

The biological interpretation of probabilistic food webs

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Community ecologists are increasingly thinking probabilistically when it comes to food webs and other ecological networks. Assuredly, the benefits of representing ecological interactions as probabilistic events (e.g., how likely are species to interact?) instead of binary objects (e.g., do species interact?) are numerous, from a better assessment of the spatiotemporal variation of trophic interactions to an increase capacity to reconstruct networks from sparse data. However, probabilities need to be used with caution when working with species interactions. Indeed, depending on the system at hand and the method used to build probabilistic networks, probabilities can have different interpretations that imply different ways to manipulate them. At the core of these differences lie the distinction between assessing the likelihood that two groups of individuals *can* interact and the likelihood that they *will* interact. This impacts the spatial, temporal, and taxonomic scaling of interaction probabilities, thus enlightening the need to properly define them in their ecological context. Published data on probabilistic species interactions are poorly documented in the literature, which impedes our ability to use them appropriately. With these challenges in mind, we propose a general approach to thinking about probabilities in regards to ecological interactions, with a strong focus on food webs, and call for better definitions and conceptualizations of probabilistic ecological networks, both at the local and regional scales.

1 Introduction

2 Cataloging species interactions across space is a gargantuan task. At the core of this challenge lies the
3 spatiotemporal variability of ecological networks (Poisot *et al.* 2012, 2015), which makes documenting the
4 location and timing of interactions difficult. Indeed, it is not sufficient to know that two species have the
5 biological capacity to interact to infer the realization of their interaction at a specific time and space
6 (Dunne 2006). Taking food webs as an example, a predator species and its potential prey must first
7 co-occur in order for a trophic interaction to take place (Blanchet *et al.* 2020). They must then encounter,
8 which is conditional on their relative abundances in the ecosystem and the matching of their phenology
9 (Poisot *et al.* 2015). Finally, the interaction occurs only if the predators have a desire to consume their prey
10 and are able to capture and ingest them (Pulliam 1974). Environmental (e.g. temperature and presence of
11 shelters) and biological (e.g. physiological state of both species and availability of other prey species)
12 factors contribute to this variability by impacting species co-occurrence (Araujo *et al.* 2011) and the
13 realization of their interactions (Poisot *et al.* 2015). In this context, the development of computational
14 methods in ecology can help alleviate the colossal sampling efforts required to document species
15 interactions across time and space (Strydom *et al.* 2021). Having a better portrait of species interactions
16 and the emerging structure of their food webs is important since it lays the groundwork for understanding
17 the functioning, dynamics, and resilience of ecosystems worldwide (e.g., Proulx *et al.* 2005; Pascual *et al.*
18 2006; Delmas *et al.* 2019).

19 The recognition of the intrinsic variability of species interactions and the emergence of numerical
20 methods have led ecologists to rethink their representation of ecological networks, slowly moving from a
21 binary to a probabilistic view of species interactions (Poisot *et al.* 2016). This has several benefits. For
22 example, probabilities represent the limit of our knowledge about species interactions and can inform us
23 about the expected number of interactions and emerging network properties despite this limited
24 knowledge (Poisot *et al.* 2016). They are also very helpful in predicting the spatial distribution of species
25 within networks (Cazelles *et al.* 2016) and the temporal variability of interactions (Poisot *et al.* 2015),
26 generating new ecological data (e.g., Strydom *et al.* 2022), and identifying priority sampling locations of
27 species interactions (see Andrade-Pacheco *et al.* 2020 for an ecological example of a sampling optimization
28 problem). Moreover, the high rate of false negatives in ecological network data, resulting from the
29 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 yes-no 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.

However, representing species interactions probabilistically can also be 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. This is worrisome, since working with probabilistic species interactions without clear guidelines could be misleading as much for field ecologists as for computational ecologists who use and generate these data. 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. Specifically, we argue that probabilities should be better documented, defined mathematically, and used with caution when describing species interactions.

Definitions and interpretations

Food-web representations

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 scales, which impacts the properties and behaviour of these systems (Guimarães 2020). A network’s nodes can thus designate distinct levels of organization, whereas the edges linking these nodes can describe a variety of interaction measures. When using a Boolean (yes-no)

58 representation of biotic interactions, the observation that one individual from group (or node) i interacts
 59 with another individual from group j is enough to set the interaction $A_{i,j}$ to 1. This simplified
 60 representation of food webs is a highly valuable source of ecological information (Pascual *et al.* 2006) even
 61 though it overlooks important factors regarding interaction strengths. These, in turn, can be represented
 62 using weighted interactions, which better describe the energy flows, demographic impacts or frequencies
 63 of interactions between nodes (Berlow *et al.* 2004; Borrett & Scharler 2019), with $A_{i,j} \in \mathbb{N}$ or \mathbb{R} depending
 64 on the measure. For example, they can be used to estimate the average number of prey individuals
 65 consumed by the predators in a given time period. This extra amount of ecological information typically
 66 comes at a cost of greater sampling effort or data requirement in predictive models (Strydom *et al.* 2021),
 67 which can lead to high uncertainties when building these types of networks. Therefore, important
 68 methodological and conceptual decisions must be made when sampling and building food webs.

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

81 The first aspect to take into consideration when estimating or interpreting probabilities of interactions is
 82 knowing if they describe the likelihood of potential or realized interactions. A potential interaction is
 83 defined as the biological capacity of two species to interact (i.e., the probability that they *can* interact)
 84 whereas a realized interaction refers to the materialization or observation of this interaction in a delineated
 85 space and time period (i.e., the probability that they interact). Here, we will use the terms *metaweb* to
 86 designate networks of potential interactions and *local networks* for those of realized interactions. Frequent
 87 confusion arises among ecologists over the use of these two terms, especially in a probabilistic context.

88 Indeed, in many studies of probabilistic ecological networks, it remains unclear when authors describe
89 potential or realized interactions, or when so-called probabilities are actually *interaction scores*. Likewise,
90 probabilistic potential interactions are often used as realized interactions (and conversely), even when the
91 type of interaction is clearly indicated. We believe that a better understanding of these differences and
92 concepts would alleviate interpretation errors and help ecologists use these numbers more appropriately.

93 **Probabilistic metawebs**

94 Metawebs are networks of potential interactions, representing the probability that two taxa can interact
95 regardless of biological plasticity, environmental variability or co-occurrence. They are the network
96 analogue to the species pool, where local networks originate from a subset of both species (nodes) and
97 interactions (edges). For this reason, they have been initially designed for broad spatial, temporal, and
98 taxonomic scales (e.g, species food webs at the continental scale). However, in the next section, we argue
99 that this concept can also be used at smaller scales, with similar ecological meaning.

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

$$P_M(i \rightarrow j), \quad (1)$$

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

105 Starting from a selected set of species, metawebs can be built using different data sources, including
106 literature review, field work, and predictive models (e.g., the metaweb of Canadian mammals inferred by
107 Strydom *et al.* 2022). Every pair of species that has been observed to interact at least once can be given a
108 probability of interaction of 1; we know that they *can* interact. This means that rare interactions can
109 technically be given high probabilities in the metaweb. Unobserved interactions, on the other hand, are
110 given lower probabilities, going as low as 0 for forbidden links. Two important nuances must however be
111 made here. Because of observation errors due to taxonomic misidentifications and ecological
112 misinterpretations, many observations of interactions are actually false positives. Similarly, forbidden

113 interactions can be false negatives if e.g. they have been assessed for specific phenotypes, locations or time.
114 Implementing a Bayesian framework, which updates prior probabilities of interactions with empirical
115 data, could lessen these errors.

116 **Probabilistic local networks**

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

125 Many factors could be taken into consideration when estimating the probability that a predator species i
126 interacts with a given prey species j locally. One of the most important is species co-occurrence, which
127 describes if both species can be found at location and time x, y, t . Surely, the probability that the
128 interaction is realized must be 0 when species do not co-occur. Similarly, species relative abundance is
129 another important predictor of the probability of interaction, because it impacts the probability that
130 species will randomly encounter (Canard *et al.* 2012; Canard *et al.* 2014; Poisot *et al.* 2015). Interaction
131 probabilities can also be conditional on other biological and environmental variables, such as temperature,
132 precipitation, presence of shelters, phenotypic plasticity, phenology, and presence of other interacting
133 species in the network. These conditions can affect species traits, which greatly impact the likelihood of
134 interactions (Poisot *et al.* 2015). When probabilities of interactions are estimated using specific values of
135 these variables, ecologists should make them explicit in their metadata, preferably using mathematical
136 equations to avoid any ambiguity. In the next section, we will see examples of why this matters when it
137 comes to spatial, temporal, and taxonomic scaling of biotic interactions. Here, we will use the variable Ω
138 as a substitute for the biological and ecological context in which interaction probabilities were estimated.
139 This gives us the following equation for the probability that species (or taxa) i and j interact in a local
140 network N :

$$P_N(i \rightarrow j | \mathbf{x}, \mathbf{y}, \mathbf{t}, \mathbf{\Omega}). \quad (2)$$

141 **From potential to realized interactions**

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

$$P_N(i \rightarrow j | \mathbf{x}, \mathbf{y}, \mathbf{t}, \mathbf{\Omega}) \leq P_M(i \rightarrow j). \quad (3)$$

152 Therefore, building local networks from their metaweb keeping the same values of interaction probability
 153 would generate systematic biases in the prediction. Second, the structure of local networks is constrained
 154 by the one of their metaweb (Saravia *et al.* 2022). This suggests that a metaweb not only constraints the
 155 pairwise interactions of its corresponding local networks, but also their emerging properties. Inferring the
 156 structure of local networks from the metaweb could thus help estimate more realistically the likelihood
 157 that potential interactions are realized and observed locally (Strydom *et al.* 2021).

158 **Scaling**

- 159 • We should expect a certain number of interactions to be realized depending on the probability value.
 160 This number depends on the number of trials, which also depends on the ecological context (e.g.,
 161 environmental conditions, scale) in which probabilities were estimated. This is in contrast with
 162 probabilities in metawebs.

163 Spatial and temporal scales

164 How do interaction probabilities scale spatially and temporally?

- 165 • Why do probabilistic local food webs scale with area and time but not probabilistic metawebs?
- 166 • In metawebs, interaction probabilities do not scale with space and time because they depend solely
167 on the biological capacity of two species to interact.
- 168 • In local food webs, interaction probabilities scale with space and time because there are more
169 opportunities of interactions (e.g., more environmental conditions) in a larger area and longer time
170 period.
- 171 • What are some network area relationships in probabilistic local food webs?
- 172 • We know that local networks can inform regional networks. However, can regional networks
173 inform local networks?

174 **Figure:** Empirical example of the association between the number of interactions in realized local food
175 webs and the number of interactions in the corresponding species subnetworks of regional networks. We
176 should expect the interaction to be linear below the 1:1 line.

177 **Papers:** there might be something in these McLeod *et al.* (2020); McLeod *et al.* (2021); Wood *et al.* (2015)

178 Taxonomic scale

179 How do interaction probabilities scale taxonomically?

- 180 • There are different biological interpretations of probabilities in food webs at the individual level and
181 at higher taxonomic levels.
- 182 • How does the scaling up of the nodes from an individual to population to any higher taxonomic
183 group change our interpretation of interaction probabilities? How does the aggregation change our
184 interpretation?
- 185 • How is it similar and different to spatial and temporal scaling? Basically, all kinds of scaling are just
186 different ways to aggregate individuals or nodes.

187 **Figure:** Conceptual figure of how a scale up of the nodes from an individual to a population to any higher
188 taxonomic group change our interpretation of the probability of interaction.

189 **Concluding remarks**

190 Here we present some advice moving forward.

- 191 • What can we learn from other systems/fields (e.g., social networks, probabilistic graph theory)?
- 192 • What even are probabilities? What is the probability that we will ever know the answer to that?
- 193 • Be careful of how we define probabilities. Be sure to be explicit about these things. Be sure to specify
- 194 the type of interaction, the spatial, temporal, and taxonomic scale when presenting new data on
- 195 interaction probabilities. We need better metadata documentation.
- 196 • Be careful to use and manipulate interaction probabilities properly depending on how they were
- 197 defined and obtained. Different interpretations imply different scaling, and thus different ways to
- 198 manipulate these numbers.
- 199 • Maybe mention thinking about a workflow to predict probabilistic local food webs from probabilistic
- 200 metawebs.

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209 **References**

- 210 Andrade-Pacheco, R., Rerolle, F., Lemoine, J., Hernandez, L., Meïté, A., Juziwelo, L., *et al.* (2020). Finding
211 hotspots: Development of an adaptive spatial sampling approach. *Scientific Reports*, 10, 10939.
- 212 Araujo, M.B., Rozenfeld, A., Rahbek, C. & Marquet, P.A. (2011). Using species co-occurrence networks to
213 assess the impacts of climate change. *Ecography*, 34, 897–908.

214 Berlow, E.L., Neutel, A.-M., Cohen, J.E., De Ruiter, P.C., Ebenman, B., Emmerson, M., *et al.* (2004).
 215 Interaction strengths in food webs: Issues and opportunities. *Journal of Animal Ecology*, 73, 585–598.

216 Blanchet, F.G., Cazelles, K. & Gravel, D. (2020). Co-occurrence is not evidence of ecological interactions.
 217 *Ecology Letters*, 23, 1050–1063.

218 Borrett, S.R. & Scharler, U.M. (2019). Walk partitions of flow in Ecological Network Analysis: Review and
 219 synthesis of methods and indicators. *Ecological Indicators*, 106, 105451.

220 Canard, E.F., Mouquet, N., Mouillot, D., Stanko, M., Miklisova, D. & Gravel, D. (2014). Empirical
 221 Evaluation of Neutral Interactions in Host-Parasite Networks. *The American Naturalist*, 183, 468–479.

222 Canard, E., Mouquet, N., Marescot, L., Gaston, K.J., Gravel, D. & Mouillot, D. (2012). Emergence of
 223 Structural Patterns in Neutral Trophic Networks. *PLOS ONE*, 7, e38295.

224 Catchen, M.D., Poisot, T., Pollock, L.J. & Gonzalez, A. (2023). The missing link: Discerning true from false
 225 negatives when sampling species interaction networks.

226 Cazelles, K., Araujo, M.B., Mouquet, N. & Gravel, D. (2016). A theory for species co-occurrence in
 227 interaction networks. *Theoretical Ecology*, 9, 39–48.

228 Delmas, E., Besson, M., Brice, M.-H., Burkle, L.A., Dalla Riva, G.V., Fortin, M.-J., *et al.* (2019). Analysing
 229 ecological networks of species interactions. *Biological Reviews*, 94, 16–36.

230 Dunne, J.A. (2006). The Network Structure of Food Webs. In: *Ecological networks: Linking structure and*
 231 *dynamics* (eds. Dunne, J.A. & Pascual, M.). Oxford University Press, pp. 27–86.

232 Elton, C.S. (2001). *Animal Ecology*. University of Chicago Press, Chicago, IL.

233 Godsoe, W., Murray, R. & Iritani, R. (2022). Species interactions and diversity: A unified framework using
 234 Hill numbers. *Oikos*, n/a, e09282.

235 Gonzalez-Varo, J.P. & Traveset, A. (2016). The Labile Limits of Forbidden Interactions. *Trends in Ecology &*
 236 *Evolution*, 31, 700–710.

237 Guimarães, P.R. (2020). The Structure of Ecological Networks Across Levels of Organization. *Annual*
 238 *Review of Ecology, Evolution, and Systematics*, 51, 433–460.

239 Jordano, P., Bascompte, J. & Olesen, J.M. (2003). Invariant properties in coevolutionary networks of
 240 plant-animal interactions. *Ecology Letters*, 6, 69–81.

241 McLeod, A., Leroux, S.J., Gravel, D., Chu, C., Cirtwill, A.R., Fortin, M.-J., *et al.* (2021). Sampling and
 242 asymptotic network properties of spatial multi-trophic networks. *Oikos*, n/a.

243 McLeod, A.M., Leroux, S.J. & Chu, C. (2020). Effects of species traits, motif profiles, and environment on
 244 spatial variation in multi-trophic antagonistic networks. *Ecosphere*, 11, e03018.

245 Ohlmann, M., Miele, V., Dray, S., Chalmandrier, L., O'Connor, L. & Thuiller, W. (2019). Diversity indices
 246 for ecological networks: A unifying framework using Hill numbers. *Ecology Letters*, 22, 737–747.

247 Olesen, J.M., Bascompte, J., Dupont, Y.L., Elberling, H., Rasmussen, C. & Jordano, P. (2010). Missing and
 248 forbidden links in mutualistic networks. *Proceedings of the Royal Society B: Biological Sciences*, 278,
 249 725–732.

250 Pascual, M., Dunne, J.A. & Dunne, J.A. (2006). *Ecological Networks: Linking Structure to Dynamics in Food*
 251 *Webs*. Oxford University Press, USA.

252 Poisot, T., Canard, E., Mouillot, D., Mouquet, N. & Gravel, D. (2012). The dissimilarity of species
 253 interaction networks. *Ecology Letters*, 15, 1353–1361.

254 Poisot, T., Cirtwill, A.R., Cazelles, K., Gravel, D., Fortin, M.-J. & Stouffer, D.B. (2016). The structure of
 255 probabilistic networks. *Methods in Ecology and Evolution*, 7, 303–312.

256 Poisot, T., Stouffer, D.B. & Gravel, D. (2015). Beyond species: Why ecological interaction networks vary
 257 through space and time. *Oikos*, 124, 243–251.

258 Proulx, S.R., Promislow, D.E.L. & Phillips, P.C. (2005). Network thinking in ecology and evolution. *Trends*
 259 *in Ecology & Evolution*, SPECIAL issue: BUMPER book REVIEW, 20, 345–353.

260 Pulliam, H.R. (1974). On the Theory of Optimal Diets. *The American Naturalist*, 108, 59–74.

261 Saravia, L.A., Marina, T.I., Kristensen, N.P., De Troch, M. & Momo, F.R. (2022). Ecological network
 262 assembly: How the regional metaweb influences local food webs. *Journal of Animal Ecology*, 91,
 263 630–642.

264 Strydom, T., Bouskila, S., Banville, F., Barros, C., Caron, D., Farrell, M.J., *et al.* (2022). Food web
 265 reconstruction through phylogenetic transfer of low-rank network representation. *Methods in Ecology*
 266 *and Evolution*, 13.

267 Strydom, T., Catchen, M.D., Banville, F., Caron, D., Dansereau, G., Desjardins-Proulx, P., *et al.* (2021). A
 268 roadmap towards predicting species interaction networks (across space and time). *Philosophical*

269 *Transactions of the Royal Society B-Biological Sciences*, 376, 20210063.

270 Wood, S.A., Russell, R., Hanson, D., Williams, R.J. & Dunne, J.A. (2015). Effects of spatial scale of

271 sampling on food web structure. *Ecology and Evolution*, 5, 3769–3782.