

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 are they occurring?) 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. These definitions are based on the distinction between the observation of an interaction at a specific time and space and its biological feasibility. We show that different network representations have different statistical properties when it comes to common ecological applications. Specifically, we argue that local probabilistic networks 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 networks from subsets of metawebs. To support our arguments, we build a spatiotemporally explicit model of probabilistic interactions and develop different case studies using empirical data on host-parasite interactions in Europe. Overall, 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.

Keywords:
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spatial scale
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Introduction

Cataloging ecological interactions is a substantial challenge. There are methodological and biological constraints that hinder our ability to observe all interactions, such as the spatial and temporal uncoupling of species (Jordano (1987)) and the large number of possible interactions in a community, of which the vast majority are rare (Jordano (2016)). Documenting the location and timing of interactions becomes even more difficult when accounting for the spatiotemporal variability of ecological networks (Poisot *et al.* (2012), Poisot *et al.* (2015)). Indeed, knowing the biological capacity of two species to interact is necessary but not sufficient for inferring their interaction at a specific time and space. For example, Golubski & Abrams (2011) presented many cases where trophic interactions in food webs depend on the presence or abundance of a third species (e.g., of a more profitable prey species). 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)). Then, they must encounter locally. Probabilities of interspecific encounters are typically low, especially for rare species with low relative abundances (Canard *et al.* (2012)). Finally, their traits must be locally compatible (Poisot *et al.* (2015)). This includes their phenology (Olesen *et al.* (2010), Singer & McBride (2012)), behavioral choices (Pulliam (1974), Choh *et al.* (2012)) and phenotypes (Bolnick *et al.* (2011), Stouffer *et al.* (2011), Gravel *et al.* (2013)). 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. 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)).

The recognition of the intrinsic variability of species interactions has led ecologists to expand their representation of ecological networks to include a probabilistic view of interactions (Poisot *et al.* (2016)). As opposed to binary deterministic networks, in which interactions are regarded as either occurring or not, probabilistic networks represent our degree of belief about the realization or feasibility of pairwise interactions at the local or regional scale, respectively. In other words, representing interactions probabilistically takes into account inherent uncertainties and variability associated with ecological data. 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). In probabilistic networks, only forbidden interactions (i.e., interactions prohibited by biological traits, Jordano *et al.* (2003), Olesen *et al.* (2010)) have a probability value of zero, provided that intraspecific trait variability is considered (Gonzalez-Varo & Traveset (2016)). However, *neutrally* forbidden interactions (i.e., improbable interactions between rare species, Canard *et al.* (2012)) could have low probability values in local networks but high probability in a regional network (metaweb) describing the biological capacity of species to interact.

By accounting for the uncertainty of interactions, probabilistic networks provide a more realistic portrait of species interactions and network structure (i.e. community-level properties), which is a major driver 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 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 networks 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 networked, 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 network predictions 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 (e.g., Bascompte *et al.* (2003), Fortuna & Bascompte (2006)), which can be used to generate underlying distributions of network measures for null hypothesis significance testing, are other examples of common probabilistic network models. 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 networks. 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 networks (Gilman *et al.* (2010)).

The lack of clear guidelines on the use of probabilistic interaction data is worrisome (Brimacombe *et al.* (2023)), both for data producers and re-users who generate and manipulate these numbers. 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 networks that necessitate distinct approaches when applied to key ecological questions: local networks of realized interactions, and regional networks (metawebs) 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 networks across space. Moreover, there is

currently no metadata standard that could guide the documentation of all types of probabilistic interactions (Salim *et al.* (2022) discuss data standards for deterministic mutualistic networks). Well-defined metadata for probabilistic networks would support more adequate manipulation and integration of interaction data from different sources and guard against the potential misinterpretations arising from ambiguous definitions of probabilistic networks. These metadata should outline the nature (i.e., potential or local) 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, 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 networks. Although our contribution focuses on food webs, our observations and advice can be applied to other types of ecological networks, from plant-pollinator 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 networks describe probabilities of direct interactions, which are conceptually and mathematically analogous regardless of their biological type (e.g., trophic and mutualistic interactions).

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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 interaction is defined as the biological capacity of two taxa to interact (i.e., the probability that they *can* theoretically interact) whereas a realized 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 networks of potential interactions and *local networks* (Poisot *et al.* (2012)) for those of realized interactions. Metawebs are the network analogues of the species pool, where local networks 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 networks describe potential or realized interactions, or if so-called probabilities are in reality *interaction scores* (i.e., non-probabilistic quantitative interactions). When probabilistic potential interactions are used and interpreted 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 networks would alleviate interpretation errors and facilitate a more adequate utilization of interaction data.

2.1. Pairwise interactions: the building blocks of ecological networks Local ecological networks 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 unit of food webs and other ecological networks are individuals that interact with each other (e.g., by predation, 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, trophic species, families) allows us to represent nodes at broader taxonomic scales, which affects our interpretation of the properties of these systems (Guimarães (2020)). Moreover, edges linking these 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 . Boolean interactions can be viewed as the result of a Bernoulli process $A_{i,j} \sim \text{Bernoulli}(P(i \rightarrow j))$, with $P(i \rightarrow j)$ being the probability of interaction between i and j that characterizes our limited knowledge of the system and its intrinsic spatiotemporal variability. Depending on the type of networks (local or metaweb), the mathematical formulation and interpretation of stochastic parameters like $P(i \rightarrow j)$ 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. In these probabilistic network representations in which $P(i \rightarrow j)$ are edge values, the only two possible outcomes are the presence ($A_{i,j} = 1$) or absence ($A_{i,j} = 0$) of an interaction between each pair of nodes. When considering uncertainties around the estimation of $P(i \rightarrow j)$, a Beta distribution $\text{Beta}(\alpha, \beta)$ can also be used to encompass all possible probability values. Observing an interaction between two taxa at a given location and time provides important information that can be used to update previous estimates of $P(i \rightarrow j)$, informing us on the biological capacity of both taxa to interact and the environmental conditions that enabled them to interact locally.

Even though binary networks constitute a highly valuable source of ecological information (Pascual *et al.* (2006)), they overlook important factors regarding interaction strengths. These are represented using quantitative interactions, which better describe the energy flows, demographic impacts or frequencies of interactions between nodes (Berlow *et al.* (2004), Borrett & Scharler (2019)), with $A_{i,j}$ being a natural number \mathbb{N} or a real number \mathbb{R} 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)). Because quantitative interactions can also describe predation pressure on prey taxa in food webs, they can be 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 networks with limited data. Just like binary networks, the uncertainty and spatiotemporal variability of quantitative interactions can be represented probabilistically. However, the need to estimate the probability distribution of all possible value of interaction strengths can make the inference of probabilities more challenging in quantitative networks compared to binary networks, which require only one probability estimate for each interaction. Quantitative interactions can follow various probability distributions depending on the measure used, the event's outcome being the value of interaction strength. For instance, quantitative interactions can follow a Poisson distribution $A_{i,j} \sim \text{Poisson}(\lambda_{i,j})$ when predicting frequencies of interactions between pairs of nodes, with $\lambda_{i,j}$ 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 networks due to their typically high sparseness (Jordano (2016)). Because of the methodological difficulties typically encountered when building deterministic quantitative networks, binary networks, which are easier to sample (Jordano (2016)) and predict (Strydom *et al.* (2021)), are much more documented and modeled in the literature. Moreover, most published probabilistic networks and methods describe Bernoulli interactions (whether interaction probabilities are regarded as constant or variable, e.g. represented by Beta distributions), which underlines the need for better guidelines regarding the interpretation and manipulation of these types of networks. For these reasons, our primary focus in this contribution will be on addressing the challenges in interpreting and using Bernoulli interactions, in both probabilistic local networks and metawebs.

2.2. Local networks: communities interacting in space and time Probabilistic local networks 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 networks, 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, Kopalke *et al.* (2017) assembled a dataset of binary local European food webs of willow-galling sawflies and their natural enemies, clearly referencing each food web in space and time. Gravel *et al.* (2019) used this dataset to infer the probabilities of locally observing interactions between co-occurring species, with the added aspect of situating local networks within the context of environmental variables. This was achieved by including temperature and precipitation as conditional variables in some of their models.

We define space as the set of geographic coordinates (x, y, z) of the spatial boundaries delineating the system, whether sampled or targeted. Ecological interactions may exhibit variations spatially and along altitudinal gradients, as evidenced by changes in hummingbird-plant interactions (Weinstein & Graham (2017b) and Weinstein & Graham (2017a)) and mosquitoes 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 networks 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 both an area 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 locally 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 $C_{i,j} \sim \text{Bernoulli}(P_{i,j}(x, y, z))$, where the probability of co-occurrence $P_{i,j}(x, y, z)$ 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., $P_N(i \rightarrow j|C = 0) = 0$), the probability of local interaction can be obtained by multiplying the probability of interaction given co-occurrence with the probability of co-occurrence:

$$P_N(i \rightarrow j) = P_N(i \rightarrow j|C = 1) \times P_{i,j}(x, y, z). \quad (1)$$

Other important factors that can impact our estimation of 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)). Here, we use the variable 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, 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 actually impacting ecological interactions.

The probability that two taxa i and j interact in a local network N can thus be conditional on the area A , the time interval t , their co-occurrence C and chosen environmental and biological conditions Ω . This gives us the following equation when all of these conditions are included in the estimation of interaction probabilities:

$$P_N(i \rightarrow j|A, t, C, \Omega). \quad (2)$$

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 $P_N(i \rightarrow j|C = 1)$ or not $P_N(i \rightarrow j)$ 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 Notation 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 network N of realized interactions. Each notation 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 networks. 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.

Notation	Type	Description	Reference
$P_M(i \rightarrow j)$	potential	biological feasibility of the interaction	Strydom <i>et al.</i> (2022)
$P_N(i \rightarrow j)$	local	realization of the interaction	Fortuna & Bascompte (2006) (null model)
$P_N(i \rightarrow j A)$	local	realization of the interaction in a given area	Galiana <i>et al.</i> (2018)*
$P_N(i \rightarrow j t)$	local	realization of the interaction during a given time period	Weinstein & Graham (2017a)
$P_N(i \rightarrow j C)$	local	realization of the interaction given that the taxa co-occur	Gravel <i>et al.</i> (2019)

Notation	Type	Description	Reference
$P_N(i \rightarrow j \Omega)$	local	realization of the interaction given environmental conditions	Gravel <i>et al.</i> (2019) (temperature and precipitation)

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. Potential interactions are by definition context-independent, i.e. they are not measured at a specific location and time. In contrast with probabilistic local networks, 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). In other words, 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. 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 one-on-one interactions, the extent of sampling effort also contributes to shaping our assessment of metaweb properties, as sampling a larger number of local networks allows us to capture more potential interactions (McLeod *et al.* (2021a)). A probability of potential interaction in a metaweb M can be expressed as

$$P_M(i \rightarrow j), \quad (3)$$

which, in contrast with eq. 2, is not conditional on any spatial, temporal, or environmental variables (tbl. 1).

Starting from a selected set of taxa, which are usually distributed within a broad region of interest, probabilistic metawebs can be built using different data sources, including literature review, fieldwork, and predictive models (e.g., the metaweb of trophic interactions between Canadian mammals inferred by Strydom *et al.* (2022)). 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 networks, in which interaction events usually remain stochastic (i.e., $P_N(i \rightarrow j) < 1$) after empirically observing interactions because of their intrinsic spatiotemporal variability. Similarly, although rare interactions typically have low probabilities in local networks, 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 metawebs and local networks, going as low as 0 for forbidden links. However, because of observation errors due to taxonomic misidentifications and ecological misinterpretations (e.g., due to cryptic species and interactions, Pringle & Hutchinson (2020)), many observations of interactions are in reality false positives. 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, has the potential to enhance the accuracy of our estimation of interaction probabilities within both local and potential networks (e.g., Bartomeus *et al.* (2016), Cirtwill *et al.* (2019)). This improvement is achieved in potential networks by leveraging prior information regarding the feasibility of interactions along with the empirical data on observed interactions.

3

Properties of probabilistic networks

Probabilistic local networks and metawebs differ in their type of interactions (i.e., local 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 networks, which could be particularly problematic when addressing crucial ecological questions about networks. Here we compare the characteristics of local networks and metawebs through the presentation of four common applications of probabilistic interactions. All code and data to reproduce these analyses are available at the Open Science Framework (TBD).

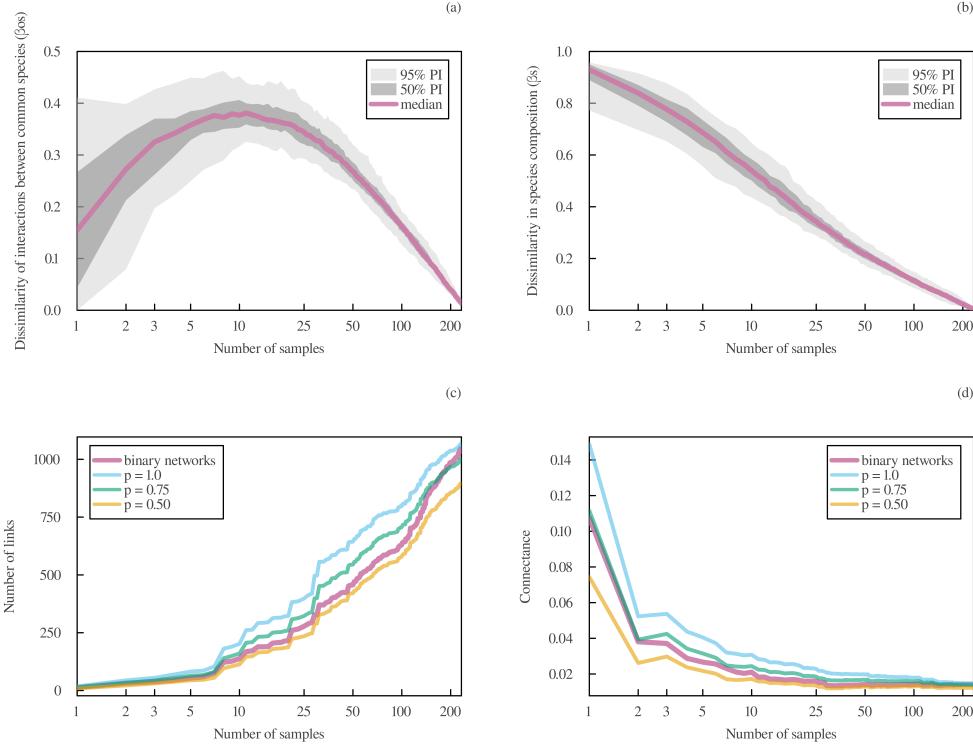


Figure 1 Network accumulation curves. (a) Dissimilarity of interactions between common species (β_{OS}) and (b) dissimilarity in species composition between aggregated local networks and the binary metaweb of host-parasite interactions. Aggregated local networks were obtained by sequentially and randomly selecting a number of binary local networks 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 networks. For a better comparison with binary networks, local probabilistic networks were derived from the probabilistic metaweb with a false positive and false negative rates of zero. A specific value of p (the local probability of interaction among potentially interacting species) was used for all local networks within a particular curve. Aggregated probabilistic local networks were obtained by sequentially and randomly selecting a number of probabilistic local networks and aggregating both their species and interactions (with the value of p adjusting according to eq. 5).

3.1. Host-parasite network data We use the collection of tripartite host-parasite networks sampled across Europe, created by Kopalke *et al.* (2017), in most of our 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 networks 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 networks, we retained those containing at least 5 species, resulting in a set of 233 georeferenced local networks. We built a binary metaweb by aggregating all local interactions, which gave us a regional metaweb 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 networks (Poisot *et al.* (2012)) vary with the number of sampled local networks. 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.

We converted these binary networks into probabilistic ones using models based on simple assumptions. Our models do not aim to precisely estimate the actual values of probabilistic interactions but rather to offer simplified networks as illustrative examples to underscore the differences between probabilistic local networks and metawebs. We created two probabilistic metawebs by employing constant false positive and false negative rates for all potential 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 networks. This gave us a probability of potential 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 capture the elevated occurrence of false negatives in ecological networks (Catchen *et al.* (2023)). Observed potential interactions were thus given a probability of 95%, whereas unobserved ones were assigned a probability of 10%.

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

$$P_N(i \rightarrow j) = P_N(i \rightarrow j|M_{i \rightarrow j} = 1) \times P_M(i \rightarrow j). \quad (4)$$

We built the probabilistic local networks from the binary ones by using the probabilistic metawebs and a constant value of p across interactions. Lower values of p indicate that feasible interactions rarely occur locally, intermediate values around 50% suggest considerable spatiotemporal variability, while higher values indicate that potential interactions are nearly always realized. Following eq. 4, the local probabilities of interaction between a given pair of taxa consistently remained equal to or below their probability of potential 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 S^2 possible links that are realized, where S represents species richness) scale with the number of sampled local probabilistic networks, according to different values of p . When aggregating local probabilistic networks, the constancy of the probability of potential interaction across the entire study area means that any rise in the probability of local interaction is solely attributable to an increase in p . The probability $p_{1,2}$ of local interaction among potentially interacting species in an aggregated network $N_{1,2}$ is obtained by:

$$p_{1,2} = 1 - (1 - p_1) \times (1 - p_2), \quad (5)$$

where p_1 and p_2 are the probabilities of local interaction among two potentially interacting species in the subnetworks N_1 and N_2 , respectively.

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

3.2. Taxonomic scaling of interactions Probabilistic networks 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 networks 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 networks is an effective approach for such analyses.

There are no inherent differences in the taxonomic scaling between local networks and metawebs, as only the nodes are defined taxonomically. In other words, the probability values of edges in both local networks (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 networks, transitioning to a broader level of organization can be accomplished directly by using probabilities from finer scales. For example, in a network with n_A species from genus A and n_B species from genus B, one can compute the probability that at least one species from genus A interacts with at least one species from genus B as follows:

$$P(A \rightarrow B) = 1 - \prod_{i=1}^{n_A} \prod_{j=1}^{n_B} (1 - P(A_i \rightarrow B_j)), \quad (6)$$

where A_i and B_j are the species of the corresponding genus. If it is known that at least two of these species interact (i.e., $P(A_i \rightarrow B_j) = 1$ for at least one pair of i,j), 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 heterogenous levels of organization (e.g., a network whose nodes are composed of

both species and trophic species). This is common in ecological networks 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 networks 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).

3.3. Spatial and temporal scaling of interactions The investigation of network-area relationships (NARs) and interaction accumulation curves (IACs) is an important area of research in network ecology. First, NARs 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, IACs describe the scaling of the number of observed interactions with sampling effort (Jordano (2016)), which can also impact various measures of network structure such as connectance (McLeod *et al.* (2021b)). Apart from sampling effort, the temporal scaling of interactions elucidates how network structure changes with the duration of the network (Poisot *et al.* (2012)), acknowledging that distinct interactions take place over time. Given that probabilistic local networks can quantify the spatiotemporal variability of interactions (eq. 2), they serve as valuable tools for developing and testing equations describing the scaling of network structure with space and time.

Metawebs and local networks exhibit distinct relationships with spatial and temporal scales. On one hand, probabilistic metawebs, being independent of any local context, feature potential interactions that do not scale with space and time. This is because potential interactions depend solely on the biological capacity of two taxa to interact, regardless of their co-occurrence and specific environmental conditions. This implies that 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. As a result, if a smaller metaweb M_1 is derived from subsampling a regional metaweb M_0 to represent potential interactions among a subset of taxa in a smaller region, their probabilities of interaction should be identical regardless of scale, i.e. $P_{M_1}(i \rightarrow j) = P_{M_0}(i \rightarrow j)$. However, because the number of taxa may be higher in the larger metaweb, it is expected that the overall number of interactions would be higher in the larger network, despite pairwise probabilities being 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 network N_1 with an area A_1 is derived from a larger network N_0 with an area A_0 , and A_1 is entirely nested within A_0 , interaction probabilities should be lower in the smaller network, i.e. $P_{N_1}(i \rightarrow j|A_1 < A_0) \leq P_{N_0}(i \rightarrow j|A_0)$. However, if A_1 and A_0 are disjoint, interaction probabilities could potentially be higher in the smaller area, contingent upon their environmental and biological conditions. Likewise, interaction probabilities are expected to be lower in networks with shorter durations when 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 potential interactions. Even though we employed local probabilities of interactions equal to potential interactions for the purpose of comparison (i.e., using $p = 1$ here), we notice that the total number of potential interactions scales more rapidly than local interactions. This is due to the fact that numerous potential interactions involve species that never co-occur, and as a result, these interactions are not captured in local networks.

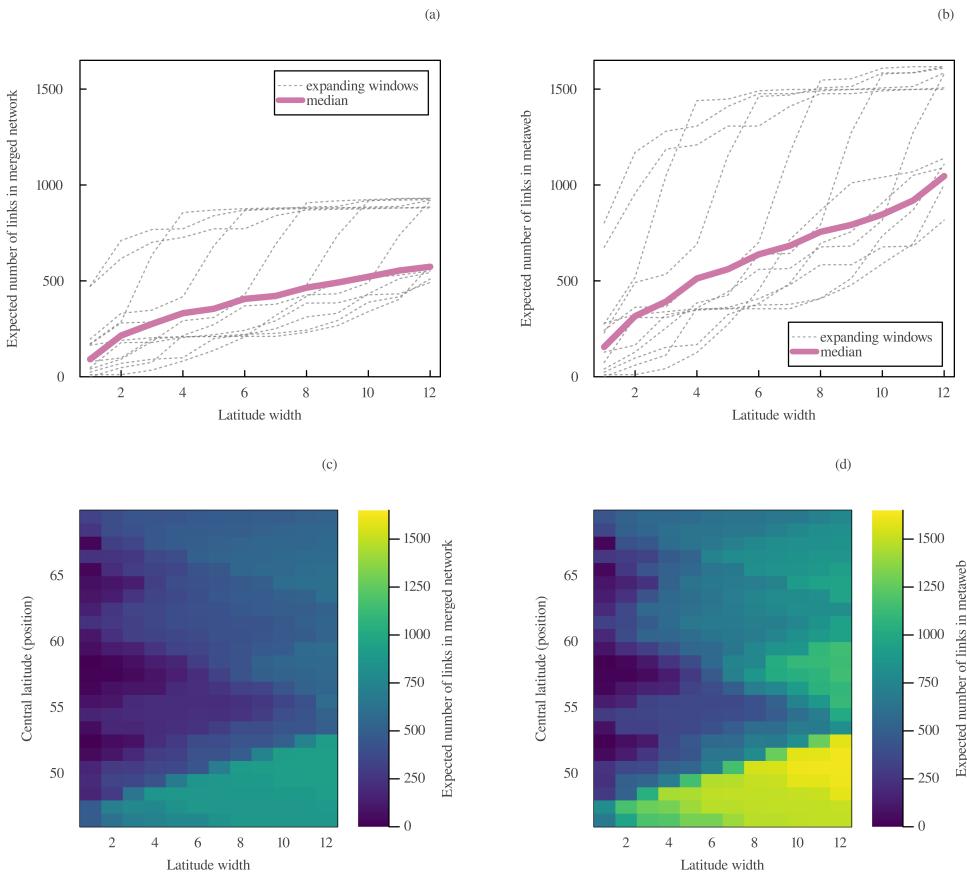


Figure 2 Spatial scaling of interactions. Expected number of host-parasite interactions in a network aggregating all probabilistic (a) local and (b) potential interactions within a latitudinal window of a given length. Every dashed curve corresponds to a different expanding window characterized by a different central latitude, with the colored solid line representing the median number of interactions. Heatmaps of the expected number of (c) local and (d) potential interactions found in windows of specified length and central latitudes. Probabilities of potential 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 (the local probability of interaction among potentially interacting species) to 1, ensuring a conservative comparison between aggregated local networks and metawebs. Aggregated local networks were obtained by aggregating both the species and interactions found within a particular latitudinal window, with the values of p remaining at their maximum value of 1 following eq. 5.

3.4. Box 1: A spatiotemporally explicit model of interactions Predicting local networks across time and space is a pivotal goal of network ecology (Strydom *et al.* (2021)). In a context of scarcity of interaction data (Jordano (2016)), ecologists must resort to predictive models for reconstructing networks at fine spatial and temporal scales. For instance, real-time biomonitoring data coupled with appropriate numerical models (Bohan *et al.* (2017)) can be employed to reconstruct local ecological networks, opening avenues for in-depth studies on local ecosystem functioning and dynamics. Apart from their predictive applications, statistical models can also be crafted for descriptive purposes, elucidating key parameters of interest such as probabilities of interactions. In such instances, the parameter values themselves offer valuable ecological insights. Various types of models (e.g., Bayesian and machine learning models) have been used for both predictive and descriptive purposes in the realm of ecological interactions (Strydom *et al.* (2021)). 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 potential 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) is 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 $P_i(x, y, z)$ and $P_j(x, y, z)$, along with the strength of association γ between their occurrences and co-occurrence (Cazelles *et al.* (2016)):

$$P_{i,j}(x, y, z) = P_i(x, y, z)P_j(x, y, z)\gamma. \quad (7)$$

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. In empirical networks, $\gamma > 1$ holds true for the majority of species pairs (Catchen *et al.* (2023)). The co-occurrence of both taxa is modeled as the outcome of a Bernoulli trial

$$C \sim \text{Bernoulli}(P_{i,j}(x, y, z)). \quad (8)$$

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:

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

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 $P_N(i \rightarrow j)$. 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:

$$I \sim \text{Bernoulli}(P_N(i \rightarrow j)) \quad (10)$$

$$P_N(i \rightarrow j) = P_i(x, y, z)P_j(x, y, z)\gamma(1 - e^{-\lambda t_0}) \quad (11)$$

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

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

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 $P_{i,j}(x, y, z)$ (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).

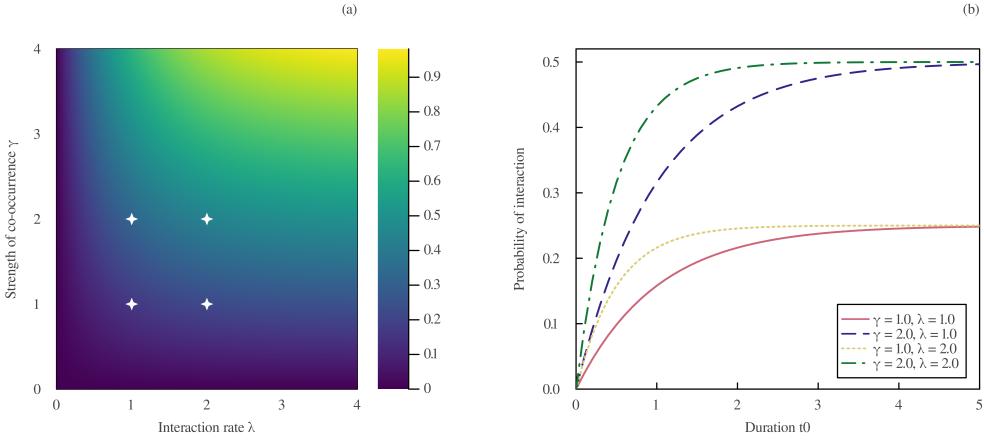


Figure 3 Parameters of the spatiotemporally explicit model of interactions. (a) Probability of local interaction given by the process model (eq. 11) under different values of λ and γ , with $t_0 = 1$. The parameter values used in the right panel are denoted by the white stars. (b) Scaling of the probability 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.

3.5. Sampling binary networks The prediction of binary interactions through random draws is an important application of probabilistic networks. This approach proves beneficial for analyzing the structural characteristics of probabilistic networks, particularly in the absence of specific analytical measures. By simulating independent Bernoulli trials for each interaction, a binary network can 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 potential 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, randomly generating binary networks across spatial and temporal dimensions aids in representing the spatiotemporal variability of network structure, allowing the testing of ecological hypotheses regarding interactions on large 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 within the region of interest based on their regional probability of potential interaction. In employing this approach, every pair of taxa predicted to interact in the binary metaweb realization will be treated as interacting in all local networks 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 networks, which can be achieved by first generating distinct probabilistic networks for each location. These local probabilistic networks 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 potential and local interactions are drawn from our host-parasite probabilistic networks, generating a number of binary network realizations for each site in the dataset. These two sampling approaches yield different outcomes, particularly for lower values of p , which denote instances when potential 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 potential interaction (i.e., when using $p = 1.0$ in eq. 4), 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 networks. 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 potential 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 regional network. However, in the second approach, local interaction probabilities are contingent on the network area. For instance, consider networks N_1 and N_2 with an area of $\frac{1}{2}A_0$, both nested within A_0 but disjoint from each other, forming N_0 . If we treat N_1 and N_2 as independent, the probability of interaction between taxa i and j in N_0 is given by:

$$P_{N_0}(i \rightarrow j) = 1 - (1 - P_{N_1}(i \rightarrow j)) \times (1 - P_{N_2}(i \rightarrow j)). \quad (14)$$

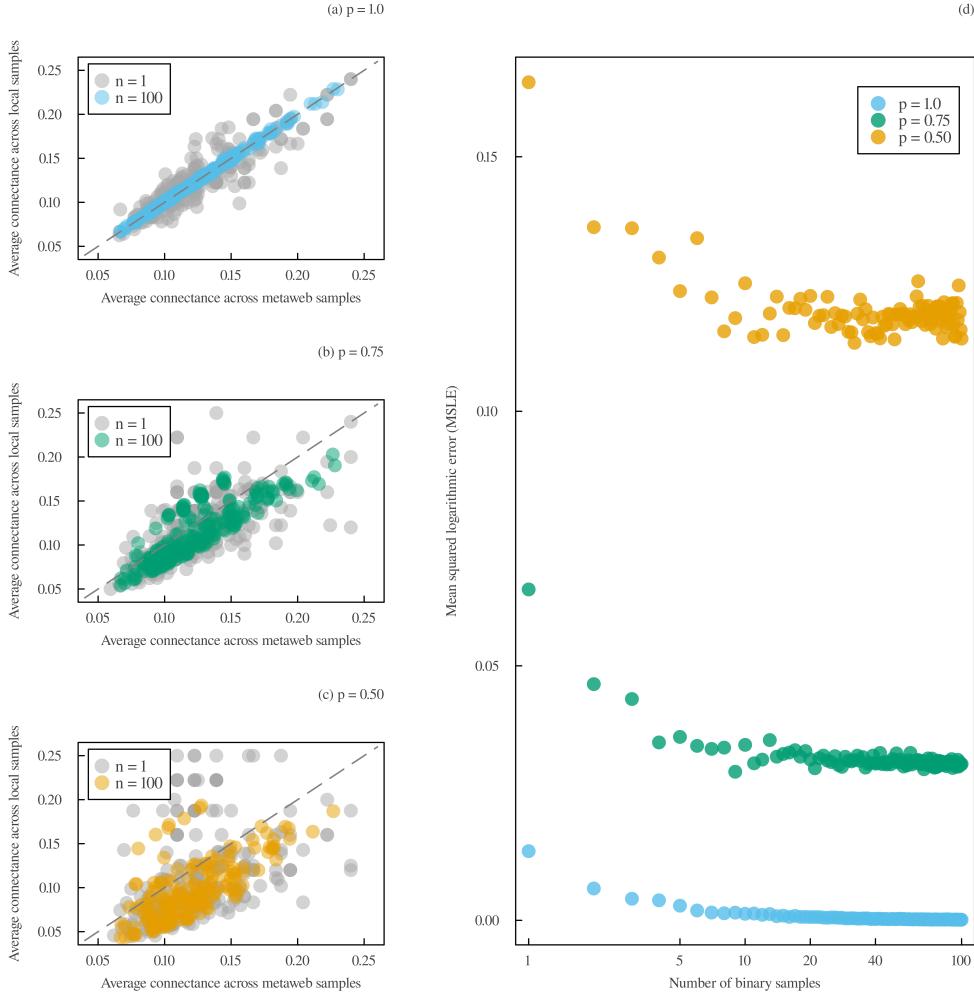


Figure 4 Connectance of sampled binary networks. Comparison between the average connectance of binary network samples obtained from the probabilistic local networks and metaweb. Each dot corresponds to a different site. The local probability of interaction between potentially interacting species was set to three different values: (a) $p = 1.0$, (b) $p = 0.75$, and (c) $p = 0.50$. 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 used in panels a-c. Probabilities of potential 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 networks that include the species potentially engaged in the interactions. Local binary networks were generated by independently sampling binary interactions for each local probabilistic network.

Due to its larger area, the probability that the two taxa interact in N_0 is equal or greater than in N_1 and N_2 . When sampling binary interactions from local networks, 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 potential systematic biases in predictions.

3.6. Prediction of local networks from metawebs Metawebs serve as a valuable source of ecological information for predicting local networks across time and space. Binary local networks 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 networks. 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 networks from the metaweb before predicting specific local pairwise interactions could hold promise (Strydom *et al.* (2021)), considering that the structure of local networks is constrained by the metaweb (Saravia *et al.* (2022)).

Building probabilistic local networks 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. 4). Therefore, inferring local networks 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, potentially leading to misinterpretations by being perceived as local interactions. As proposed by McLeod *et al.* (2021b), although metawebs lack the ability to 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 potential interaction:

$$P_N(i \rightarrow j|A, t, C, \Omega) \leq P_M(i \rightarrow j). \quad (15)$$

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 realized interactions across all spatial, temporal, and environmental conditions must be less than the probability of potential interaction, i.e.

$$\int_{\Omega} \int_A \int_t P_N(i \rightarrow j|A, t, \Omega) dt dA d\Omega \leq P_M(i \rightarrow j). \quad (16)$$

Estimating more precisely the probability p that two taxa interact locally if they can potentially interact allows for improved predictions of local networks from a probabilistic metaweb. This task is challenging due to the variability of this probability across space and time, as well as its potential variations among pairwise interactions within a network. Using simple models of p , as demonstrated in our case studies, represents an initial step toward the overarching objective of reconstructing local networks 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 potential) and the conditions in which they were estimated. We showed that probabilistic local networks and metawebs differ in their relationship to spatial and temporal scales, with potential 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 networks 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 potential 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 potential 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 networks, 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 networks 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.

5

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