The biological interpretation of probabilistic food webs

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The stochastic nature of ecological interactions has led many biologists to adopt a probabilistic view of ecological networks. Representing species interactions probabilistically (how likely are they to interact?) as opposed to deterministically (do they interact?) allows a better assessment of their spatiotemporal variability and accounts for inherent uncertainties in observations and predictions. However, despite this growing interest, general guidelines regarding 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, which are poorly documented in most published datasets. In this contribution, we review how probabilistic interactions are defined in the literature at different spatial scales, from local interactions to regional networks, with a strong emphasis on food webs. These definitions are based on the distinction between the realization of an interaction at a specific time and space and its biological feasibility. We show that these different network representations have different statistical behaviours when it comes to common ecological applications. Specifically, unlike taxonomic scaling, we argue that local and regional probabilistic networks differ in their spatial and temporal scaling of interactions, with regional interactions being scale-independent. Moreover, we suggest two approaches to sampling deterministic networks from probabilistic webs that account for these differences and argue that systematic biases arise when directly inferring local networks from subsets of regional webs. 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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Introduction

Cataloging species interactions across space and time is a gargantuan task. At the core of this challenge lies the spatiotemporal variability of ecological networks (Poisot *et al.* 2012, 2015), which makes documenting the location and timing of interactions difficult. Indeed, it is not sufficient to know that two species have the biological capacity to interact to infer the realization of their interaction at a specific time and space (Dunne 2006). Taking food webs as an example, a predator species and its potential prey must first co-occur in order for a trophic interaction to take place (Blanchet *et al.* 2020). They must then encounter, which is conditional on their relative abundances in the ecosystem and the matching of their phenology (Poisot *et al.* 2015). Finally, the interaction occurs only if the predators have a desire to consume their prey and are able to capture and ingest them (Pulliam 1974). Environmental (e.g. temperature and presence of shelters) and biological (e.g. physiological state of both species and availability of other prey species) factors contribute to this variability by impacting species co-occurrence (Araujo *et al.* 2011) and the realization of their interactions (Poisot *et al.* 2015). In this context, the development of computational methods in ecology can help alleviate the colossal sampling efforts required to document species interactions across time and space (Strydom *et al.* 2021). Having a better portrait of species interactions and the emerging structure of their food webs is important since it lays the groundwork for understanding the functioning, dynamics, and resilience of ecosystems worldwide (e.g., Proulx *et al.* 2005; Pascual *et al.* 2006; Delmas *et al.* 2019).

The recognition of the intrinsic variability of species interactions and the emergence of numerical methods have led ecologists to rethink their representation of ecological networks to include a probabilistic view of species interactions (Poisot *et al.* 2016). This has several benefits. For example, probabilities represent the limit of our knowledge about species interactions and can inform us about the expected number of interactions and emerging network properties despite this limited knowledge (Poisot *et al.* 2016). They are also very helpful in predicting the spatial distribution of species within networks (Cazelles *et al.* 2016) and the temporal variability of interactions (Poisot *et al.* 2015), generating new ecological data (e.g., Strydom *et al.* 2022), and identifying priority sampling locations of species interactions (see Andrade-Pacheco *et al.* 2020 for an ecological example of a sampling optimization problem). Moreover, the high rate of false negatives in ecological network data, resulting from the difficulty of witnessing interactions between rare species, makes it hard to interpret non-observations of species interactions ecologically (Catchen *et al.* 2023). Using probabilities instead of Boolean interactions accounts for these observation errors; in that case, only forbidden interactions (Jordano *et* *al.* 2003; Olesen *et al.* 2010) would have a probability value of zero (but see Gonzalez-Varo & Traveset 2016). 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 interactions, which shows the potential of this framework in the study of a variety of ecological phenomena.

Without clear guidelines, working with probabilistic species interactions could be misleading as much for field ecologists as for computational ecologists who use and generate these data. Indeed, representing species interactions probabilistically is challenging. Beyond methodological difficulties in estimating these numbers, there are important conceptual challenges in defining what we mean by "probability of interactions". To the best of our knowledge, because the building blocks of this mathematical representation of food webs are still being laid, there is no clear definition found in the literature or data standard when it comes to publishing data on probabilistic interactions (see Salim *et al.* 2022 for a discussion on data standardization for mutualistic networks). In this contribution, we outline different ways to define and interpret interactions probabilities in network ecology and propose an approach to thinking about them. These definitions mostly depend on the study system (e.g. local network or metaweb) and on the method used to generate them. We show that different definitions can have different ecological implications, especially regarding spatial, temporal, and taxonomic scaling. Although we will focus on food webs, our observations and advice can be applied to all types of ecological networks, from plant-pollinator to host-parasite networks. Indeed, all ecological networks, whether they are unipartite or bipartite, share fundamental commonalities in their biological conceptualization and mathematical representation that support these comparisons (i.e., they all describe groups of individuals interacting with each other). Regardless of the study system, we argue that probabilities should be better documented, defined mathematically, and used with caution when describing species interactions.

Stochastic representations of biological interactions

The first aspect to take into consideration when estimating or interpreting probabilities of interactions is knowing if they describe the likelihood of potential or realized interactions. A potential interaction is defined as the biological capacity of two species to interact (i.e., the probability that they *can* interact) whereas a realized interaction refers to the materialization or observation of this interaction in a delineated space and time period (i.e., the probability that they interact). Here, we will use the terms *metaweb* to designate networks of potential interactions and *local networks* for those of realized interactions. Frequent confusion arises among ecologists over the use of these two terms, especially in a probabilistic context. Indeed, in many studies of probabilistic ecological networks, it remains unclear when authors describe potential or realized interactions, or when so-called probabilities are actually *interaction scores*. Likewise, probabilistic potential interactions are often used as realized interactions (and conversely), even when the type of interaction is clearly indicated. We believe that a better understanding of these differences and concepts would alleviate interpretation errors and help ecologists use these numbers more appropriately.

Pairwise interactions: the building blocks of ecological networks

The basic unit of food webs and other ecological networks are individuals that interact with each others [e.g., by predation; Elton (2001)], forming individual-based networks. The aggregation of these individuals into more or less homogeneous groups (e.g., populations, species, trophic species, families) allows us to represent networks at broader taxonomic scales, which impacts our interpretation of the properties and behaviour of these systems (Guimarães 2020). Nodes can thus designate distinct levels of organization, whereas edges linking these nodes can describe a variety of interaction measures. When using a Boolean representation of biotic interactions, the observation that one individual from group (or node) i interacts with another individual from group j is enough to set the interaction $A_{i,j}$ to 1. This simplified representation of food webs is a highly valuable source of ecological information (Pascual *et al.* 2006) even though it overlooks important factors regarding interaction strengths. These, in turn, can be 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 be used to estimate the average number of prey individuals consumed by the predators in a given time period (e.g., the average number of fish in the stomach of a piscivorous species). Interaction strengths can also be used as good estimators of the parameters describing species interactions in a Lotka-Volterra model (e.g., Emmerson & Raffaelli 2004). This extra amount of ecological information typically comes at a cost of greater sampling effort or data requirement in predictive models (Strydom *et al.* 2021), which can lead to high uncertainties when building these networks.

The uncertainty and spatiotemporal variability of both types of trophic interactions (Boolean and quantitative) can be represented probabilistically. On one hand, Boolean interactions follow a Bernoulli distribution $A_{i,j} \sim \text{Bernoulli}(p)$, with p being the probability of interactions. The only two possible outcomes are the presence ($A_{i,j} = 1$) or absence ($A_{i,j} = 0$) of an interaction between the two nodes. Quantitative interactions, on the other hand, can follow various probability distributions depending on the measure used. In this case, the event's outcome is the value of interaction strength. For instance, these interaction strengths can follow a Poisson distribution $A_{i,j} \sim \text{Poisson}(\lambda)$ when predicting frequencies of interactions between pairs of nodes, with λ being the expected rate of interaction. Note that quantitative interactions can be converted to probabilistic interactions by normalizing. The definition and interpretation of parameters like p and λ are inextricably linked to environmental and biological factors such as species relative abundance, traits, area, and time, depending on the type of interaction. Because Boolean species interactions are much more documented in the literature, our primary focus in this contribution will be on addressing the challenges in defining and interpretating p for pairwise species interactions.

Local networks: communities interacting in space and time

As opposed to metawebs, probabilistic local food webs represent the likelihood that two species will interact at a specific location and within a given time period; in other words, they are context dependant. They could also represent the likelihood of observing these interactions within a given area and time. To be specific, space is defined here as the geographic coordinates (x, y) of the spatial boundaries delineating the system, whereas time is the time interval t during which interactions were sampled or for which they were predicted. We want to point out that they are not single values, but rather continued dimensions that could be outlined differently depending on the study system. Regardless of how they were defined, they always delineate a specific area A and duration t. These could refer to the sampled area and duration or to the targeted location and time period.

Many factors could be taken into consideration when estimating the probability that a predator species i interacts with a given prey species j locally. One of the most important is species co-occurrence C, which is a Boolean describing if both species can be found at location and time (x, y, t). Surely, the probability that the interaction is realized must be 0 when species do not co-occur ($C = 0$). Interaction probabilities can also be conditional on other biological and environmental variables, such as temperature, precipitation, presence of shelters, phenotypic plasticity, phenology, and presence of other interacting species in the network. These conditions can affect species traits, which greatly impact the capacity of species to interact (Poisot *et al.* 2015). Similarly, species relative abundance is another important predictor of the probability of interaction, because it impacts the probability that species will randomly encounter (Canard *et al.* 2012; Canard *et al.* 2014; Poisot *et al.* 2015). Here, we will use the variable Ω as a substitute for the biological and ecological context in which interaction probabilities were estimated, including the presence of higher-order interactions. This gives us the following equation for the probability of realized interaction between species (or taxa) i and j in a local network N:

$$P_N(i \to j | A, t, C, \Omega), \tag{1}$$

which can be read as the probability of local interaction between the two species in an area A and time interval t, given their co-occurrence C and specific environmental and biological conditions Ω. These conditions do not systematically need to be specified for all studies. However, when they are, they should be made explicit in the metadada.

Multiple difficulties of interpretation arise when the conditions are not clearly specified, which we found is often the case in the literature. For example, if $P_N(i \to j | C = 1)$ represents the probability that two co-occurring species interact (i.e., the edge's probability value), $P_N(i \to j)$ denotes instead the probability of interaction without knowing if they co-occur (i.e., the product of the nodes and edge's probability values). For practical reasons, probabilistic ecological networks are generally represented as matrices of probabilities (i.e., matrices of edges without node values), whose elements are thus hard to interpret without clear indications about C. Overall, when probabilities of interactions are estimated using specific values of A, t, C, and Ω, ecologists should make them explicit in their metadata, preferably using mathematical equations to avoid any ambiguity. Below, we will see examples of why this matters when it comes to spatial, temporal, and taxonomic scaling of biotic interactions.

Metawebs: regional catalogs of interactions

Metawebs are networks of potential interactions, representing the probability that two taxa can interact regardless of biological plasticity, environmental variability or co-occurrence. Instead of describing stochastic biological processes occurring in nature, probabilistic potential interactions can be thought of as a measure of imperfect knowledge about the capacity of two taxa to interact. They are the network analogue to the species pool, where local networks originate from a subset of both species (nodes) and interactions (edges). For this reason, they have been initially designed for broad spatial, temporal, and taxonomic scales (e.g, species food webs at the continental scale).

We can express the probability that two taxa i and j can interact in a metaweb M as

$$P_M(i \rightarrow j), \quad (2)$$

which is context independent. In other words, the probability that two species can interact is not contingent on location, time, and environmental factors. Nevertheless, one aspect of a metaweb that could be conditional on these factors is the list of species (or taxa) it is built from when assembled for a specific region.

Starting from a selected set of species, metawebs can be built using different data sources, including literature review, field work, and predictive models (e.g., the metaweb of Canadian mammals inferred by Strydom *et al.* 2022). Every pair of species that has been observed to interact at least once can be given a probability of interaction of 1; we know that they *can* interact. This means that rare interactions can technically be given high probabilities in the metaweb. Unobserved interactions, on the other hand, are given lower probabilities, going as low as 0 for forbidden links. Two important nuances must however be made here. 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 actually false positives. Similarly, forbidden interactions can be false negatives if e.g. they have been assessed for specific phenotypes, locations or time. Implementing a Bayesian framework, which updates prior probabilities of interactions with empirical data, could lessen these errors.

[Table 1 about here]. Articles using probabilistic interactions and the definitions and variables they considered.

Statistical behaviour of networks in key ecological applications

Taxonomic agglomeration and division of nodes

The properties of ecological networks depend on their level of organization (Guimarães 2020). Indeed, at different taxonomic scales, different behaviours and dynamics can be observed and distinct ecological questions can be answered (e.g., exploring evolutionary dynamics at broad taxonomic scales). Because of these reasons, it could be important to analyse the same network at different taxonomic scales. However, we want to emphasize here that many networks do not have an homogenous level of organisation (Vázquez *et al.* 2022). Indeed, different nodes within the same network can be represented at different taxonomic scales (e.g., a network composed of species and trophic species). This becomes important when we consider that the biological interpretation of interaction probabilities depends on the nodes' resolution. For example, in individual-based networks, the probability that two individuals interact could represent the degree of belief that one will actually consume the other. In species-based networks, the probability that two species interact could rather represent the degree of belief that *at least* one individual from the predator species will eat *at least* another individual from the prey species. This distinction in interpretation impacts the way probability values change with taxonomic scale.

There are a lot of similarities between taxonomic and spatiotemporal scaling of probabilistic interactions. Fundamentally, these types of scaling are just different ways to aggregate individuals into broader nodes, either spatially, temporally, or taxonomically. However, there are also important differences between them. First, in metawebs, if we know that two species have the capacity to interact, we can infer that their respective genus should also be able to interact (i.e., there should be at least two individuals within these genus that can interact). On the contrary, knowing that two genus can interact does not mean that all pairwise combinations of species within these genus can also interact among themselves. This observation also applies to local networks. When it comes to probabilistic networks, interaction probabilities at broader taxonomic scales can be directly obtained from probabilities at finer scales when aggregating nodes. For example, if we have in a network n_A species from genus A and n_B species from genus B, we can calculate the probability that the two genus interact as $P_N(A \to B) = 1 - \prod_{i=1}^{n_A} \prod_{j=1}^{n_B} (1 - P_N(A_i \to B_j))$, where A_i and B_j are the species of the corresponding genus. However, more sophisticated models need to be used when building probabilistic networks at smaller taxonomic resolutions (e.g., when building a species-level network from a genus-level network). One could, for example, estimate the probabilities of all pairwise species interactions by using a Beta distribution parametrised by the broader-scale network.

[Figure 3 about here]. Conceptual figure of how a scale up of the nodes from an individual to a population to any higher taxonomic group change our interpretation of the probability of interaction.

Spatial and temporal scaling of probabilistic interactions

Metawebs and local networks intrinsically differ in their relation to scale. On one hand, as mentioned above, probabilistic metawebs are context independent, i.e., probabilistic pairwise interactions do not scale with space and time because they depend solely on the biological capacity of the two taxa to interact. This implies that the estimated likelihood that two species can potentially interact should be the same among all metawebs in which they are present. In practice, this is rarely the case because ecologists use different methods and data to estimate these probabilities of interactions (e.g., different sampling area and time period). However, in the case where local metawebs $M_{x,y}$ are subsampled from their regional counterpart M_0, we should expect edge values to be identical among all networks, regardless of their spatial scale, i.e. $P_{M_{x,y}}(i \to j) = P_{M_0}(i \to j)$. On the other hand, local probabilistic networks are indissociable from their spatial and temporal contexts because there are more opportunities of interactions (e.g., more individuals, more trait variations, more chance of encounter) in a larger area and longer time period (McLeod *et al.* 2020). Let N_0 be a local probabilistic food web delineated in an area A_0 and N_1 a network of area $A_1 < A_0$ within A_0. We should expect the probability that i and j interacts to scale spatially, i.e. $P_{N_1}(i \to j|A < A_0) \leq P_{N_0}(i \to j|A = A_0)$. Similarly, the temporal scaling of probabilistic local food webs could be manifested through the effect of sampling effort on the observation of interactions (Jordano 2016; McLeod *et al.* 2021) or of time itself on their realization (Poisot *et al.* 2012). There are many network-area relationships (e.g., Wood *et al.* 2015; Galiana *et al.* 2018) and interaction accumulation curves (e.g, Jordano 2016) explored in the literature. These could inspire the development and testing of different equations describing the spatiotemporal scaling of probabilistic pairwise interactions in local networks, which are over the scope of this manuscript.

[Figure 2 about here]. Conceptual figure showing (1) the spatiotemporal scaling of probabilistic metawebs and local food webs and (2) the spatial sampling of metawebs and local food webs into Boolean networks.

Spatiotemporally explicit model of probabilistic interactions

The variability of species interactions spurred the development of methods aiming at predicting ecological networks at fine spatial and temporal scales. For example, Bohan *et al.* (2017) proposed a framework to reconstruct networks in real time using continuous biomonitoring. Here, we will build on these studies by proposing a simple model to make probabilistic local networks spatiotemporally explicit. These types of models could prove useful when inferring food webs across time and space from sparse data. However, they are not suitable for metawebs, which are static objects.

One way that probabilistic food webs can be made spatiotemporally explicit is by modelling interactions between co-occurring species as a Poisson process with rate λ. Specifically, if the total observation time for a location is t_0, the probability that two co-occurring species i and j will interact during this time period is $P_N(i \to j|C_{i,j} = 1, t = t_0) = 1 - e^{-\lambda t_0}$, which approaches 1 when $t \to \infty$. The value of the parameter λ could be estimated using prior data on interaction strengths, if available. Additionally, we can estimate the probability of co-occurrence at location (x, y) with $P_{x,y}(C_{i,j} = 1) = P_{x,y}(i)P_{x,y}(j)\gamma$, where $P_{x,y}(i)$ and $P_{x,y}(j)$ are respectively the probabilities of occurrence of species i and j and γ is the strength of association between occurrence and co-occurrence, as defined in Cazelles *et al.* (2016). Note that in empirical networks, γ is typically > 1 (Catchen *et al.* 2023). The observation of this interaction would thus follow a Bernoulli distribution with parameter $p = p_A(x, y)p_B(x, y)\gamma(1 - e^{-\lambda t_0})$. This simple model could be customized in many ways, e.g. by linking λ with given environmental variables or by adding in observation errors (i.e., probability of false negatives and false positives; Catchen *et al.* (2023)).

Binary conversion of probabilistic networks through random draws

Another conceptual challenge encountered when using probabilistic food webs is the prediction of Boolean networks across space. Lets take $n \times n$ grid cells each representing a probabilistic food web. If they contain potential interactions, a single random trial must be conducted for each pairwise interaction across the region (i.e., we should have only one random realization of the regional metaweb). On the contrary, if they represent probabilities of realized interactions, each food web must be independently sampled (i.e., n^2 independent random draws). This has direct implications on the spatial scaling of interactions. For example, let N_1 and N_2 be networks of area $< A_0$ within a bigger area A_0 and disjoint from each other, such as N_1 and N_2 form N_0 (think of two contiguous cells that together delineate N_0). All other things being equal, we should expect the probability that i and j interacts in A_0 to be $P_{N_0}(i \to j) = 1 - (1 - P_{N_1}(i \to j)) \times (1 - P_{N_2}(i \to j))$ if N_1 and N_2 are independently sampled. This also implies that we should expect interactions to be realized in a certain number of local networks depending on the probability value, which is not the case with metawebs. Note that spatial auto-correlation and the concept of meta-network (i.e., networks of networks) could invalidate the statistical assumption of independence. Nevertheless, the fundamental difference in sampling metawebs and local networks stands even when considering these factors. This difference in sampling further sheds light on the importance of clearly defining interaction probabilities. What we consider as a *Bernoulli trial*, when randomly drawing deterministic networks from probabilistic food webs, depends on our biological interpretation of these probabilities.

Prediction of local networks from probabilistic metawebs

Even though the spatiotemporal variability of interactions is not considered in metawebs, they can still be useful to reconstruct local networks of realized interactions. Indeed, local networks are formed from subsets of their metaweb (called subnetworks), which are obtained by selecting a subset of both species and interactions (Dunne 2006). Because a community's composition is arguably easier to sample (or predict) than its interactions, the biggest challenge is to sample links from the metaweb. This becomes a conceptual issue when we consider how potential and realized interactions differ. Despite these concerns, metawebs remain an important source of ecological information that can be leveraged for realistically predicting spatially explicit networks. First, metawebs set the upper limit of species interactions (McLeod *et al.* 2021), i.e. the probability that two species interact at a specific location is always lower or equal to the probability of their potential interaction:

$$P_N(i \to j | A, t, C, \Omega) \leq P_M(i \to j). \tag{3}$$

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 be called *spatially explicit* or *local* metawebs (i.e., smaller-scale networks of potential interactions). Second, the structure of local networks is constrained by the one of their metaweb (Saravia *et al.* 2022). This suggests that a metaweb not only constrains the pairwise interactions of its corresponding local networks, but also their emerging properties. Inferring the structure of local networks from the metaweb could thus help estimate more realistically the likelihood that potential interactions are realized and observed locally (Strydom *et al.* 2021).

[Figure 1 about here]. Empirical example of the association between the number of interactions in realized local food webs and the number of interactions in the corresponding subnetworks of their regional metaweb. We should expect the association to be linear below the 1:1 line, illustrating eq. 3.

Conclusion

The emergence of probabilistic thinking in network ecology has paved the way to a better assessment of the spatiotemporal variability and uncertainty of biotic interactions. However, measuring probabilities empirically can be strenuous given the difficulties of deciphering species and interactions (Pringle & Hutchinson 2020). In this context, the development of computational methods makes it possible to estimate interaction probabilities at large scales, which in turn can pinpoint where we should go to optimise our sampling effort for better resolving local food webs.

In this contribution, we showed that network metadata are perhaps as important as interaction data themselves when it comes to interpreting probabilistic food webs in ecological terms. First, the type of probabilistic interaction (potential or realized) impacts the importance of scale, with interactions in metawebs being scale independent, both spatially and temporally. Second, the conditions in which local networks were estimated (e.g., area, time, biological and environmental factors) and the attributes of the interacting species that were considered (e.g., species co-occurrence) are essential contextual factors that impact the mathematical representation of probabilities and their resulting behaviour. Third, the biological interpretation of probabilities changes with the level of organization of the network due to the aggregation of individuals into broader groups. All these information should be available as clear metadata so that ecologists can use probabilistic network data appropriately.

Moreover, many statistical models in ecology that yield accurate predictions of biotic interactions are black boxes difficult to interpret. Ecologists should be careful before using the output of these models as probabilistic objects, since there is often a thin line between a real probability and a non-probabilistic predictive number (or score). Probabilities are numbers between 0 and 1 that sum to 1 and either represent the expected frequency of a phenomenon or the degree of belief that it will be realized. Non-probabilistic scores, which are more akin to interaction strengths, have different mathematical properties, which impacts how we should handle these numbers in a spatially or temporally explicit context. Therefore, researchers should use their expertise to assess if their interaction data are actually probabilities or scores. This should also be added to the metadata before sharing them, as well as the methods used to build the networks.

Better metadata documentation would allow researchers to use and manipulate probabilistic ecological interactions according to how they were actually defined and obtained. This would support better scientific practices, in particular when these data are used for ecological prediction and forecasting. For instance, we showed that building a rigorous workflow to predict local networks from a probabilistic metaweb requires a good understanding of the data at hand. Similarly, explicitly stating the context in which probabilistic data were estimated would help using forecasting food-web models more rigorously under specific climate change and habitat use scenarios. Regardless of the method and application, fostering a better foundation for probabilistic reasonings in network ecology, from the very nature of probabilities and biotic interactions, is essential.

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