

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 introducing uncertainties in our knowledge of unobserved interactions. For example, the spatial and temporal
8 uncoupling of species (e.g., nocturnal and diurnal species coexisting in the same space without interacting
9 because of different daily activity timings, Jordano 1987) and the large number of rare and cryptic interactions
10 in a community, contribute to these difficulties in documenting interactions (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 after satisfying all these
27 conditions, 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 (also

34 known as ecological webs) to include a probabilistic view of interactions (Dallas *et al.* 2017; Fu *et al.* 2021;

35 Poisot *et al.* 2016). This different perspective allows us to fill in the Eltonian shortfall (Hortal *et al.* 2015) by

36 modeling the probability of occurrence of interactions (e.g., Gravel *et al.* 2019), which can be an important tool

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

38 The probabilistic representation of interactions is thus far limited to direct interactions, which are conceptually

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

40 contrast with indirect interactions (e.g., interspecific competition), which arise from distinct ecological

41 processes and are often not directly observable (Kéfi *et al.* 2015, 2016). Representing direct interactions

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

57 (Gonzalez-Varo & Traveset 2016).

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

59 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, McCann 2007; McCann 2011; Proulx *et al.* 2005; 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 (Gravel *et al.* 2013; Petchey *et al.* 2008), 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 (Godsoe *et al.* 2022; Ohlmann *et al.* 2019) 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).

Beyond 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

90 interactions, and regional webs (metawebs) describing probabilities of potential interactions. We highlight the
91 distinctions in the ecological meaning of these two representations and examine some of their properties and
92 relationships (particularly with space, time, and between each other) through empirical case studies. Moreover,
93 the lack of clear guidelines on the use of probabilistic interaction data is worrisome, as it affects both data
94 producers and re-users who generate and manipulate these numbers. This is concerning because sampling
95 strategies and decisions regarding network construction can affect our understanding of network properties
96 (Brimacombe *et al.* 2023). There is currently no metadata standard that could guide the documentation of all
97 types of probabilistic interactions (although see e.g., Salim *et al.* 2022 who discuss data standards for
98 deterministic mutualistic webs). Well-defined metadata for probabilistic interactions would support more
99 adequate manipulation and integration of interaction data from different sources and guard against possible
100 misinterpretations arising from ambiguous definitions of probabilistic interaction networks. These metadata
101 should outline the nature (i.e., local or regional) and type (e.g., predatory or pollination) of the interactions,
102 provide information regarding the taxonomic level, identities, and characteristics (e.g., life stages) of the
103 individuals involved in an interaction, present the mathematical formulation of probabilities, including clearly
104 identified conditional variables (e.g., spatial and temporal scales), and describe the methods and contexts (e.g.,
105 location, time, environmental conditions) in which interactions were estimated. Inadequately documented
106 probabilistic interaction data should be used with caution when analyzing ecological webs. Our observations
107 and advice can be applied to most types of ecological networks representing direct interactions, from food webs
108 to host-virus networks. Even though the measurement of interaction probabilities may differ between network
109 types (e.g., estimations often based on frequencies of interactions in plant-pollinator networks), the broad
110 principles underlying our findings remain relevant and applicable across diverse ecological contexts.

111 **Probabilistic representations of interactions**

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

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

125 One of the first aspects to take into consideration when estimating or interpreting probabilities of interactions is
126 knowing if they describe potential or realized interactions, as these two types of interactions have distinct
127 conceptual underpinnings and sources of uncertainty. A potential (regional) interaction is defined as the
128 biological capacity of two taxa to interact (i.e., the probability that they interact if they were to encounter each
129 other and given sufficient time) whereas a realized (local) interaction is the occurrence or observation of this
130 interaction in a well-defined space and time (i.e., the probability that they interact locally). For two co-occurring
131 taxa and over infinite time, the probability of local interaction is equivalent to the probability of regional
132 (potential) interaction. Our discussion focuses on the occurrence of local interactions rather than their direct
133 observation, as one of the primary goals of describing them probabilistically is to characterize our uncertainty
134 regarding their actual realization. We use the terms *metaweb* (Dunne 2006) to designate regional webs of
135 potential interactions and *local webs* (Poisot *et al.* 2012) for those of realized interactions. Metawebs are the
136 network analogs of the species pool, where local webs originate from a subset of both species (nodes) and
137 interactions (edges) of the regional metaweb (Saravia *et al.* 2022). Without clear documentation, it can be
138 challenging to know if published probabilistic interaction webs describe local or regional interactions (Tbl. 1
139 provides examples of studies employing both types of probabilistic interaction networks), or if so-called
140 probabilities are in reality a form of interaction score (i.e., non-probabilistic quantitative interactions analogous
141 to interaction strengths, which we won't cover further). When probabilistic regional interactions are used and
142 interpreted incorrectly as local interactions (and conversely), this may generate misleading findings during data
143 analysis. We believe that a better understanding of the differences, similarities, and interconnections between
144 these two probabilistic representations of ecological interactions would alleviate interpretation errors (e.g.,
145 when studying network-area relationships with metawebs or local webs) and facilitate a more adequate use of
146 interaction data. In the following sections, we delve into these distinctions as we scale up from pairwise
147 interactions to higher-level representations of ecological networks, i.e. local webs and metawebs.

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

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

155 Edges linking nodes may describe a variety of interaction measures. Ecologists have traditionally represented
156 interactions as binary objects that were considered realized after observing at least one individual from group i
157 interact with at least another individual from group j . In an adjacency matrix B of binary interactions, the
158 presence or absence of an interaction $B_{i \rightarrow j}$ between two taxa can be viewed as the result of a Bernoulli trial
159 $B_{i \rightarrow j} \sim \text{Bernoulli}(P(B_{i \rightarrow j}))$, with $P(B_{i \rightarrow j})$ being the probability of interaction. This interaction probability
160 characterizes our limited ecological knowledge and/or the intrinsic spatiotemporal variability of interactions. It
161 may be estimated through predictive models (e.g., those based on biological traits and species abundances) or
162 expert (prior) knowledge about the interaction. In networks of probabilistic interactions, the edge values
163 $P(B_{i \rightarrow j})$ are probabilistic events whose only two possible outcomes are the presence ($B_{i \rightarrow j} = 1$) or absence
164 ($B_{i \rightarrow j} = 0$) of an interaction between each pair of nodes. Depending on the type of probabilistic interaction
165 network (local or metaweb), the mathematical formulation and interpretation of stochastic parameters like
166 $P(B_{i \rightarrow j})$ can be linked to environmental and biological factors such as species abundance, traits, area, and time,
167 for example using logistic regression with continuous explanatory variables. Predicting the number of local
168 webs in which the interaction between two given taxa occurs can be achieved by using a Binomial distribution,
169 assuming a constant interaction probability and independence between networks (trials). When considering
170 uncertainties around the estimation of $P(B_{i \rightarrow j})$ or its spatiotemporal variability, a Beta distribution may be used
171 to represent the relative likelihood of different probability values. For example, when calculating the probability
172 of interaction between two taxa based on their local abundances, any spatiotemporal fluctuations in their
173 abundances would introduce variability in the interaction probability at the local scale. If we take into account
174 the stochasticity of the interaction probability, a Beta-Binomial distribution can be used to predict the number of
175 networks in which the interaction occurs. Empirically observing an interaction between two taxa at a given
176 location and time provides important information that can be used to update previous estimates of $P(B_{i \rightarrow j})$,
177 informing us on the biological capacity of both taxa to interact and the environmental conditions that enabled

178 them to interact locally.

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

191 Just like binary interaction networks, the uncertainty and spatiotemporal variability of interaction strengths can
192 be represented probabilistically. However, the need to estimate the probability distribution of all possible values
193 of interaction strengths can make the inference of probabilities more challenging in quantitative webs compared
194 to binary interaction webs, which require only one probability estimate for each interaction. Interaction
195 strengths can follow various probability distributions depending on the measure used. For instance, they can
196 follow a Poisson distribution $W_{i \rightarrow j} \sim \text{Poisson}(\lambda_{i \rightarrow j})$ when predicting frequencies of interactions between pairs
197 of nodes, with $\lambda_{i \rightarrow j}$ being the expected rate at which individuals of taxa i and j interact (e.g., the average
198 number of prey j consumed by all predators i in a given time period). The Poisson distribution can also be
199 0-inflated after initially modeling non-interacting taxa (e.g., Boulangeat *et al.* 2012 employ a 0-inflated model
200 to analyze species abundance following the modeling of species presence and absence), which constitute the
201 majority of taxa pairs in most local webs due to their typically high sparseness (Jordano 2016). Because of the
202 methodological difficulties typically encountered when building deterministic quantitative webs (which are only
203 partially mitigated by models such as Ecopath, Plagányi & Butterworth 2004), binary interaction webs, which
204 are easier to sample (Jordano 2016) and predict (Strydom *et al.* 2021), have been more frequently studied and
205 modeled. Moreover, most published networks of probabilistic interactions and methods describe probabilistic
206 interactions whose outcome is binary (whether interaction probabilities are regarded as constant or variable,
207 e.g. represented by a Beta distribution), which underlines the need for better guidelines regarding the

208 interpretation and manipulation of these types of webs first. For these reasons, our primary focus in this
209 contribution will be on addressing the challenges in interpreting and using interaction probabilities in Bernoulli
210 distributions, in both local webs and metawebs.

211 Local webs: communities interacting in space and time

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

220 We define space as the collection of geographic coordinates (x, y, z) , with (x, y) representing longitude and
221 latitude coordinates, and z denoting either altitudes or depths. These point coordinates delineate the spatial
222 boundaries of the system, which may be portrayed as a polyhedron. Ecological interactions may exhibit
223 variations along latitudinal and altitudinal gradients, as evidenced by changes in hummingbird-plant
224 interactions (Weinstein & Graham 2017a, b) and mosquito biting rates (e.g., Kulkarni *et al.* 2006) at different
225 elevations. In contrast, time is defined as the specific time period within which interactions were either observed
226 or predicted. Even though space and time are continuous variables that should yield probability *densities* of
227 interactions (i.e., relative likelihoods of interactions occurring at infinitesimal locations and instants in time),
228 these definitions enable them to be conceptualized as distinct patches and time segments. Treating space and
229 time as discrete dimensions aligns with the common sampling methods of ecological networks and provides
230 actual probabilities of interactions, which can be obtained by integrating probability densities over space and
231 time. Furthermore, we can quantify both an area A and a duration t , which can be readily used in spatiotemporal
232 analyses of ecological networks. For example, when studying network-area relationships (NAR, Galiana *et al.*
233 2018), we anticipate that local probabilities of interactions scale positively with area and duration because taxa
234 have more opportunities to interact as these dimensions expand.

235 The probability that two taxa i and j interact in a local web $L_{x,y,z,t}$ (spatial and temporal subscripts hereafter

236 omitted or replaced by the shorter subscript l for clarity) can be conditioned on many environmental and
 237 biological factors. In addition to network area (or volume) and duration, they may be conditioned on taxa
 238 co-occurrence $X_{i,j,l}$, which is usually a Boolean describing if the geographic distributions of both taxa overlap
 239 within the study area. Co-occurrence may be modeled probabilistically, in which case it may conform to a
 240 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 /
 241 absence) of both taxa. The probability of co-occurrence $P(X_{i,l}, X_{j,l})$ can be estimated through the application of
 242 joint species distribution models (e.g., Pollock *et al.* 2014), potentially taking into account biotic interactions
 243 (Staniczenko *et al.* 2017). Given that the probability that two non-co-occurring taxa interact locally is zero (i.e.,
 244 $P(L_{i \rightarrow j}|X_{i,j,l} = 0) = 0$), the probability of local interaction can be obtained by multiplying the probability of
 245 interaction given co-occurrence with the probability of co-occurrence:

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

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

264 The probability that two taxa i and j interact in a local web L can thus be conditioned on their co-occurrence
 265 $X_{i,j,l}$ (or more explicitly on their occurrences $X_{i,l}$ and $X_{j,l}$), local abundances $N_{i,l}$ and $N_{j,l}$, local traits
 266 distributions $T_{i,l}$ and $T_{j,l}$, local environmental conditions E_l , network area (or volume) A , time interval t , and
 267 network properties $f(L)$. Although these variables correspond to distinct ecological inquiries or mechanisms
 268 related to ecological interactions, they may covary with each other, such as the possible dependence of $X_{i,j,l}$ and
 269 E_l on spatial and temporal scales. When estimating interaction probabilities using e.g. a generalized linear
 270 model with multiple explanatory variables that might not be independent, it may become important to address
 271 collinearity. In such a case, to mitigate this issue, it may be necessary to use variable selection techniques before
 272 fitting the model to data. The probability that a local interaction is realized is described by the following
 273 expression when all these conditional variables are included:

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

274 The representation of the local context in which probabilities are estimated and the variables that should be
 275 taken into consideration depend on the study system, the objectives of the study, and the resources available to
 276 the researchers. In other words, these variables do not systematically need to be accounted for. For example, in
 277 Gravel *et al.* (2019), for the purpose of model comparison, some models incorporated environmental variables
 278 as conditions of interaction probabilities, while others did not. When accounted for, these variables should be
 279 clearly described in the documentation of the data (Brimacombe *et al.* 2023), preferentially in mathematical
 280 terms to avoid any confusion in their interpretation and to limit manipulation errors during their re-use. For
 281 instance, ecologists should be explicit about their consideration of co-occurrence in their estimation of local
 282 interaction probabilities. Indeed, it is important to specify if probability values are conditional $P(L_{i \rightarrow j} | X_{i,j,l} = 1)$
 283 or not $P(L_{i \rightarrow j})$ on co-occurrence since this can significantly impact the interpretation and analysis of the data.
 284 In Tbl. 1, we present examples of studies that used these different formulations of probabilistic interactions and
 285 conditional variables. We have included the probability of empirically observing an interaction that is realized
 286 locally $P(O_{i \rightarrow j} | L_{i \rightarrow j})$ to underscore the distinction between local observations and actual realizations of
 287 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 local web 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 webs. Note that we also included the expression for a local web 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	Uncertainty	
			sources	Reference
$P(L_{i \rightarrow j} X_{i,l}, X_{j,l}, \dots)$	local	realization of the interaction	spatiotemporal	Gravel <i>et al.</i> (2019)
		given taxa co-occurrence	variability	
$P(L_{i \rightarrow j} N_{i,l}, N_{j,l}, \dots)$	local	realization of the interaction	neutral models	Canard <i>et al.</i> (2014)
		given taxa abundances		
$P(L_{i \rightarrow j} T_{i,l}, T_{j,l}, \dots)$	local	realization of the interaction	trait matching	Gravel <i>et al.</i> (2016)
		given local traits	models	
$P(L_{i \rightarrow j} E_l, \dots)$	local	realization of the interaction	environmental-	Gravel <i>et al.</i> (2019)
		given local environmental	based models	
		conditions		
$P(L_{i \rightarrow j} A, \dots)$	local	realization of the interaction in	spatial models	Galiana <i>et al.</i> (2018)
		a given area or volume		
$P(L_{i \rightarrow j} t, \dots)$	local	realization of the interaction	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	
$P(O_{i \rightarrow j} L_{i \rightarrow j}, \dots)$	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

When testing or employing multiple models to estimate local interaction probabilities, rather than selecting a single model that best fits the data, model averaging may be used to 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 $P(L_{i \rightarrow j}|...)$ can be calculated as follows:

$$P(L_{i \rightarrow j}|...) = P(L_{i \rightarrow j}|mod_1, ...) \times P(mod_1) + P(L_{i \rightarrow j}|mod_2, ...) \times P(mod_2), \quad (3)$$

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

Metawebs: regional catalogs of interactions

Metawebs are networks of potential interactions that have been designed for broad spatial, temporal, and taxonomic scales (e.g., species food webs at the continental scale). Potential interactions describe the biological capacity of taxa to interact, which is typically assessed at the regional scale. Metawebs of probabilistic interactions are particularly useful in situations where there is high uncertainty in the ability of taxa to interact if they were to encounter each other. This uncertainty frequently arises due to insufficient interaction data, especially for taxa that have not yet been observed to co-occur, and uncertainties in trait-matching models. As data accumulates, interactions in metawebs should tend towards binarity, approaching probability values of 0

304 (repeatedly failing to observe an interaction between two co-occurring taxa) and 1 (observing an interaction at
305 least once). The extent of sampling effort thus influences our evaluation of probabilities of potential
306 interactions, as sampling over a larger area or for a longer duration enables us to capture a greater number of
307 regional interactions (McLeod *et al.* 2021). However, in contrast with local webs of probabilistic interactions,
308 which describe interaction stochasticity in local natural settings, regional interactions are not evaluated for any
309 particular local context. Although *neutrally* forbidden interactions (i.e., improbable interactions between rare
310 species, Canard *et al.* 2012) tend to have low probability values in local webs, they may have higher probabilities
311 in the metaweb (i.e., when species' biological traits can support an interaction if they were to encounter each
312 other). Likewise, non-co-occurring taxa may have a non-zero probability of interaction in the metaweb.

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

$$P(M_{i \rightarrow j} | T_i, T_j), \quad (4)$$

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

$$P(M_{i \rightarrow j} | T_i, T_j) = 1 - P(F_{i \rightarrow j} | T_i, T_j). \quad (5)$$

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

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

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

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

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

$$\int_E P(M_{i \rightarrow j}^* | T_i, T_j, E) dE \leq P(M_{i \rightarrow j} | T_i, T_j). \quad (7)$$

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

351 Starting from a selected set of taxa, which are usually distributed within a broad region of interest, metawebs

352 can be built using different data sources, including literature review (e.g., Maiorano *et al.* 2020), aggregated
353 local web data (e.g., Gravel *et al.* 2019; Saravia *et al.* 2022), trait-matching models Strydom *et al.* (2022), and
354 expert knowledge. Every pair of taxa that have confidently been observed to interact at least once can be given a
355 probability of 1 (i.e., $P(M_{i \rightarrow j}) = 1$) since we know that they *can* interact. This differs from local webs of
356 probabilistic interactions, where interaction events may remain stochastic (i.e., $P(L_{i \rightarrow j}) < 1$) even after
357 empirically observing interactions due to their spatiotemporal variability. Interactions that were never observed
358 typically have low probability values in local webs and vary from low to high values in metawebs, contingent
359 upon taxa traits distributions (reaching 0 for forbidden links).

360 When incorporating local network data to estimate probabilities of regional interactions, repeatedly failing to
361 observe an interaction between two co-occurring taxa (i.e., $P(O_{i \rightarrow j} = 0)$) should decrease the probability that
362 the interaction is biologically feasible. Using Bayes' theorem, the probability that the interaction is biologically
363 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:

$$P(M_{i \rightarrow j} = 1|O_{i \rightarrow j} = 0, \dots) = \frac{P(O_{i \rightarrow j} = 0|M_{i \rightarrow j} = 1, \dots) \times P(M_{i \rightarrow j} = 1|\dots)}{P(O_{i \rightarrow j} = 0|\dots)}. \quad (8)$$

364 The reduction in the probability of regional interaction after considering that it was never observed locally (i.e.,
365 $P(M_{i \rightarrow j} = 1|O_{i \rightarrow j} = 0, \dots) < P(M_{i \rightarrow j} = 1|\dots)$) occurs because $P(O_{i \rightarrow j} = 0|M_{i \rightarrow j} = 1, \dots)$ must be lower than
366 $P(O_{i \rightarrow j} = 0, \dots)$, i.e. there is a higher chance of observing an interaction when we know it is biologically
367 feasible.

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

375 **Properties of probabilistic interaction webs**

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

387 **Application 1: Dissimilarity of binary and probabilistic interaction webs**

388 We use the collection of tripartite host-parasite networks sampled across Europe, created by Kopelke *et al.*
389 (2017), in the following case studies. This dataset contains well-resolved binary local interactions between
390 willows (52 species), willow-galling sawflies (96 species), and their parasitoids (126 species). Given its
391 replicated webs spanning large spatiotemporal scales, this dataset is well-suited for analyzing a variety of
392 ecological hypotheses and processes. Out of a total of 374 local webs, we retained those containing at least 5
393 species, resulting in a set of 233 georeferenced local webs (networks sampled within areas of 0.1 to 0.3 km²
394 during June and/or July spanning 29 years). We built a metaweb of binary interactions by aggregating all local
395 interactions, which gave us a regional web composed of 274 species and 1080 interactions. In Fig. 1, we show
396 how the dissimilarity between the metaweb and the aggregated local webs varies with the number of sampled
397 local webs. To do so, we randomly selected one local web of binary interactions and sequentially sampled
398 additional webs while aggregating both their species and interactions. Next, we compared the metaweb and the
399 aggregated local webs using the dissimilarity of interactions between common species (β_{OS} , Fig. 1a) and the
400 dissimilarity in species composition (β_S , Fig. 1b) (Poisot *et al.* 2012). We repeated this sampling process one
401 hundred times and highlighted the median dissimilarity values across simulations, as well as the 50% and 95%
402 percentile intervals. This shows that networks of local interactions are highly dissimilar from the metaweb, both

403 in terms of species and interactions, especially when only a limited number of sites has been sampled. Both
404 dissimilarity indices were calculated based on the number of items shared by the two webs (c_{LM}) and the
405 number of items unique to the metaweb (u_M) and to the aggregated local web (u_L). The β_S dissimilarity index
406 uses species (nodes) as items being compared, while the β_{OS} index assesses dissimilarity based on interactions
407 between shared species (Poisot *et al.* 2012). Both indices were calculated following the β_W index of Whittaker
408 (1960):

$$\beta_W = \frac{c_{LM} + u_L + u_M}{(2c_{LM} + u_L + u_M)/2} - 1. \quad (9)$$

409 [Figure 1 about here.]

410 Next, we investigate the differences in scaling between networks of probabilistic or binary interactions
411 (Fig. 1c-d). We converted these binary interaction networks into probabilistic ones using models based on
412 simple assumptions. Our models are not designed to estimate the exact values of probabilistic interactions.
413 Instead, their purpose is to create plausible networks that serve as illustrative examples to highlight distinctions
414 between local webs and metawebs of probabilistic interactions. We created two metawebs of probabilistic
415 interactions by employing constant false positive and false negative rates for all regional interactions. In the first
416 metaweb, we set both false positive and false negative rates to zero to prevent artificially inflating the total
417 number of links, enabling a more accurate comparison with binary interaction webs. This gave us a probability
418 of regional interaction of 1 when at least one interaction has been observed locally and of 0 in the absence of
419 any observed interaction between a given pair of species (Fig. 1c-d). In the second metaweb (used in the next
420 applications), we introduced a 5% false positive rate to account for spurious interactions and a 10% false
421 negative rate to address the elevated occurrence of missing interactions in ecological networks (Catchen *et al.*
422 2023). We believe these rates represent reasonable estimates of missing and spurious potential interactions, but
423 confirming their accuracy is challenging due to the unavailability of data on the actual feasibility of interaction.
424 Observed interactions were thus given a probability of regional interaction of 95%, whereas unobserved ones
425 were assigned a probability of 10%.

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

429 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 sake of simplicity, with their
 430 probability of regional interaction $P(M_{i \rightarrow j})$:

$$P(L_{i \rightarrow j}) = P(L_{i \rightarrow j}|M_{i \rightarrow j} = 1) \times P(M_{i \rightarrow j} = 1). \quad (10)$$

431 We built local webs of probabilistic interactions using the taxa found in the empirical local networks and
 432 attributing pairwise interaction probabilities based on the metawebs of probabilistic interactions and a constant
 433 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
 434 occur locally, intermediate values around 50% suggest considerable spatiotemporal variability, while high
 435 values indicate that regional interactions are nearly always realized locally. Following Eq. 10, the local
 436 probability of interaction between a given pair of taxa consistently remained equal to or below their probability
 437 of regional interaction.

438 In the last two panels of Fig. 1 (c-d), we show how the aggregated number of links and connectance (i.e., the
 439 proportion of all of the non-forbidden links that are realized) scale with the number of sampled local webs,
 440 according to different values of $P(L_{i \rightarrow j}|M_{i \rightarrow j})$. When aggregating local webs of probabilistic interactions, the
 441 constancy of the probability of regional interaction across the entire study area means that any rise in the
 442 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
 443 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
 444 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
 445 these taxa interact in the aggregated web $L_{1,2}$ is obtained by:

$$P(L_{1,2,i \rightarrow j}|M_{i \rightarrow j}) = 1 - (1 - P(L_{1,i \rightarrow j}|M_{i \rightarrow j})) \times (1 - P(L_{2,i \rightarrow j}|M_{i \rightarrow j})), \quad (11)$$

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

449 By comparing the scaling relationships observed in webs of binary and probabilistic interactions; Fig. 1
 450 illustrates that high values of $P(L_{i \rightarrow j}|M_{i \rightarrow j})$ lead to systematic overestimations in the number of links and
 451 connectance, especially when $P(L_{i \rightarrow j}|M_{i \rightarrow j}) = 1$ (corresponding to the scenario where local probabilities of
 452 interactions are equivalent to the probabilities of regional interactions). However, these biases tend to diminish

453 as the number of sampled webs increases.

454 Application 2: Spatial and temporal scaling of interactions

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

461 Additionally, ecological processes occurring at distinct spatial scales, such as the spatial variability in local
462 community composition resulting from different sequences of extinction and colonization events, can also
463 contribute to this variation (Galiana *et al.* 2018). Next, interaction accumulation curves describe the scaling of
464 the number of observed interactions with sampling effort (Jordano 2016). Sampling effort, which may
465 correspond to the duration of the sampling period used to construct the network, can impact connectance
466 (Bersier *et al.* 1999) and various measures of network structure (Banašek-Richter *et al.* 2004; McLeod *et al.*
467 2021). Apart from sampling effort, the temporal scaling of interactions also elucidates how network structure
468 changes with the temporal resolution of the network (Poisot *et al.* 2012), acknowledging that distinct
469 interactions take place over time, ranging from short-term fluctuations of interactions to long-term trends. As
470 local webs of probabilistic interactions may explicitly account for the spatiotemporal variability of interactions
471 (as shown in Box 1), they offer a distinct approach to investigating the scaling of network structure with space
472 and time, in contrast to webs of binary and quantitative interactions, by making the stochasticity of interactions
473 the focal point of the modeling process.

474 Local webs and metawebs exhibit distinct relationships with spatial and temporal scales. On one hand,
475 metawebs of probabilistic interactions, representing biological feasibility, feature regional interactions that do
476 not scale with space and time. This is because regional interactions depend solely on the biological capacity of
477 two taxa to interact, regardless of their co-occurrence and local environmental conditions. However,
478 probabilities of potential interactions may change (tending to become more definitive) upon updating previous
479 estimates with increased sampling effort, even though they do not vary in a specific direction with the spatial
480 and temporal extent (boundaries) of the network. The probability of two taxa potentially interacting should
481 theoretically be the same in all metawebs in which they are present, provided that the data and methods used for

482 estimation are consistent. For example, if a smaller metaweb M_1 is derived from a larger metaweb M_0 by
483 selecting the subset of taxa present in the region described by M_1 and retaining all their interactions, their
484 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
485 equal number of taxa in M_0 as compared to M_1 , the total number of interactions is expected to be higher or at
486 least equal in the larger web, even though pairwise probabilities remain identical.

487 On the other hand, local interactions scale both spatially and temporally, given that they have more
488 opportunities to be realized and observed in larger areas and longer durations. This is attributed to factors such
489 as a higher number of individuals, greater trait variations, and increased opportunities for encounters, as
490 highlighted by McLeod *et al.* (2020). For example, if a local web of probabilistic interactions L_1 with an area
491 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
492 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,
493 interaction probabilities could be higher in the smaller area, contingent upon their environmental and biological
494 conditions. Likewise, interaction probabilities are expected to be lower in webs with shorter durations when
495 time intervals are nested. In Fig. 2, we show how the expected number of local host-parasite interactions scales
496 with area, represented as an expanding latitudinal window, in comparison with regional interactions. Even
497 though we employed local probabilities of interactions equal to regional interactions for the purpose of
498 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
499 more rapidly than local interactions. This is because numerous regional interactions involve species that never
500 co-occur, and as a result, these interactions are not captured in any local web.

501 [Figure 2 about here.]

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

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

510 simple generative mechanistic model for probabilistic local interactions that takes into consideration their
 511 spatiotemporal variability (i.e., a spatiotemporally explicit model of local interactions). It is essential to note
 512 that our model is not designed for regional interactions, which are scale-independent. Rather, it could prove
 513 valuable for predicting local interactions across time and space by generating new interaction data following
 514 parameter inference.

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

$$P(X_{i,l}, X_{j,l}) = P(X_{i,l}|X_{j,l})P(X_{j,l}) = P(X_{i,l})P(X_{j,l})\gamma. \quad (12)$$

523 When $\gamma > 1$, it signifies a positive association in the geographic distributions of both taxa, indicating that the
 524 presence of one taxon enhances the probability of occurrence of the other. Attractions may be the result of
 525 positive interactions (e.g., mutualism) or positive/negative interactions (e.g., antagonism between predators and
 526 prey, Cazelles *et al.* 2016). In empirical webs, $\gamma > 1$ holds true for the majority of species pairs (Catchen *et al.*
 527 2023). In contrast, repulsions ($\gamma < 1$) may be caused e.g. by strong interspecific competition (Cazelles *et al.*
 528 2016). We model the co-occurrence $X_{i,j,l}$ of both taxa as the outcome of a Bernoulli trial

$$X_{i,j,l} \sim \text{Bernoulli}(P(X_{i,l}, X_{j,l})). \quad (13)$$

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

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

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

538 The occurrence of an interaction between i and j can be modeled as a Bernoulli trial with a probability of
 539 $P(L_{i \rightarrow j})$. Consequently, a Bayesian inference model can be built based on the preceding equations to estimate
 540 the value of the λ_l and γ parameters and generate novel interaction data:

$$L_{i \rightarrow j} \sim \text{Bernoulli}(P(L_{i \rightarrow j})) \quad (15)$$

$$P(L_{i \rightarrow j}) = P(X_{i,l})P(X_{j,l})\gamma(1 - e^{-\lambda_l t_0}) \quad (16)$$

$$\gamma \sim \text{Gamma}(2, 0.5) \quad (17)$$

$$\lambda_l \sim \text{Exponential}(2) \quad (18)$$

541 In Fig. 3, we show the variation in the probability of interaction under different parameter values. In the right
 542 panel, we notice that, irrespective of the interaction rate λ_l , the probability of interaction converges toward an
 543 asymptote determined by the probability of co-occurrence $P(X_{i,j,l})$ (Eq. 12). This model can be customized in
 544 different ways, such as by linking λ_l with specific environmental variables or explicitly incorporating
 545 observation errors (i.e., the probabilities of false negatives and false positives).

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

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

557 There are no inherent differences in the taxonomic scaling between local and metawebs, as only the nodes are
558 defined taxonomically. In other words, the probability values of edges in both local (Eq. 2) and metawebs
559 (Eq. 4) are not conditional on any taxonomic level. The taxonomic scale is tied to the definition of the event
560 itself (i.e., the interaction between two taxa, defined at the desired taxonomical scale), not to the variables on
561 which interaction probabilities are conditional. In both types of webs, transitioning to a broader level of
562 organization (e.g., from a species-level web S to a genus-level web G) can be accomplished directly by using
563 probabilities from finer scales. For example, in a network with n_1 species from genus g_1 and n_2 species from
564 genus g_2 , one can compute the probability that at least one species from genus g_1 interacts with at least one
565 species from genus g_2 (i.e., that there is a non-zero number of species-level interactions or, equivalently, that the
566 genus-level interaction occurs) as follows:

$$P(G_{g_1 \rightarrow g_2} = 1) = 1 - \prod_{i=1}^{n_1} \prod_{j=1}^{n_2} (1 - P(S_{g_{1i} \rightarrow g_{2j}} = 1)), \quad (19)$$

567 where $g_{1,i}$ and $g_{2,j}$ are the species of the corresponding genus and assuming independence between
568 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
569 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
570 species-based network following a similar approach, by using simulated interactions between individuals
571 derived from a neutral model (i.e., a model that assumed ecological equivalence among individuals). In
572 contrast, a more sophisticated approach is necessary when transitioning from a broader to a finer level of
573 organization. This is because knowledge of an interaction between two genera does not guarantee that all

574 possible pairwise combinations of their species will also interact. One possible method is to build a finer-scale
575 network by generating probabilities of interactions through random sampling from a beta distribution,
576 parameterized by the broader-scale network.

577 Ideally, our biological interpretation of probabilistic interactions should remain consistent across a network
578 even if it incorporates heterogeneous levels of organization, such as a network whose nodes represent both
579 species and trophic species (groups of species sharing similar predators and prey). This is common in
580 ecological webs where taxonomic resolution is typically low (Hemprich-Bennett *et al.* 2021; Vázquez *et al.*
581 2022). Interaction probabilities at broader taxonomic scales should be based on probabilities of interactions
582 between individuals, for both local webs and metawebs. For instance, in local individual-based food webs, the
583 probability that two individuals interact reflects our degree of belief that one individual will consume the other.
584 Similarly, in local species-based food webs, the probability that two species interact represents our degree of
585 belief that at least one individual from the predator species consumes at least another individual from the prey
586 species. Furthermore, in local clade-based food webs, the probability that two clades interact represents our
587 degree of belief that at least two species from these clades interact with each other or, equivalently, that at least
588 two individuals from these clades interact with each other. Fundamentally, the taxonomic scaling of interactions
589 involves aggregating interactions between individuals into larger groups, which may exhibit varying degrees of
590 homogeneity based on the organisms and the study system. In that regard, taxonomic scaling is analogous to the
591 spatial and temporal scaling of interactions, as they all represent different ways to aggregate individuals into
592 broader groups (either spatially, temporally, or taxonomically).

593 Application 4: Sampling for binary interaction webs

594 The prediction of binary interactions through Bernoulli trials is an important application of probabilistic
595 interaction webs. This approach proves beneficial for analyzing the structural characteristics of probabilistic
596 interaction webs, particularly in the absence of specific analytical formulas for measures describing the structure
597 of the complete web (Poisot *et al.* 2016). By performing independent Bernoulli trials for each interaction, a
598 network of binary interactions may be generated. A probability distribution of network properties can be
599 obtained by measuring network structure across multiple randomly generated networks (Poisot *et al.* 2016).
600 This method enables the representation of the variability of network structure, albeit with possible biases when
601 connectance is low (Chagnon 2015; Poisot & Gravel 2014). Employing this strategy to generate binary
602 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 binary interactions assumes independence among interactions, which might not accurately represent reality. Covariation among interactions could exist even if we do not explicitly condition interactions on others. For example, an interaction between two taxa could be more probable when another interaction occurs. The consequences of this assumption of independence on the prediction of network structure have yet to be empirically examined.

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

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

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

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

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

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

In Fig. 4, we compare the average connectance of binary interaction networks resulting from these two sampling techniques. We drew regional and local interactions from our host-parasite networks of probabilistic interactions, generating a number of binary interaction web realizations for each site in the dataset. These two

627 sampling approaches yield different outcomes, particularly for lower values of $P(L_{i \rightarrow j} | M_{i \rightarrow j})$, which represent
628 instances where regional interactions do not consistently manifest locally. Small discrepancies between these
629 techniques are also apparent when we equate the probability of local interaction to the probability of regional
630 interaction (i.e., when using $P(L_{i \rightarrow j} | M_{i \rightarrow j}) = 1.0$ in Eq. 10, Fig. 4a), especially when the number of simulations
631 of binary interaction networks for each location is low ($n = 1$). As anticipated, we observe that sampling binary
632 interactions from the metaweb tends to overestimate connectance on average compared to sampling them from
633 local webs (Fig. 4a-c). Furthermore, we observe an increase in the variability of connectance when employing a
634 single simulation (Fig. 4, gray markers), which in our opinion is a more tangible representation of the process
635 leading to the realization of local interactions in nature.

636 [Figure 4 about here.]

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

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

643 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
644 sampling binary interactions from local webs, it is crucial to sample at the same spatial scale for which
645 probabilities were estimated. Otherwise, interaction probabilities must be adjusted to align with the intended
646 cell size, preventing systematic biases in predictions.

647 Application 5: Prediction of local webs from metawebs

648 Metawebs serve as a valuable source of ecological information for predicting local webs across time and space.
649 Local webs of binary interactions can be reconstructed by selecting a subset of taxa and interactions from the
650 metaweb (Dunne 2006). This implies that metawebs consistently contain more interactions than their
651 corresponding local webs, even though their connectance is usually much smaller than the ones of local webs

652 (Gravel *et al.* 2011). Determining the list of taxa to select can be achieved empirically or through numerical
 653 methods like range maps or species distribution models. As species composition is arguably less difficult to
 654 sample or predict than pairwise interactions, the primary challenge lies in deciding which interactions to select
 655 from the metaweb, a task that may necessitate advanced statistical models and ecological expertise. Inferring
 656 the structure of local webs from the metaweb before predicting specific local pairwise interactions could hold
 657 promise (Strydom *et al.* 2021), considering that the structure of local webs is constrained by the metaweb
 658 (Saravia *et al.* 2022).

659 Building local webs of probabilistic interactions from a metaweb of probabilistic interactions involves a
 660 reduction in the value of pairwise interaction probabilities. This decrease is attributed to the prerequisite that
 661 two taxa must initially possess the capacity to interact before engaging in local interactions (Eq. 10). Therefore,
 662 inferring local webs from their metaweb while maintaining identical interaction probability values would
 663 introduce systematic biases into the predictions. In such cases, these networks would essentially represent
 664 smaller-scale metawebs of potential interactions, possibly leading to misinterpretations by being perceived as
 665 local interactions. As proposed by McLeod *et al.* (2021), although metawebs do not capture the spatiotemporal
 666 variability of interactions, they establish an upper limit for local interactions (similarly for metawebs of
 667 probabilistic interactions, Strydom *et al.* 2023). In other words, the probability of two taxa interacting at a
 668 specific location and time is consistently lower or equal to the probability of their regional interaction:

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

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

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

673 Estimating more precisely the probability $P(L_{i \rightarrow j} | M_{i \rightarrow j})$ that two taxa interact locally if they can potentially
 674 interact allows for improved predictions of local webs from the metaweb of probabilistic interactions. This task
 675 is challenging due to the variability of this probability across space and time, as well as its variability across

676 pairwise interactions within a network. Using simple models of $P(L_{i \rightarrow j}|M_{i \rightarrow j})$, as demonstrated in our case
677 studies, represents an initial step toward the overarching objective of reconstructing local webs from metawebs.

678 Conclusion

679 In this contribution, we underline the importance of network metadata for adequately interpreting and
680 manipulating probabilistic interaction data. The mathematical representation of probabilities and their statistical
681 properties depend on the type of interactions (local or regional) and the conditions under which these
682 interactions were evaluated. We showed that local webs and metawebs of probabilistic interactions differ in their
683 relationship to spatial and temporal scales, with regional interactions remaining consistent across scales. In
684 contrast with metawebs, local interactions are measured in a specific context (e.g., in a given area, time, and
685 biological and environmental conditions) and depend on taxa co-occurrence. These differences bring to light
686 the need to use probabilistic data with caution, for instance when generating network realizations of binary
687 interactions across space and predicting local webs from metawebs. Clear metadata describing the type of
688 interaction and the variables used in their estimation are required to ensure adequate data manipulation. Sound
689 data practices and foundations for probabilistic thinking in network ecology could facilitate reliable assessments
690 of the spatiotemporal variability and uncertainty of biotic interactions.

691 Estimating local interaction probabilities independently for each taxa pair and assembling them into a network
692 of probabilistic interactions comes with limitations. Predicting local networks of binary interactions based on
693 these interaction probabilities assumes independence among interactions, a condition seldom respected in
694 practice (Golubski & Abrams 2011). Relaxing this assumption is the next logical step in the stochastic
695 representation of interactions. A more accurate representation of the stochasticity of ecological networks
696 involves creating *probabilistic networks* ($P(L|...)$ and $P(M|...)$), rather than networks of *probabilistic*
697 *interactions* ($P(L_{i \rightarrow j}|...)$ and $P(M_{i \rightarrow j}|...)$). Probabilistic networks describe the probability that a particular
698 network of binary (or quantitative) interactions (its whole adjacency matrix) is realized. For example, Young *et*
699 *al.* (2021) used a Bayesian approach to estimate the probability of different plant-pollinator network structures
700 derived from imperfect observational data. A probability distribution of ecological networks may also be
701 derived using the principle of maximum entropy given some structural constrained (e.g., Cimini *et al.* 2019;
702 Park & Newman 2004). Regardless of the method employed, generating probabilistic local webs, bypassing the
703 need to independently estimate local interaction probabilities, could lead to more accurate predictions of local

704 webs. Furthermore, probabilistic networks could serve as an alternative to null hypothesis significance testing
705 when comparing the structure of a local web to some random expectations or, as done in Pellissier *et al.* (2018),
706 to the metaweb. These random expectations are typically derived by performing a series of Bernoulli trials on
707 probabilistic interactions, assuming independence, to generate a distribution of networks of binary interactions
708 and then calculate their structure (Poisot *et al.* 2016). One could for instance compare the likelihood of an
709 observed network to the one of the most likely network structure according to the probabilistic network
710 distribution, thereby directly obtaining a measure of discrepancy of the empirical network. Generating
711 probabilistic ecological networks represents a tangible challenge, one that, in the coming years, promises to
712 unlock doors to more advanced and adequate analyses of ecological networks.

713 It is essential to enhance our comprehension of both regional and local interactions, especially considering the
714 current scarcity of interaction data. While sampling biological communities does decrease the uncertainty of
715 interactions by accumulating evidence for their feasibility and local realization, there is a limit to how much we
716 can reduce uncertainty. In metawebs, probabilities reflect our limited knowledge of interactions (i.e., our degree
717 of belief that interactions are feasible), which is expected to improve with a larger volume of data. Regional
718 interactions should become more definitive (with probabilities approaching 0 or 1) as we investigate various
719 conditions, including different combinations of species traits. In comparison, although local webs can be seen
720 as random instances of metawebs, their randomness cannot be reduced to the same extent. Local interaction
721 probabilities may represent both their uncertainty and spatiotemporal variability. Owing to environmental
722 heterogeneity, there will invariably be instances in which an interaction occurs and others in which it does not,
723 across different times and locations, irrespective of the extent to which we can improve our knowledge of its
724 biological feasibility and the local conditions that facilitate its occurrence. When local webs describe
725 probabilities of observing interactions rather than their actual occurrence, we must also consider observation
726 variability (sampling error) as an additional source of stochasticity. Every ecological process is stochastic but
727 there is also a possibility that a phenomenon goes undetected. Quantifying and partitioning this stochasticity
728 will enable us to make more accurate predictions about ecological interactions at various spatial and temporal
729 scales. This will prove to be of vital importance as our time to understand nature runs out, especially at
730 locations where the impacts of climate change and habitat loss hit harder.

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739 **References**

- 740 Abrego, N., Roslin, T., Huotari, T., Ji, Y., Schmidt, N.M., Wang, J., *et al.* (2021). [Accounting for species](#)
741 [interactions is necessary for predicting how arctic arthropod communities respond to climate change.](#)
742 *Ecography*, 44, 885–896.
- 743 Andrade-Pacheco, R., Rerolle, F., Lemoine, J., Hernandez, L., Meité, A., Juziwelo, L., *et al.* (2020). [Finding](#)
744 [hotspots: Development of an adaptive spatial sampling approach.](#) *Scientific Reports*, 10, 10939.
- 745 Angilletta, M.J., Jr., Steury, T.D. & Sears, M.W. (2004). [Temperature, Growth Rate, and Body Size in](#)
746 [Ectotherms: Fitting Pieces of a Life-History Puzzle](#)¹. *Integrative and Comparative Biology*, 44, 498–509.
- 747 Araujo, M.B., Rozenfeld, A., Rahbek, C. & Marquet, P.A. (2011). [Using species co-occurrence networks to](#)
748 [assess the impacts of climate change.](#) *Ecography*, 34, 897–908.
- 749 Banašek-Richter, C., Cattin, M.-F. & Bersier, L.-F. (2004). [Sampling effects and the robustness of quantitative](#)
750 [and qualitative food-web descriptors.](#) *Journal of Theoretical Biology*, 226, 23–32.
- 751 Bartomeus, I., Gravel, D., Tylianakis, J.M., Aizen, M.A., Dickie, I.A. & Bernard-Verdier, M. (2016). [A](#)
752 [common framework for identifying linkage rules across different types of interactions.](#) *Functional Ecology*,
753 30, 1894–1903.
- 754 Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003). [The nested assembly of plant–animal](#)
755 [mutualistic networks.](#) *Proceedings of the National Academy of Sciences*, 100, 9383–9387.

- 756 Berg, M.P. & Ellers, J. (2010). Trait plasticity in species interactions: A driving force of community dynamics.
757 *Evolutionary Ecology*, 24, 617–629.
- 758 Berlow, E.L., Neutel, A.-M., Cohen, J.E., De Ruiter, P.C., Ebenman, B., Emmerson, M., *et al.* (2004).
759 Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73, 585–598.
- 760 Bersier, L.-F., Dixon, P. & Sugihara, G. (1999). Scale-Invariant or Scale-Dependent Behavior of the Link
761 Density Property in Food Webs: A Matter of Sampling Effort? *The American Naturalist*, 153, 676–682.
- 762 Bohan, D.A., Vacher, C., Tamaddoni-Nezhad, A., Raybould, A., Dumbrell, A.J. & Woodward, G. (2017).
763 Next-Generation Global Biomonitoring: Large-scale, Automated Reconstruction of Ecological Networks.
764 *Trends in Ecology & Evolution*, 32, 477–487.
- 765 Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., *et al.* (2011). Why
766 intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26, 183–192.
- 767 Borrett, S.R. & Scharler, U.M. (2019). Walk partitions of flow in Ecological Network Analysis: Review and
768 synthesis of methods and indicators. *Ecological Indicators*, 106, 105451.
- 769 Boulangeat, I., Gravel, D. & Thuiller, W. (2012). Accounting for dispersal and biotic interactions to disentangle
770 the drivers of species distributions and their abundances. *Ecology Letters*, 15, 584–593.
- 771 Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T. & Fortin, M.-J. (2023). Shortcomings of reusing
772 species interaction networks created by different sets of researchers. *PLOS Biology*, 21, e3002068.
- 773 Broom, M. & Ruxton, G.D. (2005). You can run—or you can hide: Optimal strategies for cryptic prey against
774 pursuit predators. *Behavioral Ecology*, 16, 534–540.
- 775 Brose, U., Ostling, A., Harrison, K. & Martinez, N.D. (2004). Unified spatial scaling of species and their
776 trophic interactions. *Nature*, 428, 167–171.
- 777 Burnham, K.P. & Anderson, D.R. (2004). Multimodel Inference: Understanding AIC and BIC in Model
778 Selection. *Sociological Methods & Research*, 33, 261–304.
- 779 Canard, E.F., Mouquet, N., Mouillot, D., Stanko, M., Miklisova, D. & Gravel, D. (2014). Empirical Evaluation
780 of Neutral Interactions in Host-Parasite Networks. *The American Naturalist*, 183, 468–479.
- 781 Canard, E., Mouquet, N., Marescot, L., Gaston, K.J., Gravel, D. & Mouillot, D. (2012). Emergence of
782 Structural Patterns in Neutral Trophic Networks. *PLOS ONE*, 7, e38295.

- 783 Castoe, T.A., Spencer, C.L. & Parkinson, C.L. (2007). Phylogeographic structure and historical demography of
784 the western diamondback rattlesnake (*Crotalus Atrox*): A perspective on North American desert
785 biogeography. *Molecular Phylogenetics and Evolution*, 42, 193–212.
- 786 Catchen, M.D., Poisot, T., Pollock, L.J. & Gonzalez, A. (2023). The missing link: Discerning true from false
787 negatives when sampling species interaction networks.
- 788 Cazelles, K., Araujo, M.B., Mouquet, N. & Gravel, D. (2016). A theory for species co-occurrence in interaction
789 networks. *Theoretical Ecology*, 9, 39–48.
- 790 Chagnon, P.-L. (2015). Characterizing topology of ecological networks along gradients: The limits of metrics'
791 standardization. *Ecological Complexity*, 22, 36–39.
- 792 Choh, Y., Ignacio, M., Sabelis, M.W. & Janssen, A. (2012). Predator-prey role reversals, juvenile experience
793 and adult antipredator behaviour. *Scientific Reports*, 2, 728.
- 794 Cimini, G., Squartini, T., Saracco, F., Garlaschelli, D., Gabrielli, A. & Caldarelli, G. (2019). The statistical
795 physics of real-world networks. *Nature Reviews Physics*, 1, 58–71.
- 796 Cirtwill, A.R., Eklöf, A., Roslin, T., Wootton, K. & Gravel, D. (2019). A quantitative framework for
797 investigating the reliability of empirical network construction. *Methods in Ecology and Evolution*, 10,
798 902–911.
- 799 Dallas, T., Park, A.W. & Drake, J.M. (2017). Predicting cryptic links in host-parasite networks. *PLOS
800 Computational Biology*, 13, e1005557.
- 801 Dunne, J.A. (2006). The Network Structure of Food Webs. In: *Ecological networks: Linking structure and
802 dynamics* (eds. Dunne, J.A. & Pascual, M.). Oxford University Press, pp. 27–86.
- 803 Elmasri, M., Farrell, M.J., Davies, T.J. & Stephens, D.A. (2020). A hierarchical Bayesian model for predicting
804 ecological interactions using scaled evolutionary relationships. *The Annals of Applied Statistics*, 14,
805 221–240.
- 806 Elton, C.S. (2001). *Animal Ecology*. University of Chicago Press, Chicago, IL.
- 807 Emmerson, M.C. & Raffaelli, D. (2004). Predator–prey body size, interaction strength and the stability of a real
808 food web. *Journal of Animal Ecology*, 73, 399–409.
- 809 Fedorov, V.B., Goropashnaya, A.V., Boeskorov, G.G. & Cook, J.A. (2008). Comparative phylogeography and
810 demographic history of the wood lemming (*Myopus schisticolor*): Implications for late Quaternary history

- 811 of the taiga species in Eurasia. *Molecular Ecology*, 17, 598–610.
- 812 Fortuna, M.A. & Bascompte, J. (2006). Habitat loss and the structure of plant–animal mutualistic networks.
813 *Ecology Letters*, 9, 281–286.
- 814 Fu, X., Seo, E., Clarke, J. & Hutchinson, R.A. (2021). Link Prediction Under Imperfect Detection:
815 Collaborative Filtering for Ecological Networks. *IEEE Transactions on Knowledge and Data Engineering*,
816 33, 3117–3128.
- 817 Galiana, N., Lurgi, M., Claramunt-López, B., Fortin, M.-J., Leroux, S., Cazelles, K., et al. (2018). The spatial
818 scaling of species interaction networks. *Nature Ecology & Evolution*, 2, 782–790.
- 819 Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010). A framework for community
820 interactions under climate change. *Trends in Ecology & Evolution*, 25, 325–331.
- 821 Godsoe, W., Murray, R. & Iritani, R. (2022). Species interactions and diversity: A unified framework using Hill
822 numbers. *Oikos*, n/a, e09282.
- 823 Golubski, A.J. & Abrams, P.A. (2011). Modifying modifiers: What happens when interspecific interactions
824 interact? *Journal of Animal Ecology*, 80, 1097–1108.
- 825 Gomez, J.M., Verdu, M. & Perfectti, F. (2010). Ecological interactions are evolutionarily conserved across the
826 entire tree of life. *Nature*, 465, 918–U6.
- 827 Gonzalez, A. & Londoño, M.C. (2022). Monitor biodiversity for action. *Science*, 378, 1147–1147.
- 828 Gonzalez-Varo, J.P. & Traveset, A. (2016). The Labile Limits of Forbidden Interactions. *Trends in Ecology &*
829 *Evolution*, 31, 700–710.
- 830 Gravel, D., Albouy, C. & Thuiller, W. (2016). The meaning of functional trait composition of food webs for
831 ecosystem functioning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371,
832 20150268.
- 833 Gravel, D., Baiser, B., Dunne, J.A., Kopelke, J.-P., Martinez, N.D., Nyman, T., et al. (2019). Bringing Elton
834 and Grinnell together: A quantitative framework to represent the biogeography of ecological interaction
835 networks. *Ecography*, 42, 401–415.
- 836 Gravel, D., Massol, F., Canard, E., Mouillot, D. & Mouquet, N. (2011). Trophic theory of island biogeography.
837 *Ecology Letters*, 14, 1010–1016.

- 838 Gravel, D., Poisot, T., Albouy, C., Velez, L. & Mouillot, D. (2013). [Inferring food web structure from](#)
839 [predator–prey body size relationships](#). *Methods in Ecology and Evolution*, 4, 1083–1090.
- 840 Guimarães, P.R. (2020). [The Structure of Ecological Networks Across Levels of Organization](#). *Annual Review*
841 *of Ecology, Evolution, and Systematics*, 51, 433–460.
- 842 Guimerà, R. & Sales-Pardo, M. (2009). [Missing and spurious interactions and the reconstruction of complex](#)
843 [networks](#). *Proceedings of the National Academy of Sciences*, 106, 22073–22078.
- 844 Hemprich-Bennett, D.R., Oliveira, H.F.M., Le Comber, S.C., Rossiter, S.J. & Clare, E.L. (2021). [Assessing the](#)
845 [impact of taxon resolution on network structure](#). *Ecology*, 102, e03256.
- 846 Herrera, C.M. (1989). [Pollinator abundance, morphology, and flower visitation rate: Analysis of the “quantity”](#)
847 [component in a plant-pollinator system](#). *Oecologia*, 80, 241–248.
- 848 Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M. & Ladle, R.J. (2015). [Seven Shortfalls](#)
849 [that Beset Large-Scale Knowledge of Biodiversity](#). *Annual Review of Ecology, Evolution, and Systematics*,
850 46, 523–549.
- 851 Jordano, P. (1987). [Patterns of Mutualistic Interactions in Pollination and Seed Dispersal: Connectance,](#)
852 [Dependence Asymmetries, and Coevolution](#). *The American Naturalist*, 129, 657–677.
- 853 Jordano, P. (2016). [Sampling networks of ecological interactions](#). *Functional Ecology*, 30, 1883–1893.
- 854 Jordano, P., Bascompte, J. & Olesen, J.M. (2003). [Invariant properties in coevolutionary networks of](#)
855 [plant–animal interactions](#). *Ecology Letters*, 6, 69–81.
- 856 Kausrud, K.L., Mysterud, A., Steen, H., Vik, J.O., Østbye, E., Cazelles, B., et al. (2008). [Linking climate](#)
857 [change to lemming cycles](#). *Nature*, 456, 93–97.
- 858 Kéfi, S., Berlow, E.L., Wieters, E.A., Joppa, L.N., Wood, S.A., Brose, U., et al. (2015). [Network structure](#)
859 [beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky shores](#). *Ecology*, 96,
860 291–303.
- 861 Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., et al. (2012). [More than a](#)
862 [meal... integrating non-feeding interactions into food webs](#). *Ecology Letters*, 15, 291–300.
- 863 Kéfi, S., Miele, V., Wieters, E.A., Navarrete, S.A. & Berlow, E.L. (2016). [How Structured Is the Entangled](#)
864 [Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks Leads to Increased](#)
865 [Persistence and Resilience](#). *PLOS Biology*, 14, e1002527.

- 866 Kissner, K.J., Forbes, M.R. & Secoy, D.M. (1997). [Rattling Behavior of Prairie Rattlesnakes \(*Crotalus viridis* viridis, Viperidae\) in Relation to Sex, Reproductive Status, Body Size, and Body Temperature](#). *Ethology*,
867 103, 1042–1050.
- 868
- 869 Klecka, J. & Boukal, D.S. (2014). [The effect of habitat structure on prey mortality depends on predator and prey microhabitat use](#). *Oecologia*, 176, 183–191.
- 870
- 871 Kopelke, J.-P., Nyman, T., Cazelles, K., Gravel, D., Vissault, S. & Roslin, T. (2017). [Food-web structure of willow-galling sawflies and their natural enemies across Europe](#). *Ecology*, 98, 1730–1730.
- 872
- 873 Kulkarni, M.A., Kweka, E., Nyale, E., Lyatuu, E., Mosha, F.W., Chandramohan, D., *et al.* (2006).
874 [Entomological Evaluation of Malaria Vectors at Different Altitudes in Hai District, Northeastern Tanzania](#).
875 *Journal of Medical Entomology*, 43, 580–588.
- 876 Maiorano, L., Montemaggioli, A., Ficetola, G.F., O'Connor, L. & Thuiller, W. (2020). [TETRA-EU 1.0: A species-level trophic metaweb of European tetrapods](#). *Global Ecology and Biogeography*, 29, 1452–1457.
- 877
- 878 McCann, K. (2007). Protecting biostructure. *Nature*, 446, 29–29.
- 879 McCann, K.S. (2011). Food webs (MPB-50). In: *Food Webs (MPB-50)*. Princeton University Press.
- 880 McLeod, A., Leroux, S.J., Gravel, D., Chu, C., Cirtwill, A.R., Fortin, M.-J., *et al.* (2021). [Sampling and asymptotic network properties of spatial multi-trophic networks](#). *Oikos*, n/a.
- 881
- 882 McLeod, A.M., Leroux, S.J. & Chu, C. (2020). [Effects of species traits, motif profiles, and environment on spatial variation in multi-trophic antagonistic networks](#). *Ecosphere*, 11, e03018.
- 883
- 884 Melián, C.J., Vilas, C., Baldó, F., González-Ortegón, E., Drake, P. & Williams, R.J. (2011). [Eco-evolutionary Dynamics of Individual-Based Food Webs](#). In: *Advances in Ecological Research*, The Role of Body Size in Multispecies Systems (ed. Belgrano, A.). Academic Press, pp. 225–268.
- 885
- 886
- 887 Morales-Castilla, I., Matias, M.G., Gravel, D. & Araújo, M.B. (2015). [Inferring biotic interactions from proxies](#). *Trends in Ecology & Evolution*, 30, 347–356.
- 888
- 889 Ohlmann, M., Miele, V., Dray, S., Chalmandrier, L., O'Connor, L. & Thuiller, W. (2019). [Diversity indices for ecological networks: A unifying framework using Hill numbers](#). *Ecology Letters*, 22, 737–747.
- 890
- 891 Olesen, J.M., Bascompte, J., Dupont, Y.L., Elberling, H., Rasmussen, C. & Jordano, P. (2010). [Missing and forbidden links in mutualistic networks](#). *Proceedings of the Royal Society B: Biological Sciences*, 278,
892 725–732.
893

- 894 Park, J. & Newman, M.E.J. (2004). [Statistical mechanics of networks](#). *Physical Review E*, 70, 066117.
- 895 Pascual, M., Dunne, J.A. & Dunne, J.A. (2006). *Ecological Networks: Linking Structure to Dynamics in Food*
896 *Webs*. Oxford University Press, USA.
- 897 Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., *et al.* (2018). [Comparing species](#)
898 [interaction networks along environmental gradients](#). *Biological Reviews*, 93, 785–800.
- 899 Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2008). [Size, foraging, and food web structure](#).
900 *Proceedings of the National Academy of Sciences*, 105, 4191–4196.
- 901 Pilosof, S., Porter, M.A., Pascual, M. & Kéfi, S. (2017). [The multilayer nature of ecological networks](#). *Nature*
902 *Ecology & Evolution*, 1, 1–9.
- 903 Plagányi, É.E. & Butterworth, D.S. (2004). [A critical look at the potential of Ecopath with ecosim to assist in](#)
904 [practical fisheries management](#). *African Journal of Marine Science*, 26, 261–287.
- 905 Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D. (2012). [The dissimilarity of species interaction](#)
906 [networks](#). *Ecology Letters*, 15, 1353–1361.
- 907 Poisot, T., Cirtwill, A.R., Cazelles, K., Gravel, D., Fortin, M.-J. & Stouffer, D.B. (2016). [The structure of](#)
908 [probabilistic networks](#). *Methods in Ecology and Evolution*, 7, 303–312.
- 909 Poisot, T. & Gravel, D. (2014). [When is an ecological network complex? Connectance drives degree](#)
910 [distribution and emerging network properties](#). *PeerJ*, 2, e251.
- 911 Poisot, T., Stouffer, D.B. & Gravel, D. (2015). [Beyond species: Why ecological interaction networks vary](#)
912 [through space and time](#). *Oikos*, 124, 243–251.
- 913 Polis, G.A. (1991). [Complex Trophic Interactions in Deserts: An Empirical Critique of Food-Web Theory](#). *The*
914 *American Naturalist*, 138, 123–155.
- 915 Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O'Hara, R.B., Parris, K.M., *et al.* (2014). [Understanding](#)
916 [co-occurrence bymodelling species simultaneously with a Joint Species DistributionModel \(JSDM\)](#).
917 *Methods in Ecology and Evolution*, 5, 397–406.
- 918 Pomeranz, J.P.F., Thompson, R.M., Poisot, T. & Harding, J.S. (2019). [Inferring predator–prey interactions in](#)
919 [food webs](#). *Methods in Ecology and Evolution*, 10, 356–367.

- 920 Pringle, R.M. & Hutchinson, M.C. (2020). [Resolving Food-Web Structure](#). *Annual Review of Ecology, Evolution, and Systematics*, 51, 55–80.
- 921
- 922 Proulx, S.R., Promislow, D.E.L. & Phillips, P.C. (2005). [Network thinking in ecology and evolution](#). *Trends in Ecology & Evolution*, SPECIAL ISSUE: BUMPER BOOK REVIEW, 20, 345–353.
- 923
- 924 Pulliam, H.R. (1974). [On the Theory of Optimal Diets](#). *The American Naturalist*, 108, 59–74.
- 925 Rooney, N. & McCann, K.S. (2012). [Integrating food web diversity, structure and stability](#). *Trends in Ecology & Evolution*, 27, 40–46.
- 926
- 927 Salim, J.A., Saraiva, A.M., Zermoglio, P.F., Agostini, K., Wolowski, M., Drucker, D.P., et al. (2022). [Data standardization of plant–pollinator interactions](#). *GigaScience*, 11, giac043.
- 928
- 929 Sanders, D. & van Veen, F.J.F. (2012). [Indirect commensalism promotes persistence of secondary consumer species](#). *Biology Letters*, 8, 960–963.
- 930
- 931 Saravia, L.A., Marina, T.I., Kristensen, N.P., De Troch, M. & Momo, F.R. (2022). [Ecological network assembly: How the regional metaweb influences local food webs](#). *Journal of Animal Ecology*, 91, 630–642.
- 932
- 933 Schmeller, D.S., Julliard, R., Bellingham, P.J., Böhm, M., Brummitt, N., Chiarucci, A., et al. (2015). [Towards a global terrestrial species monitoring program](#). *Journal for Nature Conservation*, 25, 51–57.
- 934
- 935 Shaw, J.O., Dunhill, A.M., Beckerman, A.P., Dunne, J.A. & Hull, P.M. (2024). [A framework for reconstructing ancient food webs using functional trait data](#).
- 936
- 937 Singer, M.C. & McBride, C.S. (2012). [Geographic mosaics of species' association: A definition and an example driven by plant–insect phenological synchrony](#). *Ecology*, 93, 2658–2673.
- 938
- 939 Staniczenko, P.P.A., Sivasubramaniam, P., Suttle, K.B. & Pearson, R.G. (2017). [Linking macroecology and community ecology: Refining predictions of species distributions using biotic interaction networks](#). *Ecology Letters*, 20, 693–707.
- 940
- 941
- 942 Stouffer, D.B., Rezende, E.L. & Amaral, L.A.N. (2011). [The role of body mass in diet contiguity and food-web structure](#). *Journal of Animal Ecology*, 80, 632–639.
- 943
- 944 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M.J., et al. (2022). [Food web reconstruction through phylogenetic transfer of low-rank network representation](#). *Methods in Ecology and Evolution*, 13.
- 945
- 946

- 947 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M.J., *et al.* (2023). Graph embedding and
948 transfer learning can help predict potential species interaction networks despite data limitations. *Methods in*
949 *Ecology and Evolution*, 14, 2917–2930.
- 950 Strydom, T., Catchen, M.D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., *et al.* (2021). A
951 roadmap towards predicting species interaction networks (across space and time). *Philosophical*
952 *Transactions of the Royal Society B-Biological Sciences*, 376, 20210063.
- 953 Thompson, R.M. & Townsend, C.R. (2005). Food-Web Topology Varies with Spatial Scale in a Patchy
954 Environment. *Ecology*, 86, 1916–1925.
- 955 Tylianakis, J.M., Tscharntke, T. & Lewis, O.T. (2007). Habitat modification alters the structure of tropical
956 host-parasitoid food webs. *Nature*, 445, 202–205.
- 957 Vázquez, D.P., Melián, C.J., Williams, N.M., Blüthgen, N., Krasnov, B.R. & Poulin, R. (2007). Species
958 abundance and asymmetric interaction strength in ecological networks. *Oikos*, 116, 1120–1127.
- 959 Vázquez, D.P., Peralta, G., Cagnolo, L. & Santos, M. (2022). Ecological interaction networks. What we know,
960 what we don't, and why it matters. *Ecología Austral*, 32, 670–697.
- 961 Wagenmakers, E.-J. & Farrell, S. (2004). AIC model selection using Akaike weights. *Psychonomic Bulletin &*
962 *Review*, 11, 192–196.
- 963 Weinstein, B.G. & Graham, C.H. (2017a). On comparing traits and abundance for predicting species
964 interactions with imperfect detection. *Food Webs*, 11, 17–25.
- 965 Weinstein, B.G. & Graham, C.H. (2017b). Persistent bill and corolla matching despite shifting temporal
966 resources in tropical hummingbird-plant interactions. *Ecology Letters*, 20, 326–335.
- 967 Whittaker, R.H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological*
968 *Monographs*, 30, 279–338.
- 969 Wood, S.A., Russell, R., Hanson, D., Williams, R.J. & Dunne, J.A. (2015). Effects of spatial scale of sampling
970 on food web structure. *Ecology and Evolution*, 5, 3769–3782.
- 971 Woodward, G., Benstead, J.P., Beveridge, O.S., Blanchard, J., Brey, T., Brown, L.E., *et al.* (2010). Chapter 2 -
972 Ecological Networks in a Changing Climate. In: *Advances in Ecological Research*, Ecological Networks
973 (ed. Woodward, G.). Academic Press, pp. 71–138.

- 974 Woodward, G., Brown, L.E., Edwards, F.K., Hudson, L.N., Milner, A.M., Reuman, D.C., *et al.* (2012). [Climate](#)
975 [change impacts in multispecies systems: Drought alters food web size structure in a field experiment.](#)
- 976 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 2990–2997.
- 977 Young, J.-G., Valdovinos, F.S. & Newman, M.E.J. (2021). [Reconstruction of plant–pollinator networks from](#)
978 [observational data](#). *Nature Communications*, 12, 3911.

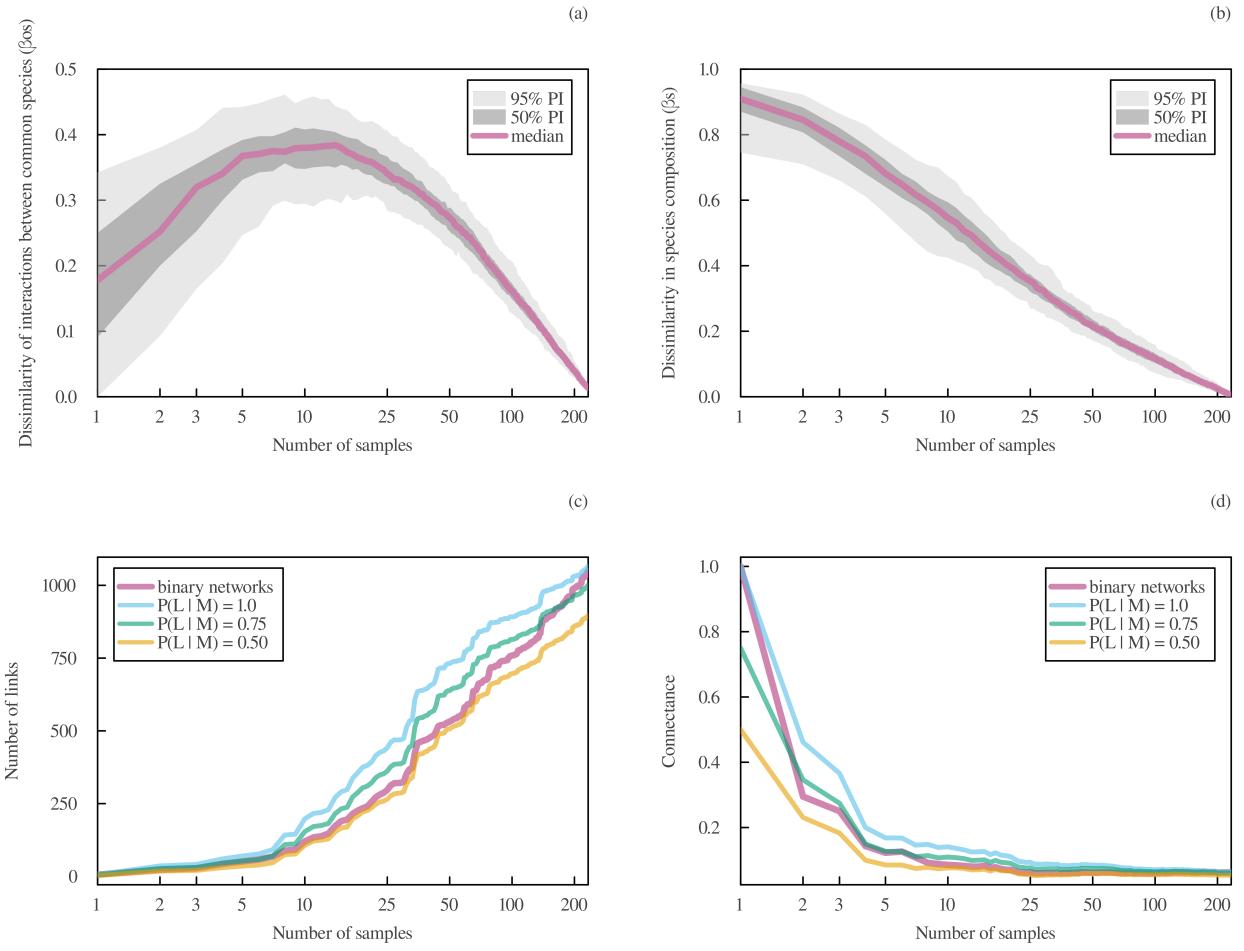


Figure 1: Network accumulation curves. (a) Dissimilarity of interactions between common species and (b) dissimilarity in species composition between aggregated local webs and the metaweb of binary host-parasite interactions. Aggregated local webs were obtained by sequentially and randomly selecting a 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. 11).

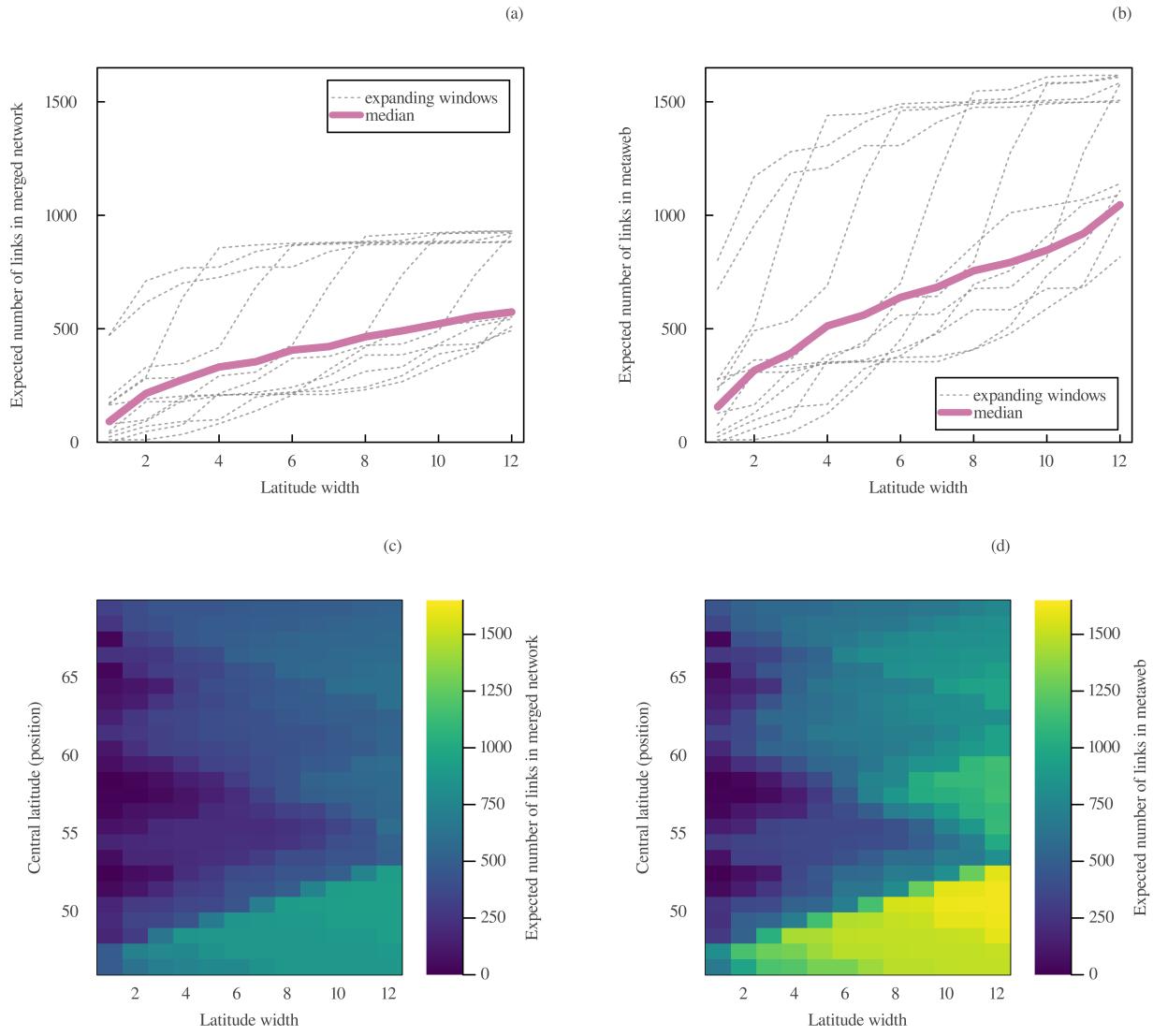


Figure 2: Spatial scaling of interactions. Expected number of host-parasite interactions in a network aggregating all (a) local and (b) regional probabilistic interactions within a latitudinal window of a given length. Every dashed curve corresponds to a different expanding window characterized by a 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. 11.

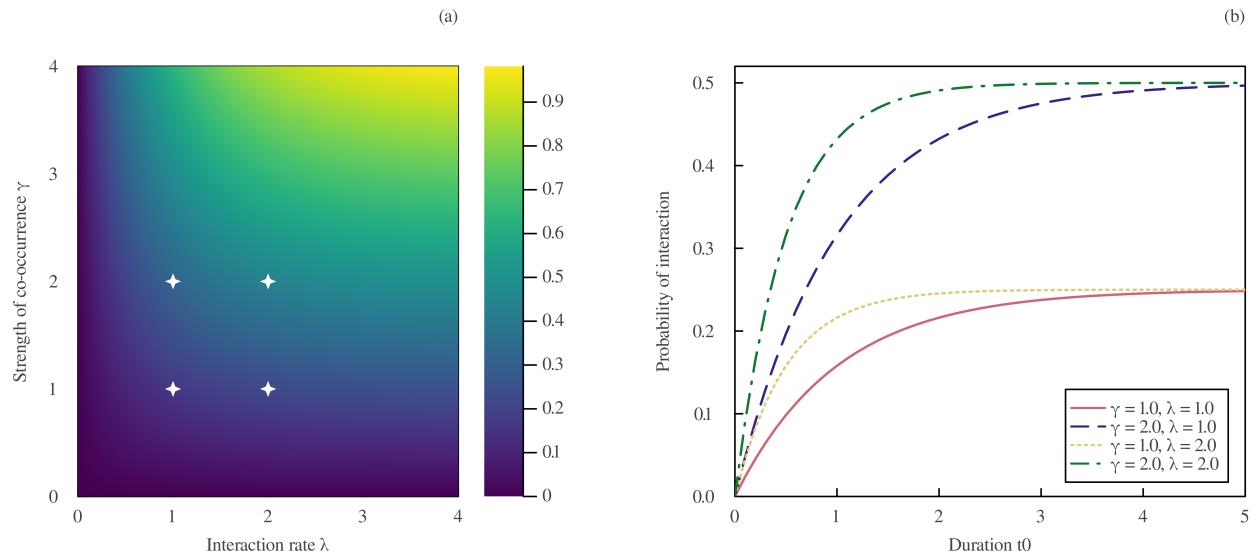


Figure 3: Parameters of the spatiotemporally explicit model of interactions. (a) Probability of local interaction given by the process model (Eq. 16) under different values of λ_l and γ , with $t_0 = 1$. The parameter values used in the right panel are denoted by the white stars. (b) Scaling of the probability of interaction with the duration parameter t_0 in Eq. 16, 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.

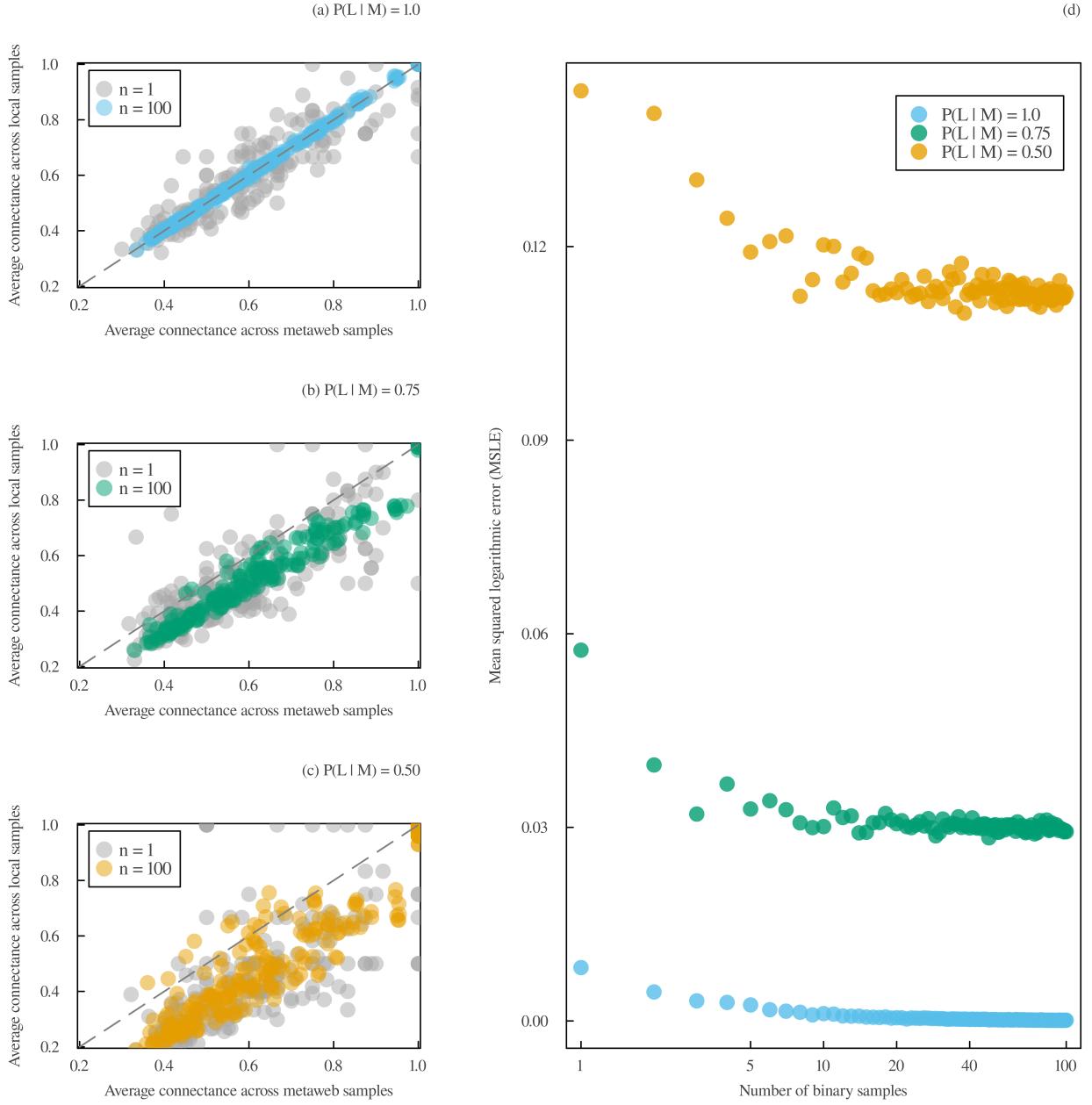


Figure 4: Connectance of sampled binary interaction webs. Comparison between the average connectance of binary interaction network samples obtained from the local webs and metawebs of probabilistic interactions. Each dot corresponds to a different site. The local probability of interaction between potentially 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 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 $P(L_{i \rightarrow j} \mid M_{i \rightarrow j})$ 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.