The biological interpretation of probabilistic food webs

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1: Community ecologists are increasingly shifting from a binary thinking of food webs and other ecological networks (e.g., do species interact?) to a more probabilistic perspective (e.g., how likely are species to interact?). Assuredly, the benefits of representing ecological interactions as probabilistic events are numerous, from a better assessment of the spatial variation of trophic interactions to an increase capacity to reconstruct networks from sparse data.

2: 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. This is rarely discussed in the literature, thus impeding our ability to use data on probabilistic interactions appropriately.

3: 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 further enlightening the need to properly define them in their ecological context.

4: 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.

Introduction

Cataloging species interactions across space is a gargantuan task. At the core of this challenge lies the spatiotemporal variability of ecological networks (Poisot *et al.* 2015), which makes documenting the location and timing of interactions difficult. Indeed, it is not sufficient to know if two species have the biological capacity to interact to infer the realization of this interaction at a specific time and space. Taking food webs as an example, a predator and its potential prey must first co-occur on the same territory in order for a trophic interaction to take place. They must then cross paths, which can happen only if their relative abundances in the ecosystem is high enough and their phenology matches. Finally, the interaction occurs only if the predator has a desire to consume its prey and is able to capture and ingest it. Environmental (e.g. temperature and presence of shelters) and biological (e.g. physiological state of both individuals and availability of other prey species) factors contribute to this variability by impacting species co-occurrence and the realization of their interactions. In this context, it is unsurprising that computational methods are being developed in ecology to help alleviate the colossal sampling efforts required to document species interactions across time and space (Strydom *et al.* 2021).

The recognition of the variability of species interactions and the emergence of numerical methods have led ecologists to rethink their representation of ecological networks, slowly moving from a binary to a probabilistic view of species interactions (**Poisot2016StrProa?**). This has several benefits. For example, probabilities represent the limit of our knowledge about species interactions and can indicate the expected frequency of two species interacting with each other. They are also very helpful in predictive models when modeling the spatial distribution and temporal variability of ecological networks, generating new ecological data, and identifying priority sampling locations.

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." Because this ecological representation is still in its infancy, there is no clear definition found in the literature. 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 related to 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. Overall, we argue that probabilities should be better documented, defined mathematically, and used with caution when describing species interactions.

Definitions and interpretations

Overview of interaction probabilities

How are interaction probabilities defined in the literature? It might not be as intuitive as one would think.

- There is a big difference in how we interpret the probability that two species *can* interact (metaweb) and the probability that they *will* interact (realized networks).
- Interaction probabilities can be used to describe Boolean interactions (e.g., the probability that two species interact) and weighted interactions (e.g., the probability distribution of the amount of energy flow between two species).
- In many studies, it is not obvious if authors use interaction scores or probabilities (in the latter case, it is rarely specified what these probabilities truly represent).

Probabilistic metawebs

What does a probability in the context of a metaweb mean?

- It means the probability that two taxa can interact, regardless of biological plasticity, environmental variability, or co-occurrence.
- One observation is enough to set this probability to one.
- Can we turn this into a local network realisation that is also probabilistic and intuitive?

Papers: (**Strydom2022FooWeb?**)

Probabilistic local networks

What does a probability in the context of a local network mean? A cautionary tale of how we define probabilities.

- It means the probability that two taxa will interact at a given location.
- What do we mean by saying that two taxa will interact? We usually mean that at least one individual from one group will interact with (e.g., predate) at least one other individual from the other group.
- The probability is conditional on the environmental and local abundance contexts.
- We should expect a certain number of interactions to be realized depending on the probability value. This number depends on the number of trials, which also depends on the ecological context (e.g., environmental conditions, scale) in which probabilities were estimated. This is in contrast with probabilities in metawebs.

Scaling

Spatial and temporal scales

How do interaction probabilities scale spatially and temporally?

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

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

Papers: there might be something in these McLeod *et al.* (2020); (**McLeod2021SamAsy?**); (**Wood2015EffSpa?**)

Taxonomic scale

How do interaction probabilities scale taxonomically?

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

Figure: 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.

Concluding remarks

Here we present some advice moving forward.

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

References

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