

Deciphering probabilistic species interaction networks

Francis Banville^{1,2,3} Tanya Strydom^{1,3} Penelope S. A. Blyth⁴ Chris Brimacombe⁵ Michael Catchen^{3,6}
Gabriel Dansereau^{1,3} Gracielle Higino² Thomas Malpas⁴ Hana Mayall⁴ Kari Norman¹
Dominique Gravel^{2,3} Timothée Poisot^{1,3}

¹ Université de Montréal ² Université de Sherbrooke ³ Quebec Centre for Biodiversity Science ⁴ University of Sheffield ⁵ University of Toronto ⁶ McGill University

Correspondance to:

Francis Banville — francis.banville@umontreal.ca

Representing species interactions probabilistically (how likely are they to occur?) as opposed to deterministically (are they occurring?) conveys 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 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) and uncertainty sources.

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1 Introduction

2 Species interactions are 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 (Poisot *et al.* 2015).
15 Probabilities of interspecific encounters are typically low, especially for rare species with low abundances.
16 While species' absolute abundances may impact interaction frequencies (Vázquez *et al.* 2007), encounter
17 probabilities are determined by their relative abundances in neutral models (Canard *et al.* 2012; Canard *et al.*
18 2014). The probability that species meet also depends on their biology, such as their phenology (Olesen *et al.*
19 2010; Singer & McBride 2012) and discoverability (Broom & Ruxton 2005). Finally, when species do come
20 into contact, an interaction occurs only if their traits, such as their phenotypes (Bolnick *et al.* 2011; Gravel *et al.*
21 2013; Stouffer *et al.* 2011) and behavior (Choh *et al.* 2012; Pulliam 1974), are locally compatible in that
22 specific environment (Poisot *et al.* 2015).

23 Documenting the location and timing of interactions becomes more difficult when accounting for the
24 spatiotemporal variability of ecological interactions (Poisot *et al.* 2012, 2015). Environmental factors, such as
25 temperature (Angilletta *et al.* 2004), drought (Woodward *et al.* 2012), climate change (Araujo *et al.* 2011;
26 Gilman *et al.* 2010; Woodward *et al.* 2010), and habitat modifications (Tylianakis *et al.* 2007), contribute to this
27 spatiotemporal variability by impacting species abundance and traits. Interactions may also be influenced by a
28 third species (e.g., a more profitable prey species, Golubski & Abrams 2011; Sanders & van Veen 2012). Even
29 under favorable circumstances, there remains a possibility that the interaction does not occur locally, either due

30 to the intricate nature of the system or simply by chance. If it does occur, it might go undetected, particularly if
31 it happens infrequently. In this context, it is unsurprising that our knowledge of ecological interactions remains
32 limited (Hortal *et al.* 2015) despite extensive biodiversity data collection (Schmeller *et al.* 2015).

33 **Species interactions as probabilistic objects**

34 Knowing the biological capacity of two species to interact directly (via e.g., trophic interactions) is necessary
35 but not sufficient for inferring their interaction at a specific time and space. The recognition of the intrinsic
36 variability of species interactions has led ecologists to expand their representation of ecological networks to
37 include a probabilistic view of interactions (Dallas *et al.* 2017; Fu *et al.* 2021; Poisot *et al.* 2016). This allows
38 filling in the Eltonian shortfall (Hortal *et al.* 2015) by modeling the probability of occurrence of interactions
39 (e.g., Gravel *et al.* 2019), which can be an important tool for directing efforts and taking action (Carlson *et al.*
40 2021), especially in places where access and resources for research are scarce. The probabilistic representation
41 of interactions has been applied to direct interactions, which are conceptually and mathematically analogous
42 regardless of their biological type (e.g., predation and pollination). This is in contrast with indirect interactions
43 (e.g., interspecific competition), which arise from distinct ecological processes and are often not directly
44 observable (Kéfi *et al.* 2015, 2016). Representing direct interactions probabilistically can capture the
45 spatiotemporal variability of the aforementioned ecological processes and the uncertainty in our knowledge of
46 interactions. By accounting for the uncertainty of interactions, networks of probabilistic interactions (which
47 differ from probabilistic networks describing the uncertainty and variability of the *whole* network) may provide
48 a more realistic portrait of species interactions. However, the absence of a standardized definition for
49 probabilistic interactions hinders our capacity to study and comprehend this uncertainty effectively.

50 We distinguish the variability of interactions from their uncertainty. Interaction variability is defined as the
51 variation of interactions along spatial, temporal, or environmental axes (Poisot *et al.* 2015). For instance, the
52 spatiotemporal variability of interactions describe the variation in the occurrence or strength of interactions
53 across space and time. It is a property of interactions that should be quantified if we aim for a comprehensive
54 understanding of ecological networks. Stochasticity is the inherent randomness or unpredictability of
55 interactions that lead to this variability. Conversely, uncertainty is defined as a lack of knowledge about the
56 occurrence of interactions. When using statistical models to infer interactions, uncertainty sources include input
57 data, parameter, and model structure uncertainties (Simmonds *et al.* 2024). Input data uncertainty arises from
58 our inability to empirically observe all interactions and from measurement errors in environmental and

59 biological variables used for inference. Parameter uncertainty represents a plausible range of values for a
60 parameter whose exact value is unknown. For example, we may calculate a range of plausible values for
61 interaction variability (e.g., there could be a 50% certainty that an interaction occurs 50% of the time). Model
62 structure uncertainty recognizes that different statistical models may adequately predict interactions. In contrast
63 to variability, uncertainty can be reduced by sampling additional data. Simmonds *et al.* (2024) underscores the
64 importance of quantifying and reporting these diverse sources of uncertainty, alongside ensuring their
65 appropriate propagation to model output (such as predicted interactions) and higher-level measures (such as
66 network structure). Finally, a probability is a measure of how likely a specific outcome is, based on both the
67 uncertainty and variability of interactions. Interaction probabilities may be uncertain when there is a
68 distribution of plausible probability values. While recognizing that these definitions may not be universally
69 accepted, they are the ones we adopt in this manuscript.

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

83 The application and development of computational methods in network ecology, often based on a probabilistic
84 representation of interactions, can alleviate (and guide) the sampling efforts required to document species
85 interactions (Strydom *et al.* 2021). For example, statistical models can be used to estimate the uncertainty of
86 pairwise interactions (Cirtwill *et al.* 2019) and the probability of missing (false negatives) and spurious (false
87 positives) interactions (Guimerà & Sales-Pardo 2009). Statistical models can generate predictions of ecological
88 networks without prior knowledge of pairwise interactions. They may do so using body size (Caron *et al.* 2024;

89 Gravel *et al.* 2013; Petchey *et al.* 2008), phylogeny (Elmasri *et al.* 2020; Strydom *et al.* 2022), or a combination
90 of niche and neutral processes (Bartomeus *et al.* 2016; Pomeranz *et al.* 2019) for inference. Topological null
91 models, which generate networks of probabilistic interactions by preserving chosen characteristics of the
92 adjacency matrix of binary interactions while intentionally omitting others (Bascompte *et al.* 2003; Fortuna &
93 Bascompte 2006), are examples of common probabilistic interaction models. Null models can be used to
94 produce underlying distributions of network measures for null hypothesis significance testing. However, how
95 the uncertainty of pairwise interactions propagates to network structure (i.e., community-level properties
96 driving the functioning, dynamics, and resilience of ecosystems, McCann 2007; McCann 2011; Proulx *et al.*
97 2005; Rooney & McCann 2012) remains to be elucidated. Many measures have been developed to describe the
98 structure (Poisot *et al.* 2016) and diversity (Godsoe *et al.* 2022; Ohlmann *et al.* 2019) of probabilistic
99 interaction networks. These models and measures support the use of this approach for the study of a wide range
100 of ecological questions, from making better predictions of species distribution (Cazelles *et al.* 2016) to
101 forecasting the impact of climate change on ecological networks (Gilman *et al.* 2010).

102 We lack clear definitions of probabilistic species interactions

103 Yet, a precise definition of probabilistic interactions appears to be lacking, making the estimation and use of
104 these data more difficult. In this manuscript, we aim to take a step back by outlining different ways in which
105 probabilistic interactions are defined and used in network ecology. We distinguish two broad categories of
106 probabilistic interaction networks that necessitate distinct approaches: local networks describing probabilities
107 of realized interactions, and regional networks (metawebs) describing probabilities of potential interactions. We
108 highlight the distinctions in the ecological meaning of these two representations and examine their properties
109 and relationships (particularly with space, time, and between each other).

110 The lack of clear guidelines on the use of probabilistic interaction data is worrisome, as it affects both data
111 producers and re-users who generate and manipulate these numbers. This is concerning because sampling
112 strategies and decisions regarding network construction can affect our understanding of network properties
113 (Brimacombe *et al.* 2023). There is currently no reporting standard that could guide the documentation of all
114 types of probabilistic interactions (Salim *et al.* 2022 discuss data standards for deterministic mutualistic
115 networks). Clear reporting standards for probabilistic interactions would support more adequate manipulation
116 and integration of interaction data from different sources and guard against possible misinterpretations arising
117 from ambiguous definitions of probabilistic interaction networks. This documentation should outline the nature

118 (i.e., local or regional) and type (e.g., predatory or pollination) of the interactions, provide information
119 regarding the taxonomic level, identities, and characteristics (e.g., life stages) of the individuals involved in an
120 interaction, present the mathematical formulation of probabilities, including clearly identified conditional
121 variables (e.g., spatial and temporal scales), and describe the methods and contexts (e.g., location, time,
122 environmental conditions) in which interactions were estimated. Inadequately documented probabilistic
123 interaction data should be used with caution when analyzing ecological networks. These broad principles
124 remain relevant and applicable across different types of direct interactions. In the following sections, we delve
125 into the definitions of probabilistic interactions as we scale up from pairwise interactions to interactions within
126 local and regional networks.

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

128 **Probabilistic interactions have different interpretations**

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

142 An important aspect to consider when using interaction probabilities is knowing if they describe potential or
143 realized interactions, as these two types of interactions have distinct conceptual underpinnings and sources of
144 uncertainty. A potential (regional) interaction is defined as the biological capacity of two taxa to interact (i.e.,
145 the probability that they interact if they were to encounter each other, given sufficient time and appropriate

146 environmental conditions) whereas a realized (local) interaction is the occurrence or observation of this
147 interaction in a well-defined space and time (i.e., the probability that they interact locally). For two co-occurring
148 taxa and over enough time, the probability of local interaction tends toward the probability of regional
149 (potential) interaction. A longer duration increases the probability that species will eventually encounter each
150 other and that local environmental conditions supporting an interaction will occur, provided that species have
151 the biological capacity to interact.

152 We use the terms *metaweb* (Dunne 2006) to designate regional networks of potential interactions and *local*
153 *networks* (Poisot *et al.* 2012) for those of realized interactions. Metawebs are the network analogs of the species
154 pool, where local networks originate from a subset of both species (nodes) and interactions (edges) of the
155 regional metaweb (Saravia *et al.* 2022). When uncertain, potential interactions in a metaweb may be
156 probabilistic (Strydom *et al.* 2023). Without clear documentation, it can be challenging to know if published
157 probabilistic interaction networks describe local or regional interactions, or if so-called probabilities are in
158 reality a form of interaction score. When probabilistic regional interactions are used and interpreted incorrectly
159 as local interactions (and conversely), this may generate misleading findings during data analysis. A better
160 understanding of probabilistic local and regional interactions would prevent interpretation errors (e.g., when
161 studying network-area relationships with metawebs or local networks) and facilitate a more adequate use of
162 interaction data.

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

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

170 Ecologists have traditionally represented interactions (edges) as binary objects that were considered realized
171 after observing at least one individual from group i interact with at least another individual from group j . In an
172 adjacency matrix B of binary interactions, the presence or absence of an interaction $B_{i,j}$ between two taxa can
173 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

174 interaction. This interaction probability characterizes our limited ecological knowledge and/or the intrinsic
175 spatiotemporal variability of interactions. It may be estimated through predictive models (e.g., those based on
176 biological traits and species abundances) or expert (prior) knowledge about the interaction. In networks of
177 probabilistic interactions, the edge values $P(B_{i,j})$ are probabilistic events whose only two possible outcomes are
178 the presence ($B_{i,j} = 1$) or absence ($B_{i,j} = 0$) of an interaction between each pair of nodes. Depending on the
179 type of probabilistic interaction network (local or metaweb), the mathematical formulation and interpretation of
180 stochastic parameters like $P(B_{i,j})$ can be linked to environmental and biological factors such as species
181 abundance, traits, area, and time, for example using logistic regression with continuous explanatory variables.

182 The variability of an interaction determines the fraction of networks in which it occurs. This can be measured
183 by using a Binomial distribution, assuming a constant interaction probability and independence between
184 interactions in different networks (trials). When considering uncertainties around the estimation of $P(B_{i,j})$ or
185 the variability of interaction probabilities, a Beta distribution may be used to represent the relative likelihood of
186 different probability values. For example, when calculating the probability of interaction between two taxa
187 based on their local abundances, any spatiotemporal fluctuations in their abundances would introduce
188 variability in the interaction probability at the local scale. If we take into account the stochasticity of the
189 interaction probability, a Beta-Binomial distribution can be used to predict the number of networks in which the
190 interaction occurs. Empirically observing an interaction between two taxa at a given location and time provides
191 important information that can be used to update previous estimates of $P(B_{i,j})$, informing us on the biological
192 capacity of both taxa to interact and the environmental conditions that enabled them to interact locally. By
193 sampling more interactions, we can estimate their local variability more precisely.

194 **Probabilistic interactions may also describe quantitative networks**

195 Even though binary interaction networks constitute a highly valuable source of ecological information (Pascual
196 *et al.* 2006), they overlook interaction strengths. Represented in a quantitative adjacency matrix W , interaction
197 strengths better describe the energy flows, demographic impacts or frequencies of interactions between nodes
198 (Berlow *et al.* 2004; Borrett & Scharler 2019), with $W_{i,j}$ being a natural \mathbb{N} or real \mathbb{R} number depending on the
199 measure. For example, they may represent local interaction rates between pairs of taxa (e.g., the flower-visiting
200 rates of pollinators in a mutualistic network, Herrera 1989). When interaction strengths characterize predation
201 pressure on prey, they can serve as parameters in a Lotka-Volterra model (e.g., Emmerson & Raffaelli 2004).
202 The extra amount of ecological information in quantitative networks typically comes at a cost of greater

203 sampling effort and data volume (Strydom *et al.* 2021), especially when using predictive models that quantify
204 the uncertainty and variability of quantitative interactions (Berlow *et al.* 2004).

205 Like binary interaction networks, the uncertainty and variability of interaction strengths can be represented
206 probabilistically. Interaction strengths can follow many probability distributions depending on the measure. For
207 instance, they can follow a Poisson distribution $W_{i,j} \sim \text{Poisson}(\lambda_{i,j}t_0)$ when predicting the number of
208 interactions between individuals, with $\lambda_{i,j}$ being the expected rate at which individuals of taxa i and j interact.
209 The product $\lambda_{i,j}t_0$ is the expected number of interactions realized by individuals during the time interval t_0
210 (e.g., the expected number of prey j consumed by all predators i). The Poisson distribution can also be
211 0-inflated when taking into account non-interacting taxa (e.g., Boulangeat *et al.* 2012 employ a 0-inflated model
212 to analyze species abundance following the modeling of species presence and absence), which constitute the
213 majority of taxa pairs in most local networks (Jordano 2016).

214 Because of the methodological difficulties typically encountered when building deterministic quantitative
215 networks, binary interaction networks, which are easier to sample (Jordano 2016) and predict (Strydom *et al.*
216 2021), have been more frequently studied and used. Mathematical models such as Ecopath (Plagányi &
217 Butterworth 2004) partially mitigate these difficulties, but the number of biological parameters required to make
218 predictions hinders their application in many systems. Moreover, most published probabilistic interaction
219 networks (e.g., Strydom *et al.* 2022) and methods (e.g., Poisot *et al.* 2016) involve probabilistic interactions
220 whose outcome is binary. This underlines the need for better guidelines on the interpretation and manipulation
221 of such probabilistic interactions, to ensure the appropriate use of these networks and methods. For these
222 reasons, our primary focus is on interpreting interaction probabilities that dictate the presence or absence of
223 interactions, in both local networks and metawebs.

224 Local networks: communities interacting in space and time

225 Species interactions occur in a local context

226 Local networks of probabilistic interactions describe how likely taxa are to interact at a given location and time
227 period. Local interactions are contingent upon the environmental conditions of the community and the matching
228 of taxa biological traits. In local networks, edges commonly represent our degree of belief that two taxa interact
229 in nature, but can also represent the probability of empirically *observing* this interaction (Catchen *et al.* 2023).

230 **Space and time**

231 We define space as the collection of geographic coordinates (x, y, z) , with (x, y) representing longitude and
232 latitude coordinates, and z denoting either altitudes or depths. These point coordinates delineate the spatial
233 boundaries of the system, which may be portrayed as a polyhedron. Ecological interactions may exhibit
234 variations along latitudinal and altitudinal gradients, as evidenced by changes in hummingbird-plant
235 interactions (Weinstein & Graham 2017a, b) and mosquito biting rates (e.g., Kulkarni *et al.* 2006) at different
236 elevations. In contrast, time is defined as the specific time period within which interactions were either observed
237 or predicted. Even though space and time are continuous variables that should yield probability *densities* of
238 interactions (i.e., relative likelihoods of interactions occurring at infinitesimal locations and instants in time),
239 these definitions enable them to be conceptualized as distinct patches and time segments. Treating space and
240 time as discrete dimensions aligns with the common sampling methods of ecological networks and provides
241 probabilities of interactions, which can be obtained by integrating probability densities over space and time. We
242 can quantify both an area A_0 and a duration t_0 , which can readily be used in spatiotemporal analyses of
243 ecological networks (Box 1).

244 **Co-occurrence**

245 The probability that two taxa i and j interact in a local network $L_{x,y,z,t}$ (spatial and temporal subscripts hereafter
246 replaced by the shorter subscript k for clarity) can be conditioned on many environmental and biological
247 factors. In addition to network area (or volume) and duration, they may be conditioned on taxa co-occurrence
248 $X_{i,j,k}$, which is usually a Boolean describing if the geographic distributions of both taxa overlap within the study
249 area. As illustrated in Box 1, co-occurrence may be modeled probabilistically, in which case it may conform to
250 a Bernoulli distribution $X_{i,j,k} \sim \text{Bernoulli}(P(X_{i,j,k}))$. The probability of co-occurrence can be calculated using
251 the individual (marginal) occurrence probabilities $P(X_{i,k})$ and $P(X_{j,k})$. Given that taxa occurrences are not
252 independent of each other, the probability of co-occurrence can be calculated by multiplying the probability of
253 occurrence of one taxon by the probability of occurrence of the other given that the first one occurs:

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

254 The probability of co-occurrence $P(X_{i,j,k})$ can be estimated through the application of joint species distribution

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

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

259 Biological and environmental factors

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

Other important factors that can impact interaction probabilities at the local scale are taxa local abundances $N_{i,k}$ and $N_{j,k}$, which affect encounter probabilities (Canard *et al.* 2012), and local traits distributions $T_{i,k}$ and $T_{j,k}$ (e.g., body mass, longevity, and habitat breadth, Caron *et al.* 2024), which determine the ability of individuals to interact after encountering each other (Poisot *et al.* 2015). Local interaction probabilities may also be conditioned on higher-level properties of the network, which we denote by $f(L)$. Many topological null models (i.e., statistical models that randomize interactions by retaining certain properties of the network while excluding others) provide interaction probabilities from selected measures of network structure, such as connectance (Fortuna & Bascompte 2006) and the degree distribution (Bascompte *et al.* 2003).

277 Local interactions must be biologically feasible

Local interactions must be biologically feasible before occurring at a specific time and space. A local probability of interaction $P(L_{i,j,k})$ can be expressed as the product of the probability of local interaction given

280 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
281 sake of simplicity, with their probability of regional interaction $P(M_{i,j})$:

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

282 Low values of $P(L_{i,j,k}|M_{i,j})$ indicate that feasible interactions rarely occur locally, intermediate values around
283 50% suggest considerable spatiotemporal variability, while high values indicate that regional interactions are
284 nearly always realized locally. The local probability of interaction between a given pair of taxa is always equal
285 to or below their probability of regional interaction.

286 **Conditional variables must be explicitly stated**

287 The probability that two taxa i and j interact in a local network L_k can thus be conditioned on their
288 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
289 traits distributions $T_{i,k}$ and $T_{j,k}$, local environmental conditions E_k , network area (or volume) A_0 , time interval
290 t_0 , network properties $f(L_k)$, and biological feasibility $M_{i,j}$. The local probability of interaction is described by
291 the following expression when all of these conditional variables are included:

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

292 Although these variables correspond to distinct ecological inquiries or mechanisms related to ecological
293 interactions, they may covary with each other, such as the possible dependence of $X_{i,j,k}$ and E_k on spatial and
294 temporal scales. When estimating interaction probabilities using e.g. a generalized linear model with multiple
295 explanatory variables that might not be independent, it may become important to address collinearity. In such a
296 case, to mitigate this issue, it may be necessary to use variable selection techniques before fitting the model to
297 data.

298 Not all of these conditional variables need to be considered at all times. The representation of the local context
299 in which probabilities are estimated and the variables that should be taken into consideration depend on the
300 study system, the objectives of the study, and the resources available to the researchers. For example, Gravel *et*
301 *al.* (2019) analyzed local European host-parasite networks of willow-galling sawflies and their natural enemies,
302 all referenced in space and time, to infer probabilities of local interactions between co-occurring species. This

303 was achieved by including temperature and precipitation as conditional variables in their models. In Box 2, we
 304 reuse these data to show the extent of variation among these local networks. We do so by measuring their
 305 dissimilarity with the regional network (metaweb aggregating all local interactions), both in terms of species
 306 composition and interactions. We build local probabilistic networks following eq. 3, showing that insufficient
 307 local variation (high probability of local interaction among potentially interacting species) results in an
 308 overestimation in both the number of interactions and connectance (i.e., the proportion of all of the
 309 non-forbidden links that are realized).

310 When accounted for, conditional variables should be clearly described in the documentation of the data
 311 (Brimacombe *et al.* 2023), preferentially in mathematical terms to avoid any confusion in their interpretation
 312 and to limit manipulation errors during their re-use. For instance, ecologists should be explicit about their
 313 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
 314 probabilities, as this can change our interpretation of the data. Understanding the scale and level of aggregation
 315 of the data enables us to more accurately study the underlying ecological processes (Clark *et al.* 2011). In
 316 Tbl. 1, we present examples of studies that used different expressions of probabilistic interactions. We included
 317 in this table the probability of empirically observing an interaction that is realized locally $P(O_{i,j,k}|L_{i,j,k})$ to
 318 underscore the 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 of realized interactions, a local network O 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 boxes in this study that discussed them are also specified. Uncertainty sources include uncertainty of model parameters, model structure, and input data. The study marked with an asterisk has been conducted on binary interaction networks.

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)

Expression	Type	Outcome	Common models	Reference
$P(L_{i,j,k} T_{i,k}, T_{j,k}, \dots)$	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)
$P(L_{i,j,k} A_0, \dots)$	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 the taxa can biologically interact	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

319 **Interaction probabilities may be estimated with multiple models**

320 When using multiple models to estimate local interaction probabilities, rather than selecting a single model that
321 best fits the data, model averaging may enhance our estimations. In this approach, the weighting is based on the
322 likelihood of each model. Model weights represent the probability that each model is the most suitable for
323 explaining the data, and may be measured using Akaike weights (Burnham & Anderson 2004; Wagenmakers &
324 Farrell 2004). For instance, considering two models mod_1 and mod_2 with respective probabilities (or weights)
325 $P(mod_1)$ and $P(mod_2)$, the average probability of interaction $P(L_{i,j,k}|...)$ can be calculated as follows:

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

326 where the ellipsis serves as a placeholder for the conditional variables incorporated in these models. Model
327 structure constitutes another source of uncertainty that needs to be documented and quantified when estimating
328 interaction probabilities.

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 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 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.

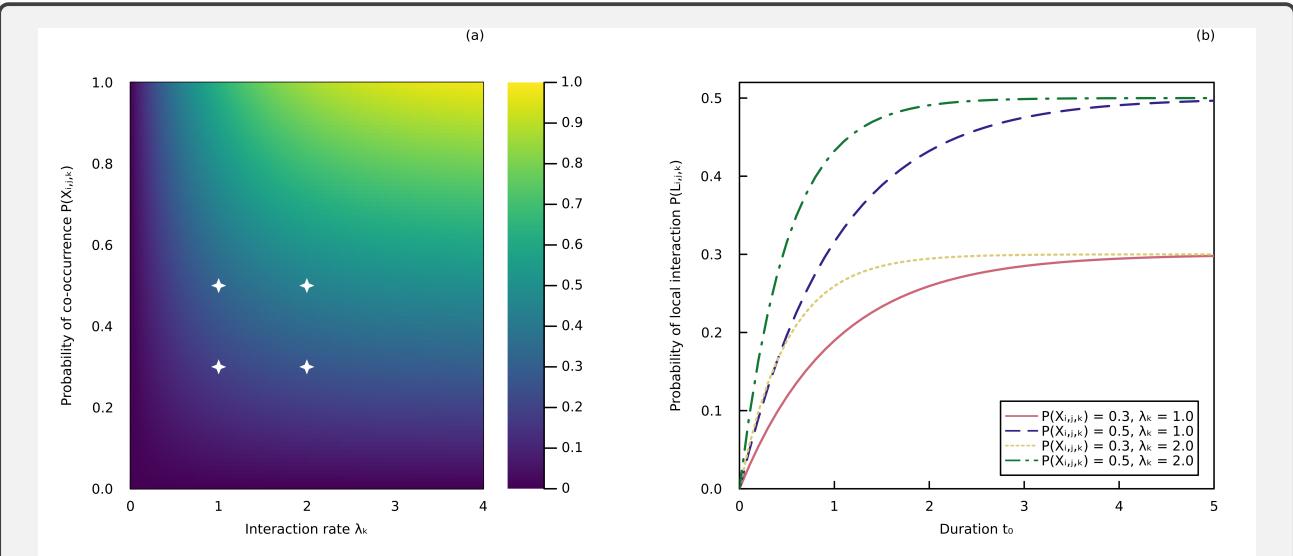


Figure 1: Parameters of the spatiotemporally explicit model of interactions. (a) Probability of local interaction given by the process model (Eq. 8) under different values of λ_k (interaction rate) and $P(X_{i,j,k})$ (probability of co-occurrence), with $t_0 = 1$ (duration). Parameters t_0 and λ_k have 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.

331

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 of interactions between common species (β_{OS} , Fig. 2b) indices (Poisot *et al.* 2012). Expectingly, local

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networks are highly dissimilar from the metaweb in terms of species composition, especially when only a limited number of sites has 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).

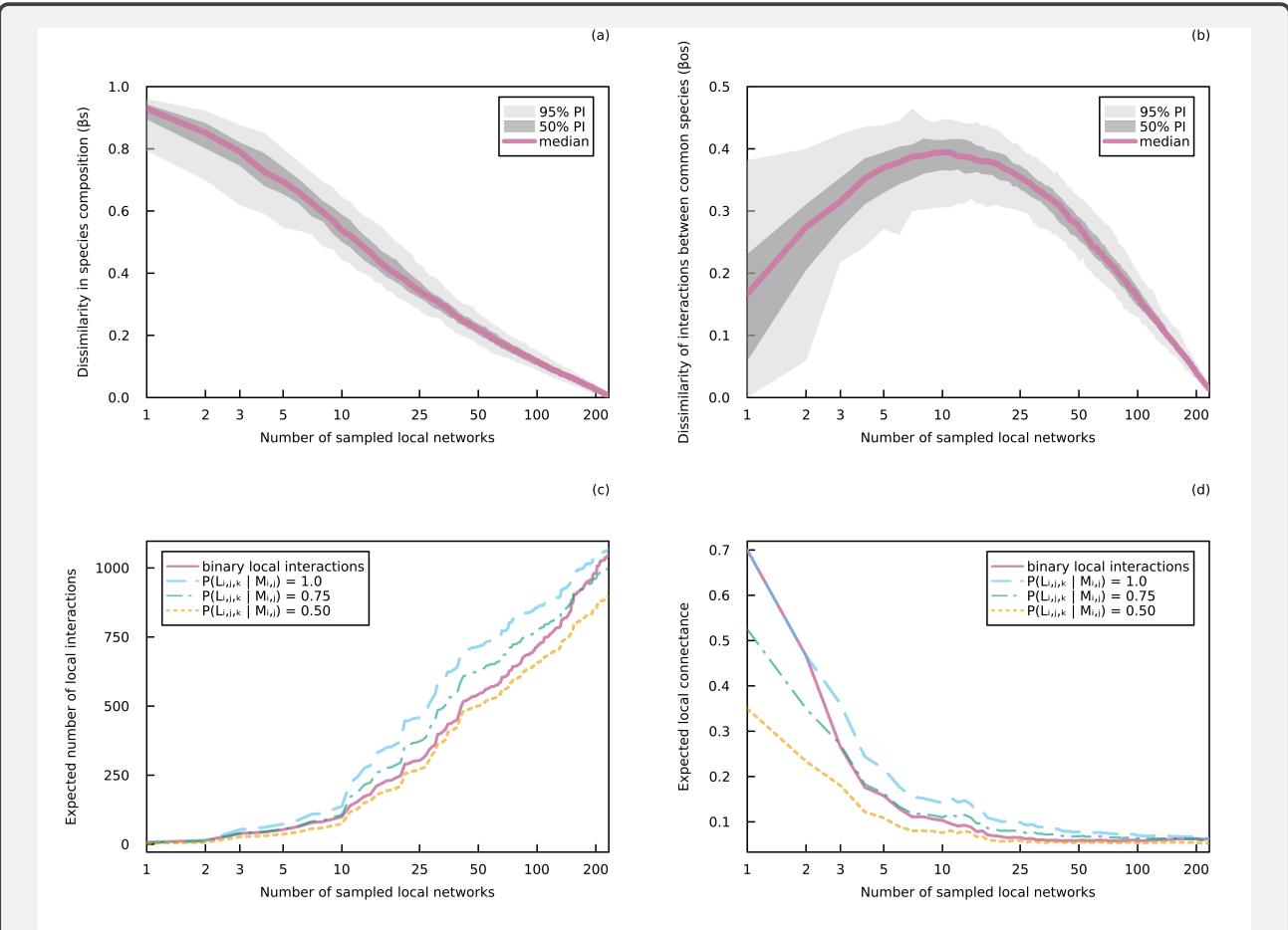


Figure 2: Network accumulation curves. (a) Dissimilarity in species composition and (b) dissimilarity of interactions between common species between aggregated local networks and the metaweb of binary host-parasite interactions. In both panels, the colored line represents the median dissimilarity across 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.

335

336 Metawebs: regional catalogs of interactions

337 Unobserved interactions should be probabilistic

338 Metawebs (Dunne 2006) are networks of potential interactions over broad spatial, temporal, and taxonomic
339 scales (e.g., food webs at the continental scale). Potential interactions describe the biological capacity of taxa to
340 interact under optimal or feasible environmental conditions, which is typically assessed at the regional scale.

341 Metawebs of probabilistic interactions are particularly useful in situations where there is uncertainty in the
342 ability of taxa to interact. They may also be used as informative priors of local interactions.

343 In contrast to local networks, where interaction probabilities arise from the processes of the interaction and the
344 lack of information on the conditions, interaction probabilities in metawebs solely result from a lack of
345 knowledge. This uncertainty arises due to insufficient interaction data, especially for taxa that have not yet been
346 observed to co-occur, and uncertainties in trait-matching models. As data accumulates, interactions in
347 metawebs should tend towards binarity, either taking a value of 1 (observing an interaction at least once) or
348 approaching 0 (repeatedly failing to observe an interaction between co-occurring taxa). Confidently observing
349 an interaction once confirms its biological feasibility, but failing to observe it (even on multiple occasions) does
350 not ensure that it is non-feasible (e.g. due to false negatives, Catchen *et al.* 2023). While local interaction
351 probabilities are irreducible because of local variability, uncertainty of regional interactions reduces to 0 with
352 the addition of information. Moreover, although *neutrally* forbidden interactions (i.e., between rare species,
353 Canard *et al.* 2012) tend to have low probability values in local networks, they may be non-random in the
354 metaweb (i.e., a probability of 1 when species' biological traits can support an interaction if they were to
355 encounter each other at high enough abundances). Likewise, non-co-occurring taxa may have a non-zero
356 probability of interaction in the metaweb. Regional interaction probabilities are thus fundamentally different

357 from local interaction probabilities, both in terms of uncertainty sources and probability values.

358 The extent of sampling effort influences our evaluation of probabilities of potential interactions, as sampling

359 over a larger area or for a longer duration enables us to capture a greater number of regional interactions

360 (McLeod *et al.* 2021). However, in contrast with local networks of probabilistic interactions, which describe

361 local interaction stochasticity, regional interactions are not evaluated for any particular local context. In Box 3,

362 we discuss the differences in spatial and temporal scaling of regional interactions compared to local interactions.

363 We do so by using the host-parasite networks of Kopelke *et al.* (2017) as an illustration of spatial scaling.

364 **Potential interactions are sometimes linked to environmental conditions**

365 **Biological feasibility**

366 Potential interactions describe what we refer to as the *biological* feasibility of interactions, which is based solely

367 on the regional traits distributions T_i and T_j of taxa i and j , respectively. We define regional trait distributions as

368 the range of phenotypes that a taxon can express across various environments. Regional traits may differ from

369 local traits $T_{i,k}$ and $T_{j,k}$, which vary spatially and temporally because of phenotypic plasticity and local

370 environmental variability (Berg & Ellers 2010). A probability of potential interaction in a metaweb M

371 describing the biological feasibility of interactions may be expressed as:

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

372 which, in contrast with local networks, is not conditioned on any spatial, temporal, co-occurrence or

373 environmental variables (Tbl. 1). Because phylogenetically close species share similar traits, we should expect

374 that closely related species will have similar interacting partners. We can thus use phylogeny to predict species

375 traits and infer regional interactions (Eklöf & Stouffer 2016; Stouffer *et al.* 2012; Strydom *et al.* 2022). The

376 taxonomic level at which interactions are evaluated also influences the distribution of regional traits. However,

377 as explained in Box 4, there is no fundamental difference in the taxonomic scaling of regional and local

378 interactions (i.e., how interaction probabilities change with taxonomic level) because they both depend on trait

379 aggregation.

380 The biological feasibility of interactions expresses our degree of belief that there exists at least one combination

381 of phenotypes that could support an interaction if they were to encounter each other, assuming they had enough

382 time to interact. Evaluating this probability is conducted without incorporating the environmental conditions
383 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
384 forbidden interactions (i.e., the probability that their traits do not support an interaction), which is based
385 uniquely on biological traits:

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

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

395 Ecological feasibility

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

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

399 where E is the environmental conditions under which potential interactions are evaluated (Tbl. 1). Unlike E_k ,
400 these environmental conditions do not represent conditions occurring at specific locations. Ecological
401 feasibility represents the probability that two taxa interact if they were to encounter each other under given
402 environmental conditions, assuming they had enough time to interact. Incorporating environmental conditions
403 into a trait-matching model may be important when there is high covariance between the environment and traits.
404 For instance, in our example involving rattlesnakes and lemmings, the probability of potential interaction

405 between these two species may be low in most environmental conditions. Western diamondback rattlesnakes
 406 may be unactive under low temperatures (Kissner *et al.* 1997), whereas wood lemmings may have low tolerance
 407 to high temperatures (Kausrud *et al.* 2008). The probability that an interaction is ecologically feasible is always
 408 lower than the probability that it is biologically feasible, even across all environmental conditions:

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

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

414 Metawebs are built with interaction data and trait-matching models

415 Starting from a selected set of taxa, which are usually distributed within a broad region of interest, metawebs
 416 can be built using different data sources, including literature review (e.g., Maiorano *et al.* 2020), aggregated
 417 interaction data (e.g., Gravel *et al.* 2019; Saravia *et al.* 2022), trait-matching models (e.g., Shaw *et al.* 2024;
 418 Strydom *et al.* 2022), and expert knowledge. Every pair of taxa that have confidently been observed to interact
 419 at least once can be given a probability of 1 (i.e., $P(M_{i,j}) = 1$) since we know that they *can* interact. This differs
 420 from local networks of probabilistic interactions, where interaction events may remain stochastic (i.e.,
 421 $P(L_{i,j,k}) < 1$) even after empirically observing interactions due to their spatiotemporal variability. Interactions
 422 that were never observed typically have low probability values in local networks and vary from low to high
 423 values in metawebs, contingent upon taxa traits distributions (reaching 0 for forbidden links).

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

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

428 The reduction in the probability of regional interaction after considering that it was never observed locally (i.e.,
429 $P(M_{i,j} = 1|O_{i,j,k} = 0, \dots) < P(M_{i,j} = 1| \dots)$) occurs because $P(O_{i,j,k} = 0|M_{i,j} = 1, \dots)$ must be lower than
430 $P(O_{i,j,k} = 0, \dots)$, i.e. there is a higher chance of observing an interaction when it is biologically feasible.
431 Observations of interactions may be false positives because of observation errors due to taxonomic
432 misidentifications and ecological misinterpretations, such as those involving phylogenetically close species or
433 cryptic species and interactions (Pringle & Hutchinson 2020). Likewise, forbidden interactions may be false
434 negatives, e.g. if they have been evaluated based on unrepresentative or incomplete traits distributions.
435 Employing Bayesian models proves valuable when estimating interaction probabilities in metawebs (e.g.,
436 Bartomeus *et al.* 2016; Cirtwill *et al.* 2019). This improvement is achieved by updating prior information
437 regarding the feasibility of interactions (e.g., experts' prior assessments of interaction probabilities) with
438 empirical data on interactions and traits. By improving our estimation of potential interaction probabilities, we
439 may build more reliable metawebs that adequately reflect our uncertainty on the biological feasibility of
440 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.

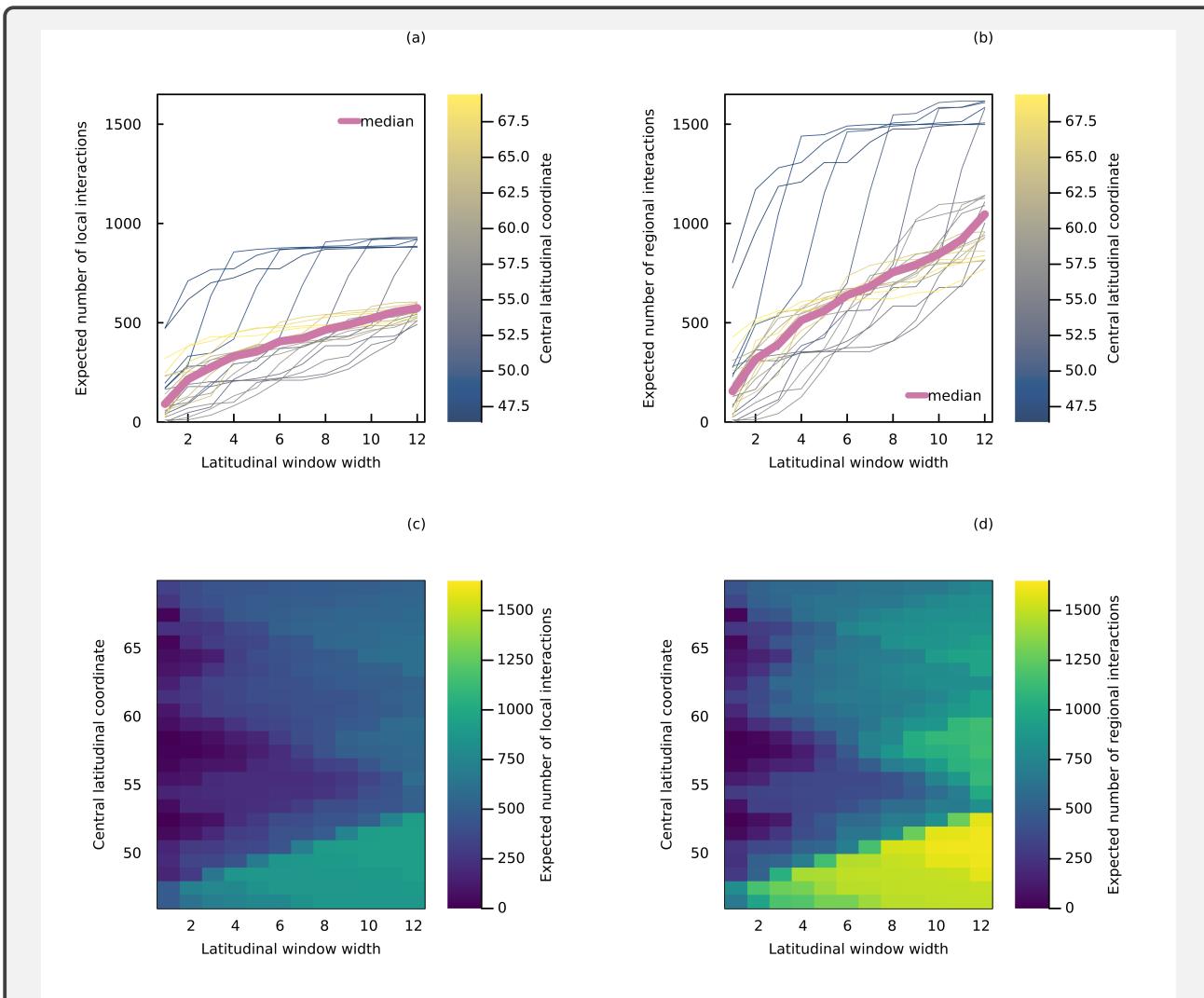


Figure 3: Spatial scaling of interactions. Expected number of host-parasite interactions in a network aggregating all (a) local and (b) regional probabilistic interactions within a latitudinal window of a given width. Every dashed curve corresponds to a different window centered at a given latitude (color 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.

443

Box 4: Taxonomic scaling of interactions

Given that our interpretation of the properties of ecological networks depends on their taxonomic level (Guimarães 2020), investigating the taxonomic scaling of interactions (i.e., how interaction probabilities

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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 be 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

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.

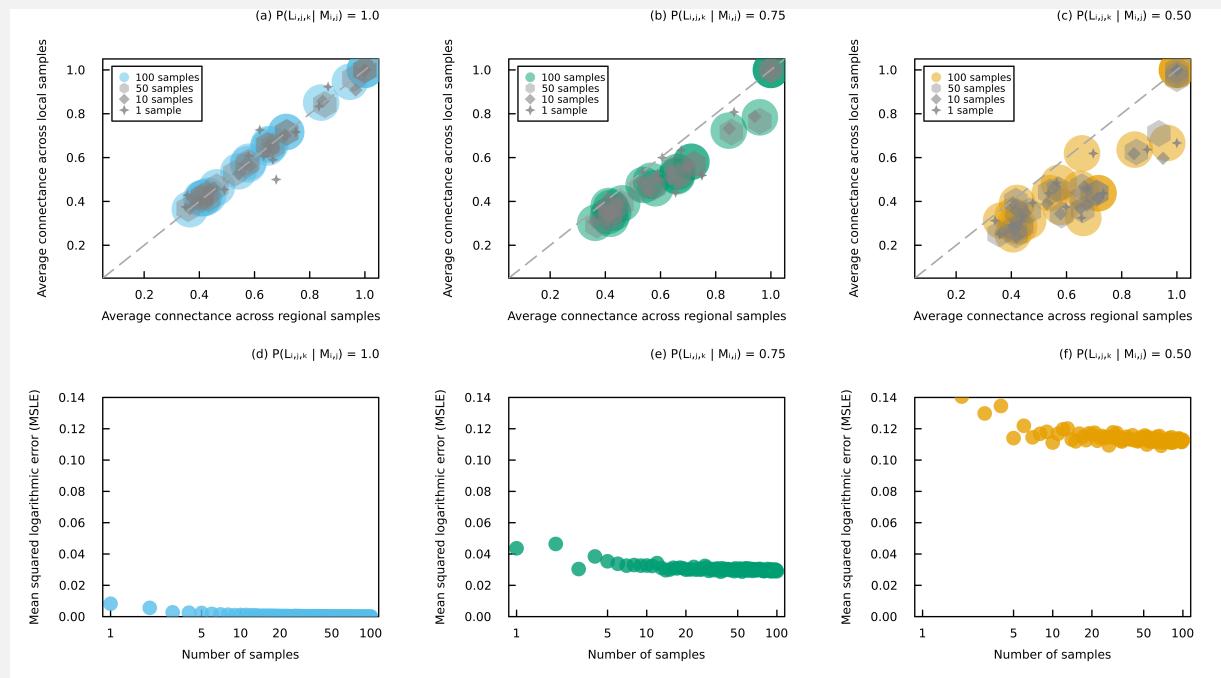


Figure 4: Connectance of sampled binary interaction networks. (a-c) Average connectance of binary interaction networks obtained from the two sampling techniques for 20 randomly selected host-parasite networks. Cross markers represent the connectance of a single sample for each network, diamond markers 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.

448

449 Future perspectives

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

463 Predicting local networks from metawebs

464 Metawebs are a valuable source of ecological information for predicting local networks across time and space.
465 Local networks of binary interactions can be reconstructed by selecting a subset of taxa and interactions from
466 the metaweb (Dunne 2006). Metawebs thus contain more interactions than local networks, even though their
467 connectance is usually much smaller than the one of local networks (Gravel *et al.* 2011). Determining the list of
468 taxa to select can be achieved empirically (e.g., observed occurrence data for a site) or numerically (e.g., species
469 distribution models). As species composition is arguably easier to sample or predict than pairwise interactions,
470 the primary challenge lies in deciding which interactions to select from the metaweb. Inferring the structure of

471 local networks from the metaweb before predicting local pairwise interactions could hold promise (Strydom *et*
 472 *al.* 2021), considering that the structure of local networks is constrained by the metaweb (Saravia *et al.* 2022).
 473 Inferring local networks of probabilistic interactions from a metaweb comes with its own set of challenges. For
 474 example, Dansereau *et al.* (2023) inferred spatially-explicit food webs from a metaweb of probabilistic trophic
 475 interactions between Canadian mammals. Their predicted localized food webs are downscaled versions of the
 476 metaweb (i.e., localized metawebs with the same interaction probabilities as those in the regional metaweb). To
 477 infer local networks as defined in this manuscript (i.e., describing local realizations of interactions), local
 478 interaction probabilities must be smaller than regional interaction probabilities. This decrease is due to the
 479 prerequisite that two taxa must initially possess the capacity to interact before engaging in local interactions
 480 (Eq. 3). Inferring local networks from a metaweb by maintaining identical interaction probability values
 481 introduces systematic biases into the predictions, as discussed in Box 2 (unless networks are seen as downscaled
 482 metawebs).

483 As suggested by McLeod *et al.* (2021), although metawebs do not capture the spatiotemporal variability of
 484 interactions, they establish an upper limit for local interactions (similarly for metawebs of probabilistic
 485 interactions, Strydom *et al.* 2023). In other words, the probability that two taxa interact at a specific location
 486 and time is consistently lower or equal to the probability of their regional interaction, regardless of the
 487 conditional variables considered:

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

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

$$\int_{E_k} \int_A \int_t P(L_{i,j,k}|E_k, A, t) dt dA dE_k \leq P(M_{i,j}|T_i, T_j). \quad (18)$$

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

495 across pairwise interactions within a network. Using simple models of $P(L_{i,j,k}|M_{i,j})$, as shown in Box 2,
496 represents an initial step toward the overarching objective of reconstructing local networks from metawebs.

497 Quantifying and reducing interaction uncertainty

498 While sampling biological communities decreases the uncertainty of interactions by accumulating evidence for
499 their feasibility and local realization, there is a limit to how much we can reduce uncertainty. In metawebs,
500 probabilities reflect our limited knowledge of interactions (i.e., our degree of belief that interactions are
501 feasible), which is expected to improve with a larger volume of data. Regional interactions should become more
502 definitive (with probabilities approaching 0 or 1) as we investigate various conditions, including different
503 combinations of species traits.

504 In comparison, although local networks can be seen as random instances of metawebs, their stochasticity cannot
505 be reduced to the same extent. Local interaction probabilities may represent both their uncertainty and
506 spatiotemporal variability. Owing to environmental heterogeneity, there will invariably be instances in which an
507 interaction occurs and others in which it does not, across different times and locations, irrespective of the extent
508 to which we can improve our knowledge of its biological feasibility and the local conditions that facilitate its
509 occurrence. When local networks describe probabilities of observing interactions rather than their actual
510 occurrence, we must also consider observation variability (sampling error) as an additional source of
511 stochasticity. Every ecological process is stochastic but there is also a possibility that a phenomenon goes
512 undetected. Quantifying and partitioning this stochasticity will enable us to make more accurate predictions
513 about ecological interactions at various spatial and temporal scales. This will prove to be of vital importance as
514 our time to understand nature runs out, especially at locations where the impacts of climate change and habitat
515 loss hit harder.

516 Relaxing the independence assumption

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

522 A more accurate representation of the stochasticity of ecological networks involves creating *probabilistic*
523 *networks* ($P(L|...)$ and $P(M|...)$), rather than networks of *probabilistic interactions* ($P(L_{i,j,k}|...)$ and $P(M_{i,j}|...)$).
524 Probabilistic networks describe the probability that a particular network of binary (or quantitative) interactions
525 (its whole adjacency matrix) is realized. For example, Young *et al.* (2021) used a Bayesian approach to estimate
526 the probability of different plant-pollinator network structures derived from imperfect observational data. A
527 probability distribution of ecological networks may also be derived using the principle of maximum entropy
528 given structural constrained (e.g., Cimini *et al.* 2019; Park & Newman 2004).

529 Regardless of the method employed, generating probabilistic local networks could lead to more accurate
530 predictions of local networks of binary interactions by bypassing the independence assumption. Probabilistic
531 networks could serve as an alternative to null hypothesis significance testing when comparing the structure of a
532 local network to some random expectations or, as done in Pellissier *et al.* (2018), to the metaweb. These random
533 expectations are typically derived by performing a series of Bernoulli trials on probabilistic interactions,
534 assuming independence, to generate a distribution of networks of binary interactions to calculate their structure
535 (Poisot *et al.* 2016). One could instead compare the likelihood of an observed network to the one of the most
536 likely network structure (according to the probabilistic network distribution), thereby directly obtaining a
537 measure of discrepancy of the empirical network. Generating probabilistic ecological networks represents a
538 tangible challenge, one that, in the coming years, promises to unlock doors to more advanced and adequate
539 analyses of ecological networks.

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