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 their biological interpretation and statistical manipulation are contingent upon the methods and variables used to estimate them. We review how probabilistic interactions are defined at different spatial scales, from local interactions to regional networks (metawebs), with a strong emphasis on food webs. 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 behaviours 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 being scale-independent. 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 and simulated data. Overall, our results emphasize the need for better documentation of probabilistic ecological networks, both at the local and regional scales, to inform the appropriate reuse of these data.

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1 Introduction

Cataloging ecological interactions is a substantial challenge. There are practical 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 potential 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 considers inherent uncertainties and variability associated with ecological data. In the broadest sense, binary networks are also a type of probabilistic network, in which the value of interactions 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 their emerging structure, which is a major driver of 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 that would yield the highest

amount of information to alleviate these 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 manipulate and generate these numbers. Indeed, beyond methodological challenges encountered when evaluating them, there are important and perhaps more fundamental conceptual challenges when it comes to defining them. There is currently no data standard that could guide the estimation and documentation of all types of probabilistic interactions (Salim *et al.* (2022) discuss data standards for deterministic mutualistic networks). General guidelines could support more adequate manipulation and integration of interaction data from different sources and prevent ecologists from being misled by ambiguous and often diverging interpretations of probabilistic networks. We aim to take a step back by outlining different ways in which they were defined and used in network ecology and propose a framework to contextualize them. We distinguish two broad categories of probabilistic networks that require distinct handling techniques when applied to key ecological questions: local networks of realized interactions, and regional networks (metawebs) of potential interactions. We show that these representations differ in their ecological interpretation and statistical outcomes, especially regarding the spatial and temporal scaling of interactions and the prediction of binary networks across space. Although we focus on food webs, our observations and advice can be applied to other types of ecological networks, from plant-pollinator to host-parasite networks. Indeed, excepting 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 parasitic interactions). We argue that probabilistic networks should be better documented, clearly defined in mathematical terms, and used with caution when analyzing ecological 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 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 refers to 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)). Frequent confusion arises

among ecologists over the use of these two terms, especially in a probabilistic context. Indeed, it can be difficult to know when published probabilistic networks describe potential or realized interactions, or when so-called probabilities are in reality *interaction scores* (i.e., non-probabilistic quantitative interactions). Likewise, probabilistic potential interactions are often used and interpreted as realized interactions (and conversely), which may generate misleading findings when analyzing these data. 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 help ecologists use these numbers more appropriately.

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 and behavior 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). 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. 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 can represent the average number of prey individuals consumed by a predator in a given time period (e.g., the average number of fish in the stomach of a piscivorous species). Because quantitative interactions can describe predation pressure on prey taxa, they can be good estimators of the parameters describing species interactions in a Lotka-Volterra model (e.g., Emmerson & Raffaelli (2004)). However, this extra amount of ecological information typically comes at a cost of greater sampling effort or 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, with the difference that 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 $A_{i,j} \sim \text{Poisson}(\lambda_{i \to j})$ when predicting frequencies of interactions between pairs of nodes, with $\lambda_{i \to j}$ 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). The Poisson distribution can also be 0-inflated when considering non-interacting taxa, 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, 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 estimating and using Bernoulli interactions, in both probabilistic local networks and metawebs.

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., they are context-dependent). In local networks, edges commonly represent our degree of belief that two taxa interact in nature, but can also document the probability of *observing* this interaction (Catchen *et al.* (2023)). For example, Kopelke *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. Because of its large

number of replicated samples, this dataset can be used to infer the probability of locally observing an interaction

between any pair of taxa by measuring the proportion of sites where an interaction was observed (Gravel *et al.*

(2019)). More generally, we define space as the geographic coordinates (x, y) of the spatial boundaries

delineating the system (sampled or targeted) and time as the time interval during which interactions were

sampled or for which they were predicted. Given that space and time are in reality continuous variables, the

probability that an interaction occurs within a particular spatial and temporal setting is given by the integral of

the probability density function describing the relative likelihood that this interaction is realized at any specific

and infinitely small location and time. Therefore, the edge value could represent a probability density or a

probability mass depending on how space and time are measured. For simplicity reasons, we will consider

space and time as discrete dimensions that provide actual probabilities of interactions, which is conform to how

ecological interactions are usually sampled. Using space and time intervals allows us to measure an area A and

duration t, which can be directly used in spatiotemporal analyses of ecological networks. For example, when

studying network-area relationships (NAR, Galiana *et al.* (2018)), we should expect local probabilities of

interactions to scale positively with area and duration because taxa have more opportunities to interact.

The probability that two taxa i and j interact locally can also 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 distribution of both taxa overlaps within the study area. In local networks, the probability that the

interaction is realized must be 0 when taxa do not co-occur, i.e. $P_N(i \to j | C = 0) = 0$. Co-occurrence can also

be modeled probabilistically. In that case, it follows a Bernoulli distribution $C_{i,j} \sim$ Bernoulli$(P_{i,j}(x, y))$, where

the probability of co-occurrence $P_{i,j}(x, y)$ can be estimated using joint species distribution models (e.g., Pollock

et al. (2014)). More generally, the probability that two taxa interact locally can be obtained by the product of

their probability of interaction given co-occurrence with their probability of co-occurrence:

$$P_N(i \to j) = P_N(i \to j | C = 1) \times P_{i,j}(x, y). \tag{1}$$

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 will 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 these conditions are included in the estimation of interaction probabilities:

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

The local context in which probabilities are estimated and the variables that should be taken into consideration depend on the study system, the objective of the study, and the resources available to the researchers. In other words, these variables do not systematically need to be accounted for. However, when they are, they should be specified in the documentation of the data (Brimacombe *et al.* (2023)), preferably in mathematical terms to avoid any confusion in their interpretation and to limit manipulation errors during their re-use. For example, 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 a handful of studies of probabilistic ecological networks and their formulation of probabilistic interactions. This table illustrates the variety of definitions of probabilistic interactions found in the literature and emphasizes the need to carefully describe interaction data before integrating and analyzing them.

Table 1: Interaction probabilities are interpreted differently in metawebs (M) and local networks (N). Each formula includes different conditional variables and is described in plain text. A non-exhaustive list of studies using these formulas is included, with the variables used specified in parentheses.

Formula	Description	Studies
$P_M(i \rightarrow j)$	probability that the interaction is biologically feasible	
$P_N(i \rightarrow j)$	probability that the interaction is realized locally	

Formula	Description	Studies
$P_N(i \to j \mid A)$	probability that the interaction is realized locally given network area	
$P_N(i \to j \mid t)$	probability that the interaction is realized locally given duration	
$P_N(i \to j \mid C)$	probability that the interaction is realized locally given co-occurrence	
$P_N(i \to j \mid \Omega)$	probability that the interaction is realized locally given chosen environmental and biological factors	
$P_N(i \to j \mid A, t, C, \Omega)$	probability that the interaction is realized locally given many conditional factors	

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 two taxa can biologically interact regardless of their co-occurrence and local environmental conditions. Indeed, 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. This probability of interaction, in a metaweb M, can be expressed as

$$P_M(i \to j), \tag{3}$$

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, 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 usually not the case in local probabilistic networks, in which probabilities 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 if the traits of both taxa match. 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 only false positives. Similarly, forbidden interactions can be false negatives in metawebs, e.g. if they have been assessed for specific phenotypes, locations or time. Implementing a Bayesian framework, which updates prior probabilities with empirical data (e.g., Bartomeus *et al.* (2016), Cirtwill *et al.* (2019)), could improve our estimation of interaction probabilities in both systems.

Statistical behaviors of probabilistic networks

The differences in the mathematical formulations of local and potential interactions can affect their statistical behaviors when applied to key ecological questions. These disparities must therefore be taken into account when analyzing probabilistic interaction data to prevent misleading results and minimize interpretation errors. Here we show four common applications of probabilistic interactions and compare the characteristics of local networks and metawebs using simulated and empirical data.

Taxonomic scaling of interactions

Probabilistic networks can be used to address a wide range of ecological questions based on their level of organization. For example, the assemblage of interactions across ecological scales can be studied using species-based networks, whereas clade-based networks can be used to study macroevolutionary processes (e.g., Gomez *et al.* (2010)). Because our interpretation of the properties and dynamics of ecological networks depends on their taxonomic scale (Guimarães (2020)), examining the phylogenetic scaling of network structure is also a promising research avenue. Analyzing the same system at different taxonomic scales can thus provide meaningful and complementary ecological information and is, in our perspective, best conducted using probabilistic networks.

There is no qualitative difference in the taxonomic scaling of local networks compared to metawebs because only the nodes are defined taxonomically. In other words, the edge probability values of local networks (eq. 2) and metawebs (eq. 3) are not conditional on any taxonomic scale. It is the definition of the event itself (i.e., the interaction of the two taxa) that has a given phylogenetic scale, not their conditional variables. In both types of networks, shifting to a broader level of organization can be directly done using probabilities at finer scales. For example, if we have a network of n_A species from genus A and n_B species from genus B, we can calculate the probability that at least one species from genus A interact with at least one species from genus B as follows:

$$P(A \rightarrow B) = 1 - \prod_{i=1}^{n_A} \prod_{j=1}^{n_B} (1 - P(A_i \rightarrow B_j)), \tag{4}$$

where A_i and B_j are the species of the corresponding genus. Knowing that two species interact (i.e., $P(A_i \rightarrow B_j) = 1$) gives a probability of genus interaction of 1. Canard *et al.* (2012) built a species-based network from neutrally simulated interactions between individuals using a similar approach. In contrast, more sophisticated models need to be built when shifting to a finer level of organization. Indeed, knowing that two genera interact does not imply that all of their pairwise species combinations can also interact. One could, for example, build a finer-scale network by generating probabilities of species interactions by randomly sampling them from a beta distribution parametrized by the broader-scale network.

Ideally, the biological interpretation of probabilistic interactions should not differ across a network even if it has heterogenous levels of organization, i.e. if different nodes are represented at different taxonomic scales (e.g., a network composed of species and trophic species). This is frequent in ecological networks where taxonomic resolution is typically low (Hemprich-Bennett *et al.* (2021), Vázquez *et al.* (2022)). Broader-scale interactions should be based on probabilities of interactions between individuals, either at the local or regional scale. For example, in local individual-based food webs, the probability that two individuals interact represents the degree of belief that one individual will actually consume the other. Similarly, in local species-based food webs, the probability that two species interact represents the degree of belief that at least one individual from the predator species consumes at least another individual from the prey species. Moreover, in local clade-based food webs, the probability that two clades interact represents the 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 is an aggregation of interactions between individuals into larger groups, which could be more or less homogeneous depending on the organisms and the study system.

This type of scaling is analogous to the spatial and temporal scaling of interactions to the extent that they represent different ways to aggregate individuals into broader groups, either spatially, temporally, or taxonomically.

Spatial and temporal scaling of interactions

The study of network-area relationships (NARs) and interaction accumulation curves (IACs) are important realms of research in network ecology. Firstly, NARs describe 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 variation of network structure across spatial scales can be the result of the scaling of species richness (species-area relationships, SARs) and the number of interactions (Brose *et al.* (2004)) with the area sampled, but can also be due to ecological processes (e.g., spatial variability in community composition and extinction and colonization events) occurring at different scales (Galiana *et al.* (2018)). Secondly, IACs describe the scaling of the number of interactions observed with sampling effort (Jordano (2016)), which can impact many measures of network structure such as connectance (McLeod *et al.* (2021)). Beyond sampling effort, the temporal scaling of interactions describes how network structure changes with the duration of the network (Poisot *et al.* (2012)) given that different interactions are occurring through time. Because probabilistic local networks can assess the spatiotemporal variability of interactions (eq. 2), they are useful tools to develop and test different equations of the scaling of network structure with space and time.

Metawebs and local networks intrinsically differ in their relationship to spatial and temporal scales. On one hand, because probabilistic metawebs are context-independent, potential interactions do not scale with space and time since they depend solely on the biological capacity of the two taxa to interact, regardless of any particular environmental conditions. This suggests that the probability that two taxa can potentially interact should theoretically be the same in all metawebs in which they are present, provided that the data and methods used to estimate them are the same. As a result, if a potential network M_1 is subsampled from a regional metaweb M_0 to represent the potential interactions between a subset of taxa found in a smaller region, their probabilities of interaction should be identical regardless of scale, i.e. $P_{M_1}(i \rightarrow j) = P_{M_0}(i \rightarrow j)$. On the other hand, local ecological networks scale both spatially and temporally since interactions have more opportunities to be realized and observed in a larger area and duration (e.g., more individuals, more trait variations, more chance of an encounter, McLeod *et al.* (2020)). For example, if a local probabilistic network N_1 of area A_1 is obtained from a larger network N_0 of area A_0, with A_1 being completely nested within A_0, interaction probabilities should

be smaller 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 be incidentally higher in the smaller area depending on their environmental and biological conditions. Similarly, interaction probabilities should be smaller in networks of shorter durations if time intervals are nested. Statistical models, such as network-area relationships and interaction accumulation curves, can be used to generate estimates of local probabilities of interactions across spatial and temporal scales.

A spatiotemporally explicit model of interactions

Predicting local networks across time and space is an important goal of network ecology (Strydom *et al.* (2021)). Indeed, in a context of scarcity of interaction data (Jordano (2016)), ecologists must rely on predictive models to reconstruct networks at fine spatial and temporal scales. For example, local ecological networks could be reconstructed using real-time biomonitoring data and adequate numerical models (Bohan *et al.* (2017)), which could pave the way for fine-scale studies of ecosystem functioning and dynamics. Besides predictive models, statistical models can also be built to describe parameters of interest, such as probabilities of interactions. In that case, parameter values provide valuable ecological information in their own rights. Different types of models (e.g., Bayesian and machine learning models) of ecological interactions have been built for predictive and descriptive purposes (Strydom *et al.* (2021)). Representing interactions probabilistically reflects the uncertainty of these models, which is usually represented in terms of probability distributions. Here we show how to build a simple generative mechanistic model of probabilistic interactions that takes into account their inherent spatiotemporal variability, i.e. a spatiotemporally-explicit model. Our model is not suitable for potential interactions, which are scale-independent. Rather, it could prove useful for predicting local interactions across time and space by generating new interaction data after parameter inference.

As stated by eq. 1, the probability that two taxa i and j interact at a given location (x, y) is given by the product of their probability of interaction given co-occurrence and their probability of co-occurrence. First, their probability of co-occurrence is given by their respective probabilities of occurrence $P_i(x, y)$ and $P_j(x, y)$ and the strength of association γ between their occurrence and co-occurrence (Cazelles *et al.* (2016)):

$$P_{i,j}(x, y) = P_i(x, y)P_j(x, y)\gamma. \tag{5}$$

When $\gamma > 1$, the geographic distributions of both taxa are positively associated, which implies that the occurrence of one taxon increases the probability of occurrence of the other. In empirical networks, $\gamma > 1$ for

most species pairs (Catchen *et al.* (2023)). The co-occurrence of both taxa is the result of a Bernoulli trial

$$C \sim Bernoulli(P_{i,j}(x,y)). \tag{6}$$

Second, the probability of interaction given co-occurrence can be made temporally explicit by modeling it as a Poisson process with rate λ. This parameter corresponds to the expected frequency of interaction between both taxa in a given time period and its value can be estimated using prior data on interaction strengths, if available. Specifically, the probability that two co-occurring taxa interact during a time period t_0 is:

$$P_N(i \rightarrow j | C = 1) = 1 - e^{-\lambda t_0}, \tag{7}$$

which approaches 1 when $t_0 \rightarrow \infty$.

The realization of the interaction between i and j is the result of a Bernoulli trial with probability $P_N(i \rightarrow j)$. A Bayesian inference model can thus be built from the previous equations to estimate the value of the λ parameter and generate new interaction data:

$$I \sim Bernoulli(P_N(i \rightarrow j)) \tag{8}$$

$$P_N(i \rightarrow j) = P_i(x,y)P_j(x,y)\gamma(1 - e^{-\lambda t_0}) \tag{9}$$

$$\gamma \sim Gamma(2, 0.5) \tag{10}$$

$$\lambda \sim Exponential(2) \tag{11}$$

This simple model can be customized in many ways, e.g. by linking λ with given environmental variables or by explicitly modeling observation errors (i.e., the probability of false negatives and false positives).

Sampling binary networks

Probabilistic networks can be used to predict binary interactions through random draws. This can be useful when analyzing the structure of a probabilistic network when analytical probabilistic measures are lacking. A binary network can be generated from independent Bernoulli trials for each interaction. The distribution of a

network's property can then be obtained after measuring the structure of all randomly generated networks (Poisot *et al.* (2016)). Doing so allows us to represent the variability of network structure, although possibly with biases when connectance is low (Poisot & Gravel (2014), Chagnon (2015)). When binary networks are generated under a null model, this method can be used for null hypothesis significance testing, in which case the observed measure is compared to a null distribution (e.g., Bascompte *et al.* (2003)). Furthermore, randomly generating binary networks across space and time can help us visualize the spatiotemporal variability of network structure and test ecological hypotheses on interactions across large spatial and temporal scales.

There are at least two different approaches when sampling binary networks from probabilistic webs across space, e.g. if we want to predict a binary network for each of $n \times n$ grid cells. The first approach is to conduct a single Bernoulli trial for each pair of taxa found in the region of interest based on their regional probability of interaction. As a result, each pair of taxa that are predicted to interact in the regional network realization will interact in all of the n^2 networks in which they co-occur. This sampling technique is best used with potential interactions that have no spatial variation. The second approach is to independently sample each of the n^2 networks. In practice, this can be done by generating a different probabilistic network for each grid cell. Depending on how they were obtained, these networks can differ in their taxa composition (nodes) and/or interaction probabilities (edges). Then, binary networks can be independently sampled for each grid cell. Because this method generates spatial variation in binary interactions, it is best used with local interactions.

The choice of sampling approach has an impact on the selection of grid cell size. In the first approach, interactions will be the same regardless of cell size because interactions are sampled only once from the regional network. However, in the second approach, local interaction probabilities depend on the network area. For example, let N_1 and N_2 be networks of area $\frac{1}{2}A_0$ nested within A_0 and disjoint from each other, i.e. two contiguous cells that form N_0. If N_1 and N_2 are independent (which is rarely the case in reality because of spatial auto-correlation), the probability that two taxa i and j interact in N_0 is given by:

$$P_{N_0}(i \rightarrow j) = 1 - (1 - P_{N_1}(i \rightarrow j)) \times (1 - P_{N_2}(i \rightarrow j)). \tag{12}$$

Because of its larger area, the probability that the two taxa interact in N_0 is higher than in N_1 and N_2. When sampling binary interactions from local networks, it is thus important to sample at the same spatial scale as the one for which probabilities were estimated. Otherwise, interaction probabilities must be adjusted to correspond to the targeted cell size and avoid systematic biases in prediction.

Prediction of local networks from metawebs

Metawebs are an important source of ecological information that can be leveraged for predicting local networks. Indeed, binary local networks can be reconstructed by selecting a subset of both taxa and interactions from the metaweb (Dunne (2006)). This implies that there are always more interactions in a metaweb compared to its corresponding local networks. In practice, because a community's composition is arguably easier to sample or predict than its interactions, the list of taxa to select can be known empirically or obtained using range maps or species distribution models. The challenge is rather to choose which interactions to select from the metaweb, which could require more sophisticated statistical models and ecological knowledge. Because the structure of local networks is constrained by the one of the metaweb (Saravia *et al.* (2022)), inferring their structure from the metaweb before predicting local pairwise interactions could prove promising (Strydom *et al.* (2021)).

When building probabilistic local networks from a probabilistic metaweb, interaction probabilities decrease. This is because two taxa must first have the capacity to interact (i.e., $M_{i,j}^* = 1$ in the binary metaweb M^*) before interacting locally:

$$P_N(i \to j) = P_M(i \to j) \times P_N(i \to j | M_{i,j}^* = 1).$$

Therefore, inferring local networks from their metaweb keeping the same values of interaction probability would generate systematic biases in the prediction. In that case, these networks would instead represent smaller-scale metawebs of potential interactions, which could be misinterpreted as local interactions. As suggested by McLeod *et al.* (2021), even though metawebs do not capture the spatiotemporal variability of interactions, they set the upper limit of local interactions. In other words, the probability that two taxa interact at a given location and time is always lower or equal to the probability of their potential interaction:

$$P_N(i \to j | A, t, C, \Omega) \leq P_M(i \to j). \tag{13}$$

Moreover, the probability that two taxa have the biological capacity to interact must be higher than the probability that they will ever interact because they might never co-occur or encounter locally. More precisely, the accumulated probability of realized interactions across all spatial, temporal, and environmental conditions must be lower than the probability of potential interaction, i.e.

$$\int_\Omega \int_A \int_t P_N(i \to j | A, t, \Omega) dt dA d\Omega \le P_M(i \to j). \tag{14}$$

Conclusion

In this contribution, we underlined the importance of network metadata for adequately interpreting and manipulating probabilistic interaction data. Indeed, the mathematical representation of probabilities and their statistical behaviors 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 being scale-independent. In contrast, local interactions are measured in a specific context (e.g., in a given area, time, and biological and environmental conditions) and are conditional 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 rigorous foundations for probabilistic thinking in network ecology could enable more reliable assessments of the spatiotemporal variability and measurement uncertainty of biotic interactions.

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