

A new model explaining the origin of different topologies in interaction networks

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Abstract. Nestedness and modularity have been recurrently observed in species interaction networks. Some studies argue that those topologies result from selection against unstable networks, and others propose that they likely emerge from processes driving the interactions between pairs of species. Here we present a model that simulates the evolution of consumer species using resource species following simple rules derived from the integrative hypothesis of specialization (IHS). Without any selection on stability, our model reproduced all commonly observed network topologies. Our simulations demonstrate that resource heterogeneity drives network topology. On the one hand, systems containing only homogeneous resources form generalized nested networks, in which generalist consumers have higher performance on each resource than specialists. On the other hand, heterogeneous systems tend to have a compound topology: modular with internally nested modules, in which generalists that divide their interactions between modules have low performance. Our results demonstrate that all real-world topologies likely emerge through processes driving interactions between pairs of species. Additionally, our simulations suggest that networks containing similar species differ from heterogeneous networks and that modules may not present the topology of entire networks.

Key words: assembly rules; compound topology; consumer-resource networks; interaction networks; modularity; nestedness; network topology; specialization; species interactions; trade-offs.

INTRODUCTION

Network science, focusing on entire systems rather than species, can be an outstanding tool for the study of species interactions (Delmas et al. 2018). This approach led to important discoveries, including the existence of widespread topologies, among which nestedness and modularity stand out (Fortuna et al. 2010). Some studies claim that the prevalence of such topologies results from a selection against unstable networks, and, thus, patterns that increase network stability are more often observed (Thebault and Fontaine 2010, Borrelli 2015). Other authors, however, argue that network patterns likely emerge from processes that drive interactions between pairs of species, and, thus, selection on network stability is not necessary to explain them (Maynard et al. 2018, Valverde et al. 2018). However, knowledge about node linkage rules is still incipient, and we know little about whether these rules can scale up and shape entire

networks (Ings et al. 2009), a critical issue to advance the debate.

Nestedness has been observed in a variety of networks (Bascompte et al. 2003). In a perfectly nested network, the links made by species with fewer interaction partners are a subset of the links made by species with more interaction partners (Bascompte and Jordano 2007). Other studies reported modularity in similar networks (Olesen et al. 2007, Guimerà et al. 2010, Krasnov et al. 2012). A modular network is characterized by each species interacting preferentially within a cohesive subgroup of species. Modules are often composed of phylogenetically related species (Krasnov et al. 2012) or species with similar traits (Mello et al. 2011).

Despite nestedness and modularity being logically different topologies (Ulrich et al. 2017) and negatively correlated with one another in real-world networks (Thebault and Fontaine 2010, Pires and Guimaraes 2012, Trøjelsgaard and Olesen 2013), several networks show combinations of them (Olesen et al. 2007, Flores et al. 2013). A potential explanation is that networks may present a compound topology: modular, but with internally nested modules (Lewinsohn et al. 2006). Compound topologies have been detected in empirical

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(Flores et al. 2013, Felix et al. 2017, Genrich et al. 2017, Mello et al. 2018) and simulated (Beckett and Williams 2013, Leung and Weitz 2016) interaction networks.

Traditionally, interaction network patterns and their underlying causes have been studied through phenomenological approaches (reviewed by Ings et al. 2009). Recently, though, this focus shifted, boosting the development of models that mimic ecological and evolutionary processes (e.g., Zhang et al. 2011, Guimarães et al. 2017, Maynard et al. 2018, Valverde et al. 2018). Despite several patterns being recovered by those models, the question of why networks present different topologies was seldom addressed (but see Leung and Weitz 2016). Here, we use recent theoretical developments on consumer-resource interactions to build a model focused on topology emergence.

The abstraction of consumer species exploiting resource species can be applied to different kinds of species interactions, such as parasite–host, pollinator–plant, and predator–prey interactions (Holland and DeAngelis 2010). An intuitive expectation is that generalist consumers should be outperformed by specialist consumers in the consumption of each resource (Futuyma and Moreno 1988). In other words, the higher the diversity of resources consumed (i.e., generalism), the lower should be the fitness obtained by the consumer on each resource (i.e., performance). The underlying assumption of this expectation is the existence of adaptive trade-offs: Different traits are necessary for a consumer to consume different resources optimally, and, thus, increased performance on one resource comes at the cost of decreased performance on the other resources (Joshi and Thompson 1995). The importance of adaptive trade-offs in consumer–resource interactions, however, remains unclear, as studies of different systems found different results (Poulin 1998, Krasnov et al. 2004, Muchhala 2007, García-Robledo and Horvitz 2012).

The integrative hypothesis of specialization (IHS), initially called the integrative hypothesis of parasite specialization (Pinheiro et al. 2016), predicts that the intensity of trade-offs on a consumer-resource network, mostly depends on the heterogeneity of resources. When resources are similar to one another, they require similar traits for efficient consumption from a consumer. However, if resources are too dissimilar, consumers likely face adaptive trade-offs. Diverse communities can also comprise clusters of similar resource species, each cluster being highly different from the other (Pinheiro et al. 2016). In this case, the IHS predicts that strong trade-offs may exist on the performance of consumers on resources from different clusters, but not within clusters.

Beyond the relationship between performance and generalism of consumers, the IHS predictions may be extended to network topology (Felix et al. 2017, Mello et al. 2018). In networks that contain narrow phylogenetic or functional subsets of species, nestedness should prevail. In diverse networks with clustered resources, on the other hand, modularity may emerge because of the

trade-offs in the performance of consumers on dissimilar clusters. However, within each cluster, as trade-offs are absent, nestedness may still emerge and produce a compound topology. These explanations do not assume selection on network stability, but assume that resource dissimilarities drive the formation of links and shape network topology.

Here, we propose a new model for interaction networks based on the IHS. Our new model simulates the evolution of consumer species using resource species, under three assumptions: (1) each resource species has a set of traits that affect its consumption by each consumer species, and thus resource species can be more or less similar to one another from the consumers' perspective. (2) Any characteristic that enhances a consumer's ability to use a given resource tends to improve the consumption of similar resources, but diminish the consumption of dissimilar resources. (3) The capacity of a consumer to use each resource on a given moment is contingent on its cumulative previous adaptations and maladaptations.

Following these simple assumptions, and adjusting a set of five parameters, the IHS model was able to (1) reproduce the diverse relationships between performance and generalism of consumers observed in natural systems, (2) reproduce the main topologies observed in interaction networks, (3) explain the general conditions that affect the emergence of those patterns, and (4) generate predictions that are consistent with ecological and evolutionary theories and coherent with real-world observations.

THE IHS MODEL

Core structure

Our model produces species-based networks. For increased text fluency, hereafter, we call consumer species “consumers” and resource species “resources.” The core of our model consists of two evolving matrices: the match matrix and the performance matrix. In addition, there are two static inputs: a matrix with pairwise dissimilarities between resources, and a vector of resource availabilities (Fig. 1).

The match between a consumer and a resource summarizes how all characteristics of the consumer (e.g., morphology, physiology, and behavior) affect its ability to consume the resource. In our approach, match values are not bounded and may be even negative. When a consumer has a negative match with a resource, it is unable to consume it. The more negative the value, the greater the mismatch with the resource, and more adaptations would be necessary for consumption.

The dissimilarity between two resources is a measure of how different they are from one another from the consumer's perspective. Similar resources require from the consumer the same adaptations for efficient consumption (i.e., there are no trade-offs). For instance, two plant

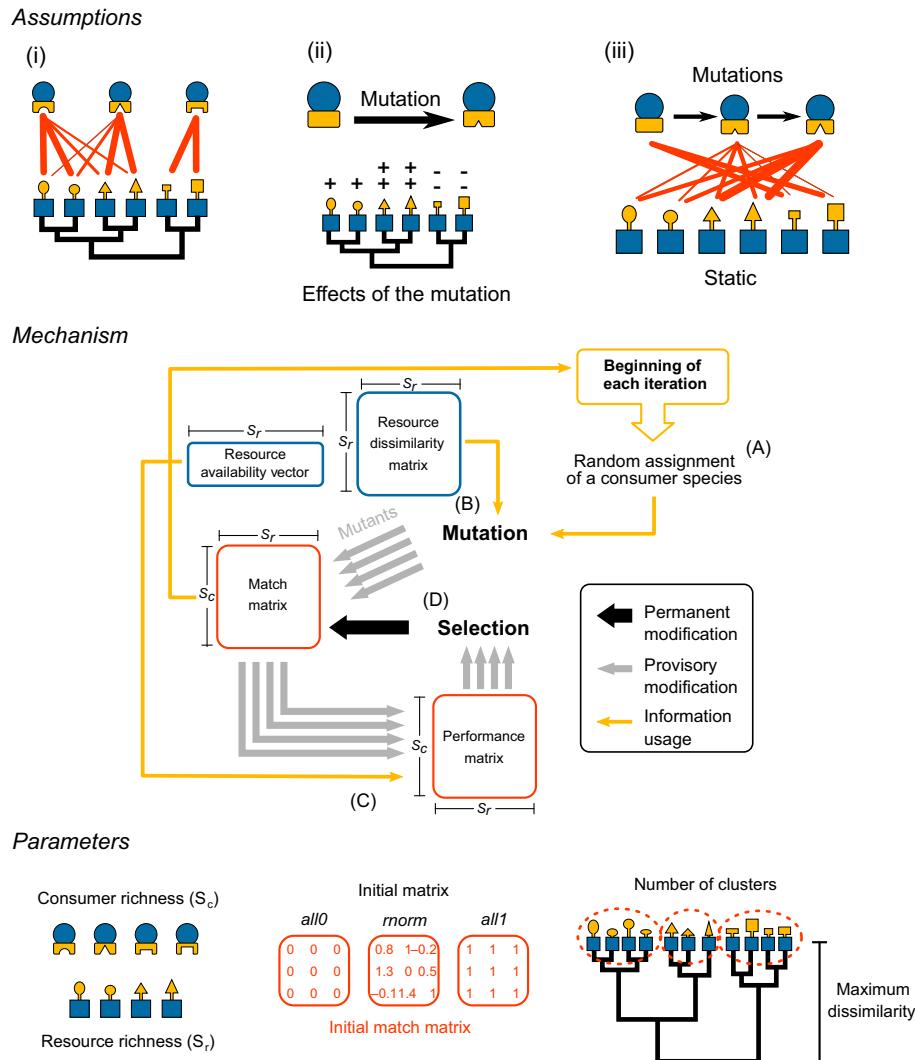


FIG. 1. The IHS model. *Assumptions*: Our model is based on three assumptions: (i) each resource species (squares) has a set of traits that affect its consumption by each consumer species (circles). Consumption efficiency is represented by the match between the yellow shapes of consumers and resources. (ii) A mutation that enhances consumer’s ability to use a given resource tends to improve the consumption of similar resources, but diminish its consumption of dissimilar resources. The figure illustrates the effect a hypothetical mutation on the capacity of a consumer to use each resource: “+” means increased consumption and “-” means decreased consumption. (iii) The capacity of a consumer to use each resource is a result of its previous adaptations and maladaptations. In our model consumers evolve through gradual mutations, which may modify their interactions with resources. However, our model does not simulate resource evolution (resource dissimilarity structure is kept static). *Mechanism*: An iteration starts with the assignment of a random consumer that will evolve (A). This consumer suffers alternative mutations, each generating a mutant with its own match with each resource. Each mutation is focused on a given resource (focal resource) but affects the consumer’s matches with all resources. The consequence of each mutation for the consumer’s match with a given resource depends on the dissimilarity between this resource and the focal resource, which is given by the resource dissimilarity matrix (B). Then the performance of each mutant is calculated taking into account resource availabilities (C). The mutant with the highest total performance is selected and replaces the original consumer in the match matrix to be used in the next iteration of the model (unless all mutations result in decreased total performance, in which case the original consumer is maintained) (D). For a detailed example of one iteration of the IHS model, see Appendix S1. Elements in blue are static inputs; they do not change during the simulation. Elements in red are evolving matrices. S_r = resource richness; S_c = consumer richness. *Parameters*: We adjusted five parameters in our simulations: (1) the resource species richness, (2) the consumer species richness, (3) the method to generate the initial match matrix (initial matrix), (4) the maximum dissimilarity between resources, and (5) the number of clusters in the structure of dissimilarities between resources.

species whose fruits have similar shape, size, and consistency require the same type of beak from frugivorous birds. Thus, a bird with the appropriate beak may

efficiently consume fruits from both plants. Resources are distant from one another when they require opposite adaptations of the consumers, and therefore, improving

the consumption of one comes at the cost of lower efficiency in consuming another (i.e., there are trade-offs). For instance, two plant species whose fruits are more easily consumed by, respectively, small-beaked and large-beaked birds. In this case, a bird may be very efficient in consuming fruits from one plant species, but not both. The availability of each resource is the limit for the overall performance of its consumers.

The performance matrix represents the strength of interactions taking place in a consumer-resource system. Consumers that have negative match with a given resource, have zero performance on it. For consumers that have positive match with a given resource, the performances are the resource's availability divided between these consumers proportionally to their matches.

Mutation phase

At the beginning of each iteration, a consumer is randomly assigned to evolve. This consumer is submitted to alternative mutations, one focused on each resource (focal resource), therefore generating S_i (resource richness) mutants of the consumer.

Each mutation changes the match of the assigned consumer with the focal resource by summing a value randomly drawn from a normal distribution with mean 1 (standard deviation: 0.3). The mutation effect on the other resources is also drawn from normal distributions whose means are defined by their dissimilarity to the focal resource. The higher this dissimilarity, the lower the mean of the normal distribution (mean = $1 - \text{dissimilarity}$). When the dissimilarity of a resource from the focal resource is more than 1, this mean is negative, and the mutation tends to decrease the match of the mutant consumer with the resource.

Selection phase

In the selection phase, the total performance of each mutant consumer is compared with the total performance of the original consumer (before mutations). If at least one mutant increased its total performance, the mutant with the largest total performance is selected, replacing the original consumer (i.e., evolutionary changes occurred). However, if all mutations result in decreased total performance, the original consumer is retained, and the simulation goes to the next iteration without evolutionary changes.

Our model has a strong optimization focus. First, because resource traits are summarized as dissimilarities, consumer mutations must be focused on the resources. That way, the model easily allows, beyond modification on the identity of resources consumed, increases and decreases in consumer generalism. The drawback of this approach is that mutations are not fully random: they always increase the match with at least one resource. This is, however, unlikely to bias the model, as fully negative mutations should not be selected anyway. Second,

in every iteration, the evolving consumer has available a wide range of mutations, which decreases the chance of it getting stuck in local minima and accelerates network evolution.

End of the simulation

The simulation ends after a pre-defined number of iterations, and the final performance matrix is used as the simulated consumer-resource network (hereafter referred to as “simulated network”). It contains the information about the consumer and resource species in the network (nodes), the consumer–resource interactions (links), and the performance of consumers on each resource (weights). The simulated network is bipartite (two-mode). For a complete example of an iteration of the IHS model, see Appendix S1.

SIMULATIONS

Inputs and parameters of the simulations

List of parameters.—In our simulations, we adjusted five parameters: consumer richness, resource richness, method used to generate the initial match matrix (initial matrix), maximum dissimilarity between two resources (maximum dissimilarity), and number of resource clusters (number of clusters).

Initial match matrix.—To start each simulation, we need to provide an initial match matrix. We built matrices with different consumer richness and resource richness. To fill the matrix we used three different methods: *allo*: all consumers score 0 in the match with all resources; *rnorm*: the match between each consumer and each resource is randomly drawn from a normal distribution with mean = 1 and standard deviation = 1; and *all1*: all consumers score 1 in the match with all resources.

Resource availability vector.—The availability of each resource was defined by randomly drawing a value from a normal distribution with mean = 200 and standard deviation = 50.

Matrix of resource dissimilarities.—The IHS predicts that network topology emerges as a function of the dissimilarity between resources and the degree of clustering of those dissimilarities. To test this prediction, we generated dissimilarity matrices with a range of values for the maximum dissimilarity between two resources and the number of clusters it contains. Those parameters define the heterogeneity of resources.

To produce the dissimilarities, we randomly assigned values for each resource in simulated dimensions and calculated the pairwise Euclidian distance, then we rescaled all distances based on the defined maximum. In simulations with clusters, each resource was first assigned to a cluster. Then, when defining values in the

dimensions, a different range of possible values was used for each cluster, forcing dissimilarities within clusters to be lower than between clusters.

Running simulations

The IHS model was coded in R version 3.4.0 (R Core Team 2017). Commented codes and details of the model are available in GitHub (<https://doi.org/10.5281/zenodo.1486121>).

Preliminary simulations.—First, we performed 40 preliminary simulations with varied parameter values, to visualize the evolution of network topology during the procedure. In these tests we analyzed the network in intermediary steps of the simulations, to check visually: (1) if its evolution follows a unique trend in all simulations or if it depends upon the parameter values, (2) whether it tends to stabilization, and (3) if so, how many iterations are necessary to achieve it. Details and complete results of these simulations are presented in Appendix S2: Section S1.

Simulated networks.—The next step was to generate a pool of simulated networks. The parameter values used were consumer richness: 5, 10, 50, 100, and 200; resource richness: 50, 100, and 200; initial matrix: *all0*, *rnorm*, and *all1*; maximum dissimilarity: 1, 1.5, 2, 2.5, 3, 3.5, and 4; and number of clusters: 1, 2, and 4. We ran one simulation for each combination of those values, totalizing 945 setups. The number of iterations for each simulation was defined as consumer richness times 50 (see Appendix S2: Section S1 for justification).

As in each iteration of the model it is possible that no evolutionary changes occur; it is also possible that the entire simulation goes on without or with few modifications from the initial matrix (Appendix S2: Section S2). In these cases, the simulated networks did not reflect the mechanism of the model, but rather mirrored the initial matrices. Therefore, we removed from our pool the simulations in which evolutionary changes occurred in <80% of iterations. After this filtering, 672 simulated networks were retained for analysis.

ANALYSIS OF SIMULATED NETWORKS

Here, we used several indices and performed several analyses to describe the topology and specialization of simulated networks. Then we fitted generalized linear and additive models to understand how these features were driven by model parameters. A complete report of all the analysis performed in this study is presented in Appendix S2.

Network specialization

First, for each simulated network, we calculated binary and weighted network specialization metrics:

connectance and H_2' , respectively (Blüthgen et al. 2008). Connectance is the proportion of potential links that are actually observed in the network, and H_2' measures the degree of mutual specialization between nodes in the network, accounting for the quantitative information.

Network topology

Modularity and nestedness.—We measured modularity and determined module composition of each simulated network using the DIRTLPawb+ algorithm for weighted bipartite networks (Beckett 2016), available at the *bipartite* package for R (Dormann et al. 2008).

To compute nestedness we used a new metric, which we named WNODA (weighted nestedness based on overlap and decreasing abundance). WNODA is a modification of WNODF index (weighted nestedness based on overlap and decreasing fill; Almeida-Neto and Ulrich 2011). Contrary to WNODF, WNODA does not demand binary decreasing fill to account for weighted nestedness, but rather decreasing marginal totals. It is, thus, less affected by weak links, and can be used to compare completely filled matrices (in which case WNODF is always 0). Detailed information about WNODA and comparisons between metrics are presented in Appendix S3.

Considering the possibility of a compound topology in our simulated networks, we used the approach proposed by Flores et al. (2013) and adapted by Felix et al. (2017), in which we separately computed the nestedness between species belonging to the same module and the nestedness between species belonging to different modules. In a network with a compound topology we expect the WNODA between species of the same module (WNODA_{SM}) to be much higher than the WNODA between species of different modules (WNODA_{DM}). An R function (*nest.smdm*) to compute these components of nestedness is now available at the *bipartite* package for R.

Null model analysis.—We used null model analysis to define which topology—modular, nested, or compound—described each simulated network best. First, we tested for nested and modular topologies with the use of free null models—null models that do not conserve the modular structure of the matrix (Felix et al. 2017). We applied a modified version of the algorithm proposed by Vázquez et al. (2007), in which randomized matrices rigidly conserve the original connectance and the total sum of weights, and probabilistically conserve the marginal sums. The original algorithm was modified to deal with continuous link weights instead of counts better (details in Appendix S2: Section S9).

A network has a compound topology when it is significantly modular and presents a significant WNODA_{SM} (i.e., modular with internally nested modules). To test for the significance of WNODA_{SM} in each modular

network we used a restricted null model: a null model that conserves the modular structure of the matrix in the randomization. As, by definition, nodes in the same modules overlap more than nodes in different modules, not conserving the modular structure on the randomized matrix would result in an inflated type I error ratio for $WNODA_{SM}$ (Felix et al. 2017).

To avoid excessively low consumer richness in each module, we excluded the networks with 10 or fewer consumer species and kept 415 simulated networks for these and subsequent analysis. Each null model was composed by 500 randomized matrices, and metric values were compared through *Z* tests. Null model analysis was performed in the Sagarana High-Performance Computing cluster from the High-Performance Processing Center, Institute of Biological Sciences, Federal University of Minas Gerais, Brazil.

Relationship between performance and generalism of consumers

Performance vs. generalism.—For each consumer in the simulated networks, we calculated the mean performance: its average performance on all resources it consumes. We also calculated two generalism indices: (1) basic resource generalism, the richness of resources consumed; and (2) structural resource generalism, the diversity of resources consumed measured with the Shannon index (Poisot et al. 2012). Then, we calculated Spearman correlations between the mean performance and the generalism indices for each simulated network.

Performance vs. between-module generalism.—To measure the between-module generalism of consumers in each modular simulated network, we calculated its participation coefficient (*P*; Guimerà and Nunes Amaral 2005). The *P* measures how much the consumer's links are divided between different modules. We also used a weighted version of *P* (Appendix S2: Section S11). Then, for each network, we calculated Spearman correlations between the mean performance and the between-module generalism of consumers (binary and weighted).

Statistical analysis

To test the effect of model parameter in each of the descriptors of simulated networks, we fitted generalized and additive linear models. After building each complete model, we performed analysis of variance to reduce it to a minimum model and used the deviance explained by each variable as a measure of effect size (Dobson and Barnett 2008). See Appendix S2 for the setup, reduction, and results of each model.

RESULTS

The evolution of networks in the preliminary simulations followed no unique trend. For instance,

connectance may increase, decrease, or remain constant in the course of the iterations, depending on model parameter values. Network topology and specialization tend to stabilize, and the number of iterations used to generate our pool of simulated networks was enough, in most of the preliminary simulations, to reach a very stable state (Appendix S2: Section S1).

The IHS model was able to generate a diverse set of simulated networks for every metric calculated in this study: from highly generalized to highly specialized (connectance: 0.12–1; H_2' : <0.01–0.79), and from highly modular to highly nested (modularity: <0.01–0.80; $WNODA$: 0.07–0.95). Also, correlation between performance and generalism varied from positive to negative (basic generalism: –1 to 0.87; structural generalism: –1 to 1). Of the 415 networks tested for topologies, 268 (65%) were modular, 198 (48%) were nested, and 51 (12%) were both modular and nested. Of the 268 modular networks, 142 (53%) presented a compound topology: modules that are internally nested.

Out of the five parameters adjusted, maximum dissimilarity and number of clusters, which are related to resource heterogeneity, disproportionately drove simulated network specialization and topology (Fig. 2). The initial matrix had weak effects in most of the analysis showing that network evolution has overcome initial patterns. Consumer richness had a moderate effect in the detection of significant nestedness, likely resulting from an increased statistical power in the analysis (Appendix S2: Section S9). But, overall, consumer and resource richness did not strongly influence the simulation outputs. For the effect of each parameter in each model see Appendix S2.

Consequently, two main different patterns have emerged in our simulations. On the one hand, simulations with homogeneous resource mostly resulted in highly generalized, highly connected, nested, and non-modular networks (Fig. 3). In these simulations, there is a positive correlation between performance and generalism of consumers.

On the other hand, simulations with heterogeneous resources mostly resulted in highly specialized, sparsely connected, nonnested, and modular networks with internally nested modules (compound topology; Fig. 4). In most of the modular networks, the performance of consumers has a negative relationship with between-module generalism (*P*): 75% of the networks for the binary metric and 84% for the weighted metric.

DISCUSSION

Topology emergence

The IHS model produced a highly diverse set of simulated consumer-resource networks. In these simulations, specialization varied widely, and we detected the three main topologies observed in real-world interaction networks: nested, modular, and compound. We also found

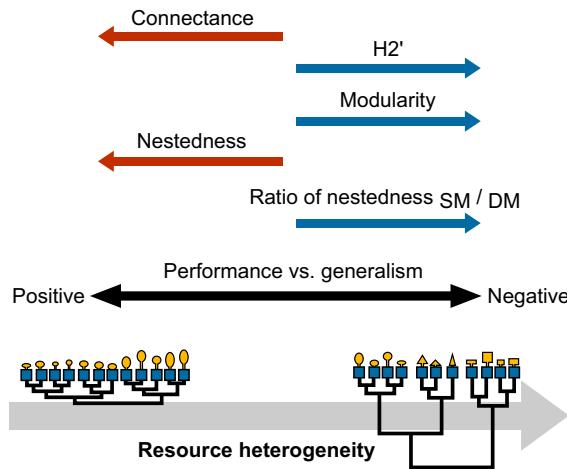


FIG. 2. Effects of resource heterogeneity in network specialization and topology. Parameters' maximum dissimilarity and number of clusters that define resource heterogeneity have mostly driven simulation outputs. Specialization increases (lower connectance and higher $H2'$), nestedness decreases, and modularity increases with increased resource heterogeneity. The ratio between nestedness of species in the same module (nestedness S_M) and nestedness of species in different modules (nestedness D_M) is higher in simulated networks with more heterogeneous resources, boosting the emergence of compound topologies. Finally, the relationship between performance and generalism of consumers shifts from highly positive to highly negative, depending on resource heterogeneity. Blue and red arrows: metric values, respectively, increase and decrease with increased maximum dissimilarity and number of clusters. Complete results in Appendix S2.

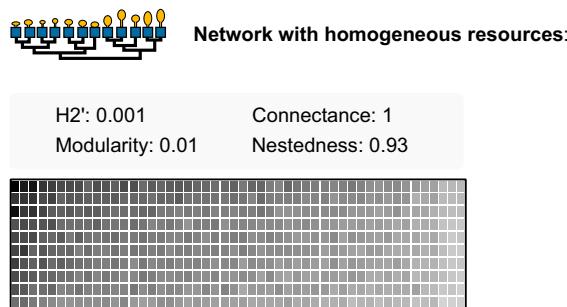


FIG. 3. Predictions of our model for networks with homogeneous resources. Here we illustrate the main pattern that emerged in simulations with highly homogeneous resources, using as example one of the simulated networks. The maximum dissimilarity between two resources in this simulation is 1; thus consumers do not face trade-offs on its performances on different resources. The simulated network is generalized, nonmodular, fully connected, and nested. Rows in the matrix are consumers, columns are resources, and the gray tones represent the weight of each interaction. Nestedness is evidenced by the general trend of decreasing weights from top-left to bottom-right corners.

positive and negative relationships between performance and generalism of consumers. Those patterns did not emerge through selection on network stability, but rather

from rules on the evolution of consumers that use different sets of resources. As far as we know, our model is the first to implement a single mechanism able to generate all those patterns under different circumstances.

The IHS predicts that modularity in interaction networks mirrors discontinuities in dissimilarities between species (Pineiro et al. 2016). Clusters are, thus, imposed on the model and drive link formation, which produces modules in the network. Our model does not address the origin of clustering on biological communities (but see Allen 2006, Scheffer and van Nes 2006). However, it is remarkable that even in simulations without clusters, modular networks emerged (see Appendix S4 for an example). This is an intriguing result, that strengthens the evidence of topology emerging from upscaling of node linkage rules.

In our model, resource heterogeneity defines the intensity of trade-offs in the performances of each consumer on different resources. When trade-offs are strong, highly generalistic consumers are very inefficient on each resource or cannot even exist and the network is highly specialized, modular, and nonnested. However, when trade-offs are weak, a consumer can consume a wide range of resources, and the network is generalized and nested.

Limitations of the model

The main limitation of the IHS model is that it only simulates the evolution of consumer species. In nature, consumption is likely to be a selective force that also drives resource species evolution (Thompson 1994, Guimarães et al. 2017). We must admit that this simplification strongly reduces the realism of our model, especially when consumption has a strong effect on resource species fitness. We decided to follow this approach, however, because the inclusion of resource evolution would result in a much more complex and intricate model.

A related limitation is that our model does not include the effect of consumer abundances on performances. In obligate interactions (e.g., endoparasitism), the abundance of the consumer species is itself a measure of interaction weight, as a consumer only survives by interacting with resources. However, when consumer abundance is less dependent on the interaction, it may be important to consider the separate effect of consumer abundances in link formation.

In our model, we explicitly favored generalism and simplicity over realism: we aimed at producing a wide range of patterns through a simple mechanism. And, despite somewhat simplistic assumptions, it was indeed able to recover the most common topological patterns observed in interaction networks.

Compound topology

On the one hand, several simulated networks presented both significant nestedness and modularity. On the other

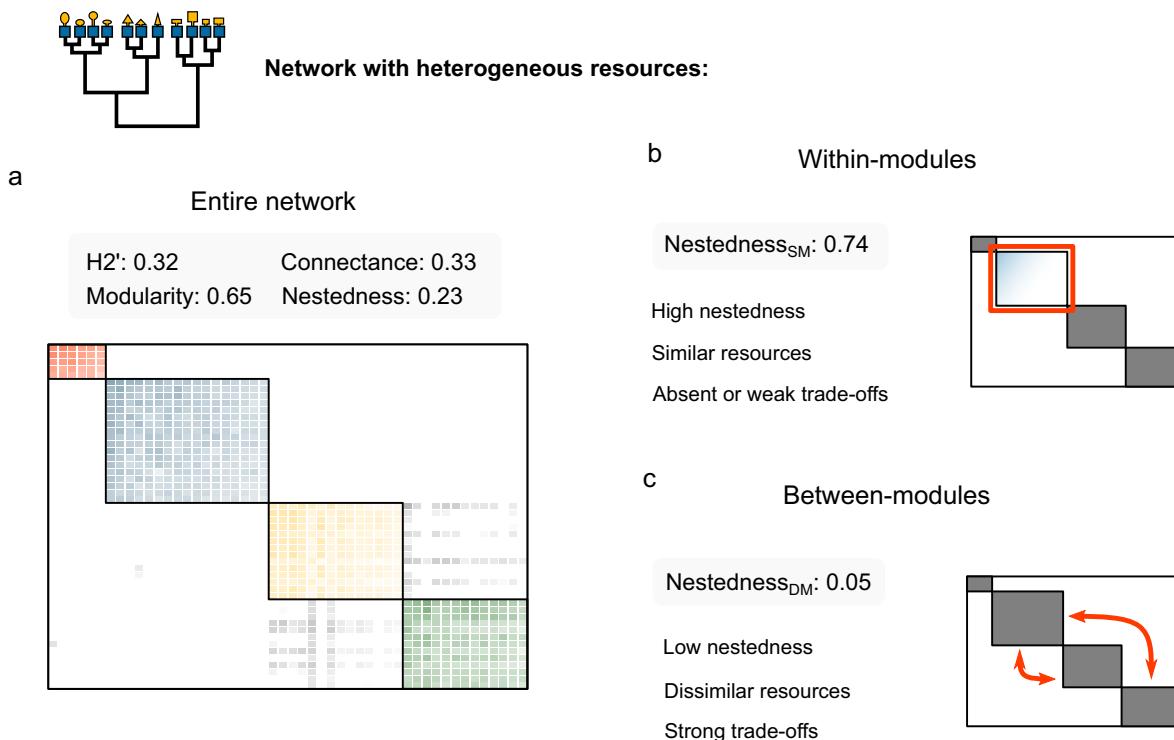


FIG. 4. Predictions of our model for networks with heterogeneous resources. Here we illustrate the main pattern that emerged in simulations with highly heterogeneous resources, using as example one of the simulated networks. The maximum dissimilarity between two resources in this simulation is 2.5 and the structure of dissimilarities is composed of 4 clusters. The simulated network is sparse, specialized, nonnested, and presents a compound topology: modular with internally nested modules (a). Within modules (b) there is high nestedness, resources are homogeneous, and consumers are submitted to weak or absent trade-offs, resembling the patterns in Fig. 3. However, between modules (c) nestedness is very low, resources are dissimilar, and multimodule generalists face strong trade-offs, which results in decreased performance. Rows in (a) are consumers, columns are resources, colors represent modules, and the tones represent the weight of each interaction. Nestedness_{SM}: nestedness between species in the same module; nestedness_{DM}: nestedness between species in different modules.

hand, nestedness and modularity are driven in opposite directions by the same main parameters and are strongly negatively correlated (Spearman ρ : -0.94 , Appendix S2: Section S7), as usually found in empirical ecological networks (Thebault and Fontaine 2010, Pires and Guimaraes 2012, Trøjelsgaard and Olesen 2013). This scenario does not support the perspective of entire networks having a mixed nested and modular topology (Fortuna et al. 2010), but supports the perspective that, in modular networks, nestedness may predominate within modules (Lewinsohn et al. 2006, Felix et al. 2017). Indeed, in nested-modular simulated networks, nestedness between species of the same module was always much higher than nestedness between species of different modules.

Our study reinforces the prediction that highly diverse networks tend to present a compound topology (Lewinsohn et al. 2006, Flores et al. 2011, Felix et al. 2017). In these networks, consumers specialize in a group of homogeneous resource species instead of a single species and multimodule generalists have decreased efficiency, which corroborates that network modules may be the real unity of specialization and coevolution (Olesen et al. 2007).

Additionally, our results show that the taxonomic, phylogenetic, and functional diversity of species included in a network may have a strong influence on the patterns observed. Interaction networks containing only similar species show patterns that are not observed in heterogeneous networks (Bezerra et al. 2009), as well as a module does not present the topology of the entire network (Flores et al. 2013). Studies are often focused on modules of the network or on taxonomically defined assemblage subsets (Olesen et al. 2007, Jordano 2016), and only a few studies investigated diverse systems (Donatti et al. 2011). Thus, the literature is probably biased toward low-diversity patterns (as suggested by Mello et al. 2011). This may explain the paradigm of mutualisms being nested (Bascompte and Jordano 2007) and the dominance of positive relationships between the performance and host range of parasites (Krasnov et al. 2004, Hellgren et al. 2009). We should expect that several of the published nested interaction networks are in fact modules of more diverse networks with compound topologies.

Other models of compound topologies

Beckett and Williams (2013) predicted a compound topology for phage–bacteria networks, using a relaxed lock-and-key model. Despite their model including a larger number of parameters and having a more complex and less general mechanism than ours, the assumptions of the IHS model are at least partially met by it. We believe that our model is not contradictory to the relaxed lock-and-key model, but rather more comprehensive.

Leung and Weitz (2016) proposed a bipartite network growth model that generates modular, nested, and compound networks. In their model, the network grows by duplication of nodes, and links, once formed, are kept constant. In our model the contrary is true, species richness is constant, and links submitted to evolution. Additionally, their model produces only binary networks. These differences make it difficult to compare both models. However, Leung and Weitz (2016) found that, when there are trade-offs, modularity emerges in networks; otherwise, hosts and parasites enter an arms race that results in nestedness. These results are highly consonant with our main predictions using the IHS model.

CONCLUSION

The proposed model based on the integrative hypothesis of specialization (IHS) reproduced the main network topologies, and its predictions are coherent to real-world observations and consonant with current evolutionary and ecological theories. Our results show that the IHS model is useful to generate weighted, bipartite, consumer-resource networks and supports the IHS as a theoretical framework to study interaction specialization and network topology.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2796/supinfo>

DATA AVAILABILITY

In this study we used only simulated data that can be reproduced using codes provided on Zenodo (<https://doi.org/10.5281/zenodo.1486121>).