A novel semantic theory of the assembly rules of interaction networks

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Abstract

In the web of life, every interaction between species tells a story of cooperation, conflict, or chance. For centuries, ecologists have charted these stories to better understand phenomena such as pollination and disease. We have been using the lens of network science to distill them into topological patterns such as nestedness or modularity. Yet, like in the old buddhist parable of the blind monks and the elephant, these separate views have often missed the bigger picture. In this Perspective, we review the history of topological studies of interaction networks, challenge the "black-and-white" paradigm, and point out a way forward: the Integrative Theory of Interaction Networks (ITIN). This theory unveils the logic of how interaction networks assemble through sequential, rule-bound processes shaped mainly by resource dissimilarity and interaction type. We show that compound topologies are likely the norm in function-oriented, taxonomically-inclusive, well-sampled networks. ITIN is deductive, predictive, and testable, mapping from first principles to real-world systems, thus helping us grasp "the whole elephant". As ecologists confront the polycrisis, from irreparable biodiversity loss to global health threats, ITIN offers a coherent framework to understand, predict, and restore the threads of the web of life.

Introduction

Ecological interactions between individual organisms of different species (i.e., species interactions) have drawn the attention of scientists, philosophers, and stakeholders for millennia [1]. This broad family of phenomena ranges from mutualistic (both sides gain fitness) to antagonistic (one or both sides lose fitness), and result in crop pollination, plant protection, seed dispersal, parasitism, and disease, among many other outcomes [2].

Species interactions have been studied from multiple perspectives and using numerous approaches [3]. One approach that has become mainstream is network science, an interdisciplinary field that provides not only tools for data analysis but also concepts that may be integrated across scientific disciplines to obtain new insights [4]. The study of interaction networks as we know it began in the late 19th century (or even earlier), through a classical effort to understand complex relationships in lake food webs [5]. Only more recently, between the late 1980s and early 2000s, the focus slowly shifted from food webs to mutualistic networks [6]. The intriguing structural patterns of interaction networks, also known as topologies, has become a fashionable research topic in itself, irrespective of the effect they may, or may not, have on the community and ecosystem dynamics [7]. This focus, although being an important first descriptive effort, seems to have led to worrisome epistemological biases, such as confounding the ecological processes with the network patterns they generate [8].

Biases in topological studies can be compared to the ancient Buddhist parable of the blind monks and the elephant (Figure 1). Once upon a time, a group of blind monks heard that a huge, strange animal had arrived near the temple, and, curious to know what it was like, decided to examine it by touch. Each monk felt a different part of the elephant and drew a different conclusion. To one monk, the trunk felt like a snake. To another, the ear felt like a fan. To others, a leg felt like a tree trunk, the belly like a wall, the tail like a rope, and a tusk like a spear. Each monk described the elephant based on their separate experience, illustrating how partial perspectives can lead to incomplete or conflicting understandings of a greater truth.

Figure 1: The blind monks and the elephant. As in the old Buddhist parable, we have been analyzing only network parts but drawing conclusions for the whole. Currently, mutualistic networks are generally assumed to be nested and antagonistic networks, modular. Gradient networks have been seldom considered, usually being associated with parasitism. Much fewer studies discussed compound topologies, although these have been drawing more interest lately. The image was modified from the original *ukiyo-e* print illustration by Itcho Hanabusa (Wikimedia Commons, public domain).

Not so different from those monks, most ecological studies have focused on interactions in only one context, ignoring that sites with different abundances will yield different networks and observed interaction preferences [8]. Moreover, by focusing on isolated interaction types, while trying to draw conclusions for all types, those studies ignore how interactions create complex systems with emergent properties [9]. Recent advances, however, show that networks require a more integrative approach to be fully understood [10]. Integration is especially needed for understanding not only the topological patterns observed in nature, but also how they emerge as a result of ecological and evolutionary processes. In other words, the assembly rules of interaction networks.

In this Perspective, we aim to demonstrate how different views about network topologies and their assembly rules could be integrated, in order to help refocus our research efforts. First, we synthesize the history of network topology studies. Second, we show how the Integrative Hypothesis of Specialization (IHS) provides a comprehensive approach to see the whole elephant, in addition to shedding light on the processes behind the patterns. Third, we point to new directions, as after a series of developments, empirical tests, and additional synthesis, IHS is evolving into a semantic theory, the Integrative Theory of Interaction Networks (ITIN), which we first introduce.

Archetypal topologies

A seminal study ahead of its time in the mid-2000s proposed a taxonomy of network topologies [11]. From its perspective, there would be four archetypal topologies (Figure 2) that capture the essence of most real-world systems (but see an alternative taxonomy [12]).

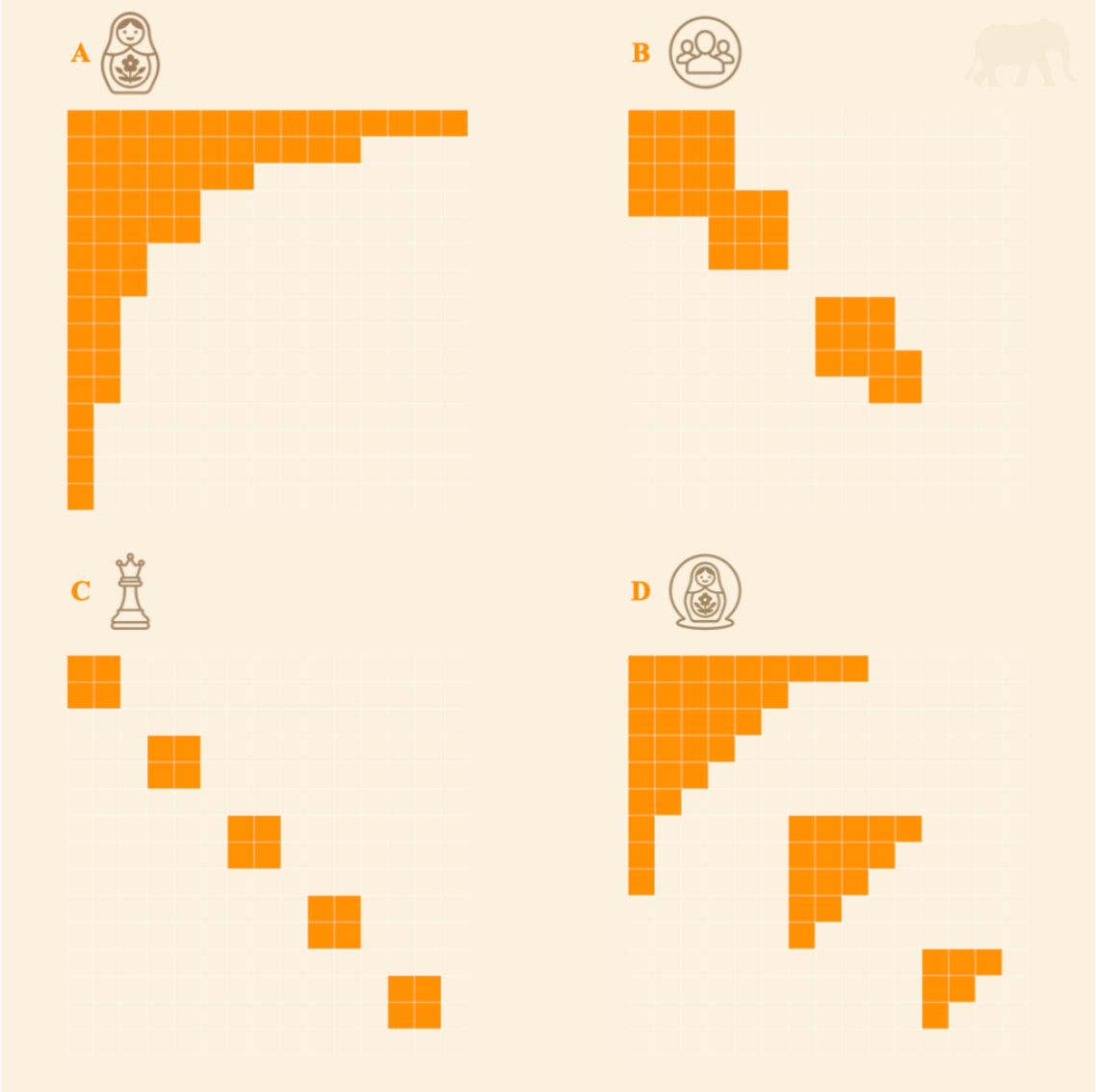

Figure 2: The four archetypal topologies. The conceptual matrices presented here were modified from those originally proposed in a seminal paper [11]. (A) A nested topology resembles a Russian doll: nodes with fewer links are connected to a subset of the links captured by the most connected nodes, sequentially, for the rows and columns separately. (B) The modular topology looks like the filter bubbles observed in social media, as the network is divided into cohesive subgroups of nodes (i.e., modules), more densely connected to one another than to other subgroups. (C) In a gradient topology, as in a chess board, there is little to no overlap in the links made by different nodes, and there are also much fewer links than in a modular network, leading to the formation of truly disconnected components. (D) A compound topology combines a modular structure in

the network, with a nested structure within its modules, resulting in “Russian dolls trapped inside filter bubbles”, and tends to be larger than a modular network.

The first archetype, nested networks (quantified as nestedness), emerges when the links made by species with fewer interactions represent a subset of those made by species with more interactions, sequentially. The second archetype, modular networks (quantified as modularity), represents systems that consist of cohesive subgroups of species (i.e., modules), which are densely interconnected but have fewer interactions with other subgroups. Gradient networks are the third and least studied archetype, usually observed when sampling in steep environmental gradients, leading to few links and almost no overlap in the interactions made by different species, therefore forming several small components (i.e., totally disconnected subgroups). Finally, the fourth archetype, compound networks, combines modularity in the network and nestedness within its modules.

Lately, different research groups have independently proposed topologies similar to the compound archetype, with slight variations in conceptualization and operationalization [13–15]. Their structure would in general resemble a polycentric heterarchy [16], almost equivalent to a dissortative network [17]. That is, in such a network there are differences in influence between nodes, with one or a few nodes dominating each module and playing the role of module hubs.

Despite the multiple options provided by the four archetypal topologies, another seminal study published a little earlier proposed the universality of nestedness in mutualistic networks [18]. By comparing food webs, pollination, and seed dispersal systems, the study invoked co-evolutionary arguments to conclude that mutualisms would form highly cohesive, nested networks in which a core of generalist species would drive the dynamics and maybe the evolution of the entire local community. In contrast, antagonisms would be characteristically modular, as traditionally assumed [19]. The almost overlooked gradient topology, which was not considered then and still remains poorly studied [20], would be found only in the most specialized systems with high interaction intimacy [21] or along steep gradients with substantial turnover in species [22].

Since nestedness was advanced, it became the dominant view in the study of interaction networks, especially mutualistic ones. Most studies have been either trying to validate a nested topology for the respective system of interest or aiming to link nestedness to the stability of the entire community, sometimes resorting to circular reasoning [23], despite how controversial this view has always been [24]. Nestedness has been pointed out as an artifact [25] or a simple byproduct of abundance [26], and not a pattern derived from a clearly defined process [27]. In addition, nestedness is also frequently found in antagonisms [28]. A striking critique emerged from a study that revealed conceptual flaws in early nestedness indices and algorithms [29]. The high nestedness scores reported for many systems were artificially inflated, and, as a more accurate index was proposed, it became clear that nestedness was indeed highly variable and lower on average than previously measured in many empirical networks [30], and even lower than expected by chance from differences in abundance [31].

What should have been the final blow to the universality of nestedness came from a naturalistic perspective. Different studies started to point out that the mutualistic interactions sampled at a local scale and low completeness levels, included in popular databases, only represent fragments, not entire networks [32–34]. This deserves attention considering that ecological functions, such as pollination, and its derived ecosystem services, such as crop pollination, are not delivered by single taxa, but by guilds composed of several taxa acting together at a local scale.

Therefore, variations in the definition of nestedness, conceptual limitations in its proxies, and a narrow taxonomic focus have raised questions regarding its universality. Nonetheless, nestedness remains a central concept in the study of mutualistic networks and continues to provide a benchmark for assessing the structure of mutualistic interactions across pristine, degraded, and restored environments [35]. More recently, however, studies started adopting conceptually refined approaches that offer fresh perspectives on network topology [36].

A way forward

Given the challenges presented above, a new theoretical perspective was needed to make sense of patterns and processes. The Integrative Hypothesis of Specialization (IHS) was proposed as a way forward, originally presented as a graphical model [37], and

197 subsequently mathematically formalized as an algorithmic model [38]. IHS was built as a
198 minimalistic mechanism that integrates sequential processes, which themselves
199 represent the mechanistic assembly rules of interaction networks.

200 In short, IHS proposes that interaction constraints of geographic, morphological,
201 physiological, or behavioral nature would lead to the formation of layers and modules in
202 interaction networks. Within these modules, the specialisation-niche breadth trade-off
203 predominates once the constraints are overcome. Consequently, we can deduce from
204 IHS that the assembly rules of interaction networks include a threshold of influence of
205 different ecological and evolutionary processes at a given hierarchical level (entire
206 network, layers, modules, motifs, and dyads), which determines which archetypal
207 topology predominates at that level.

208 To evaluate the four archetypal topologies with as much generality as possible, IHS
209 assumes that all interaction types can be viewed as pure consumer models, similarly to
210 other network models [15,39,40], but aiming at higher generality and parsimony. We know
211 that most interactions are more complex than this, but this simplification of reality has
212 proven to be surprisingly efficient in deducing topology. IHS is based on three first
213 principles that apply to evolving consumer-resource relationships in general [41]: (i) each
214 type of resource has a set of characteristics that affect its use, and the types of resources
215 may be more or less similar to each other in these characteristics; (ii) a consumer's
216 mutation that increases its ability to use a given resource tends to improve its efficiency
217 on similar resources, but worsen its on different resources, generating clusters of usable
218 and non-usable resources; and (iii) a consumer's ability to use each resource in a given
219 cluster at a given time is the result of its previous adaptations and maladaptations (i.e.
220 mutations are small). Based on this, the free parameters of IHS are: (a) consumer
221 species richness, (b) resource species richness, (c) method used to generate the initial
222 innate performance matrix (innate method), (d) maximum dissimilarity between two
223 resource species (maximum dissimilarity), and (e) number of resource species clusters
224 (number of clusters).

225 The structure of IHS leads to the logical conclusion that the topology of a given
226 interaction network depends mainly on the dissimilarity between the resources
227 contained within it, from the point of view of consumer adaptations [41]. In turn, this
228 conclusion leads to different secondary deductions, for example: the more dissimilar the
229 resources, say in traits, the more likely a modular topology emerges. Assuming that

most resources in nature tend to be organized in clusters [42], very large networks with high heterogeneity would tend to have a compound topology: modular across clusters, but nested within. In turn, small and homogeneous networks, which would actually represent clusters, would tend to be nested. At the extreme of this continuum, small networks with very high resource dissimilarity, probably resulting from very high interaction intimacy or steep environmental gradients, would be organized as a gradient.

These deductions are valid mainly for interactions studied at the community level, although further expansions of IHS to interactions between individuals have already been made [43]. Although many studies propose that coevolution is an important driver of interaction networks [44], IHS assumes that their structure can emerge without *mutual* adaptation between consumers and resources. This does not mean that coevolution is not important for understanding species interactions in general. Rather, within the scope of IHS, coevolution is not *necessary* to explain the assembly rules that generate the four archetypal topologies.

A novel theory

Starting from the realization that IHS already has all the characteristics of a semantic theory [45–47], all that remains is to formalize it as: the Integrative Theory of Interaction Networks (or ITIN, for short).

To build a novel semantic theory of the assembly rules of interaction networks, it is essential to understand the concepts and assumptions that guide this approach. Models of this type are constructed theoretically and do not directly depend on real-world data, which allows for a more flexible and adaptable approach to the conceptualization of the expected patterns in natural phenomena. The development of these models involves the application of a mathematical or logical formalism to deduce the models from the axioms, allowing a meaningful comparison with the observed phenomena. This crucial step has already been taken in building the algorithmic model used to make the proof of concept of IHS [41].

Since its proof of concept, IHS has undergone a series of empirical tests of several predictions deduced from its central axiom. IHS proved to be capable of explaining the multiplicity of network topologies in real-world networks of pathogen infection [37], parasitism [48], seed dispersal [49], pollination [50], resin collection [51], burrow sharing [52],

predation [53], resource partitioning [54], multilayered interactions [55], and food crop management [56], among many other examples, widely extending its original domain of validity.

Later studies also demonstrated that compound and modular topologies are actually much more common than previously thought [14], as expected from theory. Most interaction networks, in the end, resemble filter bubbles filled with Russian dolls, and a good example of this kind of compound topology was observed in a system formed by small mammals and their ectoparasitic fleas [48]. So, if modular and compound topologies are the most common structures observed in well-sampled, taxonomically comprehensive interaction networks studied at different spatial scales, from local to continental, what about nested and gradient topologies? Explaining the logical relationship between archetypal topologies is the next step in the development of our novel theory (Figure 3).

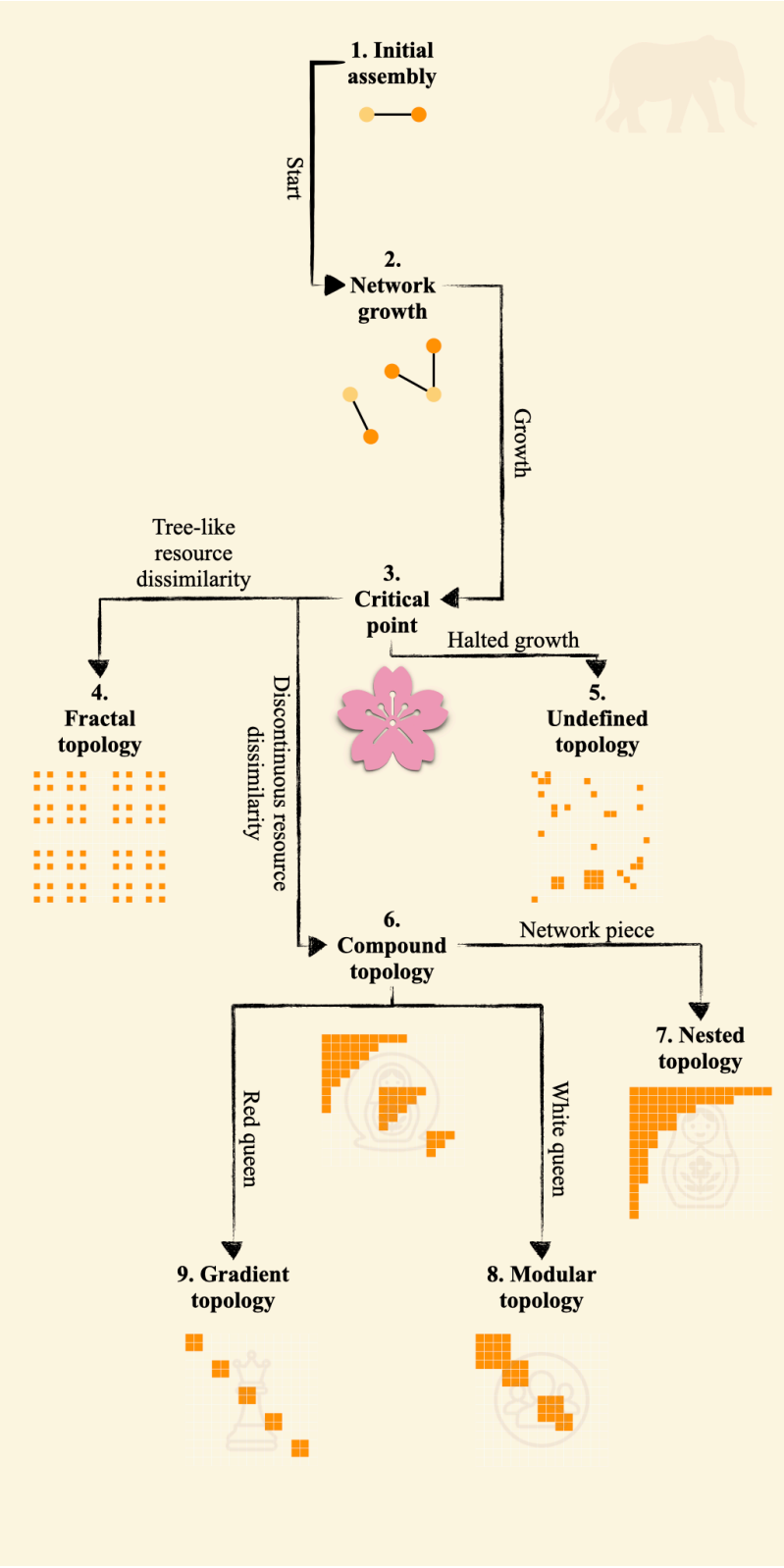

Figure 3: A roadmap to the archetypal topologies of interaction networks according to the Integrative Theory of Interaction Networks (ITIN). (1) As an example (see section Three archetypal stories), two species arrive at an open area after a disturbance, such as a forest fire, and begin to interact. (2) Ecological succession follows, bringing more

280 species and interactions, forming a shifting topology that may resemble a random
281 network. (3) A critical point is reached, a phase transition, after which the network may
282 or may not blossom, giving rise to different stable topologies. (4) When resource
283 dissimilarity follows a tree-like, hierarchical structure, the network becomes fractal,
284 resembling a Cantor matrix. (5) If network growth is halted by external factors, such as
285 hunting, its topology remains undefined. (6) When resource dissimilarity is
286 discontinuous and the network continues to grow, a compound topology emerges, with
287 modularity across scales and nestedness within modules. (7) Nested topologies,
288 therefore, represent the internal structure of modules, not the whole mature network. (8)
289 In mutualistic systems (White Queen Hypothesis), resources strengthen associations
290 with better consumers, leading to modular or compound topologies. (9) In antagonistic
291 systems (Red Queen Hypothesis), escape dynamics promote specialization, resulting in
292 gradient topologies.

293

294 Conceptual examples might help understand our rationale (Box 1).

295 *Box 1: Three archetypal stories*

296 The Integrative Theory of Interaction Networks (ITIN) is a description of how real-
297 world networks develop over time. The following "stories" exemplify possible paths
298 towards an observed network topology.

299 *The niche sequence along a steep gradient story*

300 Imagine several plant species from the same family, growing along a mountain's
301 altitudinal gradient. Evolved from the same ancestor, they still share most of their niche
302 characteristics, but differ, say, in frost tolerance. Each species has thus a position along
303 the growth-frost tolerance gradient. A set of herbivore species adapted to feeding on this
304 family will feed on all species. The network therefore will be fully connected. Over
305 time, slow-growing, high-altitude species will invest more in chemical defense, as each
306 herbivore attack leads to tissue loss, which they cannot readily compensate for by fast
307 growth given that they experience a short growing season. In response to the increased
308 chemical anti-herbivore defense, some herbivores will start avoiding these species,
309 while others will adapt and even specialize on them. The resulting topology will depend

on the degree of separation: if almost every herbivore becomes a specialist, we end up with a modular network. If most herbivores exhibit some lower preference for the species a bit higher up and lower down the gradient, we end up with a gradient topology.

The abundance story

Most species are rare [57]. The causes are multifaceted, from neutral ecological drift to competitive hierarchies [58] or statistical inevitability of random processes [59]. Either way, the evolutionary pressures to evade an abundant predator are much stronger than those to evade a rare one. Antelopes run (almost) fast enough to evade a cheetah, not only fast enough to outrun the much slower jackal. As a consequence, all antelopes face predation by common predators, and common antelopes face all predators, simply as a matter of probability. We can compute this as the matrix product of the abundance vectors of antelopes and predators, normalised to sum to 1. The resulting network is nested. Interestingly, two common predators may compete for common prey, leading to specialisation *for the most common prey* only. This will be visible as anti-nestedness for the most common prey, but still a strong nestedness signal overall. This makes "nestedness" an awkward concept: the observed competition signal leads to a *reduced* nestedness, while the overall topology is still highly nested.

The introduced species story

The effect of adding a new species to a network is likely to be extremely case-specific. Imagine a pollination network to which a non-native plant species is added [60]. If that species is similar in traits to species already present in the network, we can expect it to "slot in", maintaining whatever topology existed before. However, if the plant's attractive traits vastly exceed those of the existing species (e.g., flowers that are more nectar rich), it may actually withdraw flower visitors from other plants. The network topology is dependent on what happens next. If the pollinators keep their visitation pattern, but prefer the new plant species, then the network becomes a bit more nested. If, however, the new plant leads to a strong re-alignment of trait preferences, it may lead to network fragmentation, and a more modular structure. The point here is that the topology, in concert with the relevant traits, will in the end help us to understand what happened.

ITIN's mechanism sets the thresholds that define when one topology ends and another begins. In the simplest and least realistic scenario, considering only a tree-like distribution of resource dissimilarity, such as in a dendrogram, with progressive dissimilarity between hierarchical levels, the fundamental topology of interaction networks should be fractal, like in a Cantor matrix [61]. Nevertheless, this should not be expected in the real world, as virtually all trait distributions are discontinuous [42]. Considering even more realistic scenarios, sometimes network assembly is halted by a process, such as overhunting, that prevents the addition of new nodes or the establishment of links between them. In this case, the network might not reach an archetypal topology, remaining frozen in an undefined transitional topology.

If the network continues to grow, it might develop to a point where it becomes compound. First, because not all consumers are empirically able to use all resources [62], this leads to the formation of layers and modules. Second, because after constraints are met, there is more freedom of association within a module. Consequently, neutral processes leading to differences in abundance [63] or universal network assembly processes such as preferential attachment [64] should lead to a nested structure within the modules. Nested topologies, therefore, would represent pieces and not entire networks.

Two processes could further shape interaction networks into the remaining archetypal topologies (Figure 4). On one hand, if the interaction type is antagonistic, according to the Red Queen Hypothesis [65] the resources would tend to escape the consumers, reducing niche overlap and even the total number of links observed, maybe even resulting in the extinction of some consumers, leading to a gradient topology. On the other hand, if the interaction type that defines the links is mutualistic, then the resources would tend to strengthen their association with the most advantageous consumers, while escaping the worst consumers, which could be called a "White Queen Hypothesis". This would lead to a truly modular topology, with smaller modules that are not internally nested, because freedom of association is still limited after the main constraints are resolved.

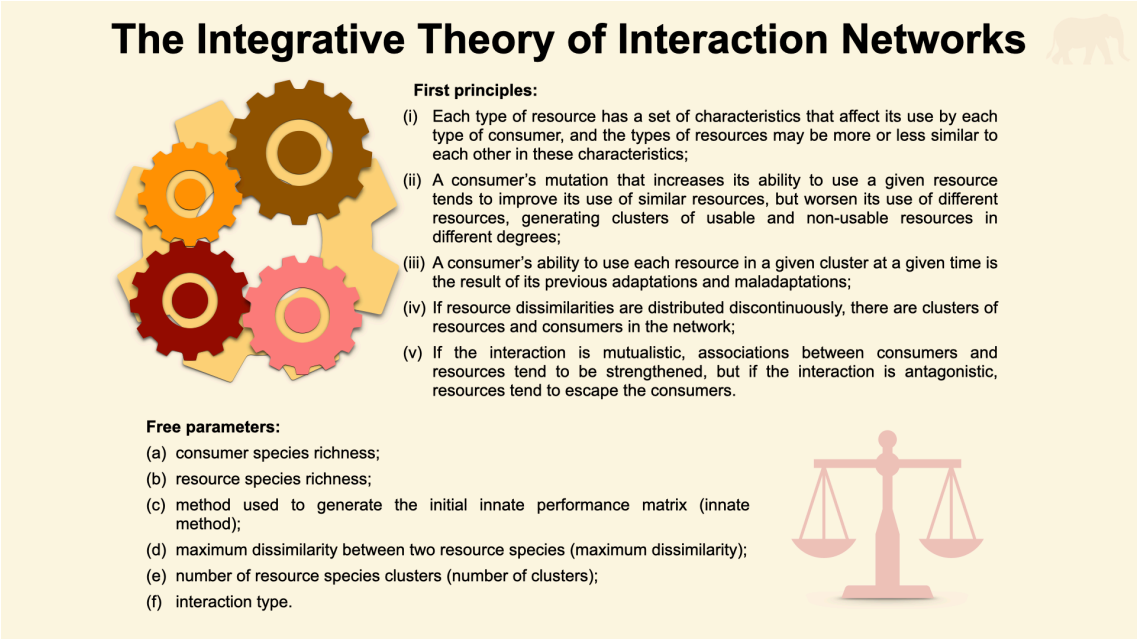

Figure 4: A novel semantic theory of the assembly rules of interaction networks. As a development of the Integrative Hypothesis of Specialization (IHS), the Integrative Theory of Interaction Networks (ITIN) has been expanded by the addition of two first principles and one free parameter. This enhances its ability to explain which processes determine where one archetypal topology ends and another begins. See also Figure 3.

Therefore, in addition to the first principles considered in the original IHS, ITIN also includes the following assumptions: (iv) if resource dissimilarities are distributed discontinuously, there are clusters of resources and consumers linked within the network; and (v) if the interaction is mutualistic, associations between consumers and resources tend to be strengthened, but if the interaction is antagonistic, resources tend to escape the consumers. Consequently, ITIN includes an additional free parameter: (f) interaction type.

From description to explanation

As discussed in the previous sections, the study of interaction networks has been guided by a multitude of metrics. Connectance, modularity, nestedness, specialization: each captures a piece of the puzzle. Yet, as in the parable of the blind monks and the elephant, these fragmented perspectives did not converge into the bigger picture. The result has been a proliferation of metrics that quantify patterns but do not explain

391 mechanistically how they arise or what they mean for ecological functions and
392 ecosystem services [8].

393 Without a mechanism that ties pattern to process, our ability to predict and intervene
394 remains limited. Conservation biologists struggle to anticipate how seed dispersal
395 networks will respond to human disturbances [66]. Agroecologists seek to design
396 sustainable crops but are left with taxon-biased network fragments that overlook the
397 functional guilds actually delivering vital ecosystem services [67]. Epidemiologists face
398 difficulties estimating the risk of pathogen spillover without understanding the assembly
399 rules that govern host-pathogen networks [68]. The black-and-white paradigm of network
400 topology has constrained both scientific inference and practical action, leaving us only
401 with numbers yet still in search for meaning.

402 ITIN provides this much needed meaning. By rooting network topologies in first
403 principles and free parameters mappable into operational variables, it shifts the focus
404 from static descriptors to dynamic assembly rules. It explains not only what structures
405 we observe, but why they emerge and where the thresholds lie between one topology
406 and another.

407 Practical applications

408 As an empirically tested semantic theory, ITIN might be used to help solve problems.
409 Not only theoretical puzzles, but also practical challenges within the frameworks
410 provided by the UN's Sustainable Development Goals [69] and the One Health Initiative
411 [70] (Figure 5).

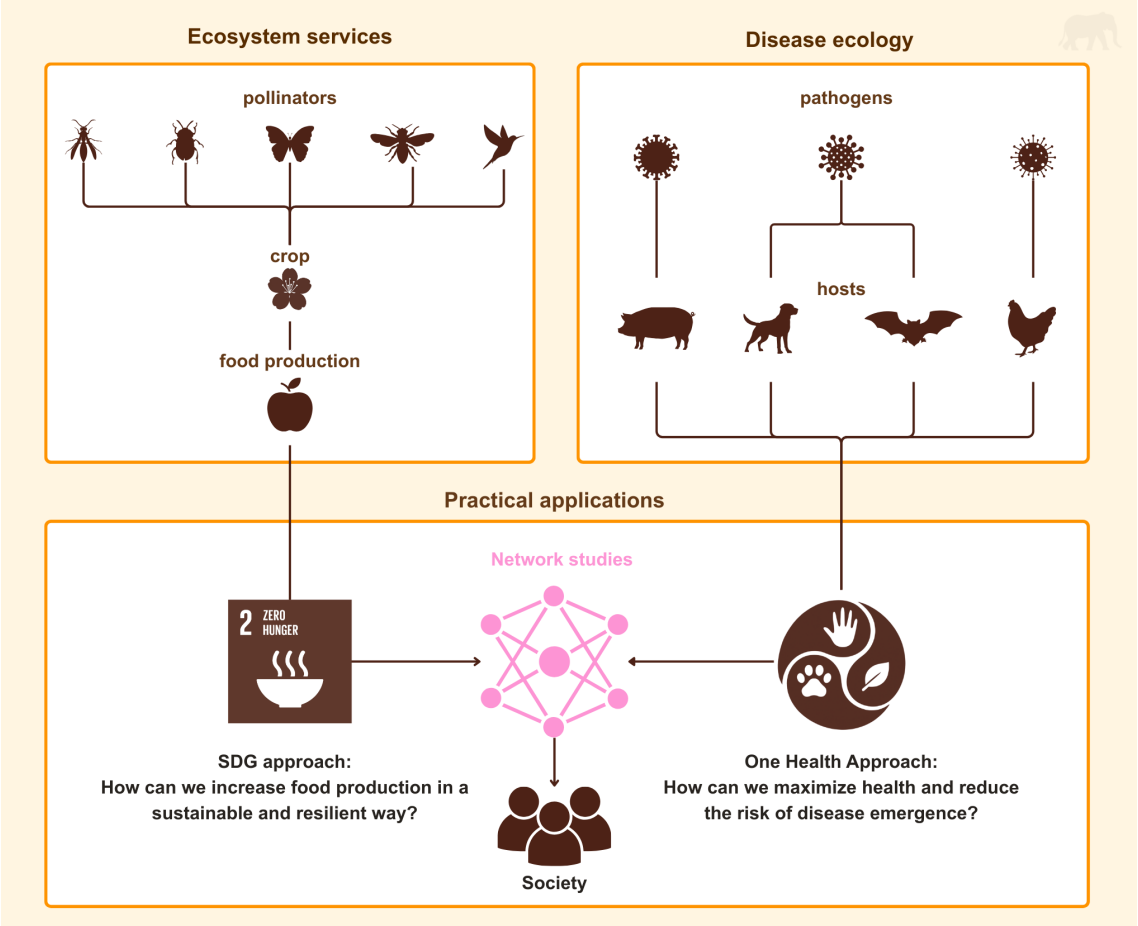

Figure 5: Conceptual framework illustrating how network studies can help translate knowledge about ecosystem services and diseases into solutions to real-world problems. On the left, pollinators contribute to ecosystem services such as crop pollination, supporting food production. On the right, animal hosts and pathogens represent the ecological interactions underlying disease emergence. By using network science, including the new framework provided by ITIN, both research areas can be aligned with the global agendas of Sustainable Development Goals and One Health.

The central driver of network topologies according to ITIN is resource dissimilarity. In order to develop practical solutions, it is of paramount importance to sample entire local networks responsible for a given ecosystem service of interest. A function-oriented modelling of interaction networks and the ecosystem services they deliver requires collaboration beyond taxonomic boundaries [9]. For example, if the aim is to restore or improve pollination services delivered to a given crop, all functional groups (e.g., buzz pollinators and oil-collectors) that compose the local guild should be considered [71].

After replacing the black-and-white paradigm and focusing on functions and services, another step would be to carefully consider what kind of phenomenon is actually being represented as a network. In other words, what is flowing from node to node: matter, energy, or information [10]? A network approach may help us better predict how pathogens flow from one host to the other, leading to spillover or outbreaks [72]. Such a network approach could be guided by ITIN adapted to transient flows [73]. This area of application highlights the need to invest in initiatives targeted at biosurveillance and big data integration [74].

There are critical interfaces across crops and diseases as well [68], uniting the ecological and social layers of real-world networks [75]. It is vital to better understand how the relationships between humans, wildlife, crops, and livestock determine economic and health gains and losses [76]. ITIN can be also helpful in this human-domestic-wildlife interface, considering the huge resource dissimilarity observed in extensively changed social-ecological systems [77].

Moving from the entire network to its layers and modules, another practical application of ITIN is the use of centrality metrics as proxies for the concept of keystone species [78]. Within this family of metrics, some have been pointed out as very useful not only for identifying the most important species responsible for maintaining different ecosystem services [71], but also to help select species to improve agroecosystems and crops in general [79], and identify pathogen superspreaders [80]. Now it is also possible to assess the topology of multilayer networks [81], as well as the multilayer centrality of a species in such a network [82], especially considering thresholds in resource dissimilarity that create constraints for consumers between and within layers.

Testing for archetypal topologies

Traditionally, ecologists have used different topological indices of avoidance [83], connectance [84], complementary specialization [85], nestedness [86], or modularity [87], just to give a few examples, to measure the structure of empirical or synthetical networks. Most commonly, the next step is to test whether the observed index is significantly different from expected by chance [31]. However, neither a topological score nor a P-value alone can mechanistically explain the structure of empirical networks if the analysis is not guided by a hypothesis-oriented, strong-inference framework [88].

Attempts to provide such a framework have been recently made in the case of nestedness [89] and compound topologies [48]. Similar hypothesis-driven efforts are still lacking for the other two archetypal topologies, modular and gradient, as is an information-theoretical way to compare the fits of these four archetypal topologies to the data. Together, these advances and gaps signal that we need to work further on conceptualization and operationalization to better understand network topologies and, most importantly, their assembly rules, so we can improve our mechanistic understanding of interaction networks.

To help fill these gaps, we provide an analytical workflow built as an R tutorial to test for network topologies, using the best solutions currently available (Supplementary Code 1). Our workflow is based on five main axioms that create a framework to interpret the results of each test. First, a network's topology is a matter of degree. Second, no single metric is able to tell the whole story of a network's topology. Third, null model analysis should be used to test hypothesis-derived predictions. Fourth, networks can have mixed topologies. Fifth, weighted interaction networks have more statistical power.

Concluding remarks

Grounded in both logic and empirical evidence, the Integrative Theory of Interaction Networks brings together a coherent set of mechanistic hypotheses from which testable predictions can be drawn. It aims for generality while focusing on the assembly rules that give rise to the four archetypal topologies observed in interaction networks. Because it maps directly onto operational variables, it offers a practical framework for studying real-world systems. Over time, our field is slowly moving from a black-and-white paradigm toward a more balanced view of network assembly, something akin to a Buddhist "middle way." Like the elephant whose parts we have long examined, the whole continues to reveal more than the sum of its parts. The moment calls for widening our view, deepening our understanding of species interactions, and applying that knowledge to the urgent challenges set by the Sustainable Development Goals. There is still much to learn, and we can only move forward together.

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Author contributions

MARM has since 2007 coordinated the research program that led to the novel theory. MARM, SES, and CFD discussed the final synthesis of the theory, wrote the first draft of the manuscript and the supplementary material, and coordinated the writing. CAK and RLM worked on the literature review and figures. MARM, CFD, and RLM worked on the supplement. All other authors contributed by discussing the ideas that form the corpus of ITIN and reviewing drafts of the manuscript and supplement.

Competing interests

None to declare.

Disclosure of generative AI-use

We used ChatGPT (OpenAI, https://chatgpt.com) in combination with GitHub Copilot (GitHub, https://github.com/features/copilot) to optimize the code provided in the supplement.

Supplementary materials

Supplementary Code 1: We have prepared a repository on GitHub with an analytical workflow that includes data, code, and tutorials aimed at helping assess the topology of empirical and synthetical interaction networks, within the framework proposed by the Integrative Theory of Interaction Networks: https://github.com/marmello77/new_theory.

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