 261 Gravel *et al.* (2019) analyzed local European trophic networks of willow-galling sawflies and their natural
 262 enemies, depicting binary interactions, all referenced in space and time, to infer probabilities of local
 263 interactions between co-occurring species. This was achieved by including temperature and precipitation as
 264 conditional variables in their models. In Box 2, we show the extent of variation among these local host-parasite
 265 networks. We do so by measuring their dissimilarity with the regional network (metaweb aggregating all local
 266 interactions), both in terms of species composition and interactions. We build local probabilistic networks
 267 following eq. 2, showing that insufficient local variation (high probability of local interaction among potentially
 268 interacting species) results in an overestimation in both the number of interactions and connectance (i.e., the
 269 proportion of all of the non-forbidden links that are realized).

270 When accounted for, conditional variables should be clearly described in the documentation of the data
 271 (Brimacombe *et al.* 2023), preferentially in mathematical terms to avoid any confusion in their interpretation
 272 and to limit manipulation errors during their re-use. For instance, ecologists should be explicit about their
 273 consideration of co-occurrence in their estimation of local interaction probabilities. Indeed, it is important to
 274 specify if probability values are conditional ($P(L_{i \rightarrow j} | X_{i,j,k} = 1)$) or not ($P(L_{i \rightarrow j})$) on co-occurrence, as this can
 275 change the interpretation of the data. In Tbl. 1, we present examples of studies that used these different
 276 formulations of probabilistic interactions and conditional variables. We have included the probability of
 277 empirically observing an interaction that is realized locally $P(O_{i \rightarrow j} | L_{i \rightarrow j})$ to underscore the distinction between
 278 local observations and actual realizations of interactions, even though the focus of this manuscript is not on the
 279 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 local network L of realized interactions and a metaweb M of potential interactions (representing the *biological* feasibility of interactions). Each expression emphasizes a different conditional variable, the ellipsis 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 networks. Note that we also included the expression for a local network O of observed interactions and a metaweb M^* of potential interactions (representing the *ecological* feasibility of interactions) as they were mentioned in the main text, even though they are not the focus of this manuscript.

Expression	Type	Outcome	Variability sources	Reference
$P(L_{i \rightarrow j} X_{i,k}, X_{j,k}, \dots)$	local	realization of the interaction	spatiotemporal	Gravel <i>et al.</i> (2019)
		given taxa co-occurrence	variability	
$P(L_{i \rightarrow j} N_{i,k}, N_{j,k}, \dots)$	local	realization of the interaction	neutral models	Canard <i>et al.</i> (2014)
		given taxa abundances		
$P(L_{i \rightarrow j} T_{i,k}, T_{j,k}, \dots)$	local	realization of the interaction	trait matching	Gravel <i>et al.</i> (2016)
		given local traits	models	
$P(L_{i \rightarrow j} E_k, \dots)$	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	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	variability	
		biologically interact		
$P(O_{i \rightarrow j} L_{i \rightarrow j}, \dots)$	local	observation of the interaction	sampling model	Catchen <i>et al.</i> (2023)
		given that it is realized locally		

Expression	Type	Outcome	Variability 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

When using multiple models to estimate local interaction probabilities, rather than selecting a single model that best fits the data, model averaging may enhance our estimations. In this approach, the weighting is based on the likelihood of each model. Model weights represent the probability that each model is the most suitable for explaining the data, and may be measured using Akaike weights (Burnham & Anderson 2004; Wagenmakers & Farrell 2004). For instance, considering two models mod_1 and mod_2 with respective probabilities (or weights) $P(mod_1)$ and $P(mod_2)$, the average probability of interaction $P(L_{i \rightarrow j} | \dots)$ can be calculated as follows:

$$P(L_{i \rightarrow j} | \dots) = P(L_{i \rightarrow j} | mod_1, \dots) \times P(mod_1) + P(L_{i \rightarrow j} | mod_2, \dots) \times P(mod_2), \quad (4)$$

where the ellipsis serves as a placeholder for the conditional variables incorporated in these models.

Box 1: A spatiotemporally explicit model of interactions

Ecologists may resort to predictive models (e.g., generative Bayesian models) to reconstruct local networks across time and space (Strydom *et al.* 2021). Uncertainty in model parameters, model structure, and input data leads to probabilistic interactions. 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). This model is not designed for regional interactions, which do not vary spatially and temporally. Rather, it may prove valuable for predicting local interactions across time and space by generating new interaction data following parameter inference.

As indicated by Eq. 1, the probability that two taxa i and j interact at a specific location and time k may be

296 determined by the product of their probability of interaction given co-occurrence and their probability of
 297 co-occurrence. First, their co-occurrence probability can be calculated using their individual (marginal)
 298 occurrence probabilities $P(X_{i,k})$ and $P(X_{j,k})$. Given that taxa occurrences are not independent of each other, the
 299 joint probability of both taxa occurring together can be calculated by multiplying the probability of one taxon
 300 being present by the conditional probability of the other occurring when the first one is present. Alternatively,
 301 the joint occurrence probability can be obtained by multiplying the marginal probabilities by the strength of
 302 association γ between the occurrences of both taxa (Cazelles *et al.* 2016):

$$P(X_{i,k}, X_{j,k}) = P(X_{i,k}|X_{j,k})P(X_{j,k}) = P(X_{i,k})P(X_{j,k})\gamma. \quad (5)$$

303 When $\gamma > 1$, there is a positive association in the geographic distributions of both taxa, indicating that the
 304 presence of one taxon enhances the probability of occurrence of the other. Attractions may be the result of
 305 positive interactions (e.g., mutualism) or positive/negative interactions (e.g., antagonism between predators and
 306 prey, Cazelles *et al.* 2016). In empirical networks, $\gamma > 1$ holds for the majority of species pairs (Catchen *et al.*
 307 2023). In contrast, repulsions ($\gamma < 1$) may be caused e.g. by strong interspecific competition (Cazelles *et al.*
 308 2016). We model the co-occurrence $X_{i,j,k}$ of both taxa as the outcome of a Bernoulli trial

$$X_{i,j,k} \sim \text{Bernoulli}(P(X_{i,k}, X_{j,k})). \quad (6)$$

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

$$P(L_{i \rightarrow j}|X_{i,j,k} = 1) = 1 - e^{-\lambda_k t_0}, \quad (7)$$

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

318 The occurrence of an interaction between i and j can be modeled as a Bernoulli trial with a probability of
 319 $P(L_{i \rightarrow j})$. Consequently, a Bayesian inference model can be built based on the preceding equations to estimate
 320 the value of the λ_k and γ parameters and generate novel interaction data:

$$L_{i \rightarrow j} \sim \text{Bernoulli}(P(L_{i \rightarrow j})) \quad (8)$$

$$P(L_{i \rightarrow j}) = P(X_{i,k})P(X_{j,k})\gamma(1 - e^{-\lambda_k t_0}) \quad (9)$$

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

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

321 In Fig. 1, we show the variation in the probability of interaction under different parameter values. In the right
 322 panel, we notice that, irrespective of the interaction rate λ_k , the probability of interaction converges toward an
 323 asymptote determined by the probability of co-occurrence $P(X_{i,j,k})$ (Eq. 5). This model can be customized in
 324 different ways, such as by linking λ_k with specific environmental variables or explicitly incorporating
 325 observation errors (i.e., the probabilities of false negatives and false positives).

326 [Figure 1 about here.]

327 **Box 2: Dissimilarity of local host-parasite networks**

328 We use the collection of tripartite host-parasite networks of Kopelke *et al.* (2017), consisting of willows,
 329 willow-galling sawflies, and their natural enemies, sampled across Europe (233 local networks used). Given its
 330 replicated networks spanning large spatiotemporal scales, this dataset is well-suited for analyzing network
 331 variability, both in terms of species composition and interactions. Further details regarding data manipulation
 332 and network construction can be found in the supplementary material.

333 In Fig. 2a-b, we show how the dissimilarity between the metaweb of binary interactions and aggregated local
 334 networks varies with the number of sampled local networks. To do so, we randomly selected one local network

335 of binary interactions and sequentially sampled additional networks while aggregating both their species and
 336 interactions. We compared the metaweb and the aggregated local networks using the dissimilarity in species
 337 composition (β_S , Fig. 2a) and the dissimilarity of interactions between common species (β_{OS} , Fig. 2b) indices
 338 (Poisot *et al.* 2012). We repeated this sampling process one hundred times and highlighted the median
 339 dissimilarity values across simulations, as well as the 50% and 95% percentile intervals. Both dissimilarity
 340 indices were calculated based on the number of items shared by the two networks (c_{LM}) and the number of
 341 items unique to the metaweb (u_M) and the aggregated local network (u_L). The β_S dissimilarity index uses
 342 species (nodes) as items being compared, while the β_{OS} index assesses dissimilarity based on interactions
 343 between shared species. Both indices were calculated following the β_W index of Whittaker (1960):

$$\beta_W = \frac{c_{LM} + u_L + u_M}{(2c_{LM} + u_L + u_M)/2} - 1. \quad (12)$$

344 [Figure 2 about here.]

345 Expectingly, local networks are highly dissimilar from the metaweb in terms of species composition, especially
 346 when only a limited number of sites has been sampled. This is because species in the metaweb form the
 347 regional species pool, and few species occur locally. Moreover, we observe a peak in the dissimilarity of
 348 interactions between common species at intermediate sampling levels. This suggests that species are collected
 349 faster than their interactions. With a limited number of sampled local networks, few regional interactions are
 350 observed locally. Adding more sites brings new species, but not always their interactions. Interactions are more
 351 comprehensively captured when the number of sampled sites is high. Quadratic relationships of network
 352 properties with sampling effort were also observed by McLeod *et al.* (2021).

353 Next, we investigate how the number of local interactions and connectance scale with the number of sampled
 354 (aggregated) local networks of probabilistic or binary interactions (Fig. 2c-d). We built probabilistic local
 355 networks following (**local_meta?**), and set $P(M_{i \rightarrow j})$ to 1 when the interaction was observed at least once, and to
 356 0 otherwise (i.e., no false positive or false negative in the metaweb). We used a constant value of $P(L_{i \rightarrow j}|M_{i \rightarrow j})$
 357 for all interactions.

358 When aggregating local networks of probabilistic interactions, the constancy of the probability of regional
 359 interaction across the entire study area means that any rise in the probability of local interaction is solely
 360 attributable to an increase in $P(L_{i \rightarrow j}|M_{i \rightarrow j})$. For example, let L_1 and L_2 be two local networks and $L_{1,2}$ the

361 aggregated network. 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 that two potentially interacting
362 taxa interact respectively in L_1 and L_2 , the probability $P(L_{1,2,i \rightarrow j}|M_{i \rightarrow j})$ that these taxa interact in the aggregated
363 network $L_{1,2}$ is obtained by:

$$P(L_{1,2,i \rightarrow j}|M_{i \rightarrow j}) = 1 - [1 - P(L_{1,i \rightarrow j}|M_{i \rightarrow j})] \times [1 - P(L_{2,i \rightarrow j}|M_{i \rightarrow j})], \quad (13)$$

364 assuming independence between the interaction of the two taxa in different networks. This equation represents
365 the probability that the interaction is realized in either (1) exclusively the local network L_1 , (2) exclusively the
366 local network L_2 or (3) both, given that the two taxa have the biological capacity to interact.

367 By comparing the scaling relationships observed in local networks of binary (empirical) and probabilistic
368 (modeled) interactions, Fig. 2c-d shows that high values of $P(L_{i \rightarrow j}|M_{i \rightarrow j})$ lead to systematic overestimations in
369 the number of interactions and connectance, especially when $P(L_{i \rightarrow j}|M_{i \rightarrow j}) = 1$ (corresponding to the scenario
370 where local probabilities of interactions are equivalent to the probabilities of regional interactions). This
371 suggests that high values of $P(L_{i \rightarrow j}|M_{i \rightarrow j})$ do not adequately capture the variability of local interactions.
372 However, these biases tend to diminish as the number of sampled networks increases, indicating that most
373 interactions are eventually captured when $P(L_{i \rightarrow j}|M_{i \rightarrow j})$ is high. In contrast, low values of $P(L_{i \rightarrow j}|M_{i \rightarrow j})$ lead to
374 missing interactions, resulting in an underestimation of the number of interactions and connectance. These
375 results underscore the importance of integrating the appropriate level of variability into our assessment of local
376 interaction probabilities.

377 Metawebs: regional catalogs of interactions

378 Metawebs (Dunne 2006) are networks of potential interactions over broad spatial, temporal, and taxonomic
379 scales (e.g., food webs at the continental scale). Potential interactions describe the biological capacity of taxa to
380 interact, which is typically assessed at the regional scale. Metawebs of probabilistic interactions are particularly
381 useful in situations where there is uncertainty in the ability of taxa to interact. This uncertainty frequently arises
382 due to insufficient interaction data, especially for taxa that have not yet been observed to co-occur, and
383 uncertainties in trait-matching models. As data accumulates, interactions in metawebs should tend towards
384 binarity, approaching probability values of 0 (repeatedly failing to observe an interaction between two
385 co-occurring taxa) and 1 (observing an interaction at least once). The extent of sampling effort thus influences

386 our evaluation of probabilities of potential interactions, as sampling over a larger area or for a longer duration
 387 enables us to capture a greater number of regional interactions (McLeod *et al.* 2021). However, in contrast with
 388 local networks of probabilistic interactions, which describe local interaction stochasticity, regional interactions
 389 are not evaluated for any particular local context. Although *neutrally* forbidden interactions (i.e., between rare
 390 species, Canard *et al.* 2012) tend to have low probability values in local networks, they may have higher
 391 probabilities in the metaweb (i.e., when species' biological traits can support an interaction if they were to
 392 encounter each other). Likewise, non-co-occurring taxa may have a non-zero probability of interaction in the
 393 metaweb.

394 Potential interactions describe what we refer to as the *biological feasibility* of interactions, which is based solely
 395 on the regional traits distributions T_i and T_j of taxa i and j , respectively. A probability of potential interaction in
 396 a metaweb M describing the biological feasibility of interactions may be expressed as:

$$P(M_{i \rightarrow j} | T_i, T_j), \quad (14)$$

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

$$P(M_{i \rightarrow j} | T_i, T_j) = 1 - P(F_{i \rightarrow j} | T_i, T_j). \quad (15)$$

406 For example, let i be a western diamondback rattlesnake (*Crotalus atrox*) and j , a wood lemming (*Myopus*
 407 *schisticolor*). These two taxa never co-occur, the rattlesnake being adapted to warm regions of North America
 408 (Castoe *et al.* 2007) and the lemming, to northern habitats of Eurasia (Fedorov *et al.* 2008). As we lack direct
 409 observations of an interaction between these two species, we have to rely on expert knowledge or trait-matching

410 models to estimate their probability of potential interaction. To accurately estimate this probability using
411 trait-matching models, it is crucial to ensure that the set of traits considered reflects the overall traits
412 distributions of both taxa. We could for instance consider their average body mass and the average phylogenetic
413 proximity of lemmings to rattlesnakes' prey. Doing so, we might find a high probability of potential interaction
414 based on these traits.

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

$$P(M_{i \rightarrow j}^* | T_i, T_j, E), \quad (16)$$

418 where E is the environmental conditions under which potential interactions are evaluated (Tbl. 1). Unlike E_k ,
419 these environmental conditions do not represent conditions occurring at specific locations. Ecological
420 feasibility represents the probability that two taxa interact if they were to encounter each other under given
421 environmental conditions, assuming they had infinite time to interact. Incorporating environmental conditions
422 into a trait-matching model may be important when there is high covariance between the environment and traits.
423 For instance, in our example involving rattlesnakes and lemmings, the probability of potential interaction
424 between these two species may be low in most environmental conditions. Western diamondback rattlesnakes
425 may be unactive under low temperatures (Kissner *et al.* 1997), whereas wood lemmings may have low tolerance
426 to high temperatures (Kausrud *et al.* 2008). The probability that an interaction is ecologically feasible is always
427 lower than the probability that it is biologically feasible, even across all environmental conditions:

$$\int_E P(M_{i \rightarrow j}^* | T_i, T_j, E) dE \leq P(M_{i \rightarrow j} | T_i, T_j). \quad (17)$$

428 This is because the biological feasibility of an interaction is a prerequisite for its ecological feasibility.
429 Biological feasibility is necessary but not sufficient for an interaction to be ecologically feasible. Our discussion
430 of metawebs will focus on the biological feasibility of interactions since most methods developed for inferring
431 probabilities of regional interactions do not explicitly take into account environmental conditions (e.g., Strydom
432 *et al.* 2022).
433 Starting from a selected set of taxa, which are usually distributed within a broad region of interest, metawebs

434 can be built using different data sources, including literature review (e.g., Maiorano *et al.* 2020), aggregated
435 interaction data (e.g., Gravel *et al.* 2019; Saravia *et al.* 2022), trait-matching models (e.g., Shaw *et al.* 2024;
436 Strydom *et al.* 2022), and expert knowledge. Every pair of taxa that have confidently been observed to interact
437 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
438 differs from local networks of probabilistic interactions, where interaction events may remain stochastic (i.e.,
439 $P(L_{i \rightarrow j}) < 1$) even after empirically observing interactions due to their spatiotemporal variability. Interactions
440 that were never observed typically have low probability values in local networks and vary from low to high
441 values in metawebs, contingent upon taxa traits distributions (reaching 0 for forbidden links).

442 When incorporating local network data to estimate probabilities of regional interactions, repeatedly failing to
443 observe an interaction between two co-occurring taxa (i.e., $P(O_{i \rightarrow j} = 0)$) should decrease the probability that
444 the interaction is biologically feasible. Using Bayes' theorem, the probability that the interaction is biologically
445 feasible given that it was never observed locally, $P(M_{i \rightarrow j} = 1|O_{i \rightarrow j} = 0, \dots)$, may be calculated as follows:

$$P(M_{i \rightarrow j} = 1|O_{i \rightarrow j} = 0, \dots) = \frac{P(O_{i \rightarrow j} = 0|M_{i \rightarrow j} = 1, \dots) \times P(M_{i \rightarrow j} = 1|\dots)}{P(O_{i \rightarrow j} = 0|\dots)}. \quad (18)$$

446 The reduction in the probability of regional interaction after considering that it was never observed locally (i.e.,
447 $P(M_{i \rightarrow j} = 1|O_{i \rightarrow j} = 0, \dots) < P(M_{i \rightarrow j} = 1|\dots)$) occurs because $P(O_{i \rightarrow j} = 0|M_{i \rightarrow j} = 1, \dots)$ must be lower than
448 $P(O_{i \rightarrow j} = 0, \dots)$, i.e. there is a higher chance of observing an interaction when we know it is biologically
449 feasible.

450 Many observations of interactions are false positives because of observation errors due to taxonomic
451 misidentifications and ecological misinterpretations (e.g., due to cryptic species and interactions, Pringle &
452 Hutchinson 2020). Likewise, forbidden interactions may be false negatives, e.g. if they have been evaluated
453 based on unrepresentative or incomplete traits distributions. Employing Bayesian models proves valuable when
454 estimating interaction probabilities in metawebs (e.g., Bartomeus *et al.* 2016; Cirtwill *et al.* 2019). This
455 improvement is achieved by updating prior information regarding the feasibility of interactions (e.g., experts'
456 prior assessments of interaction probabilities) with empirical data on interactions and traits.

457 Properties of probabilistic interaction networks

458 Local networks and metawebs of probabilistic interactions differ in their type of interactions (i.e., realized or
459 potential) and in the conditional variables upon which interaction values depend. These differences are
460 significant as they influence the characteristics of probabilistic interaction networks. Neglecting to consider
461 them may result in misleading results and interpretation errors when analyzing the properties of probabilistic
462 interaction networks, which could be particularly problematic when addressing crucial ecological questions
463 about networks. Here we compare the characteristics of local networks and metawebs through the presentation
464 of five applications of probabilistic interactions: (1) describing the dissimilarity between local networks and
465 metawebs of binary and probabilistic interactions (2) describing their spatial and temporal scaling, (3)
466 describing their taxonomic scaling, (4) sampling for binary interaction networks, and (5) reconstructing local
467 networks of probabilistic interactions from metawebs. All code and data to reproduce these analyses are
468 available at the Open Science Framework (TBD).

469 Application 2: Spatial and temporal scaling of interactions

470 Network-Area Relationships document the scaling of network properties (such as modularity and trophic chain
471 lengths) with spatial scale (e.g., Galiana *et al.* 2018; Wood *et al.* 2015). The variations in network structure
472 across spatial scales may stem from the scaling of species richness (species-area relationships, SARs), the
473 number of interactions (Brose *et al.* 2004), and many other higher-level properties of the system (e.g.,
474 environmental heterogeneity, Thompson & Townsend 2005) with the sampled area. Additionally, ecological
475 processes occurring at distinct spatial scales, such as the spatial variability in local community composition
476 resulting from different sequences of extinction and colonization events, can also contribute to this variation
477 (Galiana *et al.* 2018). Next, interaction accumulation curves describe the scaling of the number of observed
478 interactions with sampling effort (Jordano 2016). Sampling effort, which may correspond to the duration of the
479 sampling period used to construct the network, can impact connectance (Bersier *et al.* 1999) and various
480 measures of network structure (Banašek-Richter *et al.* 2004; McLeod *et al.* 2021). Apart from sampling effort,
481 the temporal scaling of interactions also elucidates how network structure changes with the temporal resolution
482 of the network, acknowledging that distinct interactions take place over time, ranging from short-term
483 fluctuations of interactions to long-term trends. As local networks of probabilistic interactions may explicitly
484 account for the spatiotemporal variability of interactions, they offer a distinct approach to investigating the

485 scaling of network structure with space and time, in contrast to networks of binary and quantitative interactions,
486 by making the stochasticity of interactions the focal point of the modeling process.

487 Local networks and metawebs exhibit distinct relationships with spatial and temporal scales. On one hand,
488 metawebs of probabilistic interactions, representing biological feasibility, feature regional interactions that do
489 not scale with space and time. This is because regional interactions depend solely on the biological capacity of
490 two taxa to interact, regardless of their co-occurrence and local environmental conditions. However,
491 probabilities of potential interactions may change (tending to become more definitive) upon updating previous
492 estimates with increased sampling effort, even though they do not vary in a specific direction with the spatial
493 and temporal extent (boundaries) of the network. The probability of two taxa potentially interacting should
494 theoretically be the same in all metawebs in which they are present, provided that the data and methods used for
495 estimation are consistent. For example, if a smaller metaweb M_1 is derived from a larger metaweb M_0 by
496 selecting the subset of taxa present in the region described by M_1 and retaining all their interactions, their
497 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
498 equal number of taxa in M_0 as compared to M_1 , the total number of interactions is expected to be higher or at
499 least equal in the larger network, even though pairwise probabilities remain identical.

500 On the other hand, local interactions scale both spatially and temporally, given that they have more opportunities
501 to be realized and observed in larger areas and longer durations. This is attributed to factors such as a higher
502 number of individuals, greater trait variations, and increased opportunities for encounters, as highlighted by
503 McLeod *et al.* (2020). For example, if a local network of probabilistic interactions L_1 with an area A_1 is derived
504 from a larger network L_0 with an area A_0 , and A_1 is entirely nested within A_0 , interaction probabilities should
505 be lower in the smaller network, 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,
506 interaction probabilities could be higher in the smaller area, contingent upon their environmental and biological
507 conditions. Likewise, interaction probabilities are expected to be lower in networks with shorter durations when
508 time intervals are nested. In Fig. 3, we show how the expected number of local host-parasite interactions scales
509 with area, represented as an expanding latitudinal window, in comparison with regional interactions. Even
510 though we employed local probabilities of interactions equal to regional interactions for the purpose of
511 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
512 more rapidly than local interactions. This is because numerous regional interactions involve species that never
513 co-occur, and as a result, these interactions are not captured in local networks.

515 **Application 3: Taxonomic scaling of interactions**

516 Probabilistic interaction networks offer a versatile approach to tackle a broad array of ecological questions,
 517 depending on their level of organization. For instance, the assemblage of interactions across ecological scales
 518 can be explored through species-based networks, while clade-based networks provide insights into
 519 macroevolutionary processes (e.g., Gomez *et al.* 2010). Given that our interpretation of the properties and
 520 dynamics of ecological networks depends on their taxonomic level (Guimarães 2020), investigating the
 521 taxonomic scaling of interactions (i.e., how interaction probabilities change with taxonomic level) emerges as a
 522 promising research avenue. Examining the same system at various taxonomic scales can yield meaningful and
 523 complementary ecological information, and, in our perspective, employing networks of probabilistic
 524 interactions is an effective approach for such analyses.

525 There are no inherent differences in the taxonomic scaling between local and metawebs, as only the nodes are
 526 defined taxonomically. In other words, the probability values of edges in both local (Eq. 3) and metawebs
 527 (Eq. 14) are not conditional on any taxonomic level. The taxonomic scale is tied to the definition of the event
 528 itself (i.e., the interaction between two taxa, defined at the desired taxonomical scale), not to the variables on
 529 which interaction probabilities are conditional. In both types of networks, transitioning to a broader level of
 530 organization (e.g., from a species-level network S to a genus-level network G) can be accomplished directly by
 531 using probabilities from finer scales. For example, in a network with n_1 species from genus g_1 and n_2 species
 532 from genus g_2 , one can compute the probability that at least one species from genus g_1 interacts with at least
 533 one species from genus g_2 (i.e., that there is a non-zero number of species-level interactions or, equivalently,
 534 that the genus-level interaction occurs) as follows:

$$P(G_{g_1 \rightarrow g_2} = 1) = 1 - \prod_{i=1}^{n_1} \prod_{j=1}^{n_2} (1 - P(S_{g_1 i \rightarrow g_2 j} = 1)), \quad (19)$$

535 where $g_{1,i}$ and $g_{2,j}$ are the species of the corresponding genus and assuming independence between
 536 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
 537 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
 538 species-based network following a similar approach, by using simulated interactions between individuals
 539 derived from a neutral model (i.e., a model that assumed ecological equivalence among individuals). In

540 contrast, a more sophisticated approach is necessary when transitioning from a broader to a finer level of
541 organization. This is because knowledge of an interaction between two genera does not guarantee that all
542 possible pairwise combinations of their species will also interact. One possible method is to build a finer-scale
543 network by generating probabilities of interactions through random sampling from a beta distribution,
544 parameterized by the broader-scale network.

545 Ideally, our biological interpretation of probabilistic interactions should remain consistent across a network
546 even if it incorporates heterogeneous levels of organization, such as a network whose nodes represent both
547 species and trophic species (groups of species sharing similar predators and prey). This is common in
548 ecological networks where taxonomic resolution is typically low (Hemprich-Bennett *et al.* 2021; Vázquez *et al.*
549 2022). Interaction probabilities at broader taxonomic scales should be based on probabilities of interactions
550 between individuals, for both local networks and metawebs. For instance, in local individual-based food webs,
551 the probability that two individuals interact reflects our degree of belief that one individual will consume the
552 other. Similarly, in local species-based food webs, the probability that two species interact represents our degree
553 of belief that at least one individual from the predator species consumes at least another individual from the
554 prey species. Furthermore, in local clade-based food webs, the probability that two clades interact represents
555 our degree of belief that at least two species from these clades interact with each other or, equivalently, that at
556 least two individuals from these clades interact with each other. Fundamentally, the taxonomic scaling of
557 interactions involves aggregating interactions between individuals into larger groups, which may exhibit varying
558 degrees of homogeneity based on the organisms and the study system. In that regard, taxonomic scaling is
559 analogous to the spatial and temporal scaling of interactions, as they all represent different ways to aggregate
560 individuals into broader groups (either spatially, temporally, or taxonomically).

561 Application 4: Sampling for binary interaction networks

562 The prediction of binary interactions through Bernoulli trials is an important application of probabilistic
563 interaction networks. This approach proves beneficial for analyzing the structural characteristics of probabilistic
564 interaction networks, particularly in the absence of specific analytical formulas for measures describing the
565 structure of the complete network (Poisot *et al.* 2016). By performing independent Bernoulli trials for each
566 interaction, a network of binary interactions may be generated. A probability distribution of network properties
567 can be obtained by measuring network structure across multiple randomly generated networks (Poisot *et al.*
568 2016). This method enables the representation of the variability of network structure, albeit with possible biases

569 when connectance is low (Chagnon 2015; Poisot & Gravel 2014). Employing this strategy to generate binary
570 interaction networks under a null model facilitates null hypothesis significance testing, wherein the observed
571 measure is compared against the simulated distribution (e.g., Bascompte *et al.* 2003). Additionally, the random
572 generation of binary interaction networks, from a probabilistic interaction network that accounts for the
573 spatiotemporal variability of interactions, may effectively capture network structure across space and time. This
574 facilitates the investigation of ecological hypotheses about interactions at broad spatial and temporal scales. Yet,
575 inferring network structure through sampling for binary interactions assumes independence among interactions,
576 which might not accurately represent reality. Covariation among interactions could exist even if we do not
577 explicitly condition interactions on others. For example, an interaction between two taxa could be more
578 probable when another interaction occurs. The consequences of this assumption of independence on the
579 prediction of network structure have yet to be empirically examined.

580 There are at least two distinct approaches to sample binary interaction networks from probabilistic interaction
581 networks across space, for example, when attempting to predict a binary interaction network for each location l
582 within a given region. Both approaches assume independence between interactions. The first approach involves
583 performing a singular Bernoulli trial for each pair of taxa based on their regional probability of interaction:

$$M_{i \rightarrow j} \sim \text{Bernoulli}(P(M_{i \rightarrow j})).$$

584 In employing this approach, we predict a single metaweb of binary interactions for each simulation. Every pair
585 of taxa predicted to interact in this metaweb will be treated as interacting in all local networks where they
586 co-occur, i.e. $L_{l,i \rightarrow j} = M_{i \rightarrow j}$ when $X_{i,j,k} = 1$. This will result in local pairwise interactions without spatial
587 variation.

588 The second approach is to independently sample each local network of probabilistic interactions:

$$L_{l,i \rightarrow j} \sim \text{Bernoulli}(P(L_{l,i \rightarrow j})).$$

589 This can be achieved by first generating distinct probabilistic interaction networks for each location. These local
590 networks of probabilistic interactions may vary in taxa composition and interaction probabilities. Because
591 binary interaction networks are sampled independently for each location, this second approach introduces
592 spatial variation in binary interactions.

593 In Fig. 4, we compare the average connectance of binary interaction networks resulting from these two sampling
 594 techniques. We drew regional and local interactions from our host-parasite networks of probabilistic
 595 interactions, generating a number of binary interaction network realizations for each site in the dataset. These
 596 two sampling approaches yield different outcomes, particularly for lower values of $P(L_{i \rightarrow j} | M_{i \rightarrow j})$, which
 597 represent instances where regional interactions do not consistently manifest locally. Small discrepancies
 598 between these techniques are also apparent when we equate the probability of local interaction to the probability
 599 of regional interaction (i.e., when using $P(L_{i \rightarrow j} | M_{i \rightarrow j}) = 1.0$ in Eq. 2, Fig. 4a), especially when the number of
 600 simulations of binary interaction networks for each location is low ($n = 1$). As anticipated, we observe that
 601 sampling binary interactions from the metaweb tends to overestimate connectance on average compared to
 602 sampling them from local networks (Fig. 4a-c). Furthermore, we observe an increase in the variability of
 603 connectance when employing a single simulation (Fig. 4, gray markers), which in our opinion is a more tangible
 604 representation of the process leading to the realization of local interactions in nature.

605 [Figure 4 about here.]

606 The choice of a sampling approach can influence the selection of grid cell size when delineating local
 607 communities within a broader region of interest. In the first approach, pairwise interactions remain constant
 608 irrespective of cell size because they are sampled only once from the metaweb. However, in the second
 609 approach, local interaction probabilities are contingent on network area. For instance, consider the local
 610 networks L_1 and 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
 611 treat L_1 and L_2 as independent, the probability of interaction between taxa i and j in L_0 is given by:

$$P(L_{0,i \rightarrow j}) = 1 - [1 - P(L_{1,i \rightarrow j})] \times [1 - P(L_{2,i \rightarrow j})]. \quad (20)$$

612 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
 613 sampling binary interactions from local networks, it is crucial to sample at the same spatial scale for which
 614 probabilities were estimated. Otherwise, interaction probabilities must be adjusted to align with the intended
 615 cell size, preventing systematic biases in predictions.

616 **Application 5: Prediction of local networks from metawebs**

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

628 Building local networks of probabilistic interactions from a metaweb of probabilistic interactions involves a
629 reduction in the value of pairwise interaction probabilities. This decrease is attributed to the prerequisite that
630 two taxa must initially possess the capacity to interact before engaging in local interactions (Eq. 2). Therefore,
631 inferring local networks from their metaweb while maintaining identical interaction probability values would
632 introduce systematic biases into the predictions. In such cases, these networks would essentially represent
633 smaller-scale metawebs of potential interactions, possibly leading to misinterpretations by being perceived as
634 local interactions. As proposed by McLeod *et al.* (2021), although metawebs do not capture the spatiotemporal
635 variability of interactions, they establish an upper limit for local interactions (similarly for metawebs of
636 probabilistic interactions, Strydom *et al.* 2023). In other words, the probability of two taxa interacting at a
637 specific location and time is consistently lower or equal to the probability of their regional interaction:

$$P(L_{i \rightarrow j} | X_{i,k}, X_{j,k}, N_{i,k}, N_{j,k}, T_{i,k}, T_{j,k}, E_k, A, t, f(L)) \leq P(M_{i \rightarrow j} | T_i, T_j). \quad (21)$$

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

$$\int_{E_k} \int_A \int_t P(L_{i \rightarrow j}|E_k, A, t) dt dA dE_k \leq P(M_{i \rightarrow j}|T_i, T_j). \quad (22)$$

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

648 Conclusion

649 In this contribution, we underline the importance of network metadata for adequately interpreting and
 650 manipulating probabilistic interaction data. The mathematical representation of probabilities and their statistical
 651 properties depend on the type of interactions (local or regional) and the conditions under which these
 652 interactions were evaluated. We showed that local networks and metawebs of probabilistic interactions differ in
 653 their relationship to spatial and temporal scales, with regional interactions remaining consistent across scales.

654 In contrast with metawebs, local interactions are measured in a specific context (e.g., in a given area, time, and
 655 biological and environmental conditions) and depend on taxa co-occurrence. These differences bring to light
 656 the need to use probabilistic data with caution, for instance when generating network realizations of binary
 657 interactions across space and predicting local networks from metawebs. Clear metadata describing the type of
 658 interaction and the variables used in their estimation are required to ensure adequate data manipulation. Sound
 659 data practices and foundations for probabilistic thinking in network ecology could facilitate reliable assessments
 660 of the spatiotemporal variability and uncertainty of biotic interactions.

661 Estimating local interaction probabilities independently for each taxa pair and assembling them into a network
 662 of probabilistic interactions comes with limitations. Predicting local networks of binary interactions based on
 663 these interaction probabilities assumes independence among interactions, a condition seldom respected in
 664 practice (Golubski & Abrams 2011). Relaxing this assumption is the next logical step in the stochastic
 665 representation of interactions. A more accurate representation of the stochasticity of ecological networks
 666 involves creating *probabilistic networks* ($P(L|...)$ and $P(M|...)$), rather than networks of *probabilistic*

667 interactions ($P(L_{i \rightarrow j} | \dots)$ and $P(M_{i \rightarrow j} | \dots)$). Probabilistic networks describe the probability that a particular
668 network of binary (or quantitative) interactions (its whole adjacency matrix) is realized. For example, Young *et*
669 *al.* (2021) used a Bayesian approach to estimate the probability of different plant-pollinator network structures
670 derived from imperfect observational data. A probability distribution of ecological networks may also be
671 derived using the principle of maximum entropy given some structural constrained (e.g., Cimini *et al.* 2019;
672 Park & Newman 2004). Regardless of the method employed, generating probabilistic local networks, bypassing
673 the need to independently estimate local interaction probabilities, could lead to more accurate predictions of
674 local networks. Furthermore, probabilistic networks could serve as an alternative to null hypothesis significance
675 testing when comparing the structure of a local network to some random expectations or, as done in Pellissier *et*
676 *al.* (2018), to the metaweb. These random expectations are typically derived by performing a series of Bernoulli
677 trials on probabilistic interactions, assuming independence, to generate a distribution of networks of binary
678 interactions and then calculate their structure (Poisot *et al.* 2016). One could for instance compare the
679 likelihood of an observed network to the one of the most likely network structure according to the probabilistic
680 network distribution, thereby directly obtaining a measure of discrepancy of the empirical network. Generating
681 probabilistic ecological networks represents a tangible challenge, one that, in the coming years, promises to
682 unlock doors to more advanced and adequate analyses of ecological networks.

683 It is essential to enhance our comprehension of both regional and local interactions, especially considering the
684 current scarcity of interaction data. While sampling biological communities does decrease the uncertainty of
685 interactions by accumulating evidence for their feasibility and local realization, there is a limit to how much we
686 can reduce uncertainty. In metawebs, probabilities reflect our limited knowledge of interactions (i.e., our degree
687 of belief that interactions are feasible), which is expected to improve with a larger volume of data. Regional
688 interactions should become more definitive (with probabilities approaching 0 or 1) as we investigate various
689 conditions, including different combinations of species traits. In comparison, although local networks can be
690 seen as random instances of metawebs, their randomness cannot be reduced to the same extent. Local
691 interaction probabilities may represent both their uncertainty and spatiotemporal variability. Owing to
692 environmental heterogeneity, there will invariably be instances in which an interaction occurs and others in
693 which it does not, across different times and locations, irrespective of the extent to which we can improve our
694 knowledge of its biological feasibility and the local conditions that facilitate its occurrence. When local
695 networks describe probabilities of observing interactions rather than their actual occurrence, we must also
696 consider observation variability (sampling error) as an additional source of stochasticity. Every ecological

697 process is stochastic but there is also a possibility that a phenomenon goes undetected. Quantifying and
698 partitioning this stochasticity will enable us to make more accurate predictions about ecological interactions at
699 various spatial and temporal scales. This will prove to be of vital importance as our time to understand nature
700 runs out, especially at locations where the impacts of climate change and habitat loss hit harder.

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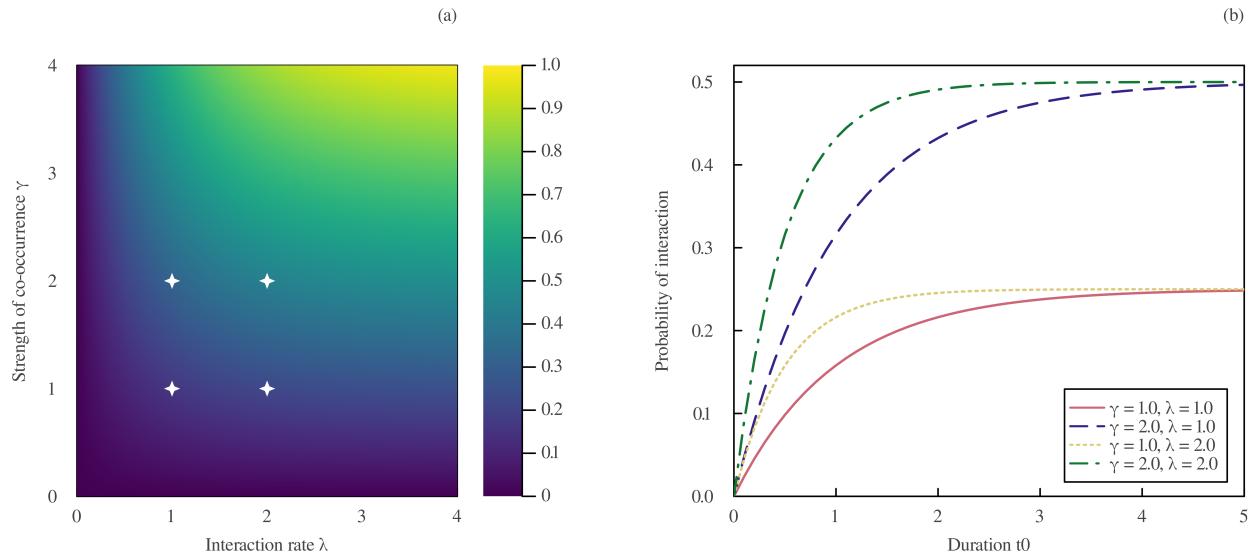


Figure 1: **Parameters of the spatiotemporally explicit model of interactions.** (a) Probability of local interaction given by the process model (Eq. 9) under different values of λ_k (interaction rate) and γ (strength of co-occurrence), with $t_0 = 1$ (duration). Parameters t_0 and λ_k have complementary units (e.g., t_0 in months and λ_k in number of interactions per month). 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. 9, for different values of λ_k and γ . In both panels, the marginal probabilities of occurrence $P(X_{i,k})$ and $P(X_{j,k})$ are set to a constant value of 0.5.

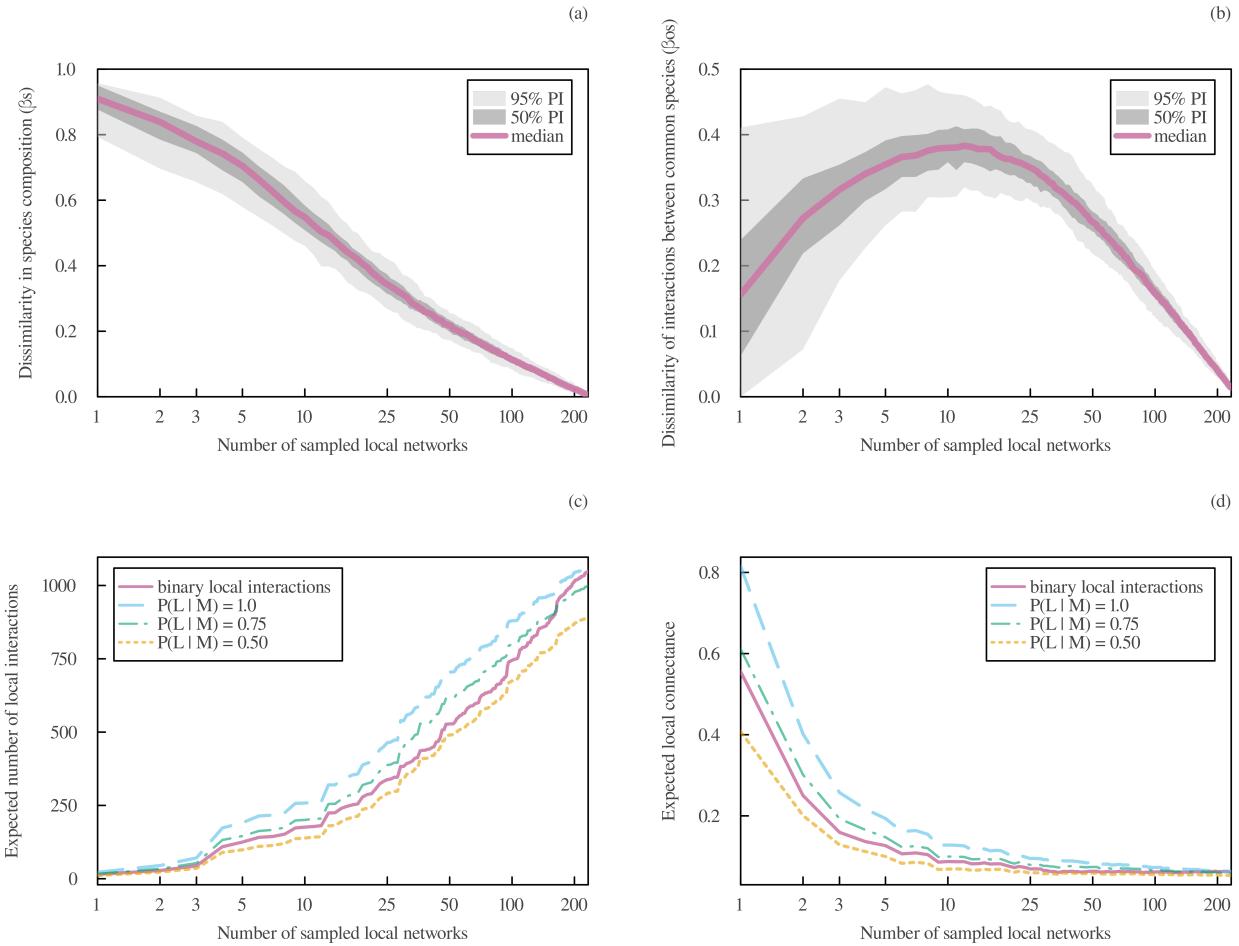


Figure 2: Network accumulation curves. (a) Dissimilarity in species composition and (b) dissimilarity of interactions between common species between aggregated local networks and the metaweb of binary host-parasite interactions. Aggregated local networks were obtained by sequentially and randomly selecting a number of local networks 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 interactions and (d) scaling of connectance with the number of sampled (aggregated) binary and probabilistic local interaction networks. For a better comparison with binary interactions, local networks of probabilistic interactions were derived from a metaweb of probabilistic interactions with a false positive and false negative rate of zero. A specific value of $P(L_{i \rightarrow j}|M_{i \rightarrow j})$ (the local probability of interaction among potentially interacting species, indices omitted in the figure for simplicity) was used for all local networks within a particular curve. Aggregated local networks of probabilistic interactions were obtained by sequentially and randomly selecting a number of local networks and aggregating both their species and interactions (with the value of $P(L_{i \rightarrow j}|M_{i \rightarrow j})$ adjusting according to Eq. 13).

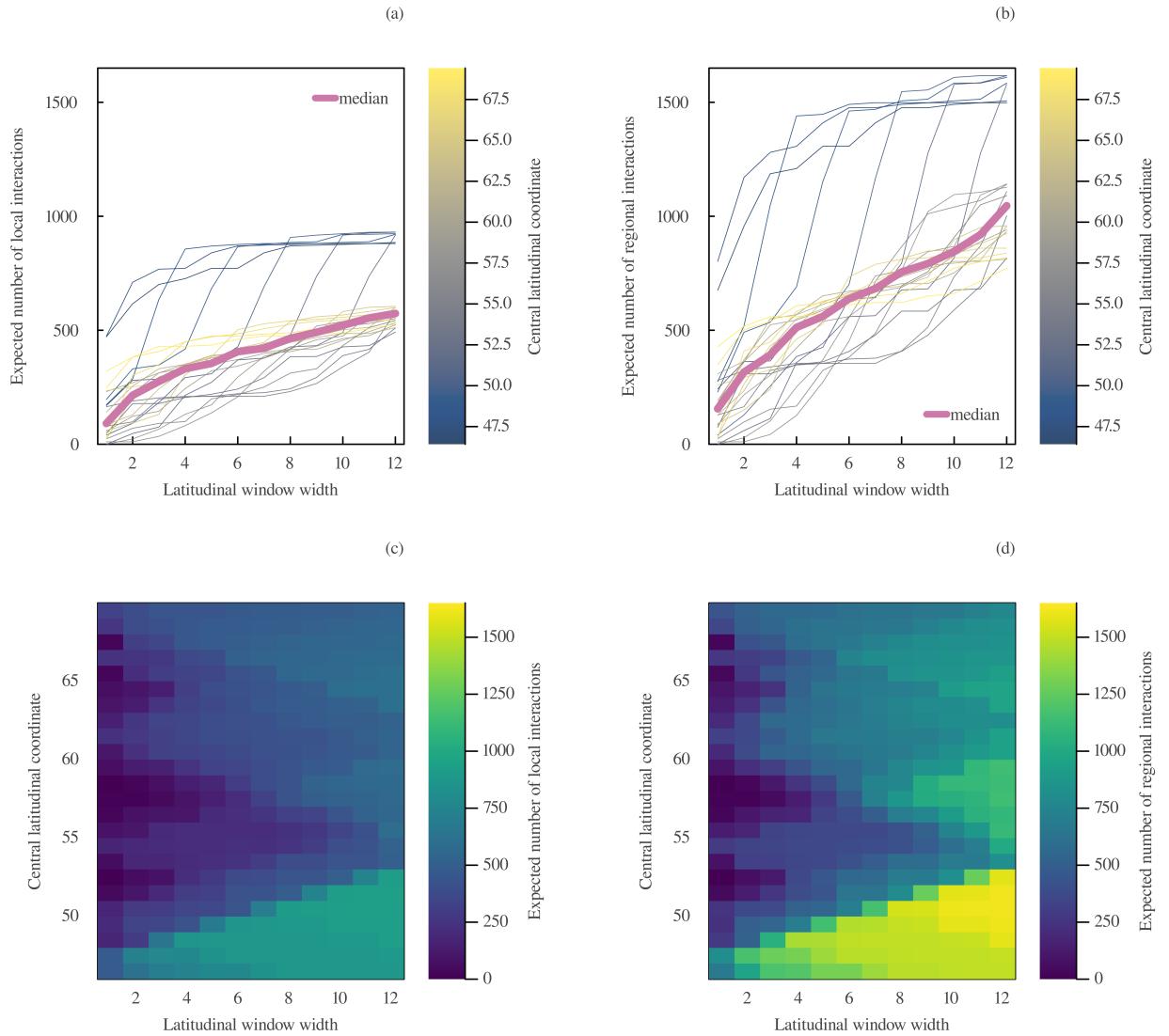


Figure 3: Spatial scaling of interactions. Expected number of host-parasite interactions in a network aggregating all (a) local and (b) regional probabilistic interactions within a latitudinal window of a given length. Every dashed curve corresponds to a different expanding window characterized by a 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 networks and metawebs. Aggregated local networks were obtained by aggregating both the species and interactions found within a particular latitudinal window, with the values of $P(L_{i \rightarrow j} | M_{i \rightarrow j})$ remaining at their maximum value of 1 following Eq. 13.

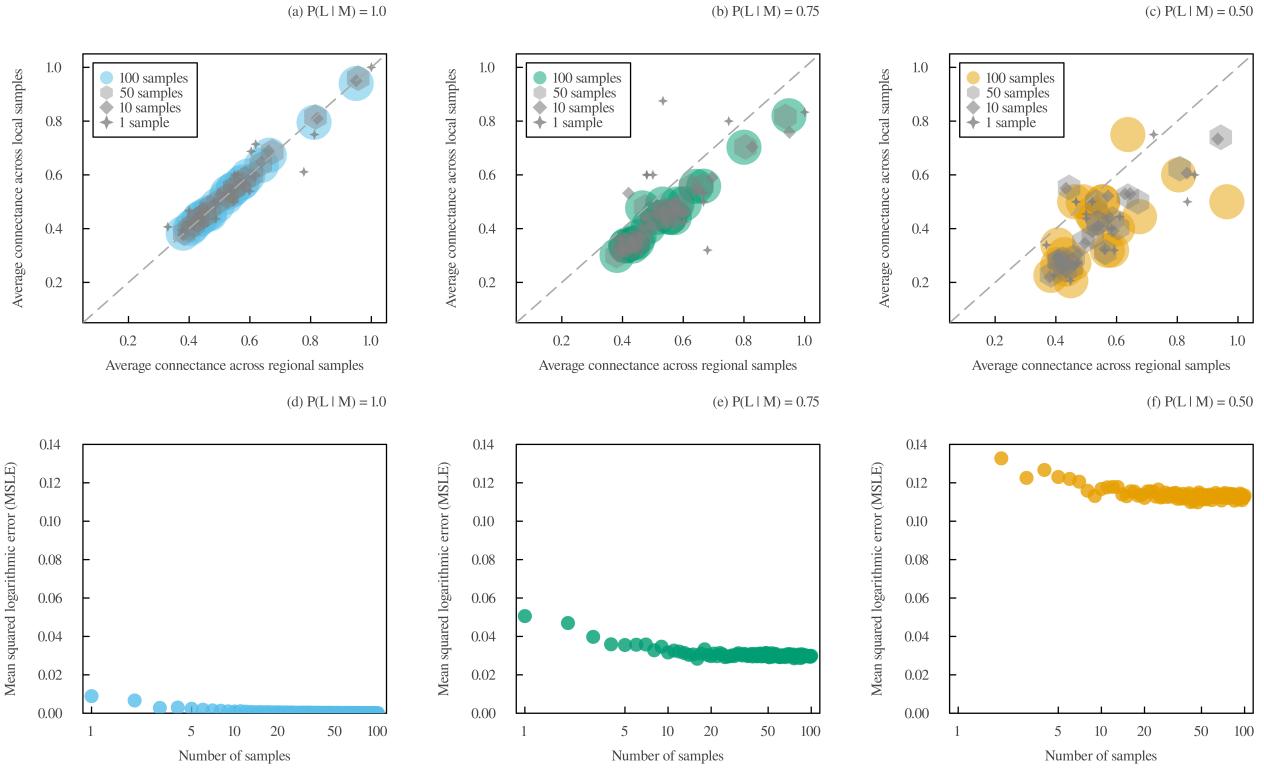


Figure 4: Connectance of sampled binary interaction networks. Comparison between the average connectance of binary interaction network samples obtained from the local networks and metawebs of probabilistic interactions. Each dot corresponds to a different site. The local probability of interaction between potentially interacting species was set to three different values: (a) $P(L_{i \rightarrow j}|M_{i \rightarrow j}) = 1.0$, (b) $P(L_{i \rightarrow j}|M_{i \rightarrow j}) = 0.75$, and (c) $P(L_{i \rightarrow j}|M_{i \rightarrow j}) = 0.50$. Grey dots represent the outcome of a single simulation, while colored dots represent the average connectance of each network across 100 simulations. (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 simulations increases, for the same values of $P(L_{i \rightarrow j}|M_{i \rightarrow j})$ 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 networks that include the species potentially engaged in the interactions. Local binary interaction networks were generated by independently sampling binary interactions for each local network of probabilistic interactions.