

The ecological interpretation of probabilistic networks

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The stochastic nature of ecological interactions has led biologists to adopt a probabilistic view of ecological networks. Representing species interactions probabilistically (how likely they are to occur?) as opposed to deterministically (are they occurring?) allows a better assessment of their spatiotemporal variability and accounts for inherent uncertainties in both observations and predictions. However, despite this growing interest in probabilistic networks, guidelines for the estimation and documentation of probabilistic interaction data are still lacking. This is concerning given that our biological understanding of probabilistic interactions and their appropriate analyses depend on the often elusive methods and variables used for their estimation. 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 web) and its biological feasibility (metaweb). We show that different network representations have different statistical properties when it comes to common ecological applications. Specifically, we argue that probabilistic local and metawebs differ in their spatial and temporal scaling of interactions, with potential interactions in metawebs remaining constant across spatial and temporal scales. This is in contrast with the taxonomic scaling of interactions, which does not qualitatively differ between both types of networks. We suggest two approaches to inferring deterministic networks from probabilistic webs that account for these differences and argue that systematic biases arise when directly inferring local webs from subsets of metawebs. To support our arguments, we develop different case studies using open empirical data on host-parasite interactions in Europe. Our results underscore the importance of clear metadata for probabilistic ecological networks, both at the local and regional scales, to inform the appropriate reuse of interaction data. Comprehensive metadata, providing explicit details on the sources of uncertainty in probabilistic webs, not only supports more rigorous statistical analyses but also broadens the scope of applications of interaction data. This clarity may help with the identification of optimal sampling locations to effectively minimize the uncertainty of trophic interactions.

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temporal scale

1

Introduction

As we try to navigate global biodiversity change, filling in knowledge gaps about biodiversity becomes instrumental to monitoring and mitigating those changes (Gonzalez & Londoño (2022), Abrego *et al.* (2021)). However, cataloging species, populations and, in particular, ecological interactions (e.g., predation, parasitism, and pollination) is a substantial challenge (Polis (1991), Pascual *et al.* (2006)). There are methodological and biological constraints that hinder our ability to observe all ecological interactions, leading to significant uncertainties in our understanding of these interactions. For example, the spatial and temporal uncoupling of species (e.g., nocturnal and diurnal species coexisting in the same space without interacting due to differences in the timing of their daily activities, Jordano (1987)) and the large number of rare and

cryptic interactions in a community contribute to these uncertainties (Jordano (2016)). More generally, a handful of conditions must be satisfied for an interaction to be observed locally. First, both species must have overlapping geographic ranges, i.e. they must co-occur within the region of interest (Blanchet *et al.* (2020)). Second, they must have some probability of meeting. Probabilities of interspecific encounters are typically low, especially for rare species with low relative abundances (Canard *et al.* (2012)). The probability that species meet each other also depends on their biological characteristics, such as the synchronization of their phenology (Olesen *et al.* (2010), Singer & McBride (2012)) and their discoverability (e.g., Broom & Ruxton (2005)). Finally, when species do come into contact, an interaction occurs only if their traits are locally compatible (Poisot *et al.* (2015)), including but not limited to their body phenotypes (Bolnick *et al.* (2011), Stouffer *et al.* (2011), Gravel *et al.* (2013)) and behavioral choices (Pulliam (1974), Choh *et al.* (2012)). Interactions may also be influenced by the presence or prevalence of a third species (e.g., of a more profitable prey species) (Golubski & Abrams (2011), Sanders & van Veen (2012)). Documenting the location and timing of interactions becomes even more difficult when accounting for the spatiotemporal variability of ecological interactions (Poisot *et al.* (2012), Poisot *et al.* (2015)). Environmental factors, such as temperature (Angilletta *et al.* (2004)), drought (Woodward *et al.* (2012)), climate change (Gilman *et al.* (2010), Woodward *et al.* (2010), Araujo *et al.* (2011)), and habitat modifications (Tylianakis *et al.* (2007)), contribute to this spatiotemporal variability of interactions by impacting species abundance and traits. Even after satisfying all these conditions, there remains a possibility that the interaction does not occur locally, either due to the intricate nature of the system or simply by chance. If it does occur, it might still go unnoticed, particularly if it happens infrequently. In this context, it is unsurprising that our knowledge of ecological interactions remains limited (Hortal *et al.* (2015)) despite extensive biodiversity data collection (Schmeller *et al.* (2015)).

Knowing the biological capacity of two species to interact directly (via e.g., trophic interactions) is necessary but not sufficient for inferring their interaction at a specific time and space. The recognition of the intrinsic variability of species interactions has led ecologists to expand their representation of ecological networks (also known as ecological webs) to include a probabilistic view of interactions (Poisot *et al.* (2016), Dallas *et al.* (2017), Fu *et al.* (2021)). This different perspective allows us to fill in the Eltonian shortfall (Hortal *et al.* (2015)) by modeling the probability of detecting interactions, which can be an important tool for directing efforts and taking action, especially in places where access and resources for research are scarce. Representing interactions probabilistically enables us to capture the spatiotemporal variability of the aforementioned ecological processes and the uncertainties associated with their measurement. As opposed to binary deterministic webs, in which interactions are regarded as either occurring or not, probabilistic webs, within a Bayesian framework, express our degree of belief (or confidence) regarding the occurrence of interactions. Based on the scale at which they are estimated, probabilistic interactions may reflect our level of confidence in whether interactions will be observed, realized, or biologically feasible. As an illustration, we could outline a situation in which there is a 50% certainty that an interaction occurs 50% of the time, or that there is a 50% certainty that it simply occurs. Our level of confidence should be more definitive (approaching either 0 or 1) as we extend our sampling to a broader area and over a longer time period, thereby diminishing the uncertainty of the interactions (but not necessarily the estimation of their variability). In the broadest sense, binary networks are also a type of probabilistic network, in which the numerical value of an interaction is restrained to 0 (non-occurring) or 1 (occurring). Yet, for the sake of clarity, we omit binary networks from our discussion of probabilistic networks in this contribution. In probabilistic webs, only forbidden interactions (i.e., interactions prohibited by biological traits or species absence, Jordano *et al.* (2003), Olesen *et al.* (2010)) have a probability value of zero by default, provided that intraspecific trait variability is considered (Gonzalez-Varo & Traveset (2016)).

By accounting for the uncertainty of interactions, probabilistic webs may provide a more realistic portrait of species interactions and network structure (i.e. community-level properties), which are major drivers of the functioning, dynamics, and resilience of ecosystems worldwide (Proulx *et al.* (2005), McCann (2007), McCann (2011), Rooney & McCann (2012)). Moreover, 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 probabilistic networks by preserving chosen characteristics of the binary adjacency matrix while intentionally omitting others (Bascompte *et al.* (2003), Fortuna & Bascompte (2006)), serve as other examples of common probabilistic network 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 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 webs 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 show that they yield different statistical outcomes regarding e.g. the spatial and temporal scaling of interactions and the prediction of binary webs across space. 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 webs would support more adequate manipulation and integration of interaction data from different sources and guard against possible misinterpretations arising from ambiguous definitions of probabilistic 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 many types of ecological networks, from food webs to host-virus networks. Indeed, excluding networks of indirect interactions such as competition and facilitation networks (Kéfi *et al.* (2015), Kéfi *et al.* (2016)), most ecological webs describe probabilities of direct interactions, which are conceptually and mathematically analogous regardless of their biological type (e.g., trophic and parasitic interactions).

Probabilistic representations of interactions

One of the first aspects to take into consideration when estimating or interpreting probabilities of interactions is knowing if they describe potential or realized interactions. A potential (regional) interaction is defined as the biological capacity of two taxa to interact (i.e., the probability that they *can* theoretically interact) whereas a realized (local) interaction is the materialization or observation of this interaction in a well-defined space and time (i.e., the probability that they interact locally). Here, we use the terms *metaweb* (Dunne (2006)) to designate regional webs of potential interactions and *local webs* (Poisot *et al.* (2012)) for those of realized interactions. Metawebs are the network analogs of the species pool, where local webs originate from a subset of both species (nodes) and interactions (edges) of the regional metaweb (Saravia *et al.* (2022)). Without clear documentation, it can be challenging to know if published probabilistic webs describe local or regional interactions (tbl. 1 provides examples of studies employing both types of probabilistic networks), or if so-called probabilities are in reality *interaction scores* (i.e., non-probabilistic quantitative interactions). When probabilistic regional interactions are used and interpreted incorrectly as local interactions (and conversely), this may generate misleading findings during data analysis. We believe that a better understanding of the differences, similarities, and relationships between these two probabilistic representations of ecological webs would alleviate interpretation errors and facilitate a more adequate utilization of interaction data.

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

Edges linking nodes can describe a variety of interaction measures. Ecologists have traditionally represented interactions as binary objects that were considered realized after observing at least one individual from group i interact with at least another individual from group j . In a binary adjacency matrix B , the presence or absence of an interaction $B_{i \rightarrow j}$ between two taxa can be viewed as the result of a Bernoulli process $B_{i \rightarrow j} \sim \text{Bernoulli}(P(B_{i \rightarrow j}))$, with $P(B_{i \rightarrow j})$ being the probability of interaction that characterizes our limited knowledge of the system and its intrinsic spatiotemporal variability. In probabilistic networks, $P(B_{i \rightarrow j})$ are edge 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 between each pair of nodes. Depending on the type of probabilistic network (local or metaweb), the mathematical formulation and interpretation of stochastic parameters like $P(B_{i \rightarrow j})$ can be linked to environmental and biological factors such as species relative abundance, traits, area, and time (tbl. 1), for example using logistic regression with a logit link function with continuous explanatory variables. Predicting the number of local webs in which the interaction occurs can be achieved by using a Binomial distribution, assuming a constant probability of interaction and independence between networks (trials). When considering uncertainties around the estimation of $P(B_{i \rightarrow j})$, a Beta distribution can also be used to encompass all possible probability values. In that case, a Beta-Binomial distribution can be used to predict the number of networks in which the interaction occurs. Observing an interaction between two taxa at a given location and time provides important information that can be used to update previous estimates of $P(B_{i \rightarrow j})$, informing us on the biological capacity of both taxa to interact and the environmental conditions that enabled them to interact locally.

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

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

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

We define space as the collection of geographic coordinates (x, y, z) , with (x, y) representing longitude and latitude coordinates, and z denoting either altitudes or depths. These point coordinates delineate the spatial boundaries of the system, which may be portrayed as a polyhedron. Ecological interactions may exhibit variations along altitudinal gradients, as evidenced by changes in hummingbird-plant interactions (Weinstein & Graham (2017b) and Weinstein & Graham (2017a)) and mosquito biting rates (e.g., Kulkarni *et al.* (2006)) at different elevations. In contrast, time is defined as the specific time period within which interactions were either observed or predicted. With these definitions in mind, space and time can be conceptualized as distinct patches or time segments. Treating them as discrete dimensions aligns with the common sampling methods of ecological webs and provides actual probabilities of interactions across space and time. This differs from the approach of treating them as continuous variables, where edge values represent probability densities (i.e., relative likelihoods of interactions occurring at infinitesimal locations and instants in time) rather than discrete probability values (which can be obtained by integrating probability densities). By employing discrete locations and time periods, we can quantify an area (or volume) A and a duration t , which can be readily used in spatiotemporal analyses of ecological networks. For example, when studying network-area relationships (NAR, Galiana *et al.* (2018)), we anticipate that local probabilities of interactions scale positively with area and duration because taxa have more opportunities to interact as these dimensions expand.

The probability that two taxa i and j interact in a local web $L_{x,y,z,t}$ (spatial and temporal subscripts hereafter omitted for clarity) can be conditional on many environmental and biological factors. One of these is their co-occurrence $C_{i,j}$, which is usually a Boolean describing if the geographic distributions of both taxa overlap within the study area. Co-occurrence can be modeled probabilistically, in which case it may conform to a Bernoulli distribution $C_{i,j} \sim \text{Bernoulli}(P(C_{i,j}))$, where the probability of co-occurrence $P(C_{i,j})$ can be estimated through the application of joint species distribution models (e.g., Pollock *et al.* (2014)). Considering that the probability that two non-co-occurring taxa interact locally is zero (i.e., $P(L_{i \rightarrow j}|C_{i,j} = 0) = 0$), the probability of local interaction can be obtained by multiplying the probability of interaction given co-occurrence with the probability of co-occurrence:

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

Other important factors that can impact interaction probabilities at the local scale are taxa relative abundance (Canard *et al.* (2012)) and traits (Poisot *et al.* (2015)), as well as environmental factors such as temperature (Angilletta *et al.* (2004)), precipitation (Woodward *et al.* (2012)), habitat structure (Klecka & Boukal (2014)), and presence of other interacting taxa in the network (Pilosof *et al.* (2017), Kéfi *et al.* (2012)), as described above. Here, we use the variable $\Omega_{x,y,z,t}$ (hereafter simply Ω) to describe the biological and ecological context in which interaction probabilities were estimated. For example, if a research team conducts a mesocosm experiment to estimate interaction probabilities between predators and prey with and without shelters (a place that offers refuge and protection for prey, shielding them from predators), Ω would represent the presence or absence of these shelters. Like co-occurrence, Ω can also be modeled probabilistically when the stochasticity or uncertainty of environmental and biological factors is considered. In sum, Ω represents all ecological and biological variables that were taken into consideration when measuring interaction probabilities and is, therefore, a subset of all factors impacting ecological interactions. It is a vector of random variables whose values determine the overall uncertainty of an interaction.

The probability that two taxa i and j interact in a local web L can thus be conditional on the area (or volume) A , the time interval t , their co-occurrence $C_{i,j}$ and chosen environmental and biological conditions Ω . Although these variables are associated with distinct questions or mechanisms related to ecological interactions, they may covary with each other, such as the possible dependence of $C_{i,j}$ and Ω on spatial and temporal scales. When estimating interaction probabilities using e.g. a generalized linear model with multiple explanatory variables that might not be independent, it may become important to address collinearity. Using variable selection techniques, for instance, may be necessary before fitting the model to mitigate this issue. The probability of local interaction is described by the following expression when all these conditional variables are included:

$$P(L_{i \rightarrow j} | A, t, C_{i,j}, \Omega) \quad (2)$$

The representation of the local context in which probabilities are estimated and the variables that should be taken into consideration depend on the study system, the objectives of the study, and the resources available to the researchers. In other words, these variables do not systematically need to be accounted for. For example, in Gravel *et al.* (2019), for the purpose of model comparison, some models incorporated environmental variables as conditional factors to estimate interaction probabilities, while others did not. When accounted for, these variables should be clearly described in the documentation of the data (Brimacombe *et al.* (2023)), preferentially in mathematical terms to avoid any confusion in their interpretation and to limit manipulation errors during their re-use. For instance, ecologists should be explicit about their consideration of co-occurrence in their estimation of local interaction probabilities. Indeed, it is important to specify if probability values are conditional $P(L_{i \rightarrow j} | C_{i,j} = 1)$ or not $P(L_{i \rightarrow j})$ on co-occurrence since this can significantly impact the interpretation and analysis of the data. In [tbl. 1](#), we present examples of studies that used these diverse formulations of probabilistic interactions and conditional variables.

Table 1 Mathematical expression of probabilistic interactions. The probability of interaction between two taxa i and j is interpreted differently in a metaweb M of potential interactions and a local web L of realized interactions. Each expression includes a different conditional variable, when applicable. An example of a study employing each of these notations and conditional variables is provided, with the specific variables used indicated in parentheses. The study marked with an asterisk has been carried out on binary webs. Note that interaction probabilities can be contingent upon multiple conditional variables, or none at all. Additionally, local interaction probabilities might represent the probability of observing an interaction, not necessarily its actual occurrence.

Expression	Type	Outcome	Reference
$P(M_{i \rightarrow j})$	regional	biological feasibility of the interaction	Strydom <i>et al.</i> (2022)
$P(L_{i \rightarrow j})$	local	realization of the interaction	Fortuna & Bascompte (2006) (null model)
$P(L_{i \rightarrow j} A)$	local	realization of the interaction in a given area or volume	Galiana <i>et al.</i> (2018)*
$P(L_{i \rightarrow j} t)$	local	realization of the interaction during a given time period	Weinstein & Graham (2017a)
$P(L_{i \rightarrow j} C_{i,j})$	local	realization of the interaction given that the taxa co-occur	Gravel <i>et al.</i> (2019)
$P(L_{i \rightarrow j} \Omega)$	local	realization of the interaction given environmental conditions	Gravel <i>et al.</i> (2019) (temperature and precipitation)
$P(L_{i \rightarrow j} M_{i \rightarrow j})$	local	realization of the interaction given that the taxa can biologically interact	this study

2.3. 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). They represent the probability that taxa can biologically interact regardless of their co-occurrence and local environmental conditions. Regional interactions are by definition context-independent, i.e. they are not measured at a specific location and time. In contrast with probabilistic local webs, which represent the stochasticity of interactions occurring in nature, probabilistic metawebs measure our degree of belief in the capacity of two taxa to interact (i.e., the probability that their traits could support an interaction in the right conditions). Consequently, although *neutrally* forbidden interactions (i.e., improbable interactions between rare species, Canard *et al.* (2012)) tend to have low probability values in local webs, they may exhibit a higher probability in the metaweb. Potential interactions describe the probability that there exists at least one combination of phenotypes of taxa i and j that can interact with each other if they were to encounter. For example, a piscivorous species may have the capacity to interact with a potential prey species if they share at least one matching combination of body sizes, such as an adult predator being able to consume juvenile prey. To reduce any biases in our calculation of this probability, it is crucial to ensure that the set of traits sampled or considered accurately reflects the overall trait distribution in both taxa. This enhances our confidence in concluding that the taxa cannot interact when no positive observation has been made and increases our capacity to detect an interaction when it is biologically feasible. In addition to pairwise interactions, the extent of sampling effort also contributes to shaping our assessment of metaweb properties, as sampling a

larger number of local webs allows us to capture more regional interactions (McLeod *et al.* (2021)). A probability of potential interaction in a metaweb M can be expressed as

$$P(M_{i \rightarrow j}), \quad (3)$$

which, in contrast with local webs, is never conditional on any spatial, temporal, co-occurrence or environmental variables (tbl. 1).

Starting from a selected set of taxa, which are usually distributed within a broad region of interest, metawebs can be built using different data sources, including literature review (e.g., Maiorano2020Tetraeu), aggregated local web data (e.g., Gravel *et al.* (2019), Saravia *et al.* (2022)), and predictive models (e.g., Strydom *et al.* (2022), Shaw *et al.* (2024)). Every pair of taxa that have confidently been observed to 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. This is not the case in local probabilistic webs, in which interaction events usually remain stochastic (i.e., $P(L_{i \rightarrow j}) < 1$) after empirically observing interactions because of their intrinsic spatiotemporal variability. Similarly, although rare interactions typically have low probabilities in local webs, they can have high probabilities in metawebs when the traits of both taxa are congruent. On the other hand, interactions that were never observed can have low probability values in both local and metawebs, going as low as 0 for forbidden links (i.e., interactions forbidden by biological traits). However, many observations of interactions are in reality false positives because of observation errors due to taxonomic misidentifications and ecological misinterpretations (e.g., due to cryptic species and interactions, Pringle & Hutchinson (2020)). Likewise, forbidden interactions can be false negatives in metawebs, e.g. if they have been assessed for specific phenotypes, locations or time. Employing Bayesian models, whether they are mechanistic or phenomenological, could improve the accuracy of our estimation of interaction probabilities within both local and regional webs (e.g., Bartomeus *et al.* (2016), Cirtwill *et al.* (2019)). This improvement is achieved in metawebs by leveraging prior information regarding the feasibility of interactions along with the empirical data on observed interactions.

3

Properties of probabilistic webs

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

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

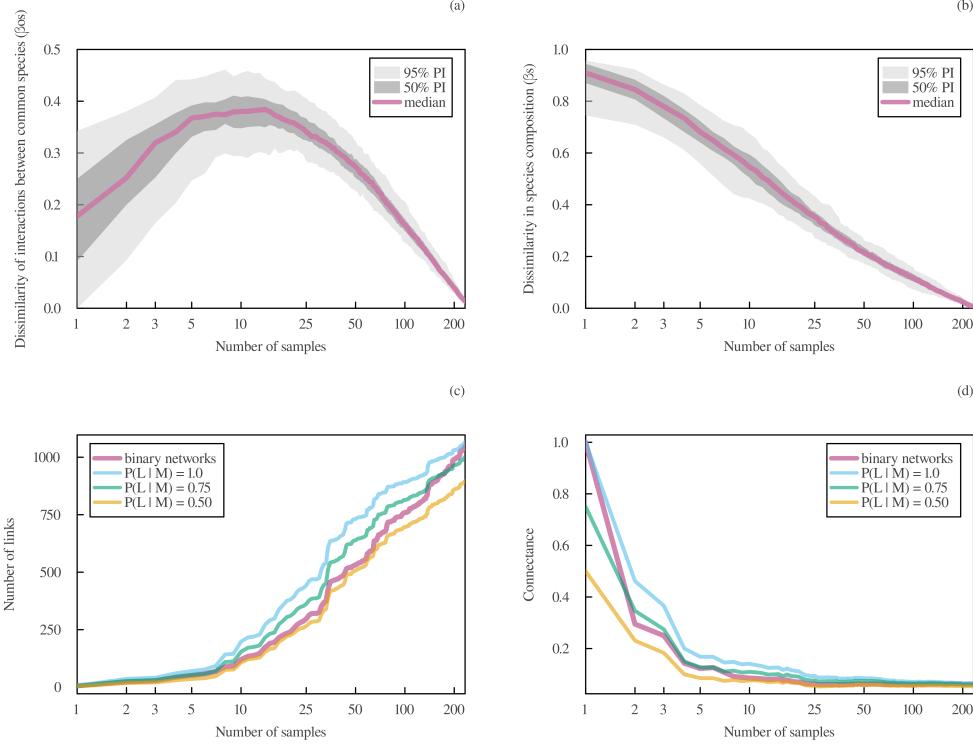


Figure 1 Network accumulation curves. (a) Dissimilarity of interactions between common species and (b) dissimilarity in species composition between aggregated local webs and the binary metaweb of host-parasite interactions. Aggregated local webs were obtained by sequentially and randomly selecting a number of binary local webs 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 webs. For a better comparison with binary webs, local probabilistic webs were derived from the probabilistic metaweb with a false positive and false negative rate of zero. A specific value of $P(L|M)$ (the local probability of interaction among potentially interacting species) was used for all local webs within a particular curve. Aggregated probabilistic local webs were obtained by sequentially and randomly selecting a number of probabilistic local webs and aggregating both their species and interactions (with the value of $P(L|M)$ adjusting according to eq. 6).

$$\beta_W = \frac{c_{LM} + u_L + u_M}{(2c_{LM} + u_L + u_M)/2} - 1. \quad (4)$$

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

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

$$P(L_{i \rightarrow j}) = P(L_{i \rightarrow j}|M_{i \rightarrow j} = 1) \times P(M_{i \rightarrow j} = 1). \quad (5)$$

We built the probabilistic local webs from the binary ones by using the probabilistic metawebs and a constant value of $P(L|M)$ across interactions. Low values of $P(L|M)$ indicate that feasible interactions rarely occur locally, intermediate values around 50% suggest considerable spatiotemporal variability, while high values indicate that regional interactions are nearly always realized locally. Following eq. 5, the local probability of interaction between a given pair of taxa consistently remained equal to or below their probability of regional interaction.

In the last two panels of fig. 1, we show how the aggregated number of links and connectance (i.e., the proportion of all of the non-forbidden links that are realized) scale with the number of sampled local probabilistic webs, according to different values of $P(L|M)$. When aggregating local probabilistic webs, the constancy of the probability of regional interaction across the entire study area means that any rise in the probability of local interaction is solely attributable to an increase in $P(L|M)$. The probability $P(L_{1,2}|M)$ of local interaction among potentially interacting species in an aggregated web $L_{1,2}$ is obtained by:

$$P(L_{1,2}|M) = 1 - (1 - P(L_1|M)) \times (1 - P(L_2|M)), \quad (6)$$

where $P(L_1|M)$ and $P(L_2|M)$ are the probabilities of local interaction among two potentially interacting species in the subnetworks L_1 and L_2 , respectively. This equation provides the probability that the interaction is realized in either (1) exclusively the local web L_1 , (2) exclusively the local web L_2 or (3) both local webs, given that the two taxa have the biological capacity to interact.

By comparing the scaling relationships observed in binary and probabilistic webs, fig. 1 illustrates that high values of $P(L|M)$ lead to systematic overestimations in the number of links and connectance, especially when $P(L|M) = 1$ (corresponding to the scenario where local probabilities of interactions are equivalent to the probabilities of regional interactions). However, these biases tend to diminish as the number of sampled webs increases.

3.2. Spatial and temporal scaling of interactions The investigation of network-area relationships and interaction accumulation curves is an important area of research in network ecology. First, network-area relationships elucidate the scaling of network properties (such as modularity and trophic chain lengths) with spatial scale (e.g., Wood *et al.* (2015), Galiana *et al.* (2018)). The variations in network structure across spatial scales may stem from the scaling of species richness (species-area relationships, SARs) and the number of interactions (Brose *et al.* (2004)) with the sampled area. Additionally, ecological processes unfolding at distinct spatial scales, such as the spatial variability in local community composition resulting from different sequences of extinction and colonization events, can also contribute to this variation (Galiana *et al.* (2018)). Next, interaction accumulation curves describe the scaling of the number of observed interactions with sampling effort (Jordano (2016)). Sampling effort, which may correspond to the duration of the sampling period used to construct the network, can impact connectance (Bersier *et al.* (1999)) and various measures of network structure (Banašek-Richter *et al.* (2004), McLeod *et al.* (2021)). Apart from sampling effort, the temporal scaling of interactions also elucidates how network structure changes with the temporal resolution of the network (Poisot *et al.* (2012)), acknowledging that distinct interactions take place over time, ranging from short-term fluctuations of interactions to long-term trends. As probabilistic local webs may explicitly account for the spatiotemporal variability of interactions, they offer a distinct approach to investigating the scaling of network structure with space and time, in contrast to binary and quantitative webs, by making the stochasticity of interactions the focal point of the modeling process.

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

On the other hand, local interactions scale both spatially and temporally, given that they have more opportunities to be realized and observed in larger areas and longer durations. This is attributed to factors such as a higher number of individuals, greater trait variations, and increased opportunities for encounters, as highlighted by McLeod *et al.* (2020). For example, if a local probabilistic web L_1 with an area 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 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, interaction probabilities could be higher in the smaller area, contingent upon their environmental and biological conditions. Likewise, interaction probabilities are expected to be lower in webs with shorter durations when

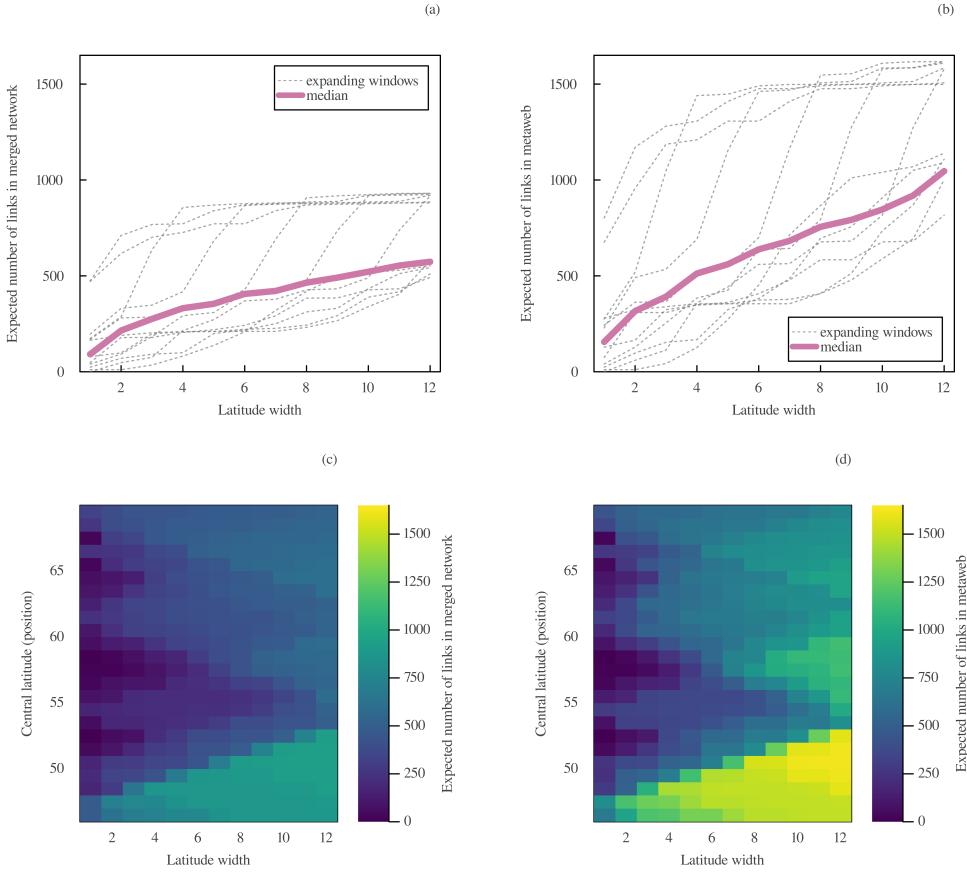


Figure 2 Spatial scaling of interactions. Expected number of host-parasite interactions in a network aggregating all probabilistic (a) local and (b) regional interactions within a latitudinal window of a given length. Every dashed curve corresponds to a different expanding window characterized by a different 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 the probabilistic metaweb by setting the value of $P(L|M)$ (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 $P(L|M)$ remaining at their maximum value of 1 following eq. 6.

time intervals are nested. In fig. 2, we show how the expected number of local host-parasite interactions scales with area, represented as an expanding latitudinal window, in comparison with regional interactions. Even though we employed local probabilities of interactions equal to regional interactions for the purpose of comparison (i.e., using $P(L|M) = 1$ here), we notice that the total number of regional interactions scales more rapidly than local interactions. This is because numerous regional interactions involve species that never co-occur, and as a result, these interactions are not captured in local webs.

3.3. Box 1: A spatiotemporally explicit model of interactions Predicting local webs across time and space is a pivotal goal of network ecology, especially given the scarcity of interaction data (Strydom *et al.* (2021)). Ecologists may resort to predictive models (e.g., generative Bayesian and machine learning models) to reconstruct networks at fine spatial and temporal scales with limited interaction data. For instance, real-time biomonitoring data coupled with appropriate numerical models (Bohan *et al.* (2017)) can be employed to reconstruct local ecological webs, opening avenues for in-depth studies on local ecosystem functioning and dynamics. The probabilistic representation of interactions acknowledges the inherent uncertainty in these models, typically expressed through probability distributions. We introduce and develop a simple generative mechanistic model for probabilistic local interactions that takes into consideration their spatiotemporal variability (i.e. a spatiotemporally explicit model of local interactions). It is essential to note that our model is not designed for regional interactions, which are scale-independent. Rather, it could prove valuable for predicting local interactions across time and space by generating new interaction data following parameter inference.

As indicated by eq. 1, the probability that two taxa i and j interact at a specific location (x, y, z) may be determined by the product of their probability of interaction given co-occurrence and their probability of co-occurrence. First, their co-occurrence probability can be calculated using their individual occurrence probabilities $P(X_i)$ and $P(X_j)$, along with the strength of association γ between their occurrences and co-occurrence (Cazelles *et al.* (2016)):

$$P(C_{i,j}) = P(X_i, X_j) = P(X_i)P(X_j)\gamma. \quad (7)$$

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

$$C_{i,j} \sim \text{Bernoulli}(P(X_i, X_j)). \quad (8)$$

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

$$P(L_{i \rightarrow j} | C_{i,j} = 1) = 1 - e^{-\lambda t_0}, \quad (9)$$

which tends toward 1 as $t_0 \rightarrow \infty$. It is important to note that the units of λ and t_0 are complementary. For instance, if the duration t_0 is measured in months, λ denote the expected number of interactions per month.

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

$$L_{i \rightarrow j} \sim \text{Bernoulli}(P(L_{i \rightarrow j})) \quad (10)$$

$$P(L_{i \rightarrow j}) = P(X_i)P(X_j)\gamma(1 - e^{-\lambda t_0}) \quad (11)$$

$$\gamma \sim \text{Gamma}(2, 0.5) \quad (12)$$

$$\lambda \sim \text{Exponential}(2) \quad (13)$$

In fig. 3, we show the variation in the probability of interaction under different parameter values. In the right panel, we notice that, irrespective of the interaction rate λ , the probability of interaction converges toward an asymptote determined by the co-occurrence $P(C_{i,j})$ (eq. 7). This model can be customized in different ways, such as by linking λ with specific environmental variables or explicitly incorporating observation errors (i.e., the probabilities of false negatives and false positives).

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

There are no inherent differences in the taxonomic scaling between local and metawebs, as only the nodes are defined taxonomically. In other words, the probability values of edges in both local (eq. 2) and metawebs (eq. 3) are not conditional on any taxonomic scale. The phylogenetic scale is tied to the definition of the event itself (i.e., the interaction between two taxa), not to the conditional variables. In both types of webs, transitioning to a broader level of organization (e.g., from a species-level web S to a genus-level web G) can be accomplished directly by using probabilities from finer scales. For example, in a network with n_1 species

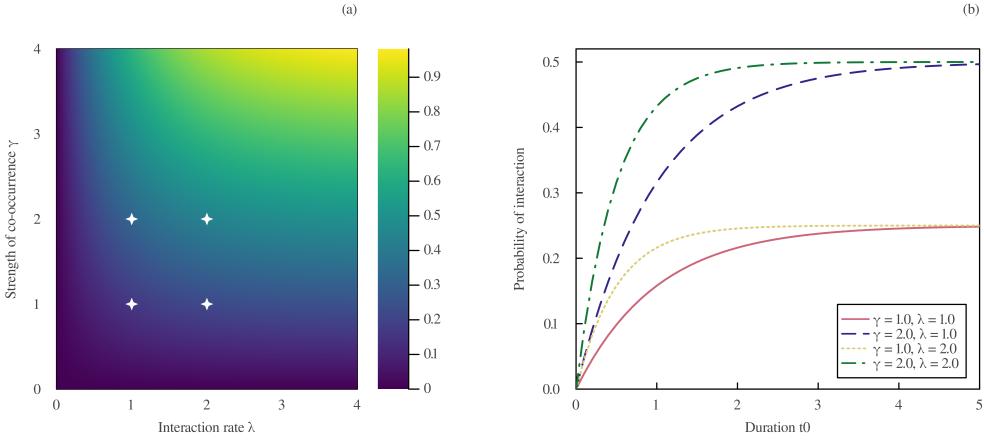


Figure 3 Parameters of the spatiotemporally explicit model of interactions. (a) Probability of local interaction given by the process model (eq. 11) under different values of λ and γ , with $t_0 = 1$. The parameter values used in the right panel are denoted by the white stars. (b) Scaling of the probability of interaction with the duration parameter t_0 in eq. 11, for different values of λ and γ . In both panels, the individual probabilities of occurrence $P_i(x, y, z)$ and $P_j(x, y, z)$ are set to a constant value of 0.5.

from genus g_1 and n_2 species from genus g_2 , one can compute the probability that at least one species from genus g_1 interacts with at least one species from genus g_2 as follows:

$$P(G_{g_1 \rightarrow g_2}) = 1 - \prod_{i=1}^{n_1} \prod_{j=1}^{n_2} (1 - P(S_{g_{1i} \rightarrow g_{2j}})), \quad (14)$$

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

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

3.5. Sampling for binary webs The prediction of binary interactions through Bernoulli trials is an important application of probabilistic webs. This approach proves beneficial for analyzing the structural characteristics of probabilistic webs, particularly in the absence of specific analytical measures. By performing independent Bernoulli trials for each interaction in a probabilistic web, a binary network may be generated. A probability distribution of network properties can be obtained by measuring network structure across multiple randomly generated networks (Poisot *et al.* (2016)). This method enables the representation of the variability of network structure, albeit with possible biases when connectance is low (Poisot & Gravel (2014), Chagnon (2015)). Employing this strategy to generate binary networks under a null model facilitates null hypothesis significance testing, wherein the observed measure is compared against the simulated distribution

(e.g., Bascompte *et al.* (2003)). Additionally, the random generation of binary networks, from a probabilistic web that accounts for the spatiotemporal variability of interactions, may effectively capture network structure across space and time. This facilitates the investigation of ecological hypotheses about interactions at broad spatial and temporal scales.

There are at least two distinct approaches to sample binary networks from probabilistic webs across space, for example, when attempting to predict a binary network for each of a number of locations within a given region. The first approach involves performing a singular Bernoulli trial for each pair of taxa based on their regional probability of interaction. In employing this approach, every pair of taxa predicted to interact in the binary metaweb will be treated as interacting in all local webs where they co-occur. This will result in local pairwise interactions without spatial variation. The second approach is to independently sample each of the local probabilistic webs, which can be achieved by first generating distinct probabilistic networks for each location. These local probabilistic webs may vary in taxa composition and interaction probabilities. Subsequently, binary networks can be independently sampled for each location, introducing spatial variation in binary interactions.

In fig. 4, we compare the average connectance of binary networks resulting from these two sampling techniques, where regional and local interactions are drawn from our host-parasite probabilistic networks, generating a number of binary web realizations for each site in the dataset. These two sampling approaches yield different outcomes, particularly for lower values of $P(L|M)$, which denote instances where regional interactions do not consistently manifest locally. Small discrepancies are also apparent between these techniques when we equate the probability of local interaction to the probability of regional interaction (i.e., when using $P(L|M) = 1.0$ in eq. 5), especially when the number of binary network samples for each location is low. As anticipated, we observe that sampling binary interactions from the metaweb tends to overestimate connectance on average compared to sampling them from local webs. Furthermore, we observe an increase in the variability of connectance when employing a single sample, representing what we consider as a more tangible process leading to the realization of local and regional interactions in nature.

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

$$P(L_{0,i \rightarrow j}) = 1 - (1 - P(L_{1,i \rightarrow j}) \times P(L_{2,i \rightarrow j})). \quad (15)$$

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

3.6. Prediction of local webs from metawebs Metawebs serve as a valuable source of ecological information for predicting local webs across time and space. Binary local webs can be reconstructed by selecting a subset of taxa and interactions from the metaweb (Dunne (2006)). This implies that metawebs consistently contain more interactions than their corresponding local webs. Determining the list of taxa to select can be achieved empirically or through methods like range maps or species distribution models. As the species composition of a community is arguably less difficult to sample or predict than its interactions, the primary challenge lies in deciding which interactions to select from the metaweb, a task that may necessitate advanced statistical models and ecological expertise. Inferring the structure of local webs from the metaweb before predicting specific local pairwise interactions could hold promise (Strydom *et al.* (2021)), considering that the structure of local webs is constrained by the metaweb (Saravia *et al.* (2022)).

Building probabilistic local webs from a probabilistic metaweb involves a reduction in the value of pairwise interaction probabilities. This decrease is attributed to the prerequisite that two taxa must initially possess the capacity to interact before engaging in local interactions (eq. 5). Therefore, inferring local webs from their metaweb while maintaining identical interaction probability values would introduce systematic biases into the predictions. In such cases, these networks would essentially represent smaller-scale metawebs of potential interactions, possibly leading to misinterpretations by being perceived as local interactions. As proposed by McLeod *et al.* (2021), although metawebs do not capture the spatiotemporal variability of interactions, they establish an upper limit for local interactions. In other words, the probability of two taxa interacting at a specific location and time is consistently lower or equal to the probability of their regional interaction:

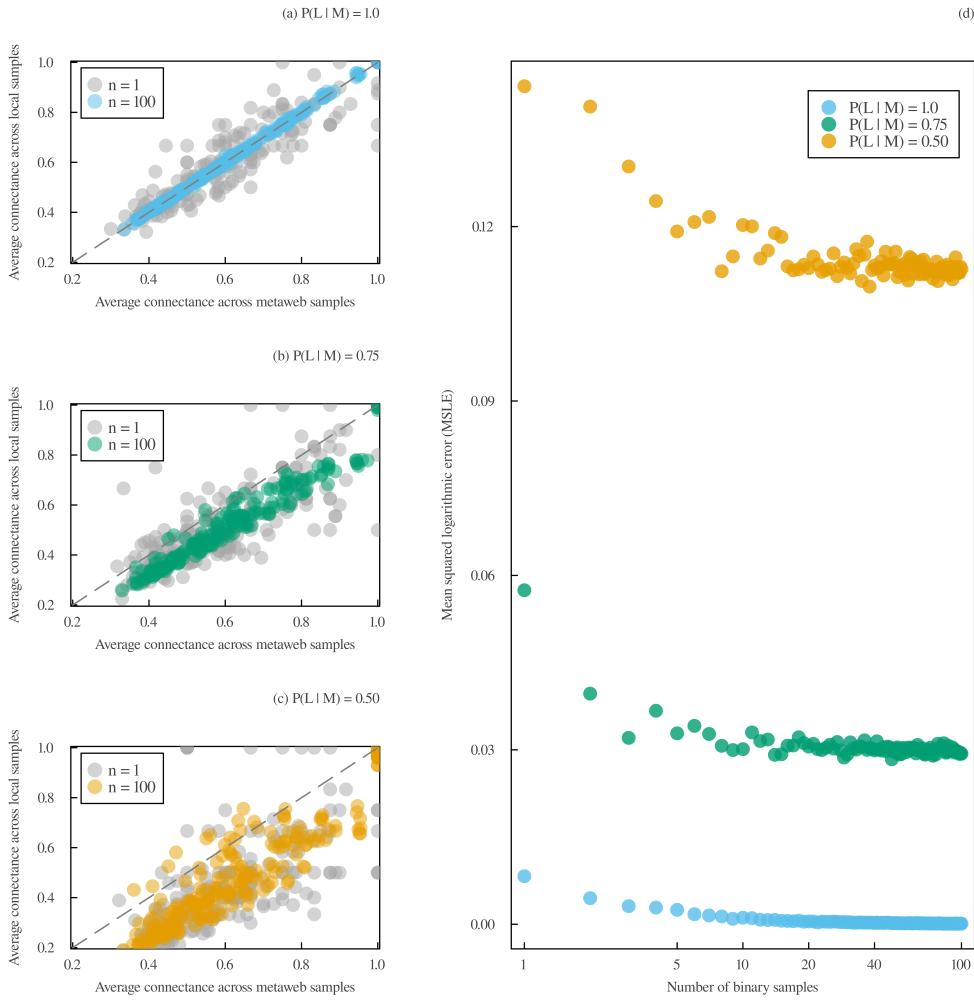


Figure 4 Connectance of sampled binary webs. Comparison between the average connectance of binary network samples obtained from the probabilistic local and metawebs. Each dot corresponds to a different site. The local probability of interaction between potentially interacting species was set to three different values: (a) $P(L|M) = 1.0$, (b) $P(L|M) = 0.75$, and (c) $P(L|M) = 0.50$. Grey dots represent the outcome of a single trial, while colored dots represent the average connectance of each network across 100 trials. (d) Reduction in the mean squared logarithmic error between the average connectance of binary networks obtained from these two sampling methods as the number of trials increases, for the same values of $P(L|M)$ 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 metaweb, and then propagating this result to all local webs that include the species potentially engaged in the interactions. Local binary webs were generated by independently sampling binary interactions for each local probabilistic web.

$$P(L_{i \rightarrow j}|A, t, C, \Omega) \leq P(M_{i \rightarrow j}). \quad (16)$$

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

$$\int_{\Omega} \int_A \int_t P(L_{i \rightarrow j}|A, t, \Omega) dt dA d\Omega \leq P(M_{i \rightarrow j}). \quad (17)$$

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

4

Conclusion

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

It is essential to enhance our comprehension of both regional and local interactions, especially considering the current scarcity of interaction data. However, while sampling biological communities does decrease the uncertainty of interactions by accumulating evidence for their feasibility and local realization, there is a limit to how much we can diminish their inherent randomness. In metawebs, probabilities reflect our limited knowledge of interactions (i.e., our degree of belief that interactions are feasible), which is expected to improve with a larger volume of data. We should anticipate that regional interactions will become more definitive (with probabilities approaching 0 or 1) as we investigate various conditions, including different combinations of species traits. Conversely, in the case of local webs, which can be seen as random instances of metawebs, randomness cannot be as reduced. In local interactions, probabilities can be divided into a component representing uncertainty and another representing spatiotemporal variability. Owing to environmental heterogeneity, there will invariably be instances in which an interaction occurs and others in which it does not, across different times and locations, irrespective of the extent to which we can improve our knowledge of its biological feasibility and the local conditions that facilitate its occurrence. When local webs depict probabilities of observing interactions rather than just their actual occurrence, we must also consider the observation variability as an additional source of randomness. Every ecological process is stochastic but there is also a possibility that a phenomenon goes undetected. Quantifying and partitioning this stochasticity will enable us to make more accurate predictions about ecological interactions at various spatial and temporal scales. This will prove to be of vital importance as our time to understand nature runs out, especially at the places where the impacts of climate change and habitat loss hit harder.

5

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References

- Abrego, N., Roslin, T., Huotari, T., Ji, Y., Schmidt, N.M., Wang, J., *et al.* (2021). Accounting for species interactions is necessary for predicting how arctic arthropod communities respond to climate change. *Ecography*, 44, 885–896.
- 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.
- 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 Puzzle¹. *Integrative and Comparative Biology*, 44, 498–509.
- 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.
- 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.
- 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.
- 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.
- Berlow, E.L., Neutel, A.-M., Cohen, J.E., De Ruiter, P.C., Ebenman, B., Emmerson, M., *et al.* (2004). Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73, 585–598.
- 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.
- Blanchet, F.G., Cazelles, K. & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions. *Ecology Letters*, 23, 1050–1063.
- Bohan, D.A., Vacher, C., Tamaddoni-Nezhad, A., Raybould, A., Dumbrell, A.J. & Woodward, G. (2017). Next-Generation Global Biomonitoring: Large-scale, Automated Reconstruction of Ecological Networks. *Trends in Ecology & Evolution*, 32, 477–487.
- 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.
- Borrett, S.R. & Scharler, U.M. (2019). Walk partitions of flow in Ecological Network Analysis: Review and synthesis of methods and indicators. *Ecological Indicators*, 106, 105451.
- Boulangeat, I., Gravel, D. & Thuiller, W. (2012). Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters*, 15, 584–593.
- Brimacombe, C., Bodner, K., Michalska-Smith, M., Poisot, T. & Fortin, M.-J. (2023). Shortcomings of reusing species interaction networks created by different sets of researchers. *PLOS Biology*, 21, e3002068.
- Broom, M. & Ruxton, G.D. (2005). You can run or you can hide: Optimal strategies for cryptic prey against pursuit predators. *Behavioral Ecology*, 16, 534–540.
- Brose, U., Ostling, A., Harrison, K. & Martinez, N.D. (2004). Unified spatial scaling of species and their trophic interactions. *Nature*, 428, 167–171.
- Canard, E., Mouquet, N., Marescot, L., Gaston, K.J., Gravel, D. & Mouillot, D. (2012). Emergence of Structural Patterns in Neutral Trophic Networks. *PLOS ONE*, 7, e38295.

- Catchen, M.D., Poisot, T., Pollock, L.J. & Gonzalez, A. (2023). The missing link: Discerning true from false negatives when sampling species interaction networks.
- Cazelles, K., Araujo, M.B., Mouquet, N. & Gravel, D. (2016). **A theory for species co-occurrence in interaction networks.** *Theoretical Ecology*, 9, 39–48.
- Chagnon, P.-L. (2015). **Characterizing topology of ecological networks along gradients: The limits of metrics' standardization.** *Ecological Complexity*, 22, 36–39.
- Choh, Y., Ignacio, M., Sabelis, M.W. & Janssen, A. (2012). **Predator-prey role reversals, juvenile experience and adult antipredator behaviour.** *Scientific Reports*, 2, 728.
- Cirtwill, A.R., Eklöf, A., Roslin, T., Wootton, K. & Gravel, D. (2019). **A quantitative framework for investigating the reliability of empirical network construction.** *Methods in Ecology and Evolution*, 10, 902–911.
- Dallas, T., Park, A.W. & Drake, J.M. (2017). **Predicting cryptic links in host-parasite networks.** *PLOS Computational Biology*, 13, e1005557.
- Dunne, J.A. (2006). The Network Structure of Food Webs. In: *Ecological networks: Linking structure and dynamics* (eds. Dunne, J.A. & Pascual, M.). Oxford University Press, pp. 27–86.
- Elmasri, M., Farrell, M.J., Davies, T.J. & Stephens, D.A. (2020). **A hierarchical Bayesian model for predicting ecological interactions using scaled evolutionary relationships.** *The Annals of Applied Statistics*, 14, 221–240.
- Elton, C.S. (2001). *Animal Ecology*. University of Chicago Press, Chicago, IL.
- Emmerson, M.C. & Raffaelli, D. (2004). **Predator-prey body size, interaction strength and the stability of a real food web.** *Journal of Animal Ecology*, 73, 399–409.
- Fortuna, M.A. & Bascompte, J. (2006). **Habitat loss and the structure of plant-animal mutualistic networks.** *Ecology Letters*, 9, 281–286.
- Fu, X., Seo, E., Clarke, J. & Hutchinson, R.A. (2021). **Link Prediction Under Imperfect Detection: Collaborative Filtering for Ecological Networks.** *IEEE Transactions on Knowledge and Data Engineering*, 33, 3117–3128.
- Galiana, N., Lurgi, M., Claramunt-López, B., Fortin, M.-J., Leroux, S., Cazelles, K., et al. (2018). **The spatial scaling of species interaction networks.** *Nature Ecology & Evolution*, 2, 782–790.
- Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010). **A framework for community interactions under climate change.** *Trends in Ecology & Evolution*, 25, 325–331.
- Godsøe, W., Murray, R. & Iritani, R. (2022). **Species interactions and diversity: A unified framework using Hill numbers.** *Oikos*, n/a, e09282.
- Golubski, A.J. & Abrams, P.A. (2011). **Modifying modifiers: What happens when interspecific interactions interact?** *Journal of Animal Ecology*, 80, 1097–1108.
- Gómez, J.M., Verdu, M. & Perfectti, F. (2010). **Ecological interactions are evolutionarily conserved across the entire tree of life.** *Nature*, 465, 918–U6.
- Gonzalez, A. & Londoño, M.C. (2022). **Monitor biodiversity for action.** *Science*, 378, 1147–1147.
- Gonzalez-Varo, J.P. & Traveset, A. (2016). **The Labile Limits of Forbidden Interactions.** *Trends in Ecology & Evolution*, 31, 700–710.
- Gravel, D., Baiser, B., Dunne, J.A., Kopelke, J.-P., Martinez, N.D., Nyman, T., et al. (2019). **Bringing Elton and Grinnell together: A quantitative framework to represent the biogeography of ecological interaction networks.** *Ecography*, 42, 401–415.
- Gravel, D., Poisot, T., Albouy, C., Velez, L. & Mouillot, D. (2013). **Inferring food web structure from predator-prey body size relationships.** *Methods in Ecology and Evolution*, 4, 1083–1090.
- Guimarães, P.R. (2020). **The Structure of Ecological Networks Across Levels of Organization.** *Annual Review of Ecology, Evolution, and Systematics*, 51, 433–460.
- Guimerà, R. & Sales-Pardo, M. (2009). **Missing and spurious interactions and the reconstruction of complex networks.** *Proceedings of the National Academy of Sciences*, 106, 22073–22078.
- Hemprich-Bennett, D.R., Oliveira, H.F.M., Le Comber, S.C., Rossiter, S.J. & Clare, E.L. (2021). **Assessing the impact of taxon resolution on network structure.** *Ecology*, 102, e03256.

- Herrera, C.M. (1989). **Pollinator abundance, morphology, and flower visitation rate: Analysis of the “quantity” component in a plant-pollinator system.** *Oecologia*, 80, 241–248.
- Hortal, J., de Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M. & Ladle, R.J. (2015). **Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity.** *Annual Review of Ecology, Evolution, and Systematics*, 46, 523–549.
- Jordano, P. (1987). **Patterns of Mutualistic Interactions in Pollination and Seed Dispersal: Connectance, Dependence Asymmetries, and Coevolution.** *The American Naturalist*, 129, 657–677.
- Jordano, P. (2016). **Sampling networks of ecological interactions.** *Functional Ecology*, 30, 1883–1893.
- Jordano, P., Bascompte, J. & Olesen, J.M. (2003). **Invariant properties in coevolutionary networks of plant-animal interactions.** *Ecology Letters*, 6, 69–81.
- Kéfi, S., Berlow, E.L., Wieters, E.A., Joppa, L.N., Wood, S.A., Brose, U., et al. (2015). **Network structure beyond food webs: Mapping non-trophic and trophic interactions on Chilean rocky shores.** *Ecology*, 96, 291–303.
- Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., et al. (2012). **More than a meal... integrating non-feeding interactions into food webs.** *Ecology Letters*, 15, 291–300.
- Kéfi, S., Miele, V., Wieters, E.A., Navarrete, S.A. & Berlow, E.L. (2016). **How Structured Is the Entangled Bank? The Surprisingly Simple Organization of Multiplex Ecological Networks Leads to Increased Persistence and Resilience.** *PLOS Biology*, 14, e1002527.
- Klecka, J. & Boukal, D.S. (2014). **The effect of habitat structure on prey mortality depends on predator and prey microhabitat use.** *Oecologia*, 176, 183–191.
- Kopelke, J.-P., Nyman, T., Cazelles, K., Gravel, D., Vissault, S. & Roslin, T. (2017). **Food-web structure of willow-galling sawflies and their natural enemies across Europe.** *Ecology*, 98, 1730–1730.
- Kulkarni, M.A., Kweka, E., Nyale, E., Lyatuu, E., Mosha, F.W., Chandramohan, D., et al. (2006). **Entomological Evaluation of Malaria Vectors at Different Altitudes in Hai District, Northeastern Tanzania.** *Journal of Medical Entomology*, 43, 580–588.
- McCann, K. (2007). Protecting biostructure. *Nature*, 446, 29–29.
- McCann, K.S. (2011). Food webs (MPB-50). In: *Food Webs (MPB-50)*. Princeton University Press.
- 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.
- 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.
- 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.
- 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.
- 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, 725–732.
- Pascual, M., Dunne, J.A. & Dunne, J.A. (2006). *Ecological Networks: Linking Structure to Dynamics in Food Webs*. Oxford University Press, USA.
- 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.
- Pilosof, S., Porter, M.A., Pascual, M. & Kéfi, S. (2017). **The multilayer nature of ecological networks.** *Nature Ecology & Evolution*, 1, 1–9.
- 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.
- Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D. (2012). **The dissimilarity of species interaction networks.** *Ecology Letters*, 15, 1353–1361.

- Poisot, T., Cirtwill, A.R., Cazelles, K., Gravel, D., Fortin, M.-J. & Stouffer, D.B. (2016). [The structure of probabilistic networks](#). *Methods in Ecology and Evolution*, 7, 303–312.
- Poisot, T. & Gravel, D. (2014). [When is an ecological network complex? Connectance drives degree distribution and emerging network properties](#). *PeerJ*, 2, e251.
- Poisot, T., Stouffer, D.B. & Gravel, D. (2015). [Beyond species: Why ecological interaction networks vary through space and time](#). *Oikos*, 124, 243–251.
- Polis, G.A. (1991). [Complex Trophic Interactions in Deserts: An Empirical Critique of Food-Web Theory](#). *The American Naturalist*, 138, 123–155.
- Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O’Hara, R.B., Parris, K.M., et al. (2014). [Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model \(JSDM\)](#). *Methods in Ecology and Evolution*, 5, 397–406.
- Pomeranz, J.P.F., Thompson, R.M., Poisot, T. & Harding, J.S. (2019). [Inferring predator-prey interactions in food webs](#). *Methods in Ecology and Evolution*, 10, 356–367.
- Pringle, R.M. & Hutchinson, M.C. (2020). [Resolving Food-Web Structure](#). *Annual Review of Ecology, Evolution, and Systematics*, 51, 55–80.
- Proulx, S.R., Promislow, D.E.L. & Phillips, P.C. (2005). [Network thinking in ecology and evolution](#). *Trends in Ecology & Evolution*, SPECIAL ISSUE: BUMPER BOOK REVIEW, 20, 345–353.
- Pulliam, H.R. (1974). [On the Theory of Optimal Diets](#). *The American Naturalist*, 108, 59–74.
- Rooney, N. & McCann, K.S. (2012). [Integrating food web diversity, structure and stability](#). *Trends in Ecology & Evolution*, 27, 40–46.
- Salim, J.A., Saraiva, A.M., Zermoglio, P.F., Agostini, K., Wolowski, M., Drucker, D.P., et al. (2022). [Data standardization of plant-pollinator interactions](#). *GigaScience*, 11, giac043.
- Sanders, D. & van Veen, F.J.F. (2012). [Indirect commensalism promotes persistence of secondary consumer species](#). *Biology Letters*, 8, 960–963.
- Saravia, L.A., Marina, T.I., Kristensen, N.P., De Troch, M. & Momo, F.R. (2022). [Ecological network assembly: How the regional metaweb influences local food webs](#). *Journal of Animal Ecology*, 91, 630–642.
- Schmeller, D.S., Julliard, R., Bellingham, P.J., Böhm, M., Brummitt, N., Chiarucci, A., et al. (2015). [Towards a global terrestrial species monitoring program](#). *Journal for Nature Conservation*, 25, 51–57.
- Shaw, J.O., Dunhill, A.M., Beckerman, A.P., Dunne, J.A. & Hull, P.M. (2024). [A framework for reconstructing ancient food webs using functional trait data](#).
- Singer, M.C. & McBride, C.S. (2012). [Geographic mosaics of species' association: A definition and an example driven by plant-insect phenological synchrony](#). *Ecology*, 93, 2658–2673.
- Stouffer, D.B., Rezende, E.L. & Amaral, L.A.N. (2011). [The role of body mass in diet contiguity and food-web structure](#). *Journal of Animal Ecology*, 80, 632–639.
- Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M.J., et al. (2022). [Food web reconstruction through phylogenetic transfer of low-rank network representation](#). *Methods in Ecology and Evolution*, 13.
- Strydom, T., Catchen, M.D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., et al. (2021). [A roadmap towards predicting species interaction networks \(across space and time\)](#). *Philosophical Transactions of the Royal Society B-Biological Sciences*, 376, 20210063.
- Tylianakis, J.M., Tscharntke, T. & Lewis, O.T. (2007). [Habitat modification alters the structure of tropical host-parasitoid food webs](#). *Nature*, 445, 202–205.
- Vázquez§, D.P., Peralta§, G., Cagnolo, L., Santos, M. & Igual, §.E. autores contribuyeron por. (2022). [Ecological interaction networks. What we know, what we don't, and why it matters](#). *Ecología Austral*, 32, 670–697.
- Weinstein, B.G. & Graham, C.H. (2017a). [On comparing traits and abundance for predicting species interactions with imperfect detection](#). *Food Webs*, 11, 17–25.

- Weinstein, B.G. & Graham, C.H. (2017b). Persistent bill and corolla matching despite shifting temporal resources in tropical hummingbird-plant interactions. *Ecology Letters*, 20, 326–335.
- Whittaker, R.H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, 30, 279–338.
- Wood, S.A., Russell, R., Hanson, D., Williams, R.J. & Dunne, J.A. (2015). Effects of spatial scale of sampling on food web structure. *Ecology and Evolution*, 5, 3769–3782.
- Woodward, G., Benstead, J.P., Beveridge, O.S., Blanchard, J., Brey, T., Brown, L.E., et al. (2010). Chapter 2 - Ecological Networks in a Changing Climate. In: *Advances in Ecological Research*, Ecological Networks (ed. Woodward, G.). Academic Press, pp. 71–138.
- Woodward, G., Brown, L.E., Edwards, F.K., Hudson, L.N., Milner, A.M., Reuman, D.C., et al. (2012). Climate change impacts in multispecies systems: Drought alters food web size structure in a field experiment. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 2990–2997.