

Deciphering ecological networks of probabilistic interactions

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

The stochastic nature of ecological interactions has led biologists to adopt a probabilistic view of ecological networks. Representing species interactions probabilistically (how likely are they to occur?) as opposed to deterministically (are they occurring?) highlights uncertainties in our knowledge of interactions. The origin of the uncertainty captured by interaction probabilities differs depending on the method used to evaluate them. It may consist of the uncertainty of predictive models, the subjective assessment of experts, or even the empirical evaluation of interaction spatiotemporal variability. Despite this growing interest in probabilistic interactions, guidelines for the estimation and documentation of probabilistic interaction data are still lacking. This is concerning because our biological understanding of interaction probabilities and the decisions made during data analysis rely heavily on the often elusive definition of the probabilistic event. We review how probabilistic interactions are defined at different spatial scales, from local interactions to regional networks (metawebs), with a strong emphasis on trophic interactions (predatory, herbivory, and parasitic interactions). These definitions are based on the distinction between the realization of an interaction at a specific time and space (local) and its biological feasibility (regional). Through case studies using open data on host-parasite interactions in Europe, we show that these two network representations have different statistical properties when it comes to common ecological applications. Specifically, we found that local and metawebs differ in their spatial and temporal scaling of probabilistic interactions, but not in their taxonomic scaling. We suggest two approaches to inferring binary interactions from probabilistic ones that account for these differences and show that systematic biases arise when directly inferring local webs from subsets of metawebs. Our results underscore the importance of clear metadata for networks of probabilistic interactions that describe the type of interaction (local or regional)

and uncertainty sources. Comprehensive metadata are particularly useful for the identification of optimal sampling locations where data collection may provide the greatest amount of new information on interactions and minimize their uncertainty.

This work is released by its authors under a CC-BY 4.0 license



Last revision: *March 16, 2024*

1 Introduction

2 As we try to navigate global biodiversity change, filling in knowledge gaps about biodiversity becomes
3 instrumental to monitoring and mitigating those changes (Gonzalez & Londoño (2022), Abrego *et al.* (2021)).
4 However, cataloging species, populations and, in particular, ecological interactions (e.g., predation, parasitism,
5 and pollination) is a substantial challenge (Polis (1991), Pascual *et al.* (2006)). There are methodological and
6 biological constraints that hinder our ability to observe all ecological interactions, leading to significant
7 uncertainties in our understanding of these interactions. For example, the spatial and temporal uncoupling of
8 species (e.g., nocturnal and diurnal species coexisting in the same space without interacting due to differences
9 in the timing of their daily activities, Jordano (1987)) and the large number of rare and cryptic interactions in a
10 community contribute to these uncertainties (Jordano (2016)). More generally, a handful of conditions must be
11 satisfied for an interaction to be observed locally. First, both species must have overlapping geographic ranges,
12 i.e. they must co-occur within the region of interest (Blanchet *et al.* (2020)). Second, they must have some
13 probability of meeting. Probabilities of interspecific encounters are typically low, especially for rare species
14 with low abundances. While species' absolute abundances may impact interaction frequencies (Vázquez *et al.*
15 (2007)), encounter probabilities are determined by their relative abundances (Canard *et al.* (2012), Canard *et al.*
16 (2012)). The probability that species meet each other also depends on their biological characteristics, such as
17 the synchronization of their phenology (Olesen *et al.* (2010), Singer & McBride (2012)) and their
18 discoverability (e.g., Broom & Ruxton (2005)). Finally, when species do come into contact, an interaction
19 occurs only if their traits are locally compatible (Poisot *et al.* (2015)), including but not limited to their body
20 phenotypes (Bolnick *et al.* (2011), Stouffer *et al.* (2011), Gravel *et al.* (2013)) and behavioral choices (Pulliam
21 (1974), Choh *et al.* (2012)). Interactions may also be influenced by the presence or prevalence of a third species
22 (e.g., of a more profitable prey species, Golubski & Abrams (2011), Sanders & van Veen (2012)). Documenting
23 the location and timing of interactions becomes even more difficult when accounting for the spatiotemporal
24 variability of ecological interactions (Poisot *et al.* (2012), Poisot *et al.* (2015)). Environmental factors, such as
25 temperature (Angilletta *et al.* (2004)), drought (Woodward *et al.* (2012)), climate change (Gilman *et al.* (2010),
26 Woodward *et al.* (2010), Araujo *et al.* (2011)), and habitat modifications (Tylianakis *et al.* (2007)), contribute
27 to this spatiotemporal variability by impacting species abundance and traits. Even after satisfying all these
28 conditions, there remains a possibility that the interaction does not occur locally, either due to the intricate
29 nature of the system or simply by chance. If it does occur, it might still go unnoticed, particularly if it happens
30 infrequently. In this context, it is unsurprising that our knowledge of ecological interactions remains limited

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

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

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

34 variability of species interactions has led ecologists to expand their representation of ecological networks (also

35 known as ecological webs) to include a probabilistic view of interactions (Poisot *et al.* (2016), Dallas *et al.*

36 (2017), Fu *et al.* (2021)). This different perspective allows us to fill in the Eltonian shortfall (Hortal *et al.*

37 (2015)) by modeling the probability of occurrence of interactions, which can be an important tool for directing

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

39 probabilistic representation of interactions is thus far limited to direct interactions, which are conceptually and

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

41 with indirect interactions (e.g., interspecific competition), which arise from distinct ecological processes and are

42 often not directly observable (Kéfi *et al.* (2015), Kéfi *et al.* (2016)). Representing direct interactions

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

58 (Gonzalez-Varo & Traveset (2016)).

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

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

network structure (i.e., community-level properties driving the functioning, dynamics, and resilience of ecosystems, Proulx *et al.* (2005), McCann (2007), McCann (2011), Rooney & McCann (2012)) remains to be elucidated. The application and development of computational methods in network ecology, often based on a probabilistic representation of interactions, can alleviate (and guide) the sampling efforts required to document species interactions (Strydom *et al.* (2021)). For example, statistical models can be used to estimate the uncertainty of pairwise interactions (Cirtwill *et al.* (2019)) and the probability of missing (false negatives) and spurious (false positives) interactions (Guimerà & Sales-Pardo (2009)). Considering the high rate of false negatives in species interaction data due to the difficulty of witnessing rare interactions (Catchen *et al.* (2023)), these models could inform the identification of priority sampling locations of ecological webs where data collection would yield the most valuable information, thereby reducing errors. Optimization models for sampling locations have mostly found applications in biological systems that are not networks, such as identifying priority sampling sites for disease hotspots (Andrade-Pacheco *et al.* (2020)), but there is substantial promise in applying them to probabilistic ecological interactions. Statistical models can also be used to generate predictions of ecological webs without prior knowledge of pairwise interactions, for instance using body size (Petchey *et al.* (2008), Gravel *et al.* (2013)), phylogeny (Elmasri *et al.* (2020), Strydom *et al.* (2022)), or a combination of niche and neutral processes (Bartomeus *et al.* (2016), Pomeranz *et al.* (2019)) for inference.

Topological null models, which generate networks of probabilistic interactions by preserving chosen characteristics of the adjacency matrix of binary interactions while intentionally omitting others (Bascompte *et al.* (2003), Fortuna & Bascompte (2006)), serve as other examples of common probabilistic interaction models.

Null models can be used to produce underlying distributions of network measures for null hypothesis significance testing. Many measures have been developed to describe the structure (Poisot *et al.* (2016)) and diversity (Ohlmann *et al.* (2019), Godsoe *et al.* (2022)) of probabilistic interaction webs. These models and measures support the use of this approach for the study of a wide range of ecological questions, from making better predictions of species distribution (Cazelles *et al.* (2016)) to forecasting the impact of climate change on ecological webs (Gilman *et al.* (2010)).

The lack of clear guidelines on the use of probabilistic interaction data is worrisome, both for data producers and re-users who generate and manipulate these numbers. This is concerning because sampling strategies and decisions regarding network construction can affect our understanding of network properties (Brimacombe *et al.* (2023)). Besides methodological difficulties that may arise when assessing probabilistic interactions, a precise definition of probabilistic interactions appears to be lacking, making the estimation and use of these data

more difficult. We aim to take a step back by outlining different ways in which probabilistic interactions are defined and used in network ecology. We distinguish two broad categories of probabilistic interaction networks that necessitate distinct approaches when applied to key ecological questions: local webs describing probabilities of realized interactions, and regional webs (metawebs) describing probabilities of potential interactions. We highlight the distinctions in the ecological meaning of these two representations and examine some of their properties and relationships (particularly with space, time, and between each other) through empirical case studies. Moreover, there is currently no metadata standard that could guide the documentation of all types of probabilistic interactions (although see e.g., Salim *et al.* (2022) who discuss data standards for deterministic mutualistic webs). Well-defined metadata for probabilistic interactions would support more adequate manipulation and integration of interaction data from different sources and guard against possible misinterpretations arising from ambiguous definitions of probabilistic interaction networks. These metadata should outline the nature (i.e., local or regional) and type (e.g., predatory or pollination) of the interactions, provide information regarding the taxonomic level, identities, and characteristics (e.g., life stages) of the individuals involved in an interaction, present the mathematical formulation of probabilities, including clearly identified conditional variables (e.g., spatial and temporal scales), and describe the methods and contexts (e.g., location, time, environmental conditions) in which interactions were estimated. Inadequately documented probabilistic interaction data should be used with caution when analyzing ecological webs. Our observations and advice can be applied to most types of ecological networks representing direct interactions, from food webs to host-virus networks. Even though the measurement of interaction probabilities may differ between network types (e.g., estimations often based on frequencies of interactions in plant-pollinator networks), the broad principles underlying our findings remain relevant and applicable across diverse ecological contexts.

Probabilistic representations of interactions

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

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

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

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

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

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

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

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

207 contribution will be on addressing the challenges in interpreting and using interaction probabilities in Bernoulli
208 distributions, in both local and metawebs.

209 Local webs: communities interacting in space and time

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

218 We define space as the collection of geographic coordinates (x, y, z) , with (x, y) representing longitude and
219 latitude coordinates, and z denoting either altitudes or depths. These point coordinates delineate the spatial
220 boundaries of the system, which may be portrayed as a polyhedron. Ecological interactions may exhibit
221 variations along latitudinal and altitudinal gradients, as evidenced by changes in hummingbird-plant interactions
222 (Weinstein & Graham (2017b), Weinstein & Graham (2017a)) and mosquito biting rates (e.g., Kulkarni *et al.*
223 (2006)) at different elevations. In contrast, time is defined as the specific time period within which interactions
224 were either observed or predicted. Even though space and time are continuous variables that should yield
225 probability *densities* of interactions (i.e., relative likelihoods of interactions occurring at infinitesimal locations
226 and instants in time), these definitions enable them to be conceptualized as distinct patches and time segments.

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

233 The probability that two taxa i and j interact in a local web $L_{x,y,z,t}$ (spatial and temporal subscripts hereafter
234 omitted or replaced by the shorter subscript l for clarity) can be conditioned on many environmental and

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

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

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

262 The probability that two taxa i and j interact in a local web L can thus be conditioned on their co-occurrence
 263 $X_{i,j,l}$ (or more explicitly on their occurrences $X_{i,l}$ and $X_{j,l}$), local abundances $N_{i,l}$ and $N_{j,l}$, local traits
 264 distributions $T_{i,l}$ and $T_{j,l}$, local environmental conditions E_l , network area (or volume) A , time interval t , and
 265 network properties $f(L)$. Although these variables correspond to distinct ecological inquiries or mechanisms
 266 related to ecological interactions, they may covary with each other, such as the possible dependence of $X_{i,j,l}$ and
 267 E_l on spatial and temporal scales. When estimating interaction probabilities using e.g. a generalized linear
 268 model with multiple explanatory variables that might not be independent, it may become important to address
 269 collinearity. In such a case, to mitigate this issue, it may be necessary to use variable selection techniques before
 270 fitting the model to data. The probability that a local interaction is realized is described by the following
 271 expression when all these conditional variables are included:

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

272 The representation of the local context in which probabilities are estimated and the variables that should be
 273 taken into consideration depend on the study system, the objectives of the study, and the resources available to
 274 the researchers. In other words, these variables do not systematically need to be accounted for. For example, in
 275 Gravel *et al.* (2019), for the purpose of model comparison, some models incorporated environmental variables
 276 as conditions of interaction probabilities, while others did not. When accounted for, these variables should be
 277 clearly described in the documentation of the data (Brimacombe *et al.* (2023)), preferentially in mathematical
 278 terms to avoid any confusion in their interpretation and to limit manipulation errors during their re-use. For
 279 instance, ecologists should be explicit about their consideration of co-occurrence in their estimation of local
 280 interaction probabilities. Indeed, it is important to specify if probability values are conditional $P(L_{i \rightarrow j} | X_{i,j,l} = 1)$
 281 or not $P(L_{i \rightarrow j})$ on co-occurrence since this can significantly impact the interpretation and analysis of the data.
 282 In [tbl. 1](#), we present examples of studies that used these different formulations of probabilistic interactions and
 283 conditional variables. We have included the probability of empirically observing an interaction that is realized
 284 locally $P(O_{i \rightarrow j} | L_{i \rightarrow j})$ to underscore the distinction between local observations and actual realizations of
 285 interactions, even though the focus of this manuscript is not on the observation of interactions.

Table 1: Mathematical expressions of probabilistic interactions. The probability of interaction between two taxa i and j is interpreted differently in a metaweb M of potential interactions (representing the *biological* feasibility of interactions), a metaweb M^* of potential interactions (representing the *ecological* feasibility of interactions), a local web L of realized interactions and a local web O of observed interactions. Each expression emphasizes a different conditional variable, the ellipsis serving as a placeholder for other variables not explicitly stated in the expression. The outcome of each of these probabilistic events, along with common uncertainty sources (often stemming from the model used for estimation), is presented alongside examples of studies that employed them (with specific variables indicated in parentheses, when applicable). The study marked with an asterisk has been conducted on binary interaction webs.

Expression	Type	Outcome	Uncertainty		Reference
			sources		
$P(L_{i \rightarrow j} X_{i,l}, X_{j,l}, \dots)$	local	realization of the interaction	spatiotemporal	Gravel <i>et al.</i> (2019)	
		given taxa co-occurrence	variability		
$P(L_{i \rightarrow j} N_{i,l}, N_{j,l}, \dots)$	local	realization of the interaction	neutral models	Canard <i>et al.</i> (2014)	
		given taxa abundances			
$P(L_{i \rightarrow j} T_{i,l}, T_{j,l}, \dots)$	local	realization of the interaction	trait matching	Gravel <i>et al.</i> (2016)	
		given local traits	models		
$P(L_{i \rightarrow j} E_l, \dots)$	local	realization of the interaction	environmental-	Gravel <i>et al.</i> (2019)	
		given local environmental	based models		(temperature and
		conditions			precipitation)
$P(L_{i \rightarrow j} A, \dots)$	local	realization of the interaction in	spatial models	Galiana <i>et al.</i> (2018)	
		a given area or volume			*
$P(L_{i \rightarrow j} t, \dots)$	local	realization of the interaction	temporal models	Weinstein & Graham (2017a)	
		during a given time period			
$P(L_{i \rightarrow j} f(L), \dots)$	local	realization of the interaction	topological null	Fortuna & Bascompte (2006) (connectance)	
		given network structure	models		
$P(L_{i \rightarrow j} M_{i \rightarrow j}, \dots)$	local	realization of the interaction	spatiotemporal	this study	
		given that the taxa can	variability		
$P(O_{i \rightarrow j} L_{i \rightarrow j}, \dots)$	local	observation of the interaction	sampling model	Catchen <i>et al.</i> (2023)	
		given that it is realized locally			

Expression	Type	Outcome	Uncertainty	
			sources	Reference
$P(M_{i \rightarrow j} T_i, T_j)$	regional	biological feasibility of the interaction given regional traits (non-forbiddenness)	trait matching models	Strydom <i>et al.</i> (2022)
$P(M_{i \rightarrow j}^* T_i, T_j, E)$	regional	ecological feasibility of the interaction given regional traits and environmental conditions	trait matching and environmental-based models	this study

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

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

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

Metawebs: regional catalogs of interactions

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

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

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

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

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

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

323 For example, let i be a western diamondback rattlesnake (*Crotalus atrox*) and j , a wood lemming (*Myopus*
324 *schisticolor*). These two taxa never co-occur, the rattlesnake being adapted to warm regions of North America
325 (Castoe *et al.* (2007)) and the lemming, to northern habitats of Eurasia (Fedorov *et al.* (2008)). As we lack

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

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

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

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

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

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

350 *et al.* (2022)).

351 Starting from a selected set of taxa, which are usually distributed within a broad region of interest, metawebs
352 can be built using different data sources, including literature review (e.g., Maiorano *et al.* (2020)), aggregated
353 local web data (e.g., Gravel *et al.* (2019), Saravia *et al.* (2022)), trait-matching models (e.g., Strydom *et al.*
354 (2022), Shaw *et al.* (2024)), and expert knowledge. Every pair of taxa that have confidently been observed to
355 interact at least once can be given a probability of 1 (i.e., $P(M_{i \rightarrow j}) = 1$) since we know that they *can* interact.
356 This differs from local webs of probabilistic interactions, where interaction events may remain stochastic (i.e.,
357 $P(L_{i \rightarrow j}) < 1$) even after empirically observing interactions due to their spatiotemporal variability. Interactions
358 that were never observed typically have low probability values in local webs and vary from low to high values in
359 metawebs, contingent upon taxa traits distributions (reaching 0 for forbidden links).
360 When incorporating local network data to estimate probabilities of regional interactions, repeatedly failing to
361 observe an interaction between two co-occurring taxa (i.e., $P(O_{i \rightarrow j} = 0)$) should decrease the probability that
362 the interaction is biologically feasible. Using Bayes' theorem, the probability that the interaction is biologically
363 feasible given that it was never observed locally, $P(M_{i \rightarrow j} = 1|O_{i \rightarrow j} = 0, \dots)$, may be calculated as follows:

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

364 The reduction in the probability of regional interaction after considering that it was never observed locally (i.e.,
365 $P(M_{i \rightarrow j} = 1|O_{i \rightarrow j} = 0, \dots) < P(M_{i \rightarrow j} = 1|\dots)$) occurs because $P(O_{i \rightarrow j} = 0|M_{i \rightarrow j} = 1, \dots)$ must be lower than
366 $P(O_{i \rightarrow j} = 0, \dots)$, i.e. there is a higher chance of observing an interaction when we know it is biologically
367 feasible.
368 Many observations of interactions are false positives because of observation errors due to taxonomic
369 misidentifications and ecological misinterpretations (e.g., due to cryptic species and interactions, Pringle &
370 Hutchinson (2020)). Likewise, forbidden interactions may be false negatives, e.g. if they have been evaluated
371 based on unrepresentative or incomplete traits distributions. Employing Bayesian models could prove valuable
372 when estimating interaction probabilities in metawebs (e.g., Bartomeus *et al.* (2016), Cirtwill *et al.* (2019)).
373 This improvement is achieved by updating prior information regarding the feasibility of interactions (e.g.,
374 experts' prior assessments of interaction probabilities) with empirical data on interactions and traits.

375 **Properties of probabilistic interaction webs**

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

385 **Host-parasite network data**

386 We use the collection of tripartite host-parasite networks sampled across Europe, created by Kopelke *et al.*
387 (2017), in the following case studies. This dataset contains well-resolved binary local interactions between
388 willows (52 species), willow-galling sawflies (96 species), and their parasitoids (126 species). Given its
389 replicated webs spanning large spatiotemporal scales, this dataset is well-suited for analyzing a variety of
390 ecological hypotheses and processes. Out of a total of 374 local webs, we retained those containing at least 5
391 species, resulting in a set of 233 georeferenced local webs (networks sampled within areas of 0.1 to 0.3 km²
392 during June and/or July spanning 29 years). We built a metaweb of binary interactions by aggregating all local
393 interactions, which gave us a regional web composed of 274 species and 1080 interactions. In the first two
394 panels of fig. 1, we show how the dissimilarity of interactions between common species (β_{OS}) and the
395 dissimilarity in species composition (β_S) between the metaweb and aggregated local webs (Poisot *et al.* (2012))
396 vary with the number of sampled local webs. This shows that networks of local interactions are highly
397 dissimilar from the metaweb, both in terms of species and interactions, especially when only a limited number
398 of sites has been sampled. Both dissimilarity indices were calculated based on the number of items shared by
399 the two webs (c_{LM}) and the number of items unique to the metaweb (u_M) and to the aggregated local web (u_L).
400 The β_S dissimilarity index uses species (nodes) as items being compared, while the β_{OS} index assesses
401 dissimilarity based on interactions between shared species (Poisot *et al.* (2012)). Both indices were calculated
402 following the β_W index of Whittaker (1960):

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

403

[Figure 1 about here.]

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

418 To build local webs of probabilistic interactions, we first recognize that local interactions must initially be
 419 biologically feasible before occurring at a specific time and space. A local probability of interaction $P(L_{i \rightarrow j})$
 420 can be expressed as the product of the probability of local interaction given that the two taxa can potentially
 421 interact $P(L_{i \rightarrow j}|M_{i \rightarrow j} = 1)$, which we denote as $P(L_{i \rightarrow j}|M_{i \rightarrow j})$ for the sake of simplicity, with their probability of
 422 regional interaction $P(M_{i \rightarrow j})$:

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

423 We built local webs of probabilistic interactions using the taxa found in the empirical local networks and
 424 attributing pairwise interaction probabilities based on the metawebs of probabilistic interactions and a constant
 425 value of $P(L_{i \rightarrow j}|M_{i \rightarrow j})$ across interactions. Low values of $P(L_{i \rightarrow j}|M_{i \rightarrow j})$ indicate that feasible interactions rarely
 426 occur locally, intermediate values around 50% suggest considerable spatiotemporal variability, while high

427 values indicate that regional interactions are nearly always realized locally. Following eq. 10, the local
428 probability of interaction between a given pair of taxa consistently remained equal to or below their probability
429 of regional interaction.

430 In the last two panels of fig. 1, we show how the aggregated number of links and connectance (i.e., the
431 proportion of all of the non-forbidden links that are realized) scale with the number of sampled local webs,
432 according to different values of $P(L_{i \rightarrow j} | M_{i \rightarrow j})$. When aggregating local webs of probabilistic interactions, the
433 constancy of the probability of regional interaction across the entire study area means that any rise in the
434 probability of local interaction is solely attributable to an increase in $P(L_{i \rightarrow j} | M_{i \rightarrow j})$. For example, let L_1 and L_2
435 be two local networks and $L_{1,2}$ the aggregated web. If $P(L_{1,i \rightarrow j} | M_{i \rightarrow j})$ and $P(L_{2,i \rightarrow j} | M_{i \rightarrow j})$ are the probabilities
436 that two potentially interacting taxa interact respectively in L_1 and L_2 , the probability $P(L_{1,2,i \rightarrow j} | M_{i \rightarrow j})$ that
437 these taxa interact in the aggregated web $L_{1,2}$ is obtained by:

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

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

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

446 Spatial and temporal scaling of interactions

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

453 Additionally, ecological processes occurring at distinct spatial scales, such as the spatial variability in local
454 community composition resulting from different sequences of extinction and colonization events, can also
455 contribute to this variation (Galiana *et al.* (2018)). Next, interaction accumulation curves describe the scaling of
456 the number of observed interactions with sampling effort (Jordano (2016)). Sampling effort, which may
457 correspond to the duration of the sampling period used to construct the network, can impact connectance
458 (Bersier *et al.* (1999)) and various measures of network structure (Banašek-Richter *et al.* (2004), McLeod *et al.*
459 (2021)). Apart from sampling effort, the temporal scaling of interactions also elucidates how network structure
460 changes with the temporal resolution of the network (Poisot *et al.* (2012)), acknowledging that distinct
461 interactions take place over time, ranging from short-term fluctuations of interactions to long-term trends. As
462 local webs of probabilistic interactions may explicitly account for the spatiotemporal variability of interactions,
463 they offer a distinct approach to investigating the scaling of network structure with space and time, in contrast to
464 webs of binary and quantitative interactions, by making the stochasticity of interactions the focal point of the
465 modeling process.

466 Local and metawebs exhibit distinct relationships with spatial and temporal scales. On one hand, metawebs of
467 probabilistic interactions, representing biological feasibility, feature regional interactions that do not scale with
468 space and time. This is because regional interactions depend solely on the biological capacity of two taxa to
469 interact, regardless of their co-occurrence and local environmental conditions. However, probabilities of
470 potential interactions may change (tending to become more definitive) upon updating previous estimates with
471 increased sampling effort, even though they do not vary in a specific direction with the spatial and temporal
472 extent (boundaries) of the network. The probability of two taxa potentially interacting should theoretically be
473 the same in all metawebs in which they are present, provided that the data and methods used for estimation are
474 consistent. For example, if a smaller metaweb M_1 is derived from a larger metaweb M_0 by selecting the subset
475 of taxa present in the region described by M_1 and retaining all their interactions, their probabilities of
476 interaction should be identical regardless of scale, i.e. $P(M_{1,i \rightarrow j}) = P(M_{0,i \rightarrow j})$. With a larger or equal number of
477 taxa in M_0 as compared to M_1 , the total number of interactions is expected to be higher or at least equal in the
478 larger web, even though pairwise probabilities remain identical.

479 On the other hand, local interactions scale both spatially and temporally, given that they have more
480 opportunities to be realized and observed in larger areas and longer durations. This is attributed to factors such
481 as a higher number of individuals, greater trait variations, and increased opportunities for encounters, as
482 highlighted by McLeod *et al.* (2020). For example, if a local web of probabilistic interactions L_1 with an area

483 A_1 is derived from a larger web L_0 with an area A_0 , and A_1 is entirely nested within A_0 , interaction probabilities
484 should be lower in the smaller web, i.e. $P(L_{1,i \rightarrow j}|A_1 < A_0) \leq P(L_{0,i \rightarrow j}|A_0)$. However, if A_1 and A_0 are disjoint,
485 interaction probabilities could be higher in the smaller area, contingent upon their environmental and biological
486 conditions. Likewise, interaction probabilities are expected to be lower in webs with shorter durations when
487 time intervals are nested. In fig. 2, we show how the expected number of local host-parasite interactions scales
488 with area, represented as an expanding latitudinal window, in comparison with regional interactions. Even
489 though we employed local probabilities of interactions equal to regional interactions for the purpose of
490 comparison (i.e., using $P(L_{i \rightarrow j}|M_{i \rightarrow j}) = 1$ here), we notice that the total number of regional interactions scales
491 more rapidly than local interactions. This is because numerous regional interactions involve species that never
492 co-occur, and as a result, these interactions are not captured in any local web.

493 [Figure 2 about here.]

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

495 Predicting local webs across time and space is a pivotal goal of network ecology, especially given the scarcity of
496 interaction data (Strydom *et al.* (2021)). Ecologists may resort to predictive models (e.g., generative Bayesian
497 and machine learning models) to reconstruct networks at fine spatial and temporal scales with limited
498 interaction data. For instance, real-time biomonitoring data coupled with appropriate numerical models (Bohan
499 *et al.* (2017)) can be employed to reconstruct local ecological webs, opening avenues for in-depth studies on
500 local ecosystem functioning and dynamics. The probabilistic representation of interactions describes the
501 inherent uncertainty in these models, typically expressed through probability distributions. We introduce and
502 develop a simple generative mechanistic model for probabilistic local interactions that takes into consideration
503 their spatiotemporal variability (i.e., a spatiotemporally explicit model of local interactions). It is essential to
504 note that our model is not designed for regional interactions, which are scale-independent. Rather, it could
505 prove valuable for predicting local interactions across time and space by generating new interaction data
506 following parameter inference.

507 As indicated by eq. 1, the probability that two taxa i and j interact at a specific location and time l may be
508 determined by the product of their probability of interaction given co-occurrence and their probability of
509 co-occurrence. First, their co-occurrence probability can be calculated using their individual (marginal)
510 occurrence probabilities $P(X_{i,l})$ and $P(X_{j,l})$. Given that taxa occurrences are not independent of each other, the

511 joint probability of both taxa occurring together can be calculated by multiplying the probability of one taxon
 512 being present by the conditional probability of the other occurring when the first one is present. Alternatively,
 513 the joint occurrence probability can be obtained by multiplying the marginal probabilities by the strength of
 514 association γ between the occurrences of both taxa (Cazelles *et al.* (2016)):

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

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

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

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

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

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

530 The occurrence of an interaction between i and j can be modeled as a Bernoulli trial with a probability of
 531 $P(L_{i \rightarrow j})$. Consequently, a Bayesian inference model can be built based on the preceding equations to estimate

532 the value of the λ_l and γ parameters and generate novel interaction data:

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

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

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

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

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

538 [Figure 3 about here.]

539 **Taxonomic scaling of interactions**

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

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

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

559 where $g_{1,i}$ and $g_{2,j}$ are the species of the corresponding genus and assuming independence between
 560 species-level interactions. If it is known that at least two of these species interact (i.e., $P(S_{g_{1,i} \rightarrow g_{2,j}}) = 1$ for at
 561 least one pair of $(g_{1,i}, g_{2,j})$), it implies a probability of genus interaction equal to 1. Canard *et al.* (2012) built a
 562 species-based network following a similar approach, by using simulated interactions between individuals
 563 derived from a neutral model (i.e., a model that assumed ecological equivalence among individuals). In
 564 contrast, a more sophisticated approach is necessary when transitioning from a broader to a finer level of
 565 organization. This is because knowledge of an interaction between two genera does not guarantee that all
 566 possible pairwise combinations of their species will also interact. One possible method is to build a finer-scale
 567 network by generating probabilities of interactions through random sampling from a beta distribution,
 568 parameterized by the broader-scale network.

569 Ideally, our biological interpretation of probabilistic interactions should remain consistent across a network
 570 even if it incorporates heterogeneous levels of organization, such as a network whose nodes represent both
 571 species and trophic species (groups of species sharing similar predators and prey). This is common in
 572 ecological webs where taxonomic resolution is typically low (Hemprich-Bennett *et al.* (2021), Vázquez *et al.*
 573 (2022)). Interaction probabilities at broader taxonomic scales should be based on probabilities of interactions
 574 between individuals, for both local and metawebs. For instance, in local individual-based food webs, the
 575 probability that two individuals interact reflects our degree of belief that one individual will consume the other.

576 Similarly, in local species-based food webs, the probability that two species interact represents our degree of
577 belief that at least one individual from the predator species consumes at least another individual from the prey
578 species. Furthermore, in local clade-based food webs, the probability that two clades interact represents our
579 degree of belief that at least two species from these clades interact with each other or, equivalently, that at least
580 two individuals from these clades interact with each other. Fundamentally, the taxonomic scaling of interactions
581 involves aggregating interactions between individuals into larger groups, which may exhibit varying degrees of
582 homogeneity based on the organisms and the study system. In that regard, taxonomic scaling is analogous to the
583 spatial and temporal scaling of interactions, as they all represent different ways to aggregate individuals into
584 broader groups (either spatially, temporally, or taxonomically).

585 Sampling for binary interaction webs

586 The prediction of binary interactions through Bernoulli trials is an important application of probabilistic
587 interaction webs. This approach proves beneficial for analyzing the structural characteristics of probabilistic
588 interaction webs, particularly in the absence of specific analytical measures. By performing independent
589 Bernoulli trials for each interaction, a network of binary interactions may be generated. A probability
590 distribution of network properties can be obtained by measuring network structure across multiple randomly
591 generated networks (Poisot *et al.* (2016)). This method enables the representation of the variability of network
592 structure, albeit with possible biases when connectance is low (Poisot & Gravel (2014), Chagnon (2015)).
593 Employing this strategy to generate binary interaction networks under a null model facilitates null hypothesis
594 significance testing, wherein the observed measure is compared against the simulated distribution (e.g.,
595 Bascompte *et al.* (2003)). Additionally, the random generation of binary interaction networks, from a
596 probabilistic interaction web that accounts for the spatiotemporal variability of interactions, may effectively
597 capture network structure across space and time. This facilitates the investigation of ecological hypotheses
598 about interactions at broad spatial and temporal scales. Yet, inferring network structure through sampling for
599 binary interactions assumes independence among interactions, which might not accurately represent reality.
600 Covariation among interactions could exist even if we do not explicitly condition interactions on others. For
601 example, an interaction between two taxa could be more probable when another interaction occurs. The
602 consequences of this assumption of independence on the prediction of network structure have yet to be
603 empirically examined.
604 There are at least two distinct approaches to sample binary interaction networks from probabilistic interaction

605 webs across space, for example, when attempting to predict a binary interaction network for each location l
606 within a given region. Both approaches assume independence between interactions. The first approach involves
607 performing a singular Bernoulli trial for each pair of taxa based on their regional probability of interaction:

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

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

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

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

616 In fig. 4, we compare the average connectance of binary interaction networks resulting from these two sampling
617 techniques, where regional and local interactions are drawn from our host-parasite networks of probabilistic
618 interactions, generating a number of binary interaction web realizations for each site in the dataset. These two
619 sampling approaches yield different outcomes, particularly for lower values of $P(L_{i \rightarrow j}|M_{i \rightarrow j})$, which represent
620 instances where regional interactions do not consistently manifest locally. Small discrepancies between these
621 techniques are also apparent when we equate the probability of local interaction to the probability of regional
622 interaction (i.e., when using $P(L_{i \rightarrow j}|M_{i \rightarrow j}) = 1.0$ in eq. 10), especially when the number of simulations of
623 binary interaction networks for each location is low. As anticipated, we observe that sampling binary
624 interactions from the metaweb tends to overestimate connectance on average compared to sampling them from
625 local webs. Furthermore, we observe an increase in the variability of connectance when employing a single
626 simulation, representing what we consider as a more tangible process leading to the realization of local
627 interactions in nature.

629 The choice of a sampling approach can influence the selection of grid cell size when delineating local
630 communities within a broader region of interest. In the first approach, pairwise interactions remain constant
631 irrespective of cell size because they are sampled only once from the metaweb. However, in the second
632 approach, local interaction probabilities are contingent on network area. For instance, consider the local webs
633 L_1 and L_2 with an area of $\frac{1}{2}A_0$, both nested within A_0 but disjoint from each other, forming L_0 . If we treat L_1
634 and L_2 as independent, the probability of interaction between taxa i and j in L_0 is given by:

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

635 Due to its larger area, the probability that the two taxa interact in L_0 is equal or greater than in L_1 and L_2 . When
636 sampling binary interactions from local webs, it is crucial to sample at the same spatial scale for which
637 probabilities were estimated. Otherwise, interaction probabilities must be adjusted to align with the intended
638 cell size, preventing systematic biases in predictions.

639 Prediction of local webs from metawebs

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

651 Building local webs of probabilistic interactions from a metaweb of probabilistic interactions involves a
652 reduction in the value of pairwise interaction probabilities. This decrease is attributed to the prerequisite that
653 two taxa must initially possess the capacity to interact before engaging in local interactions (eq. 10). Therefore,
654 inferring local webs from their metaweb while maintaining identical interaction probability values would

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

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

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

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

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

670 Conclusion

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

678 the need to use probabilistic data with caution, for instance when generating network realizations of binary
679 interactions across space and predicting local webs from metawebs. Clear metadata describing the type of
680 interaction and the variables used in their estimation are required to ensure adequate data manipulation. Sound
681 data practices and foundations for probabilistic thinking in network ecology could facilitate reliable assessments
682 of the spatiotemporal variability and uncertainty of biotic interactions.

683 Estimating local interaction probabilities independently for each taxa pair and assembling them into a network
684 of probabilistic interactions comes with limitations. Predicting local networks of binary interactions based on
685 these interaction probabilities assumes independence among interactions, a condition seldom respected in
686 practice (Golubski & Abrams (2011)). Relaxing this assumption is the next logical step in the stochastic
687 representation of interactions. A more accurate representation of the stochasticity of ecological networks
688 involves creating *probabilistic networks* ($P(L|...)$ and $P(M|...)$), rather than networks of *probabilistic*
689 *interactions* ($P(L_{i \rightarrow j}|...)$ and $P(M_{i \rightarrow j}|...)$). Probabilistic networks describe the probability that a particular
690 network of binary (or quantitative) interactions (its whole adjacency matrix) is realized. For example, Young *et*
691 *al.* (2021) used a Bayesian approach to estimate the probability of different plant-pollinator network structures
692 derived from imperfect observational data. A probability distribution of ecological networks may also be
693 derived using the principle of maximum entropy given some structural constrained (e.g., Park & Newman
694 (2004), Cimini *et al.* (2019)). Regardless of the method employed, generating probabilistic local webs,
695 bypassing the need to independently estimate local interaction probabilities, could lead to more accurate
696 predictions of local webs. Furthermore, probabilistic networks could serve as an alternative to null hypothesis
697 significance testing when comparing the structure of a local web to some random expectations or, as done in
698 Pellissier *et al.* (2018), to the metaweb. These random expectations are typically derived by performing a series
699 of Bernoulli trials on probabilistic interactions, assuming independence, to generate a distribution of networks
700 of binary interactions and then calculate their structure (Poisot *et al.* (2016)). One could for instance compare
701 the likelihood of an observed network to the one of the most likely network structure according to the
702 probabilistic network distribution, thereby directly obtaining a measure of discrepancy of the empirical network.
703 Generating probabilistic ecological networks represents a tangible challenge, one that, in the coming years,
704 promises to unlock doors to more advanced and adequate analyses of ecological networks.

705 It is essential to enhance our comprehension of both regional and local interactions, especially considering the
706 current scarcity of interaction data. While sampling biological communities does decrease the uncertainty of
707 interactions by accumulating evidence for their feasibility and local realization, there is a limit to how much we

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

723 Acknowledgment

724 We acknowledge that this study was conducted on land within the traditional unceded territory of the Saint
725 Lawrence Iroquoian, Anishinabewaki, Mohawk, Huron-Wendat, and Omàmiwininiwak nations. This work was
726 supported by the Institute for Data Valorisation (IVADO) and the Natural Sciences and Engineering Research
727 Council of Canada (NSERC) Collaborative Research and Training Experience (CREATE) program, through the
728 Computational Biodiversity Science and Services (BIOS²) program. A special thanks to all members of the
729 Black Holes and Revelations working group (organized by BIOS²) for their insightful discussions and valuable
730 feedback on this manuscript.

731 References

- 732 Abrego, N., Roslin, T., Huotari, T., Ji, Y., Schmidt, N.M., Wang, J., *et al.* (2021). Accounting for species
733 interactions is necessary for predicting how arctic arthropod communities respond to climate change.

- 734 *Ecography*, 44, 885–896.
- 735 Andrade-Pacheco, R., Rerolle, F., Lemoine, J., Hernandez, L., Meïté, A., Juziwelo, L., *et al.* (2020). [Finding hotspots: Development of an adaptive spatial sampling approach](#). *Scientific Reports*, 10, 10939.
- 736
- 737 Angilletta, M.J., Jr., Steury, T.D. & Sears, M.W. (2004). [Temperature, Growth Rate, and Body Size in Ectotherms: Fitting Pieces of a Life-History Puzzle](#)1. *Integrative and Comparative Biology*, 44, 498–509.
- 738
- 739 Araujo, M.B., Rozenfeld, A., Rahbek, C. & Marquet, P.A. (2011). [Using species co-occurrence networks to assess the impacts of climate change](#). *Ecography*, 34, 897–908.
- 740
- 741 Banašek-Richter, C., Cattin, M.-F. & Bersier, L.-F. (2004). [Sampling effects and the robustness of quantitative and qualitative food-web descriptors](#). *Journal of Theoretical Biology*, 226, 23–32.
- 742
- 743 Bartomeus, I., Gravel, D., Tylianakis, J.M., Aizen, M.A., Dickie, I.A. & Bernard-Verdier, M. (2016). [A common framework for identifying linkage rules across different types of interactions](#). *Functional Ecology*, 30, 1894–1903.
- 744
- 745
- 746 Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. (2003). [The nested assembly of plant–animal mutualistic networks](#). *Proceedings of the National Academy of Sciences*, 100, 9383–9387.
- 747
- 748 Berg, M.P. & Ellers, J. (2010). [Trait plasticity in species interactions: A driving force of community dynamics](#). *Evolutionary Ecology*, 24, 617–629.
- 749
- 750 Berlow, E.L., Neutel, A.-M., Cohen, J.E., De Ruiter, P.C., Ebenman, B., Emmerson, M., *et al.* (2004).
- 751 [Interaction strengths in food webs: Issues and opportunities](#). *Journal of Animal Ecology*, 73, 585–598.
- 752
- 753 Bersier, L.-F., Dixon, P. & Sugihara, G. (1999). [Scale-Invariant or Scale-Dependent Behavior of the Link Density Property in Food Webs: A Matter of Sampling Effort?](#) *The American Naturalist*, 153, 676–682.
- 754 Blanchet, F.G., Cazelles, K. & Gravel, D. (2020). [Co-occurrence is not evidence of ecological interactions](#). *Ecology Letters*, 23, 1050–1063.
- 755
- 756 Bohan, D.A., Vacher, C., Tamaddoni-Nezhad, A., Raybould, A., Dumbrell, A.J. & Woodward, G. (2017).
- 757 [Next-Generation Global Biomonitoring: Large-scale, Automated Reconstruction of Ecological Networks](#).
- 758 *Trends in Ecology & Evolution*, 32, 477–487.
- 759
- 760 Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., *et al.* (2011). [Why intraspecific trait variation matters in community ecology](#). *Trends in Ecology & Evolution*, 26, 183–192.

- 761 Borrett, S.R. & Scharler, U.M. (2019). [Walk partitions of flow in Ecological Network Analysis: Review and](#)
762 [synthesis of methods and indicators](#). *Ecological Indicators*, 106, 105451.
- 763 Boulangeat, I., Gravel, D. & Thuiller, W. (2012). [Accounting for dispersal and biotic interactions to disentangle](#)
764 [the drivers of species distributions and their abundances](#). *Ecology Letters*, 15, 584–593.
- 765 Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T. & Fortin, M.-J. (2023). [Shortcomings of reusing](#)
766 [species interaction networks created by different sets of researchers](#). *PLOS Biology*, 21, e3002068.
- 767 Broom, M. & Ruxton, G.D. (2005). [You can run—or you can hide: Optimal strategies for cryptic prey against](#)
768 [pursuit predators](#). *Behavioral Ecology*, 16, 534–540.
- 769 Brose, U., Ostling, A., Harrison, K. & Martinez, N.D. (2004). [Unified spatial scaling of species and their](#)
770 [trophic interactions](#). *Nature*, 428, 167–171.
- 771 Burnham, K.P. & Anderson, D.R. (2004). [Multimodel Inference: Understanding AIC and BIC in Model](#)
772 [Selection](#). *Sociological Methods & Research*, 33, 261–304.
- 773 Canard, E.F., Mouquet, N., Mouillot, D., Stanko, M., Miklisova, D. & Gravel, D. (2014). [Empirical Evaluation](#)
774 [of Neutral Interactions in Host-Parasite Networks](#). *The American Naturalist*, 183, 468–479.
- 775 Canard, E., Mouquet, N., Marescot, L., Gaston, K.J., Gravel, D. & Mouillot, D. (2012). [Emergence of](#)
776 [Structural Patterns in Neutral Trophic Networks](#). *PLOS ONE*, 7, e38295.
- 777 Castoe, T.A., Spencer, C.L. & Parkinson, C.L. (2007). [Phylogeographic structure and historical demography of](#)
778 [the western diamondback rattlesnake \(*Crotalus Atrox*\): A perspective on North American desert](#)
779 [biogeography](#). *Molecular Phylogenetics and Evolution*, 42, 193–212.
- 780 Catchen, M.D., Poisot, T., Pollock, L.J. & Gonzalez, A. (2023). [The missing link: Discerning true from false](#)
781 [negatives when sampling species interaction networks](#).
- 782 Cazelles, K., Araujo, M.B., Mouquet, N. & Gravel, D. (2016). [A theory for species co-occurrence in interaction](#)
783 [networks](#). *Theoretical Ecology*, 9, 39–48.
- 784 Chagnon, P.-L. (2015). [Characterizing topology of ecological networks along gradients: The limits of metrics'](#)
785 [standardization](#). *Ecological Complexity*, 22, 36–39.
- 786 Choh, Y., Ignacio, M., Sabelis, M.W. & Janssen, A. (2012). [Predator-prey role reversals, juvenile experience](#)
787 [and adult antipredator behaviour](#). *Scientific Reports*, 2, 728.

- 788 Cimini, G., Squartini, T., Saracco, F., Garlaschelli, D., Gabrielli, A. & Caldarelli, G. (2019). [The statistical](#)
789 [physics of real-world networks](#). *Nature Reviews Physics*, 1, 58–71.
- 790 Cirtwill, A.R., Eklöf, A., Roslin, T., Wootton, K. & Gravel, D. (2019). [A quantitative framework for](#)
791 [investigating the reliability of empirical network construction](#). *Methods in Ecology and Evolution*, 10,
792 902–911.
- 793 Dallas, T., Park, A.W. & Drake, J.M. (2017). [Predicting cryptic links in host-parasite networks](#). *PLOS*
794 [Computational Biology, 13, e1005557.](#)
- 795 Dunne, J.A. (2006). The Network Structure of Food Webs. In: *Ecological networks: Linking structure and*
796 *dynamics* (eds. Dunne, J.A. & Pascual, M.). Oxford University Press, pp. 27–86.
- 797 Elmasri, M., Farrell, M.J., Davies, T.J. & Stephens, D.A. (2020). [A hierarchical Bayesian model for predicting](#)
798 [ecological interactions using scaled evolutionary relationships](#). *The Annals of Applied Statistics*, 14,
799 221–240.
- 800 Elton, C.S. (2001). *Animal Ecology*. University of Chicago Press, Chicago, IL.
- 801 Emmerson, M.C. & Raffaelli, D. (2004). [Predator–prey body size, interaction strength and the stability of a real](#)
802 [food web](#). *Journal of Animal Ecology*, 73, 399–409.
- 803 Fedorov, V.B., Goropashnaya, A.V., Boeskorov, G.G. & Cook, J.A. (2008). [Comparative phylogeography and](#)
804 [demographic history of the wood lemming \(*Myopus schisticolor*\): Implications for late Quaternary history](#)
805 [of the taiga species in Eurasia](#). *Molecular Ecology*, 17, 598–610.
- 806 Fortuna, M.A. & Bascompte, J. (2006). [Habitat loss and the structure of plant–animal mutualistic networks](#).
807 *Ecology Letters*, 9, 281–286.
- 808 Fu, X., Seo, E., Clarke, J. & Hutchinson, R.A. (2021). [Link Prediction Under Imperfect Detection:](#)
809 [Collaborative Filtering for Ecological Networks](#). *IEEE Transactions on Knowledge and Data Engineering*,
810 33, 3117–3128.
- 811 Galiana, N., Lurgi, M., Claramunt-López, B., Fortin, M.-J., Leroux, S., Cazelles, K., et al. (2018). [The spatial](#)
812 [scaling of species interaction networks](#). *Nature Ecology & Evolution*, 2, 782–790.
- 813 Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010). [A framework for community](#)
814 [interactions under climate change](#). *Trends in Ecology & Evolution*, 25, 325–331.

- 815 Godsoe, W., Murray, R. & Iritani, R. (2022). Species interactions and diversity: A unified framework using Hill
816 numbers. *Oikos*, n/a, e09282.
- 817 Golubski, A.J. & Abrams, P.A. (2011). Modifying modifiers: What happens when interspecific interactions
818 interact? *Journal of Animal Ecology*, 80, 1097–1108.
- 819 Gomez, J.M., Verdu, M. & Perfectti, F. (2010). Ecological interactions are evolutionarily conserved across the
820 entire tree of life. *Nature*, 465, 918–U6.
- 821 Gonzalez, A. & Londoño, M.C. (2022). Monitor biodiversity for action. *Science*, 378, 1147–1147.
- 822 Gonzalez-Varo, J.P. & Traveset, A. (2016). The Labile Limits of Forbidden Interactions. *Trends in Ecology &*
823 *Evolution*, 31, 700–710.
- 824 Gravel, D., Albouy, C. & Thuiller, W. (2016). The meaning of functional trait composition of food webs for
825 ecosystem functioning. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371,
826 20150268.
- 827 Gravel, D., Baiser, B., Dunne, J.A., Kopelke, J.-P., Martinez, N.D., Nyman, T., et al. (2019). Bringing Elton
828 and Grinnell together: A quantitative framework to represent the biogeography of ecological interaction
829 networks. *Ecography*, 42, 401–415.
- 830 Gravel, D., Massol, F., Canard, E., Mouillot, D. & Mouquet, N. (2011). Trophic theory of island biogeography.
831 *Ecology Letters*, 14, 1010–1016.
- 832 Gravel, D., Poisot, T., Albouy, C., Velez, L. & Mouillot, D. (2013). Inferring food web structure from
833 predator–prey body size relationships. *Methods in Ecology and Evolution*, 4, 1083–1090.
- 834 Guimarães, P.R. (2020). The Structure of Ecological Networks Across Levels of Organization. *Annual Review*
835 *of Ecology, Evolution, and Systematics*, 51, 433–460.
- 836 Guimerà, R. & Sales-Pardo, M. (2009). Missing and spurious interactions and the reconstruction of complex
837 networks. *Proceedings of the National Academy of Sciences*, 106, 22073–22078.
- 838 Hemprich-Bennett, D.R., Oliveira, H.F.M., Le Comber, S.C., Rossiter, S.J. & Clare, E.L. (2021). Assessing the
839 impact of taxon resolution on network structure. *Ecology*, 102, e03256.
- 840 Herrera, C.M. (1989). Pollinator abundance, morphology, and flower visitation rate: Analysis of the “quantity”
841 component in a plant-pollinator system. *Oecologia*, 80, 241–248.

- 842 Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M. & Ladle, R.J. (2015). [Seven Shortfalls](#)
843 [that Beset Large-Scale Knowledge of Biodiversity](#). *Annual Review of Ecology, Evolution, and Systematics*,
844 46, 523–549.
- 845 Jordano, P. (1987). [Patterns of Mutualistic Interactions in Pollination and Seed Dispersal: Connectance,](#)
846 [Dependence Asymmetries, and Coevolution](#). *The American Naturalist*, 129, 657–677.
- 847 Jordano, P. (2016). [Sampling networks of ecological interactions](#). *Functional Ecology*, 30, 1883–1893.
- 848 Jordano, P., Bascompte, J. & Olesen, J.M. (2003). [Invariant properties in coevolutionary networks of](#)
849 [plant–animal interactions](#). *Ecology Letters*, 6, 69–81.
- 850 Kausrud, K.L., Mysterud, A., Steen, H., Vik, J.O., Østbye, E., Cazelles, B., *et al.* (2008). [Linking climate](#)
851 [change to lemming cycles](#). *Nature*, 456, 93–97.
- 852 Kéfi, S., Berlow, E.L., Wieters, E.A., Joppa, L.N., Wood, S.A., Brose, U., *et al.* (2015). [Network structure](#)
853 [beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky shores](#). *Ecology*, 96,
854 291–303.
- 855 Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., *et al.* (2012). [More than a](#)
856 [meal... integrating non-feeding interactions into food webs](#). *Ecology Letters*, 15, 291–300.
- 857 Kéfi, S., Miele, V., Wieters, E.A., Navarrete, S.A. & Berlow, E.L. (2016). [How Structured Is the Entangled](#)
858 [Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks Leads to Increased](#)
859 [Persistence and Resilience](#). *PLOS Biology*, 14, e1002527.
- 860 Kissner, K.J., Forbes, M.R. & Secoy, D.M. (1997). [Rattling Behavior of Prairie Rattlesnakes \(*Crotalus viridis*](#)
861 [viridis, Viperidae\) in Relation to Sex, Reproductive Status, Body Size, and Body Temperature](#). *Ethology*,
862 103, 1042–1050.
- 863 Klecka, J. & Boukal, D.S. (2014). [The effect of habitat structure on prey mortality depends on predator and](#)
864 [prey microhabitat use](#). *Oecologia*, 176, 183–191.
- 865 Kopelke, J.-P., Nyman, T., Cazelles, K., Gravel, D., Vissault, S. & Roslin, T. (2017). [Food-web structure of](#)
866 [willow-galling sawflies and their natural enemies across Europe](#). *Ecology*, 98, 1730–1730.
- 867 Kulkarni, M.A., Kweka, E., Nyale, E., Lyatuu, E., Mosha, F.W., Chandramohan, D., *et al.* (2006).
868 [Entomological Evaluation of Malaria Vectors at Different Altitudes in Hai District, Northeastern Tanzania](#).
869 *Journal of Medical Entomology*, 43, 580–588.

- 870 Maiorano, L., Montemaggiori, A., Ficetola, G.F., O'Connor, L. & Thuiller, W. (2020). [TETRA-EU 1.0: A species-level trophic metaweb of European tetrapods](#). *Global Ecology and Biogeography*, 29, 1452–1457.
- 871
- 872 McCann, K. (2007). Protecting biostructure. *Nature*, 446, 29–29.
- 873 McCann, K.S. (2011). Food webs (MPB-50). In: *Food Webs (MPB-50)*. Princeton University Press.
- 874 McLeod, A., Leroux, S.J., Gravel, D., Chu, C., Cirtwill, A.R., Fortin, M.-J., et al. (2021). [Sampling and asymptotic network properties of spatial multi-trophic networks](#). *Oikos*, n/a.
- 875
- 876 McLeod, A.M., Leroux, S.J. & Chu, C. (2020). [Effects of species traits, motif profiles, and environment on spatial variation in multi-trophic antagonistic networks](#). *Ecosphere*, 11, e03018.
- 877
- 878 Melián, C.J., Vilas, C., Baldó, F., González-Ortegón, E., Drake, P. & Williams, R.J. (2011). [Eco-evolutionary Dynamics of Individual-Based Food Webs](#). In: *Advances in Ecological Research, The Role of Body Size in Multispecies Systems* (ed. Belgrano, A.). Academic Press, pp. 225–268.
- 879
- 880
- 881 Ohlmann, M., Miele, V., Dray, S., Chalmandrier, L., O'Connor, L. & Thuiller, W. (2019). [Diversity indices for ecological networks: A unifying framework using Hill numbers](#). *Ecology Letters*, 22, 737–747.
- 882
- 883 Olesen, J.M., Bascompte, J., Dupont, Y.L., Elberling, H., Rasmussen, C. & Jordano, P. (2010). [Missing and forbidden links in mutualistic networks](#). *Proceedings of the Royal Society B: Biological Sciences*, 278,
- 884
- 885 725–732.
- 886
- 887 Park, J. & Newman, M.E.J. (2004). [Statistical mechanics of networks](#). *Physical Review E*, 70, 066117.
- 888
- 889 Pascual, M., Dunne, J.A. & Dunne, J.A. (2006). *Ecological Networks: Linking Structure to Dynamics in Food Webs*. Oxford University Press, USA.
- 890
- 891 Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., et al. (2018). [Comparing species interaction networks along environmental gradients](#). *Biological Reviews*, 93, 785–800.
- 892
- Petchey, O.L., Beckerman, A.P., Riede, J.O. & Warren, P.H. (2008). [Size, foraging, and food web structure](#). *Proceedings of the National Academy of Sciences*, 105, 4191–4196.
- 893
- 894 Pilosof, S., Porter, M.A., Pascual, M. & Kéfi, S. (2017). [The multilayer nature of ecological networks](#). *Nature Ecology & Evolution*, 1, 1–9.
- 895
- Plagányi, É.E. & Butterworth, D.S. (2004). [A critical look at the potential of Ecopath with ecosim to assist in practical fisheries management](#). *African Journal of Marine Science*, 26, 261–287.
- 896

- 897 Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D. (2012). [The dissimilarity of species interaction](#)
898 [networks](#). *Ecology Letters*, 15, 1353–1361.
- 899 Poisot, T., Cirtwill, A.R., Cazelles, K., Gravel, D., Fortin, M.-J. & Stouffer, D.B. (2016). [The structure of](#)
900 [probabilistic networks](#). *Methods in Ecology and Evolution*, 7, 303–312.
- 901 Poisot, T. & Gravel, D. (2014). [When is an ecological network complex? Connectance drives degree](#)
902 [distribution and emerging network properties](#). *PeerJ*, 2, e251.
- 903 Poisot, T., Stouffer, D.B. & Gravel, D. (2015). [Beyond species: Why ecological interaction networks vary](#)
904 [through space and time](#). *Oikos*, 124, 243–251.
- 905 Polis, G.A. (1991). [Complex Trophic Interactions in Deserts: An Empirical Critique of Food-Web Theory](#). *The*
906 [American Naturalist, 138, 123–155.](#)
- 907 Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O’Hara, R.B., Parris, K.M., *et al.* (2014). [Understanding](#)
908 [co-occurrence by modelling species simultaneously with a Joint Species DistributionModel \(JSDM\)](#).
909 [Methods in Ecology and Evolution, 5, 397–406.](#)
- 910 Pomeranz, J.P.F., Thompson, R.M., Poisot, T. & Harding, J.S. (2019). [Inferring predator–prey interactions in](#)
911 [food webs](#). *Methods in Ecology and Evolution*, 10, 356–367.
- 912 Pringle, R.M. & Hutchinson, M.C. (2020). [Resolving Food-Web Structure](#). *Annual Review of Ecology,*
913 [Evolution, and Systematics, 51, 55–80.](#)
- 914 Proulx, S.R., Promislow, D.E.L. & Phillips, P.C. (2005). [Network thinking in ecology and evolution](#). *Trends in*
915 [Ecology & Evolution, SPECIAL ISSUE: BUMPER BOOK REVIEW, 20, 345–353.](#)
- 916 Pulliam, H.R. (1974). [On the Theory of Optimal Diets](#). *The American Naturalist*, 108, 59–74.
- 917 Rooney, N. & McCann, K.S. (2012). [Integrating food web diversity, structure and stability](#). *Trends in Ecology*
918 [& Evolution, 27, 40–46.](#)
- 919 Salim, J.A., Saraiva, A.M., Zermoglio, P.F., Agostini, K., Wolowski, M., Drucker, D.P., *et al.* (2022). [Data](#)
920 [standardization of plant–pollinator interactions](#). *GigaScience*, 11, giac043.
- 921 Sanders, D. & van Veen, F.J.F. (2012). [Indirect commensalism promotes persistence of secondary consumer](#)
922 [species](#). *Biology Letters*, 8, 960–963.

- 923 Saravia, L.A., Marina, T.I., Kristensen, N.P., De Troch, M. & Momo, F.R. (2022). Ecological network
924 assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, 91, 630–642.
- 925 Schmeller, D.S., Julliard, R., Bellingham, P.J., Böhm, M., Brummitt, N., Chiarucci, A., et al. (2015). Towards a
926 global terrestrial species monitoring program. *Journal for Nature Conservation*, 25, 51–57.
- 927 Shaw, J.O., Dunhill, A.M., Beckerman, A.P., Dunne, J.A. & Hull, P.M. (2024). A framework for reconstructing
928 ancient food webs using functional trait data.
- 929 Singer, M.C. & McBride, C.S. (2012). Geographic mosaics of species' association: A definition and an
930 example driven by plant–insect phenological synchrony. *Ecology*, 93, 2658–2673.
- 931 Staniczenko, P.P.A., Sivasubramaniam, P., Suttle, K.B. & Pearson, R.G. (2017). Linking macroecology and
932 community ecology: Refining predictions of species distributions using biotic interaction networks.
933 *Ecology Letters*, 20, 693–707.
- 934 Stouffer, D.B., Rezende, E.L. & Amaral, L.A.N. (2011). The role of body mass in diet contiguity and food-web
935 structure. *Journal of Animal Ecology*, 80, 632–639.
- 936 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M.J., et al. (2022). Food web
937 reconstruction through phylogenetic transfer of low-rank network representation. *Methods in Ecology and
938 Evolution*, 13.
- 939 Strydom, T., Catchen, M.D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., et al. (2021). A
940 roadmap towards predicting species interaction networks (across space and time). *Philosophical
941 Transactions of the Royal Society B-Biological Sciences*, 376, 20210063.
- 942 Thompson, R.M. & Townsend, C.R. (2005). Food-Web Topology Varies with Spatial Scale in a Patchy
943 Environment. *Ecology*, 86, 1916–1925.
- 944 Tylianakis, J.M., Tscharntke, T. & Lewis, O.T. (2007). Habitat modification alters the structure of tropical
945 host–parasitoid food webs. *Nature*, 445, 202–205.
- 946 Vázquez, D.P., Melián, C.J., Williams, N.M., Blüthgen, N., Krasnov, B.R. & Poulin, R. (2007). Species
947 abundance and asymmetric interaction strength in ecological networks. *Oikos*, 116, 1120–1127.
- 948 Vázquez, D.P., Peralta, G., Cagnolo, L., Santos, M. & Igual, §.E. autores contribuyeron por. (2022). Ecological
949 interaction networks. What we know, what we don't, and why it matters. *Ecología Austral*, 32, 670–697.

- 950 Wagenmakers, E.-J. & Farrell, S. (2004). [AIC model selection using Akaike weights](#). *Psychonomic Bulletin &*
951 *Review*, 11, 192–196.
- 952 Weinstein, B.G. & Graham, C.H. (2017a). [On comparing traits and abundance for predicting species](#)
953 [interactions with imperfect detection](#). *Food Webs*, 11, 17–25.
- 954 Weinstein, B.G. & Graham, C.H. (2017b). [Persistent bill and corolla matching despite shifting temporal](#)
955 [resources in tropical hummingbird-plant interactions](#). *Ecology Letters*, 20, 326–335.
- 956 Whittaker, R.H. (1960). [Vegetation of the Siskiyou Mountains, Oregon and California](#). *Ecological*
957 *Monographs*, 30, 279–338.
- 958 Wood, S.A., Russell, R., Hanson, D., Williams, R.J. & Dunne, J.A. (2015). [Effects of spatial scale of sampling](#)
959 [on food web structure](#). *Ecology and Evolution*, 5, 3769–3782.
- 960 Woodward, G., Benstead, J.P., Beveridge, O.S., Blanchard, J., Brey, T., Brown, L.E., *et al.* (2010). [Chapter 2 -](#)
961 [Ecological Networks in a Changing Climate](#). In: *Advances in Ecological Research*, Ecological Networks
962 (ed. Woodward, G.). Academic Press, pp. 71–138.
- 963 Woodward, G., Brown, L.E., Edwards, F.K., Hudson, L.N., Milner, A.M., Reuman, D.C., *et al.* (2012). [Climate](#)
964 [change impacts in multispecies systems: Drought alters food web size structure in a field experiment](#).
965 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 2990–2997.
- 966 Young, J.-G., Valdovinos, F.S. & Newman, M.E.J. (2021). [Reconstruction of plant–pollinator networks from](#)
967 [observational data](#). *Nature Communications*, 12, 3911.

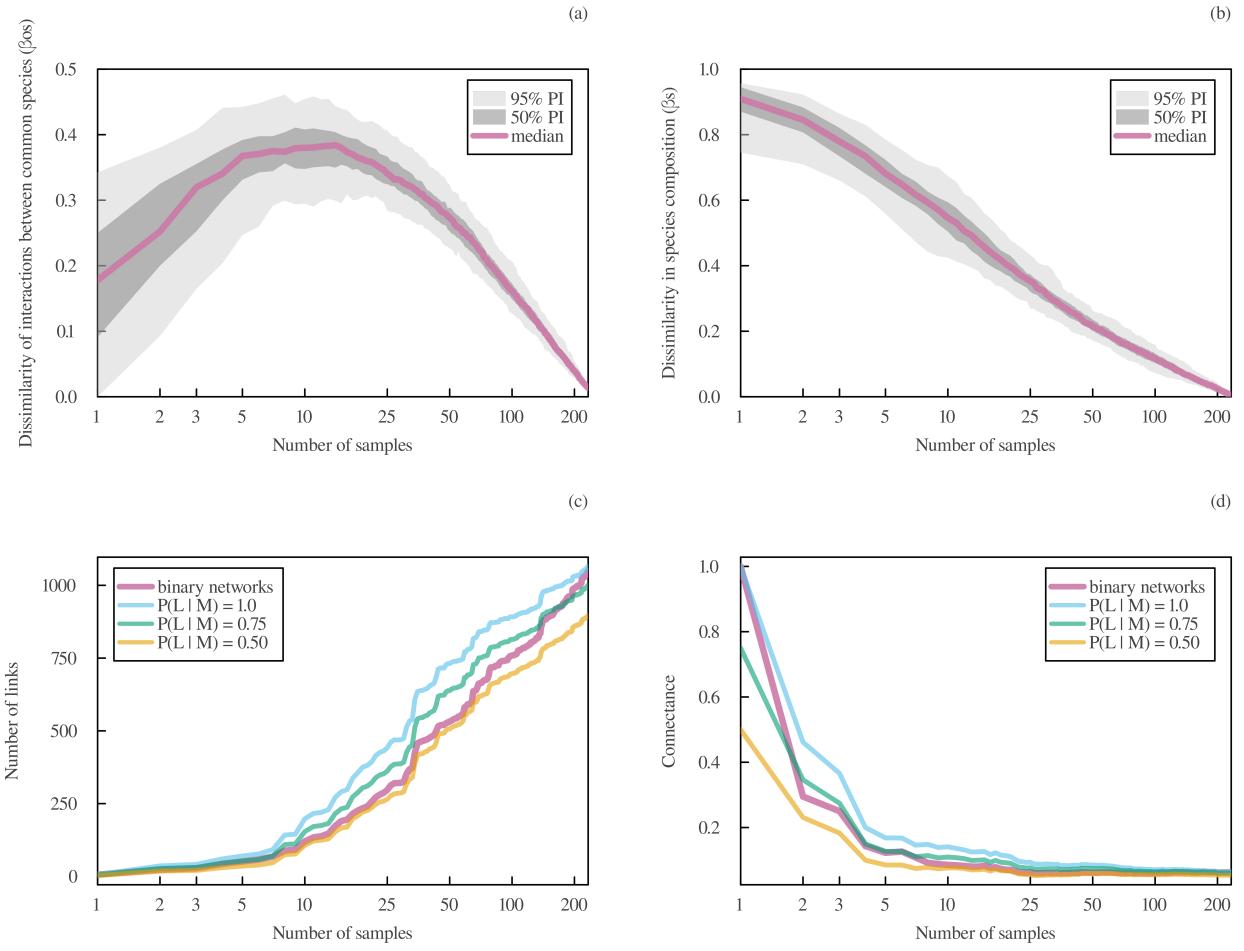


Figure 1: Network accumulation curves. (a) Dissimilarity of interactions between common species and (b) dissimilarity in species composition between aggregated local webs and the metaweb of binary host-parasite interactions. Aggregated local webs were obtained by sequentially and randomly selecting a number of local webs of binary interactions and aggregating both their species and interactions. In both panels, the colored line represents the median dissimilarity across simulations and the grey areas cover the 50% and 95% percentile intervals. (c) Scaling of the number of links and (d) scaling of connectance with the number of sampled binary and probabilistic local interaction webs. For a better comparison with binary interactions, local webs of probabilistic interactions were derived from the metaweb of probabilistic interactions with a false positive and false negative rate of zero. A specific value of $P(L_{i \rightarrow j} \mid M_{i \rightarrow j})$ (the local probability of interaction among potentially interacting species, indices omitted in the figure for simplicity) was used for all local webs within a particular curve. Aggregated local webs of probabilistic interactions were obtained by sequentially and randomly selecting a number of local webs and aggregating both their species and interactions (with the value of $P(L_{i \rightarrow j} \mid M_{i \rightarrow j})$ adjusting according to eq. 11).

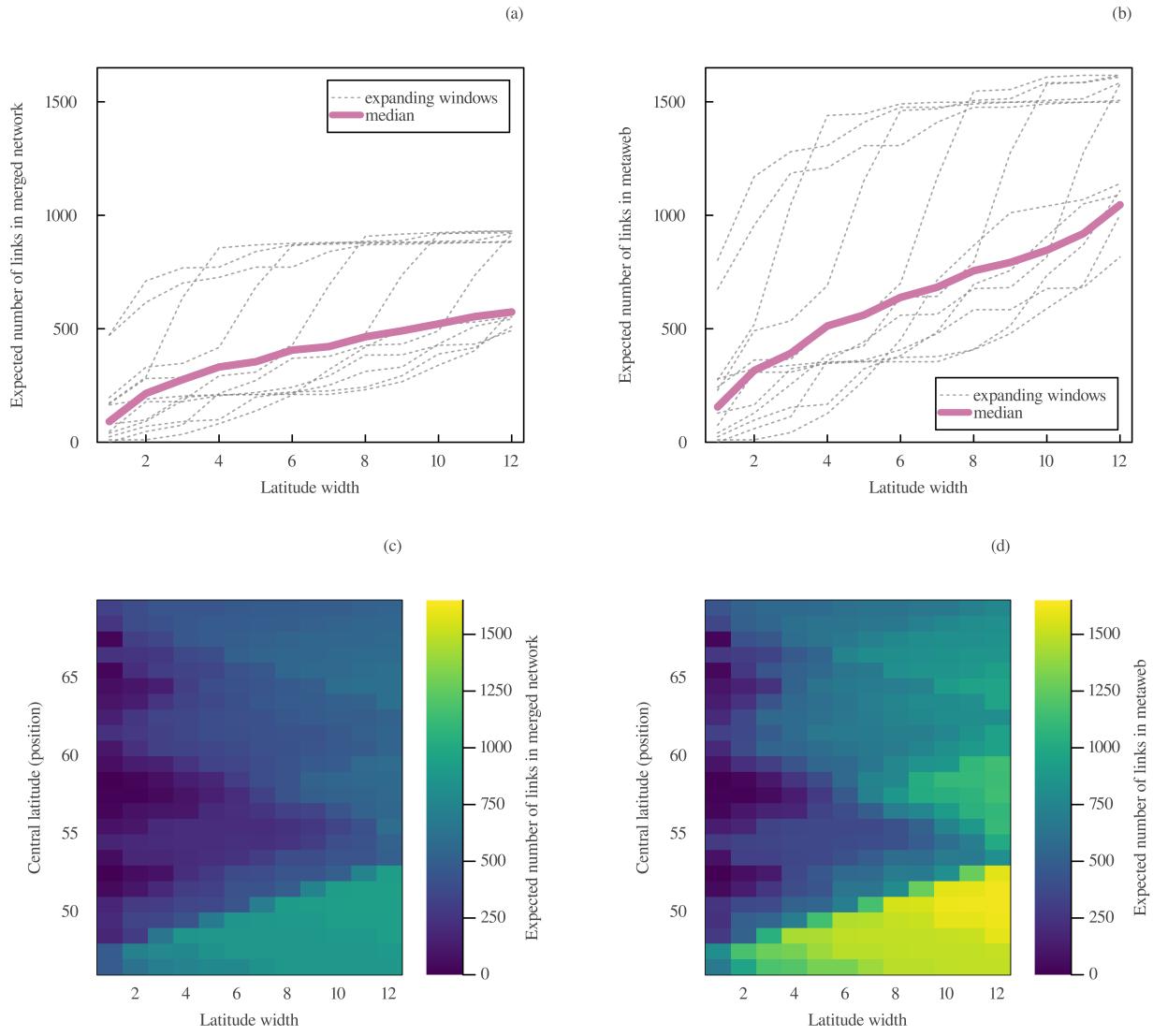


Figure 2: Spatial scaling of interactions. Expected number of host-parasite interactions in a network aggregating all (a) local and (b) regional probabilistic interactions within a latitudinal window of a given length. Every dashed curve corresponds to a different expanding window characterized by a different central latitude, with the colored solid line representing the median number of interactions. Heatmaps of the expected number of (c) local and (d) regional interactions found in windows of specified length and central latitudes. Probabilities of regional interactions were obtained with a false positive rate of 5% and a false negative rate of 10%. Local probabilistic interactions were derived from probabilistic regional interactions by setting the value of $P(L_{i \rightarrow j} | M_{i \rightarrow j})$ (the local probability of interaction among potentially interacting species) to 1, ensuring a conservative comparison between aggregated local webs and metawebs. Aggregated local webs were obtained by aggregating both the species and interactions found within a particular latitudinal window, with the values of $P(L_{i \rightarrow j} | M_{i \rightarrow j})$ remaining at their maximum value of 1 following eq. 11.

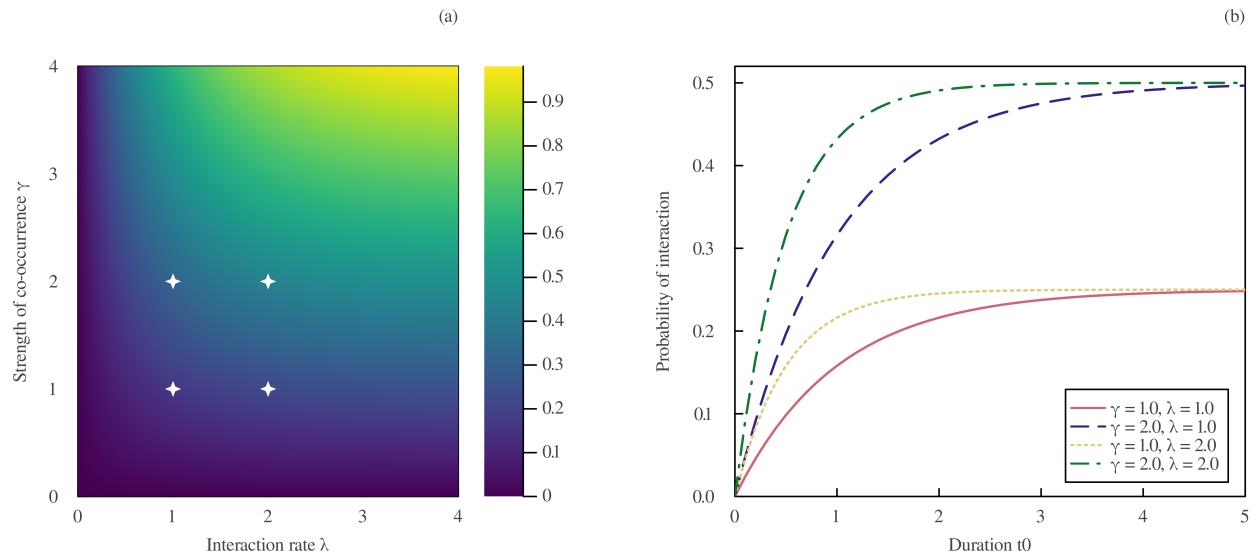


Figure 3: **Parameters of the spatiotemporally explicit model of interactions.** (a) Probability of local interaction given by the process model (eq. 16) under different values of λ_l and γ , with $t_0 = 1$. The parameter values used in the right panel are denoted by the white stars. (b) Scaling of the probability of interaction with the duration parameter t_0 in eq. 16, for different values of λ_l and γ . In both panels, the marginal probabilities of occurrence $P(X_{i,l})$ and $P(X_{j,l})$ are set to a constant value of 0.5.

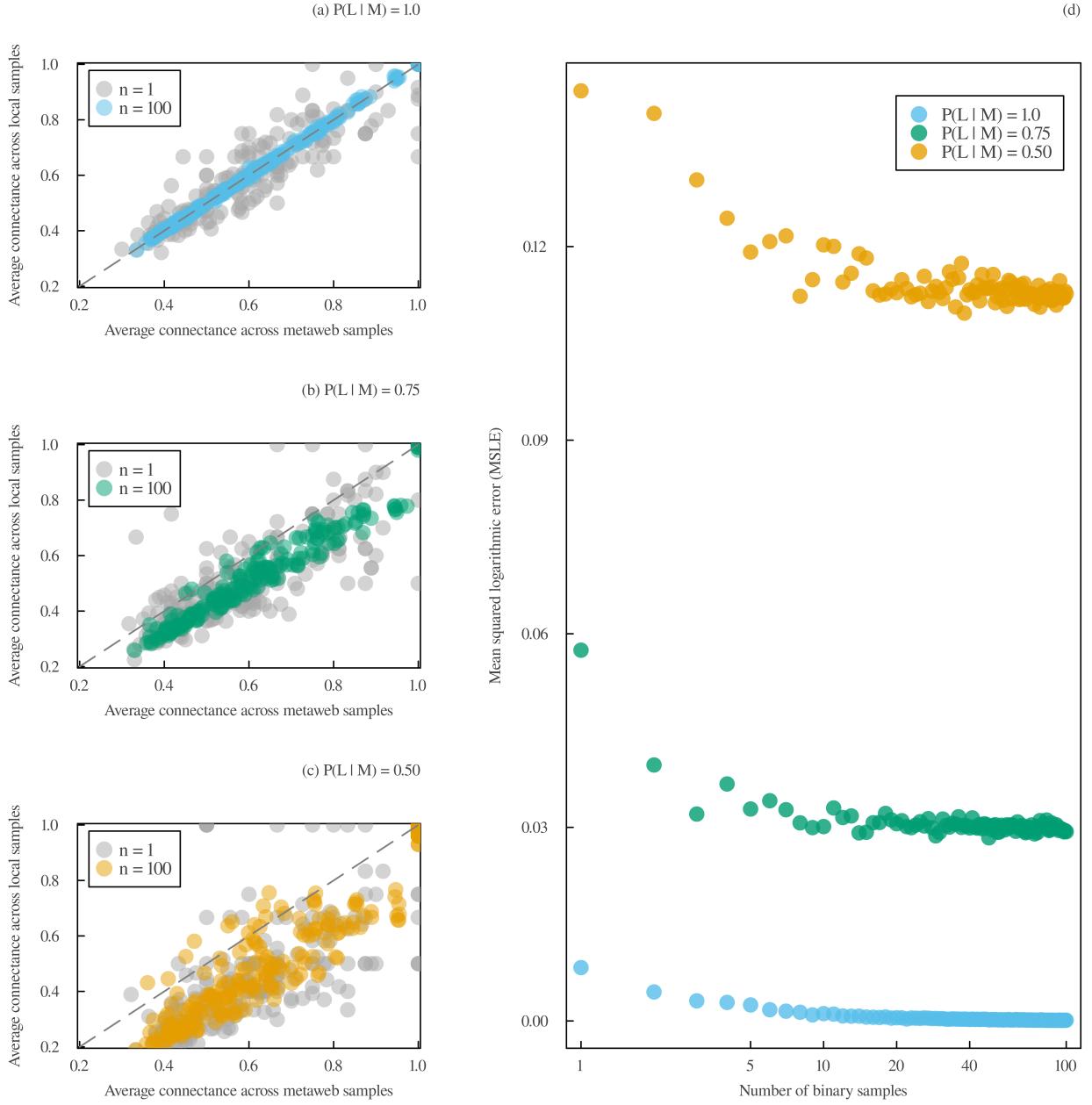


Figure 4: Connectance of sampled binary interaction webs. Comparison between the average connectance of binary interaction network samples obtained from the local and metawebs of probabilistic interactions. Each dot corresponds to a different site. The local probability of interaction between potentially interacting species was set to three different values: (a) $P(L_{i \rightarrow j} \mid M_{i \rightarrow j}) = 1.0$, (b) $P(L_{i \rightarrow j} \mid M_{i \rightarrow j}) = 0.75$, and (c) $P(L_{i \rightarrow j} \mid M_{i \rightarrow j}) = 0.50$. Grey dots represent the outcome of a single simulation, while colored dots represent the average connectance of each network across 100 simulations. (d) Reduction in the mean squared logarithmic error between the average connectance of binary interaction networks obtained from these two sampling methods as the number of simulations increases, for the same values of $P(L_{i \rightarrow j} \mid M_{i \rightarrow j})$ used in panels a-c. Probabilities of regional interactions were obtained with a false positive rate of 5% and a false negative rate of 10%. Metaweb samples were obtained by randomly sampling binary interactions from the probabilistic interaction metaweb, and then propagating this result to all local webs that include the species potentially engaged in the interactions. Local binary interaction webs were generated by independently sampling binary interactions for each local web of probabilistic interactions.