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WE NEED TO TALK ABOUT THE TOPOLOGY OF INTERACTION NETWORKS

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Abstract: In the past decades, studies on interaction networks may have zoomed in too much on arbitrary subsets of ecological communities. Consequently, the current "nestedness paradigm" is biased towards restricted taxonomic groups. This bias leads to a myopic understanding of ecological functions and ecosystem services, with serious consequences for basic and applied ecology.

Keywords: assembly rules; ecological synthesis; network science; species interactions; theoretical ecology.

Everything in the world is connected. From public transport lines to smartphones in our pockets, no entity operates alone (Vespignani 2018). Connections are also crucial for reaching most of UN's Sustainable Development Goals (SDGs, United Nations 2015), considering how interactions between humans, animals, plants, fungi, microbes, and their environments affect crop productivity and disease outbreaks, for example (Stanworth *et al.* 2024). This interconnectedness is scientifically daunting, and zooming into interaction subsets is tempting. However, what if we have zoomed in too much?

Let us zoom out a little. Network science, with roots back in the 18th century, became a pervasive approach to study connections. In ecology, it is widely used to study species interactions. Initially focusing on unweighted unipartite foodwebs in the 1880s, between the 1980s and the 2000s, the hype shifted to weighted bipartite mutualistic networks (Ings & Hawes 2018). Since then, a new paradigm has emerged, as we have assumed that mutualisms were nested like Russian dolls (Bascompte *et al.* 2003). In other words, the interactions of least connected species would represent a subset of the interactions of the most connected species. However, how well does the nestedness paradigm represent real-world systems? Recent analyses and models show that we need to talk.

To smooth our conversation, let us consider the old Buddhist parable of the elephant and the blind monks. It seems that, like those monks, we all have been looking only at network pieces instead of entire systems, which has led to a myopic perspective. This is worrisome, as the nestedness paradigm predominates not only in basic ecology but is also a fledging standard for conservation and restoration, in the sense that it is assumed that a pristine or fully restored interaction network should have a nested topology, especially in the case of mutualisms (Howe 2016, Windsor *et al.* 2022, Lussier *et al.* 2024). This raises serious concerns, as our studies and many others have shown that nestedness is more like a by-product (Staniczenko *et al.* 2013, Valverde *et al.* 2018) than a true topology observed in natural systems. In addition, nestedness as measured by binary indices is even more context-sensitive than its weighted versions (Corso *et al.* 2015), missing finer details about realized niches (Fründ *et al.* 2016), so network studies at a local scale should prefer using weighted nestedness metrics whenever possible.

Therefore, using nestedness as a proxy for ecosystem health can easily lead to misguided inferences and recommendations.

Gold standards should always be taken with a grain of salt. Divergent discoveries have led different research teams, including ours, to question the nestedness paradigm (Dormann 2023, Blüthgen & Staab 2024). For example, when studying networks formed by oil-collecting bees and oil flowers, we noticed, on the one hand, that they were much more nested and less modular than many pollination networks were (Bezerra *et al.* 2009). On the other hand, pollination networks formed by mixed taxonomic groups were reported to be non-nested, and rather modular, such as the filter bubbles observed on social media (Bezerra *et al.* 2009).

After taking a close look at the divergent evidence discussed in the previous paragraphs, we felt like the blind monks examining the elephant. At that time, in the vast majority of studies, ecologists were analyzing interaction networks at a local scale formed by a single taxonomic group. Therefore, they were looking at unrepresentative pieces but drawing conclusions for the whole (Mello *et al.* 2011). This strong bias caused by spatial scale, taxonomic scope, and sampling methods, which markedly differ between studies conducted by different research groups, was only recently investigated in detail (Brimacombe 2024). Network topology, especially when measured with binary metrics, is strongly dependent on spatial scale, which varies considerably across studies (Corso *et al.* 2015, Poisot *et al.* 2020, Brimacombe *et al.* 2023). Thus, we need to consider that a monolayer interaction network at a local scale should be delimited based on the ecological function, for example pollination, that results from the interaction type under scrutiny. The relationships among spatial scale, taxonomic scope, and ecological function are more intricate than they initially appear, as we discuss in the following paragraphs. The elephant's leg may feel like a temple column, but it is neither an elephant nor a temple.

Sometimes, a leg is just a leg. Over time, we discovered that other mutualistic networks, such as those formed by bats, birds, bees, moths, wasps, ants, and flies, but especially those with mixed taxonomic groups (Donatti *et al.* 2011, Mello *et al.* 2011, Sarmento *et al.* 2014, Schleuning *et al.* 2014, Costa *et al.* 2016), were incompatible with the nestedness paradigm. Furthermore, in addition to nestedness and modularity, some networks seem to have a gradient topology, with highly specialized, non-overlapping interactions (Fonseca & Ganade 1996). A fourth structural archetype, a compound topology (later referred to as "in-block nestedness", Lampo *et al.* 2024), which was proposed years ago as a modular network with internally nested modules (Lewinsohn *et al.* 2006), could be the key to integrate divergent evidence. This realization allowed us to conclude that, although nestedness and modularity are not actually two sides of the same coin (Fortuna *et al.* 2010), there is a balance between those two archetypical topologies, which depends mainly on the diversity contained in the network. As we zoom out from single-taxon systems, embracing whichever groups contribute to the ecological function under scrutiny at a site of interest, nested subnetworks aggregate into the elephant of network topology.

Aiming to look at the whole elephant, the Integrative Hypothesis of Specialization (IHS, first proposed by Pinheiro *et al.* 2016) reconciles divergent evidence and explains the coexistence of seemingly mutually exclusive topologies. For the sake of generality, we refer to the two groups in a bipartite network as consumers and resources. The IHS is based on three principles (formulated in detail by Pinheiro *et al.* 2019). First, the unique characteristics of each resource species affect its use by each consumer species. Second, any consumer mutation that improves the use of one resource also tends to enhance its use of similar resources while diminishing the value of dissimilar resources. Third, a consumer's ability to use a resource at a given time results from its previous adaptations and maladaptations. These three principles articulate five parameters that affect one another: (1) resource species richness, (2) consumer species richness, (3) method to generate the initial matrix, (4) maximum resource dissimilarity, and (5) number of resource clusters. Among those parameters, resource dissimilarity stands out as the most important in determining where one topology ends and another begins.

With this structure, the deductive argument of the IHS leads to the conclusion that the topology of an interaction network is primarily determined by resource dissimilarity from the consumer's perspective. This conclusion leads to secondary deductions, such as that networks with high resource dissimilarity tend to have a modular topology, whereas networks with low resource dissimilarity become nested. A compound topology would emerge in sufficiently large networks that contain high resource dissimilarity distributed in clusters. After being conceived as a graphical model (Pinheiro *et al.* 2016), which was later turned into an algorithmic model that underwent a proof of concept through computer simulations (Pinheiro *et al.* 2019), predictions deduced from the IHS were submitted to several empirical tests showing that compound topologies are indeed much more common than previously thought (*e.g.*, Pinheiro *et al.* 2022). Interaction networks, therefore, resemble filter bubbles filled with Russian dolls.

A good example of this kind of compound topology was observed in a system formed by small mammals and their ectoparasitic fleas (Felix *et al.* 2022). By considering different orders of mammals together at both the local scale and the continental scale, the interaction constraints were strong for the ectoparasites (*i.e.*, not all flea species can infest all mammals), consequently leading to the formation of modules in most networks (Felix *et al.*, 2022). In addition, those modules had an internally nested structure, as ectoparasites have more freedom of interaction after they overcome those major interaction constraints. A compound topology also becomes evident when the taxa included in a network are even farther phylogenetically apart. This is the case for a nocturnal pollination network formed by bats and hawkmoths (Queiroz *et al.* 2021).

Both its logical structure and the empirical support reported in the studies cited above indicate that rather than being just a hypothesis, the IHS could be seen as a budding scientific theory, offering testable predictions based on operational variables within a coherent framework, in addition to a dedicated toolset (check out a reproducibility tutorial at: https://github.com/marmello77/Restricted-Null-Model). Moreover, it could become an axiomatic theory of the semantic type, which is rare in ecology and represents a significant advancement (Travassos-Britto *et al.* 2021). Other models also aim at explaining network assembly but have much broader scope, such as allometric trophic networks (Martinez 2020), or narrower scope, such as a microbial network model (Flores *et al.* 2013). There are even other models focusing on compound topologies, but they differ from the IHS in that they propose that nestedness limits modularity and not the other way round (Palazzi *et al.* 2019) or assume an intrinsic or necessary relationship between topology and stability (Lampo *et al.* 2024). The IHS, in turn, focuses on explaining the assembly rules of archetypical topologies in the most parsimonious way, without evoking a circular relationship with stability. Its semantic nature and direct mapping to measurable operational variables make it quite helpful for studying real-world systems. Nevertheless, all comprehensive models of the assembly rules of interaction networks, which consider that different topologies may arise from an interplay between key factors, should be studied and thoroughly tested, as they have different scopes and thus serve different purposes.

In summary, together as a community, we have learned a lot in the past decades, coming a bit closer to a Buddhist "middle way". The elephant offers enough to marvel, even after recognizing its parts as what they are: elements of a bigger picture. It is now time to broaden our perspective, so we can not only improve our theoretical understanding of species interactions but also allow its application to the challenges posed by the SDGs.

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