

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?) conveys uncertainties in our knowledge of interactions and information on their variability. 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 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 or ecological feasibility (regional). 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), conditional variables and uncertainty sources.

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1 Introduction

2 Species interactions are variable and uncertain

3 As we try to navigate global biodiversity change, filling in knowledge gaps about biodiversity becomes
4 instrumental to monitoring and mitigating those changes (Abrego *et al.* 2021; Gonzalez & Londoño 2022;
5 Hortal *et al.* 2015). However, cataloging species, populations and, in particular, ecological interactions (e.g.,
6 predation, parasitism, and pollination) is a substantial challenge (Pascual *et al.* 2006; Polis 1991). There are
7 methodological and biological constraints that hinder our ability to document species interactions, inevitably
8 leading to uncertainty in our knowledge of interactions. For example, the spatial and temporal uncoupling of
9 species (e.g., nocturnal and diurnal species coexisting in the same space with different daily activity timings,
10 Jordano 1987) and the large number of rare and cryptic interactions in a community, contribute to these
11 knowledge gaps by making it more difficult to observe interactions (Jordano 2016).

12 Several conditions must be satisfied for an interaction to be observed locally. First, both species must have
13 overlapping geographic ranges, i.e. they must co-occur within the region of interest (Cazelles *et al.* 2016;
14 Morales-Castilla *et al.* 2015). Second, they must have some probability of meeting within a defined time frame
15 (Poisot *et al.* 2015). Probabilities of interspecific encounters are typically low, especially for rare species with
16 low abundances (Canard *et al.* 2012; Canard *et al.* 2014; Vázquez *et al.* 2007). 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, such as their phenotypes (Bolnick *et al.* 2011; Gravel *et al.* 2013; Stouffer *et al.* 2011) and
20 behavior (Choh *et al.* 2012; Pulliam 1974), are locally compatible in that specific environment (Poisot *et al.*
21 2015). Because these conditions are not consistently met locally, there will inevitably be instances where
22 interactions will be observed and others where they will not.

23 Documenting the location and timing of interactions is difficult when accounting for the spatiotemporal
24 variability of ecological interactions (Poisot *et al.* 2012, 2015). Knowing the biological capacity of two species
25 to interact directly (via e.g., trophic interactions) is necessary but not sufficient for inferring their interaction at a
26 specific time and space. Environmental factors, such as temperature (Angilletta *et al.* 2004), drought
27 (Woodward *et al.* 2012), climate change (Araujo *et al.* 2011; Gilman *et al.* 2010; Woodward *et al.* 2010),
28 habitat characteristics (e.g., presence of refuges where prey can hide from predators,
29 **Grabowski2004Habitat?**), and land use change (Tylianakis *et al.* 2007), contribute to this spatiotemporal

30 variability by impacting species abundance and traits. Interactions may also be influenced by a third species
31 (e.g., a more profitable prey species, Golubski & Abrams 2011; Sanders & van Veen 2012). Even under
32 favorable circumstances, there remains a possibility that the interaction does not occur locally, either due to the
33 intricate nature of the system or simply by chance. If it does occur, it might go undetected, particularly if it
34 happens infrequently. In this context, it is unsurprising that our knowledge of ecological interactions remains
35 limited (Hortal *et al.* 2015) despite extensive biodiversity data collection (Schmeller *et al.* 2015).

36 We distinguish the variability of interactions from their uncertainty. Interaction variability is defined as the
37 changes in the occurrence or strength of interactions along spatial, temporal, or environmental axes (Poisot *et al.*
38 2015). It is a property of interactions that should be quantified if we aim for a comprehensive understanding of
39 ecological networks. Stochasticity is the inherent randomness or unpredictability of interactions that lead to this
40 variability. Conversely, uncertainty is defined as a lack of knowledge about the occurrence of interactions.
41 When using statistical models to infer interactions, uncertainty sources include input data, parameter, and model
42 structure uncertainties (Simmonds *et al.* 2024). Input data uncertainty arises from our inability to empirically
43 observe all interactions and from measurement errors in environmental and biological variables used for
44 inference. Parameter uncertainty represents a plausible range of values for a parameter whose exact value is
45 unknown. For example, we may calculate a range of plausible values for interaction variability (e.g., there could
46 be a 50% certainty that an interaction occurs 50% of the time). Model structure uncertainty recognizes that
47 different statistical models may adequately predict interactions. In contrast to variability, uncertainty can be
48 reduced by sampling additional data (except for model uncertainty, which will persist regardless of sampling
49 effort). Simmonds *et al.* (2024) underscores the importance of quantifying and reporting these diverse sources
50 of uncertainty, alongside ensuring their appropriate propagation to model output (such as predicted interactions)
51 and higher-level measures (such as network structure). While recognizing that these definitions may not be
52 universally accepted, clarifying the distinction between variability and uncertainty enables us to better
53 comprehend the sources of our knowledge gaps about ecological interactions.

54 Species interactions as probabilistic objects

55 The recognition of the intrinsic variability and uncertainty of species interactions has led ecologists to expand
56 their representation of ecological networks to include a probabilistic view of interactions (Dallas *et al.* 2017; Fu
57 *et al.* 2021; Poisot *et al.* 2016). This allows filling in the Eltonian shortfall (i.e., the gap between our current
58 knowledge and a comprehensive understanding of interactions, Hortal *et al.* 2015) by modeling the probability

59 of occurrence of interactions (e.g., Gravel *et al.* 2019), which can be an important tool for directing efforts and
60 taking action (Carlson *et al.* 2021), especially in places where access and resources for research are scarce. A
61 probability is a measure of how likely a specific outcome is, based on both the uncertainty and variability of
62 interactions. Interaction probabilities may be uncertain when there is a distribution of plausible probability
63 values. The probabilistic representation of interactions has been applied to direct interactions, which are
64 conceptually and mathematically analogous regardless of their biological type (e.g., predation and pollination).
65 This is in contrast with indirect interactions (e.g., interspecific competition), which arise from distinct
66 ecological processes and are often not directly observable (Kéfi *et al.* 2015, 2016). By accounting for the
67 uncertainty and variability of direct interactions, networks of probabilistic interactions (which differ from
68 *probabilistic networks* describing the uncertainty and variability of the *whole* network) may provide a more
69 realistic portrait of species interactions.

70 Probabilistic interactions differ from binary interactions. Networks of probabilistic interactions, within a
71 Bayesian perspective, express our degree of belief (or confidence) regarding the occurrence or observation of
72 interactions. In a frequentist approach, they represent the expected relative frequencies of interactions over
73 many repeated trials or sampling events. In contrast, interactions are simply regarded as either occurring or not
74 in networks of deterministic binary interactions. Based on the scale at which they are estimated, interaction
75 probabilities may reflect our level of confidence in whether interactions will be observed, realized locally, or
76 biologically feasible. Our level of confidence should be more definitive (approaching either 0 or 1) as we extend
77 our sampling to a broader area and over a longer duration, thereby diminishing the uncertainty of our knowledge
78 of interactions (but not necessarily the estimation of their variability). In the broadest sense, binary interactions
79 are also a type of probabilistic interaction, in which the numerical value of an interaction is restrained to 0
80 (non-occurring) or 1 (occurring). In networks of probabilistic interactions, only forbidden interactions (i.e.,
81 interactions prohibited by biological traits or species absence, Jordano *et al.* 2003; Olesen *et al.* 2010) have a
82 probability value of zero, provided that intraspecific trait variability is considered (Gonzalez-Varo & Traveset
83 2016). Understanding the nuances between probabilistic and binary interactions is essential for accurately
84 modeling and interpreting ecological networks.

85 The application and development of computational methods in network ecology, often based on a probabilistic
86 representation of interactions, can alleviate (and guide) the sampling efforts required to document species
87 interactions (Strydom *et al.* 2021). For example, statistical models can be used to estimate the uncertainty of
88 pairwise interactions (Cirtwill *et al.* 2019) and the probability of missing (false negatives) and spurious (false

positives) interactions (Guimerà & Sales-Pardo 2009), helping us identify places where sampling is most needed to reduce this uncertainty. Statistical models can also predict networks without prior knowledge of pairwise interactions. They may do so using body size (Caron *et al.* 2024; 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. Before being used to test ecological hypotheses, predicted networks must be validated against empirical data (Brimacombe *et al.* 2024), which could be sampled strategically to optimize the validation process. 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), are examples of common probabilistic interaction models. Null models can produce underlying distributions of network measures for null hypothesis significance testing. 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. 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 networks. These models and measures support the use of probabilistic interactions 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 networks (Gilman *et al.* 2010).

We lack a clear understanding of probabilistic species interactions

We still lack a precise definition of probabilistic interactions, which makes the estimation and use of these data more difficult. In this manuscript, 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: local networks describing probabilities of realized interactions, and regional networks (metawebs) describing probabilities of potential interactions. We highlight the distinctions in the ecological meaning of these two representations of interactions and examine their properties and relationships (particularly with space, time, and between each other).

The lack of clear guidelines on the use of probabilistic interaction data is worrisome, as it affects both data producers and re-users who generate and manipulate these numbers. This is concerning because sampling strategies and decisions regarding network construction can affect our understanding of network properties

118 (Brimacombe *et al.* 2023). There is currently no reporting standard that could guide the documentation of all
119 types of probabilistic interactions (Salim *et al.* 2022 discuss data standards for deterministic mutualistic
120 networks). Clear reporting standards for probabilistic interactions would support more adequate manipulation
121 and integration of interaction data from different sources and guard against possible misinterpretations arising
122 from ambiguous definitions of probabilistic interaction networks. Data documentation should outline the nature
123 (i.e., local or regional) and type (e.g., predatory or pollination) of interactions, provide information regarding
124 the taxonomic level, identities, and characteristics (e.g., life stages) of the individuals involved in an interaction,
125 present the mathematical formulation of probabilities, including clearly identified conditional variables (e.g.,
126 spatial and temporal scales), and describe the methods and contexts (e.g., location, time, environmental
127 conditions) in which interactions were estimated. Inadequately documented probabilistic interaction data should
128 be used with caution when analyzing ecological networks. These broad principles remain relevant and
129 applicable across different types of direct interactions. In the following sections, we discuss the definitions,
130 conditions, and estimation of probabilistic interactions as we scale up from pairwise interactions to interactions
131 within local and regional networks.

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

133 **What are probabilistic interactions?**

134 Consider a scenario where an avian predator has just established itself in a northern habitat home to a small
135 rodent. Suppose their interaction has not been previously observed, either because these species have never
136 co-occurred before or because previous sampling failed to detect an interaction despite their co-occurrence.
137 What is the probability that the rodent is part of the diet of the avian predator, or put differently, what is the
138 probability that they interact? Answering this question requires some clarification, as there are multiple ways to
139 interpret and calculate interaction probabilities. We could calculate the probability that the traits of these
140 species match, i.e. that the avian predator possesses the biological attributes to capture and consume the rodent.
141 We could also calculate the probability that their traits support an interaction under the typical environmental
142 conditions of the new habitat. For example, because avian predators hunt by sight, predation could be possible
143 in the absence of snow but highly improbable when snow is present, as rodents may use it as a shelter to hide
144 from predators. Finally, we could calculate the probability that the avian predator will consume the rodent at
145 *that* particular location, for which the spatial and temporal boundaries need to be specified. The estimation of

146 the probability of interaction between these two species, whether through predictive models or informative prior
147 probabilities, hinges on our understanding of these probabilities and the specific ecological processes we aim to
148 capture.

149 An important aspect to consider when estimating or using interaction probabilities is knowing if they describe
150 the probability of potential or realized interactions, as these two types of interactions have distinct meanings and
151 sources of uncertainty and variability. A potential (regional) interaction is defined as the biological or
152 ecological capacity of two taxa to interact (i.e., the probability that they interact if they were to encounter each
153 other, given sufficient time and appropriate environmental conditions) whereas a realized (local) interaction is
154 the occurrence or observation of this interaction in a well-defined space and time (i.e., the probability that they
155 interact locally). For two co-occurring taxa and over enough time, the probability of local interaction tends
156 toward the probability of regional (potential) interaction. A longer duration increases the probability that
157 species will eventually encounter each other and that local environmental conditions supporting an interaction
158 will occur, provided that species have the biological capacity to interact. Recognizing the distinction between
159 probabilistic regional and local interactions is crucial for accurately interpreting interaction probabilities in
160 ecological networks.

161 We use the terms *metaweb* (Dunne 2006) to designate regional networks of potential interactions and *local*
162 *networks* (Poisot *et al.* 2012) for those of realized interactions. Metawebs are the network analogs of the species
163 pool, where local networks originate from a subset of both species (nodes) and interactions (edges) of the
164 regional metaweb (Saravia *et al.* 2022). Without clear documentation, it can be challenging to know if published
165 probabilistic interaction networks describe local or regional interactions. When probabilistic local interactions
166 are used and interpreted incorrectly as regional interactions (and conversely), this may generate misleading
167 findings during data analysis. A better understanding of probabilistic local and regional interaction networks
168 would facilitate a more adequate use of interaction data (e.g., when studying network-area relationships in local
169 networks and metawebs) and prevent misinterpretations of the biological meaning of probabilistic interactions.

170 **What is the outcome of probabilistic interactions?**

171 **The outcome of probabilistic interactions is usually binary**

172 Local networks and metawebs, like any type of network, are made of nodes and edges that may be represented
173 at different levels of organization. The basic units of ecological networks are individuals that interact with each

174 other (e.g., by predation in food webs, Elton 2001), forming individual-based networks (Melián *et al.* 2011).
175 The aggregation of these individuals into more or less homogeneous groups (e.g., populations, species, families,
176 feeding guilds) allows us to represent nodes at broader taxonomic scales, which affects our interpretation of the
177 properties of these systems (Guimarães 2020; Hemprich-Bennett *et al.* 2021).

178 Ecologists have traditionally represented interactions (edges) as binary objects that were considered realized
179 after observing at least one individual from group i interact with at least another individual from group j . In an
180 adjacency matrix B of binary interactions, the presence or absence of an interaction $B_{i,j}$ between two taxa can
181 be viewed as the result of a Bernoulli trial $B_{i,j} \sim \text{Bernoulli}(P(B_{i,j}))$, with $P(B_{i,j})$ being the probability of
182 interaction. This interaction probability characterizes our limited ecological knowledge and/or the intrinsic
183 spatiotemporal variability of the interaction. It may be estimated through predictive models (e.g., those based
184 on biological traits and species abundances) or expert (prior) knowledge about the interaction. In networks of
185 probabilistic interactions, the edge values $P(B_{i,j})$ are probabilistic events whose only two possible outcomes are
186 the presence ($B_{i,j} = 1$) or absence ($B_{i,j} = 0$) of an interaction between each pair of nodes. Depending on the
187 type of probabilistic interaction network (local network or metaweb), the mathematical formulation and
188 interpretation of stochastic parameters like $P(B_{i,j})$ can be linked to environmental and biological factors such as
189 species abundances, species traits, area, and time, for example using logistic regression with continuous
190 explanatory variables. This allows us to model the probability that at least two individuals interact under these
191 conditions.

192 The variability of an interaction determines the fraction of networks in which it occurs. This fraction can be
193 predicted by using a Binomial distribution, assuming a constant interaction probability and independence
194 between interactions in different networks (trials). When considering uncertainties around the estimation of
195 $P(B_{i,j})$, a Beta distribution may be used to represent the relative likelihood of different probability values. For
196 example, when calculating the probability of interaction between two taxa based on their local abundances, any
197 uncertainty in their abundances would introduce uncertainty in the interaction probability at the local scale. If
198 we take into account the uncertainty of the interaction probability, a Beta-Binomial distribution can be used to
199 predict the number of networks in which the interaction occurs. Empirically observing an interaction between
200 two taxa at a given location and time provides important information that can be used to update previous
201 estimates of $P(B_{i,j})$, informing us of the conditions that enabled them to interact locally. By sampling binary
202 interactions in different contexts, we can thus estimate their local variability more precisely.

203 **The outcome of probabilistic interactions may also be quantitative**

204 Even though binary interaction networks constitute a highly valuable source of ecological information (Pascual
205 *et al.* 2006), they overlook interaction strengths. Represented in a quantitative adjacency matrix W , interaction
206 strengths better describe the energy flows, demographic impacts or frequencies of interactions between nodes
207 (Berlow *et al.* 2004; Borrett & Scharler 2019), with $W_{i,j}$ being a natural \mathbb{N} or real \mathbb{R} number depending on the
208 measure. For example, they may represent local interaction rates (e.g., the flower-visiting rates of pollinators in
209 a mutualistic network, Herrera 1989). Relative frequencies of interactions may be used as a measure of both the
210 strength and probability of local interactions that are biologically feasible. When interaction strengths
211 characterize predation pressure on prey, they can serve as parameters in a Lotka-Volterra model (e.g.,
212 Emmerson & Raffaelli 2004). The extra amount of ecological information in quantitative networks typically
213 comes at a cost of greater sampling effort and data volume (Strydom *et al.* 2021), especially when using
214 predictive models that quantify the uncertainty and variability of quantitative interactions (Berlow *et al.* 2004).
215 However, if two taxa are repeatedly found together without interacting, there may be more uncertainty about
216 their capacity to interact than their interaction strength (which would assuredly be close to 0).

217 Like binary interaction networks, the uncertainty and variability of interaction strengths can be represented
218 probabilistically. Interaction strengths can follow many probability distributions depending on the measure. For
219 instance, they can follow a Poisson distribution $W_{i,j} \sim \text{Poisson}(\lambda_{i,j}t_0)$ when predicting the number of
220 interactions between individuals during a time interval t_0 , with $\lambda_{i,j}$ being the expected rate at which individuals
221 of taxa i and j interact (e.g., the expected number of prey j consumed by all predators i). The Poisson
222 distribution can also be 0-inflated when taking into account non-interacting taxa (e.g., Boulangeat *et al.* 2012
223 employ a 0-inflated model to analyze species abundance following the modeling of species presence and
224 absence), which constitute the majority of taxa pairs in most local networks (Jordano 2016). Regardless of the
225 measure, estimating the uncertainty of quantitative interactions enables us to consider a range of possible values
226 of interaction strength.

227 Because of the methodological difficulties typically encountered when building deterministic quantitative
228 networks, binary interaction networks, which are usually easier to sample (Jordano 2016) and predict (Strydom
229 *et al.* 2021), have been more frequently studied and used. Mathematical models such as Ecopath (Plagányi &
230 Butterworth 2004) partially mitigate these difficulties, but the number of biological parameters required to make
231 predictions hinders their application in many systems. Moreover, most published probabilistic interaction

232 networks (e.g., Strydom *et al.* 2022) and methods (e.g., Poisot *et al.* 2016) involve probabilistic interactions
233 whose outcome is binary. This underlines the need for better guidelines on the interpretation and manipulation
234 of probabilistic interactions with binary outcomes first, to ensure the appropriate use of these networks and
235 methods. For these reasons, the primary focus of the remainder of this manuscript is on the interpretation of
236 interaction probabilities that determine the presence or absence of interactions, in both local networks and
237 metawebs.

238 Local networks: communities interacting in space and time

239 What are local probabilistic interactions?

240 Local networks of probabilistic interactions describe how likely taxa are to interact in a local context. Local
241 interactions are contingent upon the environmental conditions experienced by the community and the matching
242 of taxa's local biological traits. In local networks, edges commonly represent our degree of belief that two taxa
243 interact in nature, but can also represent the probability of empirically *observing* this interaction (Catchen *et al.*
244 2023). Local interactions may thus arise from both the ecological (realized interactions) and sampling
245 (observed interactions) processes taking place locally.

246 Local networks are delineated within a particular location and time. We define space as the collection of
247 geographic coordinates (x, y, z) , with (x, y) representing longitude and latitude coordinates, and z denoting
248 either altitudes or depths. These point coordinates delineate the spatial boundaries of the system, which may be
249 portrayed as a polyhedron. Ecological interactions may vary along latitudinal and altitudinal gradients, as
250 evidenced by changes in hummingbird-plant interactions (Weinstein & Graham 2017a, b) and mosquito biting
251 rates (e.g., Kulkarni *et al.* 2006) at different elevations. On the other hand, time is defined as the specific time
252 period within which interactions were either observed or predicted. Even though space and time are continuous
253 variables that should yield probability *densities* of interactions (i.e., relative likelihoods of interactions
254 occurring at infinitesimal locations and instants in time), these definitions enable them to be conceptualized as
255 distinct patches and time segments. Treating space and time as discrete dimensions aligns with the common
256 sampling methods of ecological networks and provides probabilities of interactions, which can be obtained by
257 integrating probability densities over space and time. We can quantify both an area A_0 and a duration t_0 with
258 these definitions. By studying probabilistic local interaction networks, we may thus conduct spatiotemporal
259 analyses of local interactions (Box 1), enhancing our understanding of interactions occurring in distinct

260 environmental contexts.

261 **What are local probabilistic interactions conditioned on?**

262 **Local interactions may be conditioned on co-occurrence**

263 The probability that two taxa i and j interact in a local network $L_{x,y,z,t}$ (spatial and temporal subscripts hereafter
264 replaced by the shorter subscript k for clarity) can be conditioned on many environmental and biological factors.
265 In addition to network area (or volume) A_0 and duration t_0 , they may be conditioned on taxa co-occurrence
266 $X_{i,j,k}$, which is usually Boolean, describing if the geographic distributions of both taxa overlap within the study
267 area. As illustrated in Box 1, co-occurrence may be modeled probabilistically, in which case it may conform to
268 a Bernoulli distribution $X_{i,j,k} \sim \text{Bernoulli}(P(X_{i,j,k}))$. The probability of co-occurrence can be calculated using
269 the individual (marginal) occurrence probabilities $P(X_{i,k})$ and $P(X_{j,k})$. Given that taxa occurrences are not
270 independent of each other, the probability of co-occurrence can be calculated by multiplying the probability of
271 occurrence of one taxon by the probability of occurrence of the other given that the first one is present:

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

272 The probability of co-occurrence $P(X_{i,j,k})$ can be estimated through the application of joint species distribution
273 models (e.g., Pollock *et al.* 2014), potentially taking into account biotic interactions (Staniczenko *et al.* 2017).
274 Given that the probability that two non-co-occurring taxa interact locally is zero (i.e., $P(L_{i,j,k}|X_{i,j,k} = 0) = 0$),
275 the probability of local interaction can be obtained by multiplying the probability of interaction given
276 co-occurrence with the probability of co-occurrence:

$$P(L_{i,j,k}) = P(L_{i,j,k}|X_{i,j,k}) \times P(X_{i,j,k}). \quad (2)$$

277 Knowing that two taxa co-occur improves our estimation of the probability that they interact locally by
278 mitigating a potential source of uncertainty.

279 **Local interactions may be conditioned on different environmental and biological factors**

280 Local interactions may also be conditioned on local environmental factors such as temperature (Angilletta *et al.*
281 2004), precipitation (Woodward *et al.* 2012), habitat structure (Klecka & Boukal 2014), and presence of other
282 taxa in the network (Kéfi *et al.* 2012; Pilosof *et al.* 2017). We use the variable E_k to describe the local
283 environmental context in which interaction probabilities were estimated. For example, in a mesocosm
284 experiment estimating interaction probabilities between predators and prey with and without refuges, E_k would
285 represent the presence or absence of these refuges. Like co-occurrence, E_k can also be modeled
286 probabilistically when the variability or uncertainty of environmental factors is considered. E_k represents all
287 environmental variables that were taken into consideration when measuring interaction probabilities; it is
288 therefore a subset of all environmental factors acting on ecological interactions.

289 Other important factors that can impact interaction probabilities at the local scale are taxa local abundances $N_{i,k}$
290 and $N_{j,k}$, which affect encounter probabilities (Canard *et al.* 2012), and local traits $T_{i,k}$ and $T_{j,k}$ (e.g., movement
291 rates, **Beardsell2021Derivation?**; **Cherif2024Environment?**), which may also impact encounter probabilities
292 as well as the ability of individuals to interact after encountering each other (Caron *et al.* 2024; Poisot *et al.*
293 2015). Local interaction probabilities may also be conditioned on higher-level properties of the community (i.e.,
294 the emerging structure of ecological networks), which we denote by $f(L_k)$. Many topological null models (i.e.,
295 statistical models that randomize interactions by retaining certain properties of the network while excluding
296 others) provide interaction probabilities from selected measures of network structure, such as connectance
297 (Fortuna & Bascompte 2006) and the degree distribution (Bascompte *et al.* 2003). Biological factors, whether
298 at the scale of individual taxa pairs or the community, may thus impact how we estimate and define interaction
299 probabilities.

300 **Local interactions may be conditioned on biological feasibility**

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

$$P(L_{i,j,k}) = P(L_{i,j,k}|M_{i,j} = 1) \times P(M_{i,j} = 1). \quad (3)$$

305 Low values of $P(L_{i,j,k}|M_{i,j})$ indicate that feasible interactions rarely occur locally, intermediate values around
306 50% suggest considerable spatiotemporal variability, while high values indicate that regional interactions are
307 nearly always realized locally. The local probability of interaction between a given pair of taxa is thus always
308 equal to or below their probability of regional interaction. Taking into account biological feasibility in our
309 estimation of local interaction probabilities leverages information from the metaweb to better predict the local
310 occurrence of interactions (Dansereau *et al.* 2023; Strydom *et al.* 2021).

311 **Conditional variables must be explicitly stated**

312 The probability that two taxa i and j interact in a local network L_k can thus be conditioned on their
313 co-occurrence $X_{i,j,k}$ (or more explicitly on their occurrences $X_{i,k}$ and $X_{j,k}$), local abundances $N_{i,k}$ and $N_{j,k}$, local
314 traits $T_{i,k}$ and $T_{j,k}$, local environmental conditions E_k , network area (or volume) A_0 , time interval t_0 , network
315 properties $f(L_k)$, and biological feasibility $M_{i,j}$. When these conditions are not explicit, it may be because they
316 have been marginalized over, which would be reflected in the overall uncertainty of the interaction. The local
317 probability of interaction is described by the following expression when all of these conditional variables are
318 included:

$$P(L_{i,j,k}|X_{i,k}, X_{j,k}, N_{i,k}, N_{j,k}, T_{i,k}, T_{j,k}, E_k, A_0, t_0, f(L_k), M_{i,j}). \quad (4)$$

319 These conditional variables do not all need to be considered at all times. The representation of the local context
320 in which probabilities are estimated and the variables that should be taken into consideration depend on the
321 study system, the objectives of the study, and the resources available to the researchers. For example, Gravel *et*
322 *al.* (2019) analyzed local European host-parasite networks of willow-galling sawflies and their natural enemies,
323 all referenced in space and time, to infer probabilities of local interactions between co-occurring species. This
324 was achieved by including temperature and precipitation as conditional variables in their models. In Box 2, we
325 reuse these data to show the extent of variation among these local networks. We do so by measuring their
326 dissimilarity with the regional network (metaweb aggregating all local interactions), both in terms of species
327 composition and interactions. We built local probabilistic networks following eq. 3, showing that insufficient
328 local variation (high probability of local interaction among potentially interacting species) results in an
329 overestimation in both the number of interactions and connectance (i.e., the proportion of all of the
330 non-forbidden links that are realized). This analysis was conducted for illustrative purposes, and other

331 conditional variables could have been used to make these comparisons.
 332 When accounted for, conditional variables should be clearly described in the documentation of the data
 333 (Brimacombe *et al.* 2023), preferentially in mathematical terms to avoid any confusion in their interpretation
 334 and to limit manipulation errors during their re-use. For instance, ecologists should be explicit about their
 335 consideration ($P(L_{i,j,k}|X_{i,j,k})$) or not ($P(L_{i,j,k})$) of co-occurrence in their estimation of local interaction
 336 probabilities, as this can change our interpretation of the data and understanding of potential uncertainty
 337 sources. Reporting the scale and level of aggregation of the data enables us to more accurately study the
 338 underlying ecological processes (Clark *et al.* 2011) and manipulate or propagate uncertainty to different
 339 aggregation levels (Simmonds *et al.* 2024). In Tbl. 1, we present examples of studies that used different
 340 expressions of probabilistic interactions with different conditional variables. We included in this table the
 341 probability of empirically observing an interaction that is realized locally $P(O_{i,j,k}|L_{i,j,k})$ to underscore the
 342 distinction between local observations and actual realizations of interactions.

Table 1: Mathematical expressions of probabilistic interactions. The probability of interaction between two taxa i and j is interpreted differently in a local network L_k of realized interactions, a local network O_k of observed interactions, a metaweb M of potential interactions (representing the *biological* feasibility of interactions), and a metaweb M^* of potential interactions (representing the *ecological* 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 models used for estimation, is presented alongside examples of studies that employed them (with specific variables indicated in parentheses, when applicable). The study marked with an asterisk has been conducted on binary interaction networks. The boxes in our study that discuss these expressions are also specified.

Expression	Type	Outcome	Common models	Reference
$P(L_{i,j,k} X_{i,k}, X_{j,k}, \dots)$	local	realization of the interaction given taxa co-occurrence	species distribution models	Gravel <i>et al.</i> (2019), Dansereau <i>et al.</i> (2023), Boxes 1 and 5
$P(L_{i,j,k} N_{i,k}, N_{j,k}, \dots)$	local	realization of the interaction given taxa abundances	neutral models	Canard <i>et al.</i> (2014)
$P(L_{i,j,k} T_{i,k}, T_{j,k}, \dots)$	local	realization of the interaction given local traits	trait matching models	Caron <i>et al.</i> (2024), Box 4
$P(L_{i,j,k} E_k, \dots)$	local	realization of the interaction given local environmental conditions	environmental- based models	Gravel <i>et al.</i> (2019) (temperature and precipitation)

Expression	Type	Outcome	Common models	Reference
$P(L_{i,j,k} A_0, \dots)$	local	realization of the interaction in a given area or volume	spatial models	Galiana <i>et al.</i> (2018) *, Box 3
$P(L_{i,j,k} t_0, \dots)$	local	realization of the interaction during a given time period	temporal models	Weinstein & Graham (2017a), Boxes 1 and 3
$P(L_{i,j,k} f(L_k), \dots)$	local	realization of the interaction given network structure	topological models	Fortuna & Bascompte (2006) (connectance), Stock <i>et al.</i> (2017)
$P(L_{i,j,k} M_{i,j}, \dots)$	local	realization of the interaction given that it is biologically feasible	spatiotemporal models	Dansereau <i>et al.</i> (2023), Boxes 2, 3, and 5
$P(O_{i,j,k} L_{i,j,k}, \dots)$	local	observation of the interaction given that it is realized locally	sampling models	Catchen <i>et al.</i> (2023)
$P(M_{i,j} T_i, T_j)$	regional	biological feasibility of the interaction given regional traits (non-forbiddenness)	trait matching models	Strydom <i>et al.</i> (2022), Box 4
$P(M_{i,j}^* T_i, T_j, E)$	regional	ecological feasibility of the interaction given regional traits and environmental conditions	trait matching and environmental-based models	this study

343 How are local probabilistic interactions estimated?

344 Various statistical models can be used to estimate local interaction probabilities, some of which are presented in
 345 Tbl. 1. These models can be based on multiple conditional variables. Although these variables correspond to
 346 distinct ecological inquiries or mechanisms related to ecological interactions, they may covary with each other,
 347 such as the possible dependence of $X_{i,j,k}$ and E_k on spatial and temporal scales. When estimating interaction
 348 probabilities using e.g. a generalized linear model with multiple explanatory variables that might not all be
 349 independent, it may become important to address collinearity. In such cases, it may be necessary to use variable

350 selection techniques before fitting the model to data to mitigate this issue. Other challenges and opportunities
351 associated with predictive models of species interactions are reviewed in Strydom *et al.* (2021).

352 When using multiple competing models to estimate local interaction probabilities, rather than selecting a single
353 model that best fits the data, model averaging may enhance our estimations. Model weights represent the
354 probability that each model is the most suitable for explaining the data, and may be measured using Akaike
355 weights (Burnham & Anderson 2004; Wagenmakers & Farrell 2004). For instance, given two competing
356 models mod_1 and mod_2 with respective probabilities (or weights) $P(mod_1)$ and $P(mod_2)$, the average
357 probability of interaction $P(L_{i,j,k})$ can be calculated as follows:

$$P(L_{i,j,k}) = P(L_{i,j,k}|mod_1) \times P(mod_1) + P(L_{i,j,k}|mod_2) \times P(mod_2). \quad (5)$$

358 Model averaging takes into account the uncertainty of model structure in our estimation of local interaction
359 probabilities. Regardless of the model used for prediction, it is crucial to quantify and disclose all sources of
360 uncertainty to understand better the validity and limitations of our predictions (Simmonds *et al.* 2024).

Box 1: A spatiotemporally explicit model of interactions

Ecologists may resort to predictive models to reconstruct local networks across time and space. We introduce and develop a simple generative Bayesian model for probabilistic local interactions, which explicitly accounts for their spatiotemporal variability. Our model is not designed for regional interactions, which do not vary spatially nor temporally. Rather, it could prove valuable for generating new data on local interactions across time and space, following parameter inference.

As indicated by Eq. 2, the probability that two taxa i and j interact locally can be obtained by multiplying their probability of interaction given co-occurrence with their probability of co-occurrence. The probability of interaction given co-occurrence can be made temporally explicit by modeling it as a Poisson process with rate parameter λ_k . This parameter represents the local expected frequency of interaction between co-occurring taxa. The probability that two co-occurring taxa interact at least once during a time interval t_0 can be given by:

$$P(L_{i,j,k}|X_{i,j,k}) = 1 - e^{-\lambda_k t_0}, \quad (6)$$

which tends toward 1 as $t_0 \rightarrow \infty$ if $\lambda_k > 0$. In other words, two co-occurring taxa with a nonzero rate of

interaction will inevitably interact at least once in a sufficiently long time interval.

The occurrence of an interaction between i and j may be the result of a Bernoulli trial with probability $P(L_{i,j,k})$. A Bayesian model can be built using the preceding equations to generate new interaction data, following the inference of the λ_k and $P(X_{i,j,k})$ parameters.

$$L_{i,j,k} \sim \text{Bernoulli}(P(L_{i,j,k})) \quad (7)$$

$$P(L_{i,j,k}) = P(X_{i,j,k})(1 - e^{-\lambda_k t_0}) \quad (8)$$

$$P(X_{i,j,k}) \sim \text{Beta}(2, 2) \quad (9)$$

$$\lambda_k \sim \text{Exponential}(2) \quad (10)$$

In Fig. 1, we show the variation in the probability of interaction under different parameter values. In the right panel, we notice that the probability of interaction always converges toward the probability of co-occurrence $P(X_{i,j,k})$, for all positive values of the interaction rate.

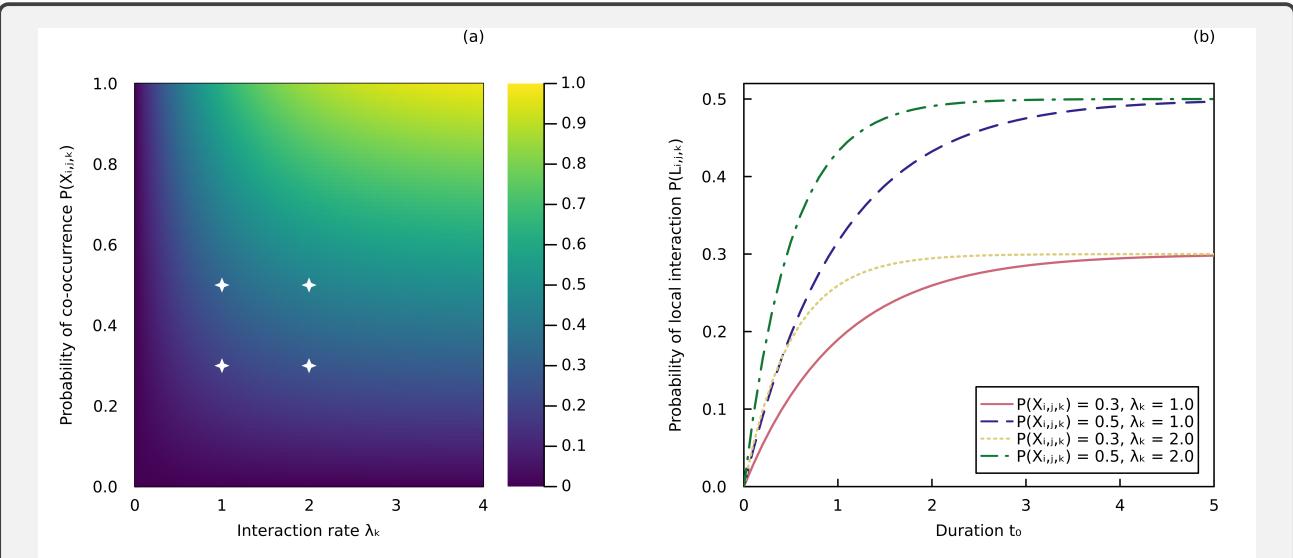


Figure 1: Parameters of the spatiotemporally explicit model of interactions. (a) Probability of local interaction given by the process model (Eq. 8) under different values of λ_k (interaction rate) and $P(X_{i,j,k})$ (probability of co-occurrence), with $t_0 = 1$ (duration). The probability of local interaction represents the probability that the two taxa will interact at least once within the given time interval. Parameters t_0 and λ_k have complementary units (e.g., t_0 in months and λ_k in number of interactions per month). The parameter values used in the right panel are denoted by the white stars. (b) Scaling of the probability of interaction with the duration parameter t_0 , for different values of λ_k and $P(X_{i,j,k})$.

This model can be customized in different ways, such as linking both parameters to specific environmental or biological variables. For instance, the probability of co-occurrence could be modeled as a function of climatic variables, while the interaction rate parameter could be modeled based on taxa abundances.

363

Box 2: Dissimilarity of local host-parasite networks

We present a way to assess local network variability and dissimilarity regarding species composition and interactions. We do so by comparing local tripartite host-parasite networks to the metaweb using data from Kopelke *et al.* (2017). This collection of networks consists of interactions between willows, willow-galling sawflies, and their natural enemies sampled across Europe. All data manipulation and methods are described in Appendix 1. All code and data to reproduce these analyses are available at the Open Science Framework (TBD).

In Fig. 2a-b, we show how the dissimilarity between the metaweb of binary interactions and aggregated local networks changes with the number of sampled local networks. We compared the metaweb and the aggregated local networks using the dissimilarity in species composition (β_S , Fig. 2a) and the dissimilarity

364

of interactions between common species (β_{OS} , Fig. 2b) indices (Poisot *et al.* 2012). Expectedly, local networks are highly dissimilar from the metaweb in terms of species composition, especially when only a limited number of sites have been sampled. This is because few species from the metaweb (species pool) occur locally. Moreover, we observe a peak in the dissimilarity of interactions between common species at intermediate sampling levels. This suggests that species are collected faster than their interactions. With a limited number of sampled local networks, few regional interactions are observed locally. Adding more sites brings new species, but not always their interactions. Quadratic relationships of network properties with sampling effort were also observed by McLeod *et al.* (2021).

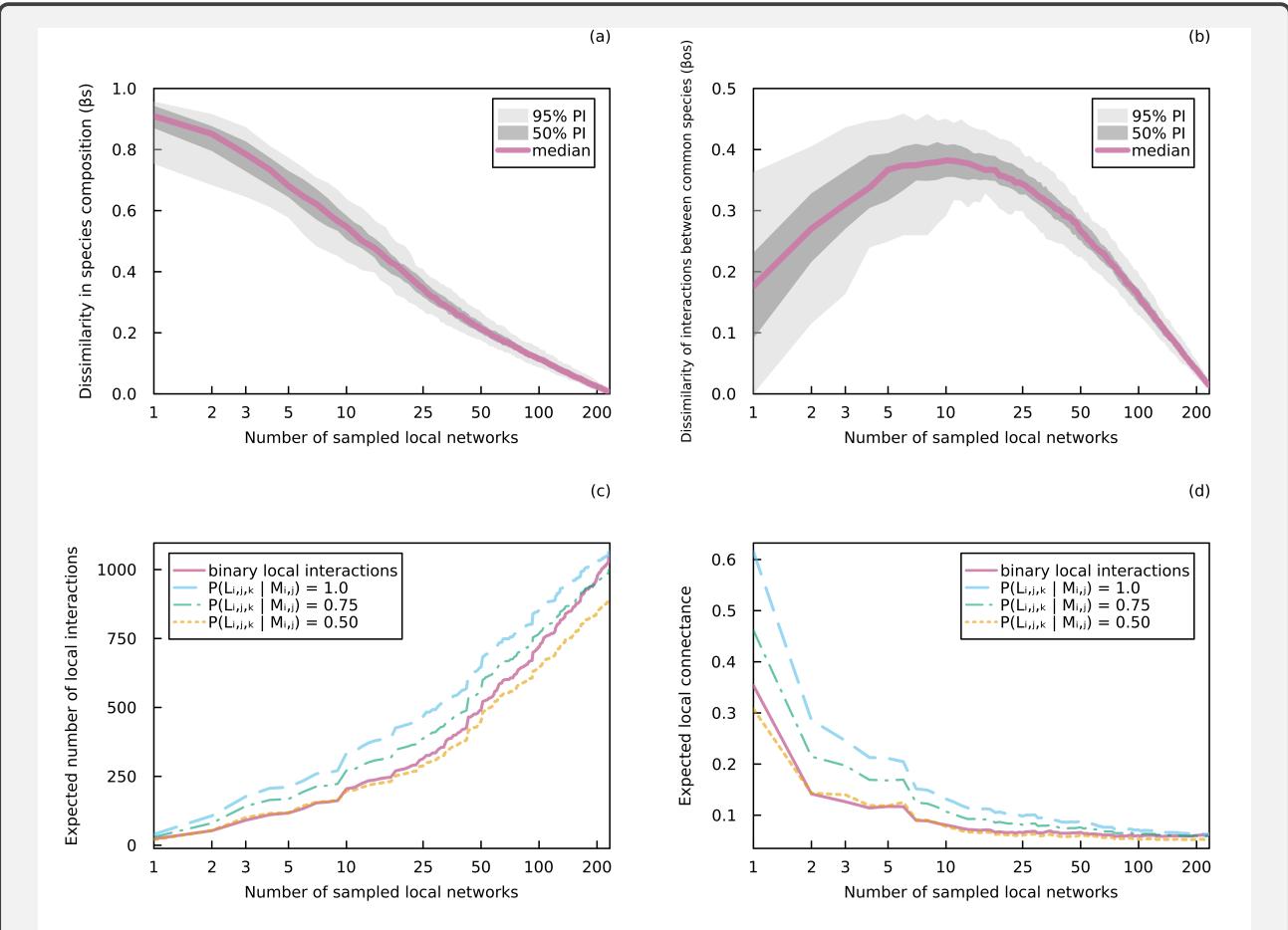


Figure 2: Network accumulation curves. (a) Dissimilarity in species composition and (b) dissimilarity of interactions between common species between aggregated local networks and the metaweb of binary host-parasite interactions. In both panels, the colored line represents the median dissimilarity across simulations and the grey areas cover the 50% and 95% percentile intervals. (c) Scaling of the number of interactions and (d) scaling of connectance with the number of sampled (aggregated) binary and probabilistic local interaction networks. For a better comparison with binary interactions, local networks of probabilistic interactions were derived from a metaweb of probabilistic interactions with a false positive and false negative rate of zero. A specific value of $P(L_{i,j,k}|M_{i,j})$ (the local probability of interaction among potentially interacting species) was used for all non-aggregated local networks within a particular curve. Aggregated local networks were obtained by sequentially and randomly selecting a number of local networks and aggregating both their species and interactions (with the value of $P(L_{i,j,k}|M_{i,j})$ increasing in aggregated local networks of probabilistic interactions).

Next, we investigate how the number of local interactions and connectance scale with the number of sampled (aggregated) local networks of probabilistic or binary interactions (Fig. 2c-d). By comparing the scaling relationships observed in local networks of binary and probabilistic interactions, we observe that high values of $P(L_{i,j,k}|M_{i,j})$ lead to systematic overestimations in the number of interactions and connectance, especially when $P(L_{i,j,k}|M_{i,j}) = 1$ (i.e., when local and regional probabilities of interactions

are equivalent). This suggests that high values of $P(L_{i,j,k}|M_{i,j})$ do not adequately capture the variability of local interactions. However, these biases tend to diminish as the number of sampled networks increases, indicating that most interactions are eventually captured when $P(L_{i,j,k}|M_{i,j})$ is high. In contrast, low values of $P(L_{i,j,k}|M_{i,j})$ lead to missing interactions, resulting in an underestimation of the number of interactions and connectance. These results underscore the importance of using the appropriate level of variability when estimating local interaction probabilities.

367

368 Metawebs: regional catalogs of interactions

369 What are regional probabilistic interactions?

370 Metawebs (Dunne 2006) are networks of potential interactions over broad spatial, temporal, and taxonomic
371 scales (e.g., food webs at the continental scale). They correspond to the temporal and spatial asymptotes of
372 local interactions (Box 1). Potential interactions describe the biological capacity of taxa to interact under
373 optimal or feasible environmental conditions given enough time, which is typically assessed at the regional
374 scale. Metawebs of probabilistic interactions are particularly useful in situations where there is uncertainty in
375 the ability of taxa to interact (Strydom *et al.* 2023). They may also be used as informative priors of local
376 interactions. Therefore, building a metaweb of probabilistic interactions may be an important first step before
377 predicting networks at finer scales.

378 In contrast to local networks, where interaction probabilities arise from the variability of interactions and the
379 lack of information on the conditions, interaction probabilities in metawebs solely result from a lack of
380 knowledge. This uncertainty arises due to insufficient interaction data, especially for taxa that have not yet been
381 observed to co-occur, and uncertainties in trait-matching models. As data accumulates, interactions in
382 metawebs should tend towards binarity, either taking a value of 1 (observing an interaction at least once) or
383 approaching 0 (repeatedly failing to observe an interaction between co-occurring taxa). Confidently observing
384 an interaction once confirms its biological feasibility, but failing to observe it (even on multiple occasions) does
385 not ensure that it is non-feasible (e.g., due to false negatives, Catchen *et al.* 2023). While local interaction
386 probabilities are irreducible because of local variability, the uncertainty of regional interactions reduces to 0
387 with the addition of information. Moreover, although *neutrally* forbidden interactions (i.e., forbidden
388 interactions between rare species, Canard *et al.* 2012) have low probability values in local networks, they would

389 have a probability of 1 in the metaweb (this is because the species' traits could support an interaction if they
390 were to encounter each other at high enough abundances). Likewise, non-co-occurring taxa may have a
391 non-zero probability of interaction in the metaweb. Regional interaction probabilities are thus fundamentally
392 different from local interaction probabilities, both in terms of uncertainty sources and probability values.

393 The extent of sampling effort influences our evaluation of probabilities of regional interactions, as sampling
394 over a larger area or for a longer duration enables us to capture a greater number of interactions (Box 1, McLeod
395 *et al.* 2021). However, in contrast with local networks of probabilistic interactions, regional interactions are not
396 evaluated for any particular local context (they are rather a collection of local contexts), which impacts how they
397 scale with space and time (notably through the extent of the region covered and sampling duration). In Box 3,
398 we discuss the differences in spatial and temporal scaling of regional interactions compared to local
399 interactions. We do so using the host-parasite networks of Kopelke *et al.* (2017) as an illustration of spatial
400 scaling (Box 3). Understanding the effect of spatial and temporal scales (including sampling effort) on local and
401 regional interaction probabilities is important for effectively propagating uncertainty across scales and
402 highlighting the fundamental differences between these two types of networks.

403 **What are regional probabilistic interactions conditioned on?**

404 **Regional interactions describing biological feasibility are conditioned on traits**

405 Potential interactions describe what we refer to as the *biological* feasibility of interactions, which is based solely
406 on the regional traits distributions T_i and T_j of taxa i and j , respectively. We define regional traits distributions
407 as the range of phenotypes that a taxon can express across various environments. Local traits $T_{i,k}$ and $T_{j,k}$,
408 which vary spatially and temporally because of phenotypic plasticity and local environmental variability (Berg
409 & Ellers 2010), are a subset of regional traits. A probability of potential interaction in a metaweb M describing
410 the biological feasibility of interactions may be expressed as:

$$P(M_{i,j}|T_i, T_j), \quad (11)$$

411 which, in contrast with local networks, is not conditioned on any spatial, temporal, co-occurrence or
412 environmental variables (Tbl. 1). Because phylogenetically close species often share similar traits, we should
413 expect that closely related species will have similar interacting partners. We can thus use phylogeny to predict

414 species traits and infer regional interactions (Eklöf & Stouffer 2016; Stouffer *et al.* 2012; Strydom *et al.* 2022).
415 The taxonomic level at which interactions are evaluated also influences the distribution of regional traits.
416 However, as explained in Box 4, there is no fundamental difference in the taxonomic scaling of regional and
417 local interactions (i.e., how interaction probabilities change with taxonomic level) because they both depend on
418 trait aggregation.

419 The biological feasibility of interactions expresses our degree of belief that there exists at least one combination
420 of phenotypes that could support an interaction if they were to encounter each other, assuming they had enough
421 time to interact. Evaluating this probability is conducted without incorporating the environmental conditions
422 under which they encounter each other into the model. It is the complement of the probability $P(F_{i,j}|T_i, T_j)$ of
423 forbidden interactions (i.e., the probability that their traits do not support an interaction), which is based
424 uniquely on biological traits:

$$P(M_{i,j}|T_i, T_j) = 1 - P(F_{i,j}|T_i, T_j). \quad (12)$$

425 For example, let i be a western diamondback rattlesnake (*Crotalus atrox*) and j , a wood lemming (*Myopus*
426 *schisticolor*). These two taxa never co-occur, the rattlesnake being adapted to warm regions of North America
427 (Castoe *et al.* 2007) and the lemming, to northern habitats of Eurasia (Fedorov *et al.* 2008). As we lack direct
428 observations of an interaction between these two species, we have to rely on expert knowledge or trait-matching
429 models to estimate their probability of potential interaction. To accurately estimate this probability using
430 trait-matching models, it is crucial to ensure that the set of traits considered reflects the overall traits
431 distributions of both taxa. We could for instance consider their average body mass and the average phylogenetic
432 distance of lemmings to rattlesnakes' prey. Doing so, we might find a high probability of potential interaction
433 based on these traits. This example illustrates how regional interactions describing biological feasibility may be
434 estimated solely based on traits, without taking into account environmental conditions (which could be
435 important to consider when e.g. an interaction is forbidden at all temperature values).

436 **Regional interactions describing ecological feasibility are conditioned on traits and environmental
437 conditions**

438 The biological feasibility of interactions should not be confused with what we refer to as the *ecological*
439 feasibility of interactions. A probability of potential interaction in a metaweb M^* describing the ecological

440 feasibility of interactions may be expressed as:

$$P(M_{i,j}^*|T_i, T_j, E), \quad (13)$$

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

$$\int_E P(M_{i,j}^*|T_i, T_j, E) dE \leq P(M_{i,j}|T_i, T_j). \quad (14)$$

451 This is because the biological feasibility of an interaction is a prerequisite for its ecological feasibility. In other
452 words, biological feasibility is necessary but not sufficient for an interaction to be ecologically feasible. Our
453 discussion of metawebs focuses on the biological feasibility of interactions since most methods developed for
454 inferring probabilities of regional interactions do not explicitly take into account environmental conditions (e.g.,
455 Strydom *et al.* 2022).

456 How are regional probabilistic interactions estimated?

457 Starting from a selected set of taxa, which are usually distributed within a broad region of interest, metawebs
458 can be built using different data sources, including literature review (e.g., Maiorano *et al.* 2020), aggregated
459 interaction data (e.g., Gravel *et al.* 2019; Saravia *et al.* 2022), trait-matching models (e.g., Shaw *et al.* 2024;
460 Strydom *et al.* 2022), and expert knowledge, which is not a trivial challenge. Every pair of taxa that have
461 confidently been observed to interact at least once can be given a probability of 1 (i.e., $P(M_{i,j}) = 1$) since we
462 know that they *can* interact. This differs from local networks of probabilistic interactions, where interaction

463 events may remain stochastic (i.e., $P(L_{i,j,k}) < 1$) even after empirically observing interactions due to their
464 spatiotemporal variability. Interactions that were never observed typically have low probability values in local
465 networks and vary from low to high values in metawebs, contingent upon taxa traits distributions (reaching 0 for
466 forbidden links). The aggregation of model predictions and data from different sources thus tends to raise the
467 number of potential interactions in metawebs.

468 When using local interaction data to estimate probabilities of regional interactions, repeatedly failing to observe
469 an interaction between two co-occurring taxa should decrease the probability that the interaction is biologically
470 feasible. Using Bayes' theorem, the probability that the interaction is biologically feasible given that it was
471 never observed locally, $P(M_{i,j} = 1|O_{i,j,k} = 0)$, may be calculated as follows:

$$P(M_{i,j} = 1|O_{i,j,k} = 0) = \frac{P(O_{i,j,k} = 0|M_{i,j} = 1) \times P(M_{i,j} = 1)}{P(O_{i,j,k} = 0)}. \quad (15)$$

472 The reduction in the probability of regional interaction after considering that it was never observed locally (i.e.,
473 $P(M_{i,j} = 1|O_{i,j,k} = 0) < P(M_{i,j} = 1)$) occurs because $P(O_{i,j,k} = 0|M_{i,j} = 1)$ must be lower than $P(O_{i,j,k} = 0)$,
474 i.e. there is a higher chance of observing an interaction when it is biologically feasible.

475 Observations of interactions may be false positives because of observation errors due to taxonomic
476 misidentifications and ecological misinterpretations, such as those involving phylogenetically close species or
477 cryptic species and interactions (Pringle & Hutchinson 2020). Likewise, forbidden interactions may be false
478 negatives, e.g. if they have been evaluated based on unrepresentative or incomplete traits distributions.

479 Employing Bayesian models proves valuable when estimating interaction probabilities in metawebs (e.g.,
480 Bartomeus *et al.* 2016; Cirtwill *et al.* 2019). This improvement is achieved by updating prior information
481 regarding the feasibility of interactions (e.g., experts' prior assessments of interaction probabilities) with
482 empirical data on interactions and traits. By improving our estimation of potential interaction probabilities, we
483 may build more reliable metawebs that adequately reflect our uncertainty on the biological feasibility of
484 interactions.

Box 3: Spatial and temporal scaling of interactions

Local networks and metawebs have distinct relationships with space (area or volume) and time (sampling effort or duration). Local probabilities of interaction scale both spatially and temporally, because local interactions have more opportunities to be realized in larger areas and longer durations. In a larger

sampling area and duration, we increase the likelihood of sampling favorable conditions for interactions to occur. If a local network of probabilistic interactions L_1 with an area A_1 is compared to a larger network L_0 with an area A_0 , and A_1 is entirely nested within A_0 , interaction probabilities should be lower in the smaller network, i.e. $P(L_{i,j,1}|A_1 < A_0) \leq P(L_{i,j,0}|A_0)$. However, if A_1 and A_0 are disjoint, interaction probabilities could be higher in the smaller area, contingent upon local environmental and biological conditions. In contrast, regional probabilities of interaction do not scale with space and time. The probability of two taxa potentially interacting should be the same in all metawebs in which they are present regardless of scale, provided that the data and methods used for estimation are consistent. This is because they depend solely on the biological capacity of two taxa to interact, regardless of co-occurrence and local environmental conditions. However, probabilities of regional interactions may change, tending to become more definitive, with increased sampling effort.

In Fig. 3, we show how the expected *number* of local host-parasite interactions scales with the spatial boundary of the network (represented by an expanding latitudinal window) in comparison with regional interactions. We do so using the host-parasite networks of Kopelke *et al.* (2017). The increase in the number of regional interactions is due to the inclusion of more species in a larger area. To ensure a conservative comparison between aggregated local and regional networks, we employed equal interaction probabilities (i.e., using $P(L_{i,j,k}|M_{i,j}) = 1$) in both types of network. This means that local interaction probabilities could not increase further when aggregating them. Despite this, we notice that the total number of regional interactions scales more rapidly than local interactions. This is because numerous regional interactions involve species that never co-occur, and as a result, these interactions are not captured in local networks. All data manipulation and methods are described in Appendix 1.

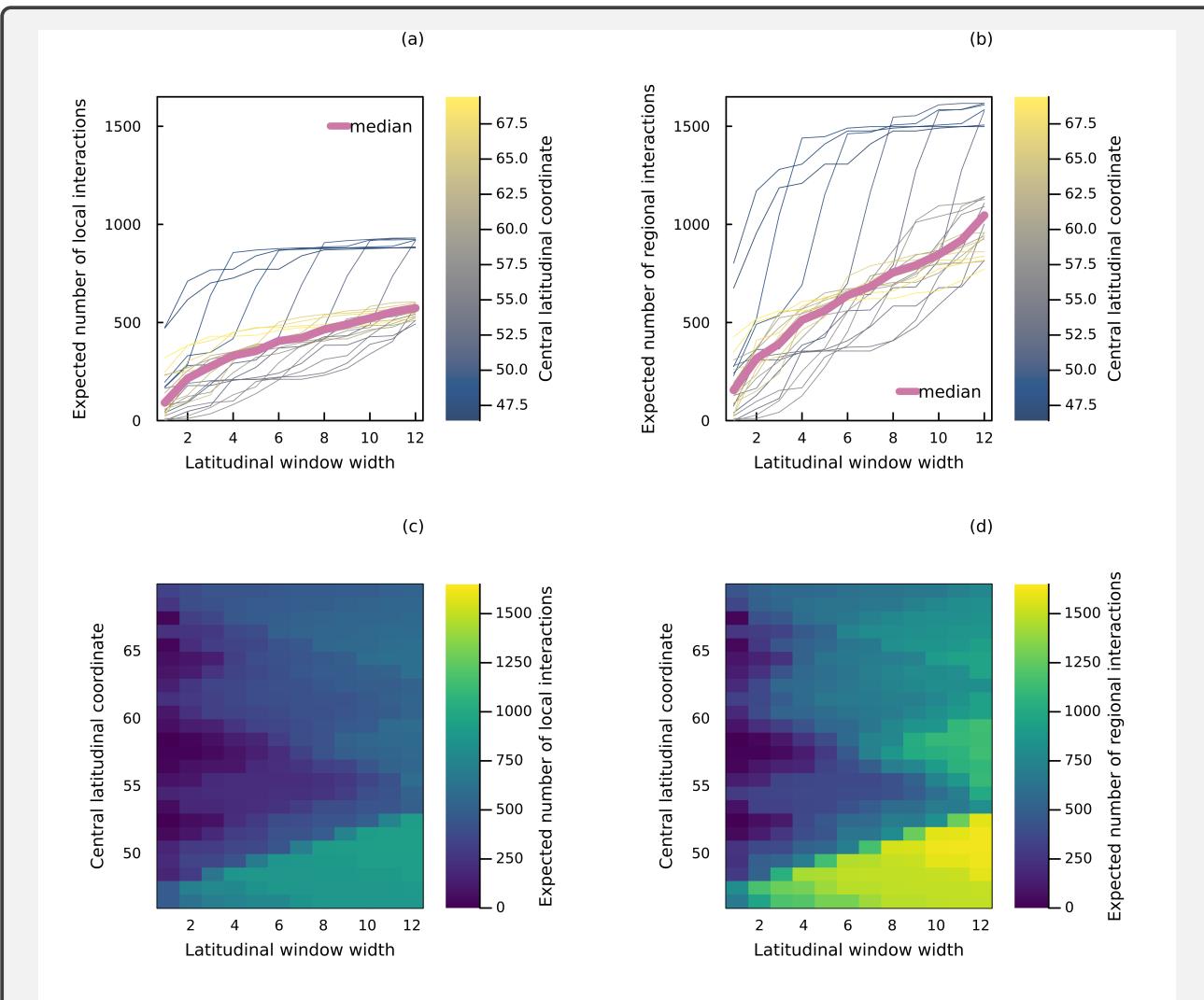


Figure 3: Spatial scaling of interactions. Expected number of host-parasite interactions in a network aggregating all (a) local and (b) regional probabilistic interactions within a latitudinal window of a given width. Every dashed curve corresponds to a different window centered at a given latitude (color bar), with the pink solid line representing the median number of interactions across windows. Heatmaps of the expected number of (c) local and (d) regional interactions found in windows of specified width and position (central latitude). 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 regional probabilistic interactions by setting the value of $P(L_{i,j,k}|M_{i,j})$ (the local probability of interaction among potentially interacting species) to 1. Aggregated local networks were obtained by aggregating both the species and interactions found within a particular latitudinal window, with the values of $P(L_{i,j,k}|M_{i,j})$ remaining at their maximum value of 1.

487

Box 4: Taxonomic scaling of interactions

Given that our interpretation of the properties of ecological networks depends on their taxonomic level (Melián *et al.* 2011), investigating the taxonomic scaling of interactions (i.e., how interaction probabilities

488

change with taxonomic level) is important. There are no inherent differences between the taxonomic scaling of local and regional interactions. The taxonomic level of interactions impacts the definition of nodes. Local and regional interaction probabilities are not directly conditioned on taxonomic scale. However, some conditional variables (e.g., trait distribution) may covary with taxonomic scale. In such cases, local and regional interaction probabilities would change taxonomically following the scaling of these variables.

In both types of interactions, transitioning to a broader level of organization (e.g., from a species-level network S to a genus-level network G) can be done using interaction probabilities from finer scales. For example, in a network with n_1 species of genus g_1 and n_2 species of genus g_2 , one can calculate the probability that at least one species from genus g_1 interacts with at least one species from genus g_2 (i.e., the probability that the genus-level interaction occurs) as follows:

$$P(G_{g_1,g_2}) = 1 - \prod_{i=1}^{n_1} \prod_{j=1}^{n_2} (1 - P(S_{g_1,i,g_2,j})), \quad (16)$$

where $g_{1,i}$ and $g_{2,j}$ are the species of the corresponding genus and assuming independence between species-level interactions. In contrast, a different approach is necessary when transitioning from a broader to a finer level of organization. This is because the knowledge of an interaction between two genera does not guarantee that all possible pairwise species combinations will also interact. One possible method is to build a finer-scale network by generating probabilities of interaction through random sampling from a beta distribution, parameterized by the broader-scale network.

Fundamentally, the taxonomic scaling of interactions involves aggregating interactions between individuals into larger groups. Interaction probabilities at broader taxonomic scales should thus conform to probabilities of interactions between individuals. For example, Canard *et al.* (2012) built a species-based network using simulated individual-based networks. In local individual-based food webs, the probability that two individuals interact reflects our degree of belief that one individual will consume the other. Likewise, in local species-based food webs, the probability that two species interact represents our degree of belief that *at least* one individual from the predator species will consume at least another individual from the prey species. In that regard, taxonomic scaling is analogous to the spatial and temporal scaling of interactions, as they all represent different ways to aggregate individuals into broader groups (either spatially, temporally, or taxonomically).

Box 5: Sampling for binary interaction networks

Local networks of binary interactions may be predicted by performing independent Bernoulli trials for each probabilistic interaction. This is particularly useful when analyzing the structure of probabilistic interaction networks in the absence of specific analytical formulas (Poisot *et al.* 2016), even though it may introduce biases in our estimations when connectance is low (Chagnon 2015; Poisot & Gravel 2014). There are at least two techniques to sampling binary interaction networks across space, each predicting a binary interaction network for each location k within a given region. The first technique involves performing a single Bernoulli trial for each pair of taxa based on their regional probability of interaction:

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

In employing this technique, 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 localized networks where they co-occur, i.e. $L_{i,j,k} = M_{i,j}$ when $X_{i,j,k} = 1$. This will result in local pairwise interactions without spatial variation.

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

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

This can be achieved by first generating distinct probabilistic interaction networks for each location. Because binary interactions are sampled independently for each location, this second technique captures network structure across space and time more effectively. When sampling binary interactions from local interaction probabilities, it is crucial to sample at the same spatial scale for which probabilities were estimated to prevent systematic biases in predictions.

In Fig. 4, we compare the average connectance of binary interaction networks resulting from these two sampling techniques. We sampled regional and local interactions from our host-parasite networks of probabilistic interactions (Kopelke *et al.* 2017), generating a number of binary interaction network realizations for each site in the dataset. These two sampling techniques yield different outcomes, particularly for intermediate values of $P(L_{i,j,k}|M_{i,j})$ of 0.50, which represent instances where regional

interactions do not consistently manifest locally (i.e., with the largest local variability). As anticipated, we observe that sampling binary interactions from the metaweb tends to overestimate connectance on average compared to sampling them from local networks (Fig. 4). We also observe an increase in the variability of connectance when employing a single simulation (Fig. 4a-c, cross markers), which is a more tangible representation of the process leading to the realization of local interactions in nature. All data manipulation and methods are described in Appendix 1.

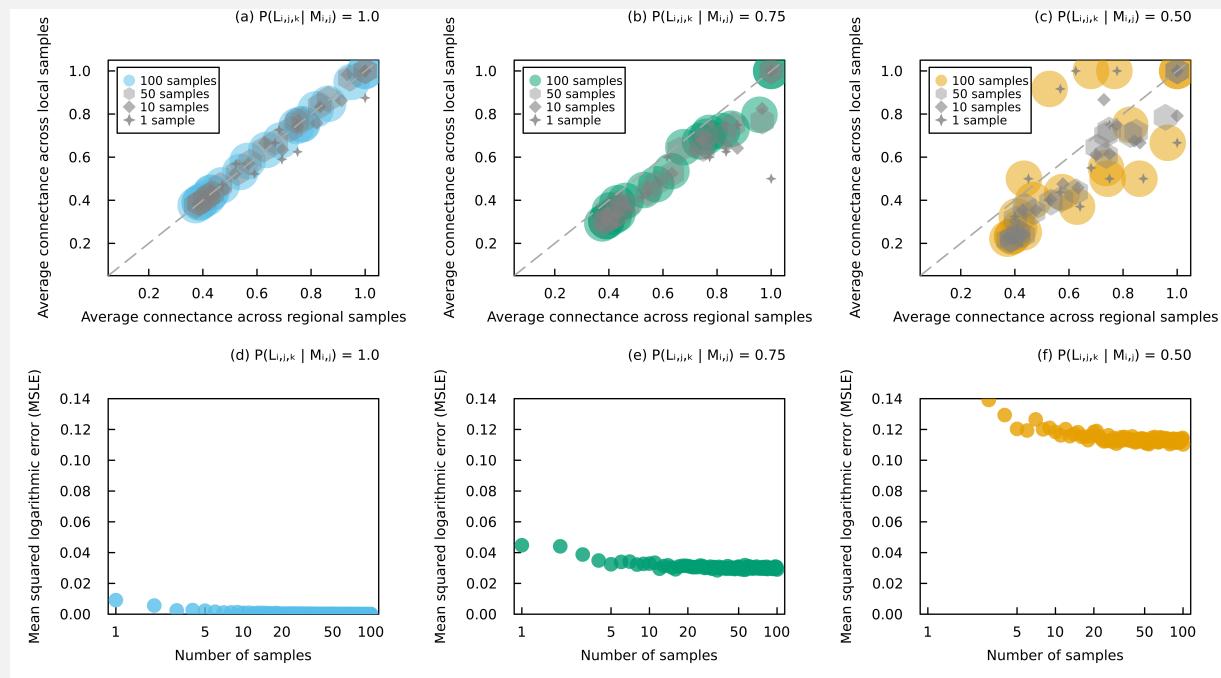


Figure 4: Connectance of sampled binary interaction networks. (a-c) Average connectance of binary interaction networks obtained from the two sampling techniques for 20 randomly selected host-parasite networks. Cross markers represent the connectance of a single sample for each network, diamond markers the average connectance across 10 samples, hexagon markers the average connectance across 50 samples, and the colored circles the average connectance across 100 samples (marker size proportional to the number of samples). (d-f) Reduction in the mean squared logarithmic error between the average connectance of binary interaction networks (all 233 host-parasite networks) obtained from these two sampling techniques as the number of samples increases. The local probability of interaction between potentially interacting species was set to three different values: (a,d) $P(L_{i,j,k}|M_{i,j}) = 1.0$, (b,e) $P(L_{i,j,k}|M_{i,j}) = 0.75$, and (c,f) $P(L_{i,j,k}|M_{i,j}) = 0.50$. Probabilities of regional interactions were obtained with a false positive rate of 5% and a false negative rate of 10%. Regional samples were obtained by randomly sampling binary interactions from the probabilistic interaction metaweb, and then propagating this result to all local networks that include the species potentially engaged in the interactions. Local samples were obtained by independently sampling binary interactions for each local network of probabilistic interactions.

Both sampling techniques assume independence between interactions, which might not hold true in 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. Sampling whole networks (or graphs) instead of pairwise interactions may eliminate the need for this assumption of independence (**Battiston2020Networks?**).

492

493 Future perspectives

494 In this contribution, we underline the importance of network documentation for adequately interpreting and
495 manipulating probabilistic interaction data. The mathematical representation of probabilities and their statistical
496 properties depend on the type of interactions (local or regional) and the conditions under which these
497 interactions were evaluated. We show that local networks and metawebs of probabilistic interactions differ in
498 their relationship to spatial and temporal scales (Box 3), with regional interactions remaining consistent across
499 scales. In contrast with metawebs, local interactions are measured in a specific context (e.g., in a given area,
500 time, and biological and environmental conditions) and depend on taxa co-occurrence. These differences bring
501 to light the need to use probabilistic data with caution, for instance when generating network realizations of
502 binary interactions across space (Box 5). Clear documentation describing the type of interaction and the
503 variables used in their estimation are required to ensure adequate data manipulation. Sound data practices and
504 foundations for probabilistic thinking in network ecology facilitate reliable assessments of the spatiotemporal
505 variability and uncertainty of biotic interactions. Here we identify key research priorities for improving our
506 understanding of probabilistic local and regional interactions.

507 Predicting local networks from metawebs

508 Metawebs are a valuable source of ecological information for predicting local networks across time and space.
509 Local networks of binary interactions can be reconstructed by selecting a subset of taxa and interactions from
510 the metaweb (Dunne 2006). Determining the list of taxa to select can be achieved empirically (e.g., observed
511 occurrence data for a site) or numerically (e.g., species distribution models). As species composition is
512 arguably easier to sample and predict than pairwise interactions, the primary challenge lies in deciding which
513 interactions to select from the metaweb. Inferring the structure of local networks from the metaweb before

514 predicting local pairwise interactions could hold promise (Strydom *et al.* 2021), considering that the structure
515 of local networks is constrained by the metaweb (Saravia *et al.* 2022).

516 While predicting local binary interactions from a metaweb is not be a simple task, inferring local networks of
517 probabilistic interactions from a metaweb comes with its own set of challenges. For example, Dansereau *et al.*
518 (2023) inferred spatially-explicit food webs from a metaweb of probabilistic trophic interactions between
519 Canadian mammals. Their predicted localized food webs are downscaled versions of the metaweb (i.e.,
520 localized metawebs with the same interaction probabilities as those in the regional metaweb). To infer local
521 networks as defined in this manuscript (i.e., describing local realizations of interactions), local interaction
522 probabilities must be smaller than regional interaction probabilities. Inferring local networks from a metaweb
523 by maintaining identical interaction probability values introduces systematic biases into the predictions, as
524 discussed in Box 2 (unless networks are seen as downscaled metawebs).

525 As suggested by McLeod *et al.* (2021), metawebs establish an upper limit for local interactions (similarly for
526 metawebs of probabilistic interactions, Strydom *et al.* 2023). In other words, the probability that two taxa
527 interact at a specific location and time is consistently lower or equal to the probability of their regional
528 interaction, regardless of the conditional variables considered:

$$P(L_{i,j,k}|...) \leq P(M_{i,j}|T_i, T_j). \quad (17)$$

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

$$\int_{E_k} \int_{A_0} \int_{t_0} P(L_{i,j,k}|E_k, A_0, t_0) dt_0 dA_0 dE_k \leq P(M_{i,j}|T_i, T_j). \quad (18)$$

533 Estimating more precisely the probability $P(L_{i,j,k}|M_{i,j})$ that two taxa interact locally if they can potentially
534 interact allows for improved predictions of local networks from the metaweb of probabilistic interactions. This
535 task is challenging due to the variability of this probability across space and time, as well as its variability
536 across pairwise interactions within a network. Using simple models of $P(L_{i,j,k}|M_{i,j})$, as shown in Appendix 1,
537 represents an initial step toward the overarching objective of reconstructing local networks from metawebs.

538 **Quantifying and reducing interaction uncertainty**

539 While sampling biological communities decreases the uncertainty of interactions by accumulating evidence for
540 their feasibility and local realization, there is a limit to how much we can reduce uncertainty. In metawebs,
541 probabilities reflect our limited knowledge of interactions, which is expected to improve with a larger volume of
542 data. Regional interactions should become more definitive (with probabilities approaching 0 or 1) as we
543 investigate various conditions, including different combinations of species traits.

544 In comparison, local interaction probabilities represent both our knowledge uncertainty and their spatiotemporal
545 variability. Owing to environmental heterogeneity, there will invariably be instances in which an interaction
546 occurs and others in which it does not, across different times and locations, irrespective of the extent to which
547 we can improve our knowledge of its biological feasibility and the local conditions that facilitate its occurrence.

548 When local networks describe probabilities of observing interactions rather than their realization, we must also
549 consider observation uncertainty (sampling error) as an additional source of uncertainty. Quantifying and
550 partitioning this uncertainty will enable us to make more accurate predictions about ecological interactions at
551 various spatial and temporal scales, and to identify priority sampling locations to reduce this uncertainty. This
552 will prove to be of vital importance as our time to understand nature runs out, especially at locations where the
553 impacts of climate change and habitat loss hit harder.

554 **Relaxing the independence assumption**

555 Estimating local interaction probabilities independently for each taxa pair and assembling them into a network
556 of probabilistic interactions comes with limitations. Predicting local networks of binary interactions based on
557 these interaction probabilities assumes independence among interactions, a condition seldom respected in
558 practice (Golubski & Abrams 2011). Relaxing this assumption is the next logical step in the stochastic
559 representation of interactions.

560 A more accurate representation of the uncertainty and variability of ecological networks involves creating
561 *probabilistic networks* ($P(L_k)$ and $P(M)$), rather than networks of *probabilistic interactions* ($P(L_{i,j,k})$ and
562 $P(M_{i,j})$). Probabilistic networks describe the probability that a particular network of binary (or quantitative)
563 interactions (its whole adjacency matrix) is realized. For example, Young *et al.* (2021) used a Bayesian
564 approach to estimate the probability of different plant-pollinator network structures derived from imperfect
565 observational data. A probability distribution of ecological networks may also be derived using the principle of

566 maximum entropy given structural constrained (e.g., Cimini *et al.* 2019; Park & Newman 2004).
567 Regardless of the method used, generating probabilistic local networks could lead to more accurate predictions
568 of local networks of binary interactions by bypassing the independence assumption. Probabilistic networks
569 could serve as an alternative to null hypothesis significance testing when comparing the structure of a local
570 network to some random expectations or, as done in Pellissier *et al.* (2018) and Box 2, to the metaweb. These
571 random expectations are typically derived by performing a series of Bernoulli trials on probabilistic
572 interactions, assuming independence, to generate a distribution of networks of binary interactions to calculate
573 their structure (Poisot *et al.* 2016). One could instead compare the likelihood of an observed network to the one
574 of the most likely network structure (according to the probabilistic network distribution), thereby directly
575 obtaining a measure of discrepancy of the empirical network. Generating probabilistic ecological networks
576 represents a tangible challenge, one that, in the coming years, promises to unlock doors to more advanced and
577 adequate analyses of ecological networks.

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