

Bipartite structural evaluation: Extended network generation model and corrected randomization techniques

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Understanding the structural organization of bipartite networks is essential for characterizing the architecture and dynamics of complex systems, from ecological communities to technological and social interactions. Such networks often exhibit recurring patterns—nestedness, modularity, in-block nestedness—that shape system stability, diversity, and function. Yet, despite extensive research, assessing the statistical significance of these patterns remains problematic, as existing null models may introduce systematic biases that can lead to contradictory interpretations. Here, we develop a generative framework that analytically constructs synthetic bipartite networks spanning the most common structural regimes and use it to perform a comprehensive evaluation of state-of-the-art null models. Across large synthetic and empirical ensembles, we show how commonly used null models inconsistently estimate the significance of nested, modular, and compound architectures, depending on how degree constraints are imposed. Building on these insights, we introduce a corrected probabilistic model that reconciles, to some extent, these inconsistencies, providing a more balanced basis for significance testing. Our work thus establishes a unified theoretical and computational framework for generating, analyzing, and interpreting structure in bipartite networks, offering conceptual and methodological guidance for future research in ecology and beyond.

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I. INTRODUCTION

Over twenty years ago, research in community ecology was deeply challenged by the evidence that biota interactions, rather than being randomly assembled, manifest clear architectural patterns. In 2003, the pioneer paper of Bascompte *et al.* [1] showed that a significant amount of mutualistic plant-animal networks are organized according to well-defined nested arrangements. Along the same line, Olesen *et al.* [2] unveiled the prevalence of modular configuration among pollination communities with a high (>150) number of species. The observation of these patterns in real ecological networks fuelled a large body of research aimed at establishing how the organization of species interactions affects the resulting community dynamics: Nestedness was recognized to be linked to the promotion of diversity [3], the maximization of abundances [4], and feasibility [5–7]. On the other hand, modularity was associated to the improvement of local asymptotic stability [8,9]. These results led to a great consensus about the crucial role of structural arrangements in the behavior of natural systems [10–14]. These findings spurred the development of many methodological advances and tools emerged to

measure and identify those interaction patterns in an automatic and efficient way [15–21].

One would think that these theoretical and methodological achievements rest on well-developed tools to assess their statistical validity. This would imply both the capability to generate large ensembles of networks with prescribed structural features and solid procedures to randomize networks to disentangle genuine emergent properties from mere byproducts. However, many studies have so far addressed these problems with *ad hoc* strategies: The former, by testing the presence of a given pattern over networks with a random organization [6,7,10,13] or by controlling the structure in a contrived way [9,12]. The latter are typically addressed by shuffling network edges with methods that may render biased results.

Another pressing issue relates to the structural arrangements under consideration. In addition to nestedness and modularity, there are other patterns worth being considered, e.g., in-block nestedness, which describes networks made up from weakly interlinked blocks with internal nested organization [22–24]. This pattern was hypothesized by Lewinsohn *et al.* in 2006 [22], and it has received much attention in the last few years [23,25] due to its predicted emergence from micro- [26,27] and macroscopic [28] mechanisms, and also because of its identification in real mutualistic communities [29]. If the production of synthetic ensembles of structured bipartite networks was feebly addressed for nested or modular structures, it has been virtually absent for hybrid in-block nested arrangements (but see Ref. [30]).

In this work, we fill these methodological gaps by, first, introducing BUNGen (Bipartite and Unipartite Network

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Generator), an integrated synthetic benchmark that generates uni- or bipartite networks, with varying levels of prescribed planted structures with few and simple parameters. The model we present is a generalization of the model proposed in Ref. [24] to construct networks with a specified number of blocks (with equal or different sizes) and connectance, inducing different structural signatures. The model is defined by an exact mathematical recipe, reminiscent of that of Beckett *et al.* [31], although the latter does not include any functionality to generate modules nor hybrid structures. In developing an analytically grounded generative model, our contribution aligns with current efforts in structural network analysis that emphasize probabilistic formulations, such as stochastic block models and Bayesian inference [32]. While Bayesian inference is not employed in this work, the proposed generative model can serve as a foundation for such inference-based applications.

Then, on top of BUNGen, we analyze the statistical significance—in terms of *z*scores—of three rich sets of bipartite matrices with nested, modular, and in-block nested configuration. We consider four different null models from the literature, and detect the presence of ambiguities in assessing the various network descriptors, corresponding to over- (or under-) estimations of the given arrangements. To address the observed inconsistencies, we introduce an alternative approach, the corrected probabilistic model, that helps reduce under- and overestimation and highlights the need for the development of frameworks that take into account those biases. These contributions are wrapped into a single compact framework, consisting of software repositories that enable the generation of the synthetic networks with the specified planted structures, the calculation of nestedness under different formulations, optimization algorithms for the maximization of modularity and in-block nestedness, and the construction of the reviewed null models.

The remainder of the article is organized as follows: Sec. II introduces the formulation of our synthetic network generation model. Sec. III starts with a brief recapitulation of some representative randomization schemes for bipartite networks, highlighting their pros and cons. Then, we introduce our probabilistic rewiring strategy, which retains some desirable features while diminishing the disadvantages of those reference models. Finally, Sec. V discusses the main open challenges for further developments.

II. SYNTHETIC BENCHMARK

In this section, we present the analytical foundations of the generative model aimed to cover the variety of structures introduced so far, namely, to build networks with planted nested, modular, and in-block nested arrangements, as well as completely random ones. As a reminder, a description of nestedness, modularity, and in-block nestedness is available in Sec. S1 of the Supplemental Material [33]. For convenience, the software implementing the models is available as an open-source package. The formulation below corresponds to the case of bipartite networks (e.g., N animal and M plant species). While the model can be easily tweaked to include unipartite ones, this possibility is not considered here.

The generation of an $N \times M$ adjacency matrix with a given pattern depends first on the number of blocks $B \geq 1$ with row and column numbers provided, respectively, by $\{r_\alpha\}$ and $\{c_\alpha\}$ ($\alpha = 1, \dots, B$). Note that $\sum_{\alpha=1}^B r_\alpha = N$ and $\sum_{\alpha=1}^B c_\alpha = M$.

The intrablock structure is obtained by first generating a perfect nested configuration, whose shape depends on the parameter ξ as

$$y = f_\xi(x) = 1 - (1 - x^{1/\xi})^\xi, \quad x \in [0, 1], \quad y \in [0, 1]. \quad (1)$$

Inspired by the unit ball equation, ξ governs the shape of the separatrix—ranging from convex ($0 < \xi < 1$), to diagonal ($\xi = 1$), to concave ($\xi > 1$); see top row in Fig. 1.

Specifically, the α th block presenting r_α rows and c_α columns is constructed by tessellating the unit ball domain in Eq. (1) into $r_\alpha \times c_\alpha$ cells, and adding a link into each entry whose center lies above the curve. In other words, after tessellation, the center of the cell associated with edge e_{ij} is located at

$$x_j = \frac{j - \frac{1}{2}}{c_\alpha} \quad \text{and} \quad y_i = \frac{i - \frac{1}{2}}{r_\alpha}, \quad (2)$$

where the row and column indices i and j range from 1 to r_α and c_α , respectively. Then, the function defining the edge e_{ij} is then given by

$$e_{ij} = \begin{cases} 1, & \text{if } y_i \geq f_\xi(x_j), \\ 0, & \text{otherwise.} \end{cases} \quad (3)$$

Finally, in the resulting adjacency matrix, we set the first row and the first column to 1, to prevent disconnection at large ξ values. Note that the parameter ξ , defining the slimness of the block-nested profile, fixes the number of links E and so uniquely determines the density of the network (or connectance, in the network ecology jargon), $d = E/(NM)$.

As mentioned, perfectly nested patterns are rarely found in real systems. Thus, we introduce the parameter p_α , expressing the fraction of links in block α lying above the curve in Eq. (1) that are randomly selected and distributed across the empty entries of the block. Whenever such intrablock noise is the same $\forall \alpha \in \{1, \dots, B\}$, it will be expressed simply as p .

Similarly, perfectly compartmentalized networks (disconnected blocks) are not frequent. To introduce interblock perturbations, we assume that each intrablock link is removed with probability μ , and then reassigned uniformly at random to any position of the $N \times M$ adjacency matrix. This procedure follows closely other widely used block-structure benchmarks, in which a probability is defined such that links are “exported” outside their native community [34,35].

The generative process outlined above can be analytically described in terms of edge probabilities, simplifying the process of algorithmic design. The probability of a link between nodes i and j can be expressed as a combination of two contributions. One corresponding to links that remain inside their original block, and one corresponding to links that are exported outside their block and placed uniformly at random. Formally,

$$P_{ij} = (1 - u)P_{ij}^{\alpha\alpha} + uP_{ij}^{\alpha\beta}, \quad (4)$$

where u , the relative weight of the interblock process, is not a free parameter but is rather fully determined by $\mu \in [0, 1]$

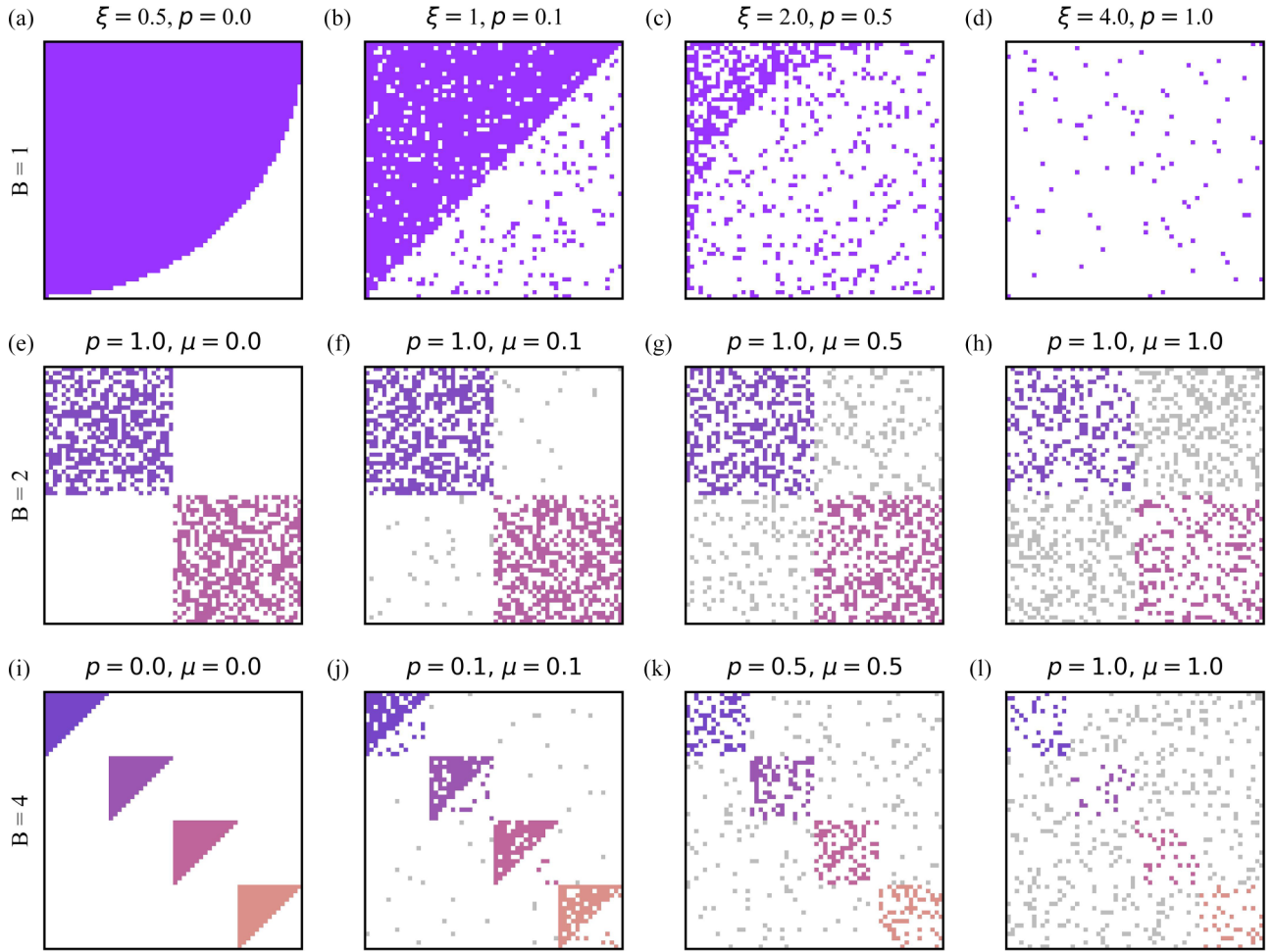


FIG. 1. Examples of synthetic network generation with the model introduced here. (a)–(d) Generation of nested networks ($B = 1$) and the effects of varying the intrablock noise parameter p and ξ . (e)–(h) Two-block modular ($p = 1$) networks ($B = 2$) with varying levels of interblock noise parameter μ and ξ fixed to 1.0. (i)–(l) In-block nested networks ($B = 4$) illustrating the combined effect of the noise parameters p and μ with ξ fixed to 1.

and the block sizes:

$$u = \mu \left(1 - \frac{\sum_{\alpha=1}^B r_{\alpha} c_{\alpha}}{NM} \right). \quad (5)$$

The first contribution to P_{ij} in Eq. (4) corresponds to the intrablock edge allocation as

$$P_{ij}^{\alpha\alpha} = [(1 - p_{\alpha} + p_{\alpha} l_{\alpha}) \Theta(x) + l_{\alpha} (1 - \Theta(x))] \delta_{\alpha, \alpha_j}, \quad (6)$$

with the Heaviside function $\Theta(x) = 1$ when $x = i/r_{\alpha} - f_{\xi}(j/c_{\alpha}) > 0$. The term l_{α} corresponds to the probability of selecting links among the removed ones:

$$l_{\alpha} = \frac{p_{\alpha} E_{\alpha}}{r_{\alpha} c_{\alpha} - E_{\alpha} + p_{\alpha} E_{\alpha}}, \quad (7)$$

with E_{α} being the number of links in block α . Note that the numerator represents the number of links selected for reallocation, while the denominator corresponds to the number of empty positions (i.e., possible places where the reallocated link can be placed).

With this in mind, the probabilistic interpretation of Eq. (6) is as follows. For block α to have a link between i and j ,

we distinguish between the originally nested part (the one that initially contains all links), identified by $\Theta(x)$, and the remaining part of the block. For the nested part to contain a link, either it has not been selected for reallocation [with probability $(1 - p_{\alpha})$], or, if it has been chosen (with probability p_{α}), it is placed back in the same position (l_{α}). The rest of the equation, $l_{\alpha}(1 - \Theta(x))$, describes the alternative probability of a link being reallocated outside the nested part. Finally, the Kronecker delta $\delta_{\alpha, \alpha_j}$ guarantees that nodes i and j belong to the same block; i.e., $\alpha_i = \alpha_j$.

On the other hand, the interblock link allocation contribution (involving nodes $i \in \alpha$ and $j \in \beta$) is

$$P_{ij}^{\alpha\beta} = \frac{1}{NM - \sum_{\alpha=1}^B r_{\alpha} c_{\alpha}} (1 - \delta_{\alpha, \alpha_j}). \quad (8)$$

This expression is uniform over all off-diagonal block positions ($\alpha_i \neq \alpha_j$), and zero otherwise.

With all the parameters laid out, Fig. 1 can be explained in length. Panels (a)–(d) illustrate the effect of increasing p levels (from left to right), toward a completely random setting ($p = 1$). Note that nested matrices are obtained by setting $B =$

1, i.e., considering only one block, and are fully characterized by the choice of ξ and p . Panels (e)–(h) display purely modular networks (with $B = 2$), obtained setting $p = 1$: blocks lack any internal structure. Finally, in-block nested arrangements are shown in panels (i)–(l) with increasing intra- (p) and interblock (μ) noise levels. Interestingly, panels (h) and (l) represent well the joint effect of p and μ , which renders, in the extreme case $p = \mu = 1$, an Erdős-Rényi graph.

III. NULL MODELS

The appropriate selection of a null model has been a center of debate in network ecology for decades [36,37]. In general, the approaches for the generation of random networks can be classified under three large families, which we summarize below. Following the nomenclature employed in Ref. [38], we will refer to them as EE, FF, and PP models.

The equiprobable-column or equiprobable-row (EE) model represents the least constrained scheme. EE is a probabilistic binary null model that assumes that all the interactions between pairs of nodes—row-to-column links—are equally probable, and that such connection is given with probability $p_{ij} = \frac{L}{NM}$, where L is the total number of connections in the original matrix. This model generates Erdős-Rényi networks with nodes exhibiting a varying number of connections around a well-defined average degree $\langle k \rangle$, preserving L on average. The model tends to falsely detect significant nested patterns; i.e., it is prone to Type I statistical errors [31,39,40].

Fixed column/fixed row (FF) models lie in the other extreme of the spectrum [17], enforcing row-nodes' and column-nodes' degrees to be strictly preserved. It is thus the most restrictive null model. The usage of this type of model to assess the probability that an observed pattern could be explained by chance alone has been applied since the 1970s [37]. A typical way for generating random networks under this constraint is through the application of some form of swap algorithm, performing exchanges between pairs of interacting nodes without altering the network's degree sequence [41].

Notably, generating random matrices by exactly preserving row and column degrees is far from being a trivial task, and so implementations of FF models are quite sophisticated. Swap methods tend to generate similar realizations that closely resemble the original network. Thus, in order to produce a truly representative set of matrices within the universe of possible matrix configurations, a very large number of matrices need be generated [42], which might not be possible in some scenarios. As a consequence, this model is susceptible to Type II errors, particularly, when it comes to the assessment of nested patterns [38,40]. On the other hand, it also tends to generate matrices with more checkerboard units, i.e., 2×2 submatrices containing 1s in the main diagonal and 0s outside, or vice versa, than expected by chance [43], producing a biased sample. To solve the latter downside, scholars have introduced variations of the swap methods, and alternative methods that are able to generate a uniform sample of null matrices with fixed row and column degrees [43–47].

In this work, we employ the Curveball algorithm as the representative FF model. It was introduced by Strona *et al.* [44] as a fast and efficient alternative to generate random matrices with fixed nodes' degrees, guaranteeing a uniform

sample [48]. The algorithm was introduced as a computationally cheap method to perform permutations on binary matrices, producing uniformly distributed random matrices with fixed degrees. The functioning of the algorithm goes as follows: Starting from a binary bipartite matrix—e.g., representing species per site or plant-pollinator matrices, in the ecological context—for each row (column) node, a list is created containing all the column (row) indices with nonzero elements. Then, the algorithm iteratively chooses at random two row lists (columns), identifies the column (row) indices that are present in list, but not in the other, and vice versa, and performs random “trades” of the column (row) indices. The number of trades for each pair of lists will go from zero to the size of the smallest list of column indices. In this work, we resort to the Python implementation of the algorithm that was provided by the authors in Ref. [44].

Row-proportional/column-proportional (PP) models stand somewhere between the extremes—and limitations—described above [17]. They represent an intermediate alternative to generate networks that preserve node degrees on average, thus mitigating the bias toward Type II (FF) or Type I (EE) errors. In these models, interactions between node pairs are defined independently for each individual link on the basis of a Bernoulli trial. From this general principle, there exist different variants along the loose-strict continuum. We introduce here two variants which, like Curveball, will be used for comparison against our proposal.

Bascompte's probabilistic model [1] is perhaps the most popular for the assessment of statistically significant structural patterns (particularly nested ones). In this model, the probability of interaction of a pair of nodes is proportional to the nodes' degrees of the original network as

$$p_{ij} = \frac{1}{2} \left(\frac{k_i^{(r)}}{M} + \frac{k_j^{(c)}}{N} \right), \quad (9)$$

where $k_i^{(r)}$ is the degree of the i th row, $k_j^{(c)}$ is the degree of the j th column, and N and M are the number of row and column nodes, respectively.

On the other hand, we consider maximum-entropy exponential random graphs (max-entropy for short), which were introduced in the last decade [49]. This randomizing framework is based on the maximization of the entropy of an ensemble of random networks, leading to the exponential random graph model [50]. This framework facilitates the analytic computation of statistics over an ensemble of networks with a given set of fixed properties (e.g., connectance). Under this formulation, the expected values and standard deviation of the network properties are calculated by finding a probability distribution over an ensemble of networks which, on average, preserve the network's degree sequence. This approach can be applied to both uni- and bipartite networks, and has been recently exploited to assess the significance of nestedness structural arrangements in economic [51] and ecological [52] networks.

More to the detail, one aims to find a probability distribution $P(G)$ over the ensemble of graphs G , with G^* as the graph corresponding to the real network, that maximizes the Shannon-Gibbs entropy $S = -\sum_G P(G) \ln P(G)$, and that keeps the average nodes' degree fixed. This maximization has

a solution given by the canonical distribution

$$P(G) = \frac{e^{-H(G, \theta)}}{Z(\theta)}, \quad (10)$$

where Z is the partition function, $H(G, \theta) = \theta \cdot C(G)$ is the graph Hamiltonian, and θ is a vector of Lagrange multipliers resulting from the maximization of the Shannon-Gibbs entropy under the chosen constraints C . The next step consists on the calculation of the exact values of the Lagrange multipliers. Following the approach presented in Ref. [49], these multipliers are determined by imposing that the chosen constraints of the network are found in the ensemble with maximum probability. This is achieved by rewriting the log-likelihood of observing the real network as $L(\theta) = -H(G^*, \theta) - \ln Z(\theta)$ and maximizing this quantity in order to find the optimal variables θ^* that define the ensemble. For the case of a bipartite network subjected to constraints on the average degree sequences, Eq. (10) takes the form

$$P(G | \vec{\alpha}, \vec{\beta}) = \frac{e^{-\vec{\alpha} \cdot \vec{v} - \vec{\beta} \cdot \vec{h}}}{\sum_G e^{-\vec{\alpha} \cdot \vec{v} - \vec{\beta} \cdot \vec{h}}},$$

where $\vec{\alpha}$ and $\vec{\beta}$ are the two sets of Lagrange multipliers for rows and columns nodes, respectively, $\vec{v}$ corresponds to the degree sequence of row nodes, and $\vec{h}$ to the degree sequence for column nodes. This probability can be rewritten in terms of the probability of existence of a link between a pair of nodes p_{ij} as

$$P(G | \vec{\alpha}, \vec{\beta}) = \prod_{i,j} p_{ij}^{a_{ij}} (1 - p_{ij})^{1-a_{ij}},$$

with p_{ij} only depending on the Lagrange multipliers as

$$p_{ij} = \frac{x_i y_j}{1 + x_i y_j}, \quad (11)$$

with $x_i = e^{-\alpha_i}$ and $y_j = e^{-\beta_j}$. The Lagrange multipliers from Eq. (11) can be determined computationally by solving the optimization problem for the likelihood $L(\vec{x}, \vec{y}) = \sum_{i=1}^{N_r} v_i \ln(x_i) + \sum_{j=1}^{N_c} h_j \ln(y_j) - \sum_{i=1}^{N_r} \sum_{j=1}^{N_c} \ln(1 + x_i y_j)$, and imposing $\vec{\nabla} L(\vec{x}, \vec{y}) = \vec{0}$. Finally, one can obtain the probabilistic bipartite matrix that can be used to sample the random ensemble of networks.

Finally, we introduce a scheme that pivots on Bascompte's approach. To do so, we revisit Eq. (9). Considering Eq. (9) as a probability, both summands can likewise be interpreted as probabilities. In this interpretation, summing them models the probability that at least one of the two events occurs. Indeed, each event corresponds to a distinct sampling process. One in which we sample the links of each row homogeneously at random, retaining the link only half of the times ($k_i^{(r)}/2M$), and a second sampling process in which we do the equivalent procedure per columns ($k_j^{(c)}/2N$). Understanding the process this way, we can reveal two aspects that affect the model performance in maintaining, in average, row and column degree of the original network.

The first aspect regards the oversampling of links per row (and column), and is a consequence of maintaining the two random sampling processes independent. Consider we first distribute links along the rows. Then, when distributing per

columns, there are already some links present that need to be considered when sampling the degree of the columns, or else this dual step process will generate more links than expected. We can quantify this excess of degree by computing, on the basis of Eq. (9), the expected degree of a row in the ensemble:

$$\begin{aligned} \langle k_i^{(r)} \rangle &= \sum_j p_{ij} = \frac{1}{2M} \sum_j k_i^{(r)} + \frac{1}{2N} \sum_j k_j^{(c)} \\ &= \frac{1}{2} k_i^{(r)} + \frac{L}{2N}, \end{aligned} \quad (12)$$

where $L = \sum_j k_j^{(c)}$ is the number of links of the network. As we can see, the error basically depends on the ratio between L and the number of row nodes, which is, in essence, the average degree. Considering the magnitude of this error and the heavy tail distribution of nodes' degrees usually observed in ecological networks, a significant overestimation on low degree nodes is expected.

The second aspect that needs to be addressed regards the chance to sampling twice the same link, which will decrease the overall expected connectance of the network and consequently the expected degree of some nodes. The probability of sampling twice a link is equivalent to the probability the adjacency matrix takes weight 2 during the dual step process, $a_{ij} = 2$, which can be obtained jointly considering the sampling of the same link by rows, $k_i^{(r)}/2M$, and by columns, $k_j^{(c)}/2N$:

$$P(a_{ij} = 2) = \left(\frac{k_i^{(r)}}{2M} \right) \left(\frac{k_j^{(c)}}{2N} \right). \quad (13)$$

Note that we usually consider a presence/absence adjacency obtained by thresholding the values of the adjacency matrix if a weight is larger than 1. This threshold is implicit in Eq. (9). From Eq. (13), we can see that the larger the degree of nodes, the higher the chance of sampling twice the edge that joins them. Then, the larger the undersampling of its degree on the ensemble. This is particularly problematic in larger degree nodes, which turn out to be the most important nodes of the network.

Our corrected probabilistic model, inspired by the original model by Bascompte, introduces a variation that alleviates the degree deviations in Eqs. (12) and (13). As in the original formulation, the interaction between pairs of species will be estimated considering the nodes' degrees of the observed interaction matrix. Although we eventually provide analytical expressions for the probability of having an interaction between species, we consider it important to describe the process behind these expressions. The corrected probabilistic model is based on two steps: In the first one, we distribute homogeneously at random the interactions of each row among the existing columns of the adjacency matrix; then, in the second step, we proceed to do the same process for each column. However, in the second step, since we already have links placed by the first step, we need to prevent resampling links already established, so as to not exceed the expected degree of columns. This process is illustrated in Fig. 2. Probabilistically, the chance of placing a link in between species i and j in the first step is equivalent to the original model: $k_i^{(r)}/M$. Then, in order to probabilistically prevent two links

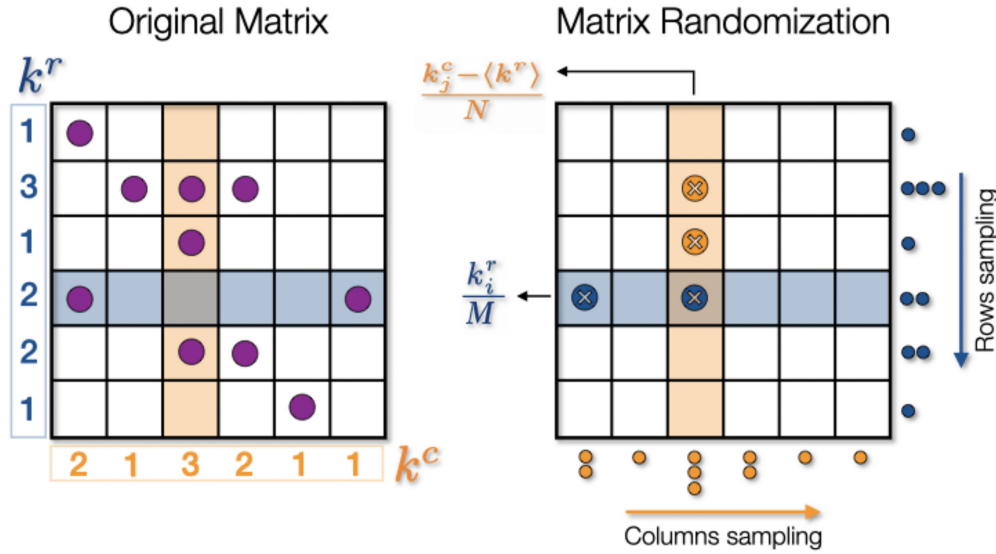


FIG. 2. Illustration of the corrected probabilistic model. In the left we have the original matrix, while on the right the result of the null model randomization is shown. In the model, the presence of a link is ruled by Eq. (14), which extends Bascompte's model by taking into account the fact that row and column sampling processes are not independent. Particularly, the figure shows a situation where the row sampling introduces a link (in the fourth row), which affects the third column degree. Accordingly, the probability to have links in a given column is corrected by subtracting a quantity embodying the probability that a fraction of these links already exists because of the row sampling.

from being placed on the same edge, we must enforce column sampling only when no link has already been placed by the row sampling process, that is, with probability $1 - k_i^{(r)}/M$. Additionally, we need to compensate the column degree induced by the sampling of rows (first step). Considering $\langle k^{(r)} \rangle$ as the average degree of rows, this induced degree can be calculated as $\sum_{i=1}^N k_i^{(r)}/M = 1/M \sum_{i=1}^N k_i^{(r)} \approx \frac{N}{M} \langle k^{(r)} \rangle$, which becomes simply $\langle k^{(r)} \rangle$ if $N = M$. The induced degree needs to be discounted when sampling links in the second step. Finally this sampling becomes: $\frac{k_j^{(c)} - \frac{N}{M} \langle k^{(r)} \rangle}{N} = \frac{k_j^{(c)}}{N} - \frac{\langle k^{(r)} \rangle}{M}$. Note that the aforementioned process will exactly maintain on average the degree of rows, and will attempt to maintain the degree of columns. It is worth mentioning that although we can compensate for the degree induced by row sampling, the process cannot remove links when the number of sampled rows already exceeds the expected column degree for a particular column. In such cases, $\frac{k_j^{(c)}}{N} - \frac{\langle k^{(r)} \rangle}{M} < 0$, and column sampling has no additional effect. To balance this induced error between rows and columns, we can assume that half the time this dual process starts by rows, and the other half by columns. Considering all of the above, we can now obtain the corrected probability of interaction between species i and j as follows:

$$p_{ij} = \frac{1}{2} \left[\frac{k_i^{(r)}}{M} + \left(1 - \frac{k_i^{(r)}}{M} \right) \left(\frac{k_j^{(c)}}{N} - \frac{\langle k^{(r)} \rangle}{M} \right) \right] + \frac{1}{2} \left[\frac{k_j^{(c)}}{N} + \left(1 - \frac{k_j^{(c)}}{N} \right) \left(\frac{k_i^{(r)}}{M} - \frac{\langle k^{(c)} \rangle}{N} \right) \right]. \quad (14)$$

The accuracy of the three PP models in nested matrices is illustrated in Fig. 3. Taking a sparse ($\xi = 2.1$) synthetic network with planted nestedness and low noise level ($p = 0.1$), the top panels show, from left to right, the pairwise interaction probabilities p_{ij} that result from the max-entropy,

Bascompte's probabilistic, and corrected probabilistic models. The bottom panels confront expected (actual) degree against the obtained one, after sampling the probability matrices for 100 times. Notably, the max-entropy model recovers exactly (with minor fluctuations) the degree sequence of the reference network. Also, it is apparent that, as predicted, lower degree nodes suffer from a significant overestimation in the probabilistic model, while the opposite happens for the largest degrees. The corrected probabilistic model largely resolves the inaccuracies of its antecedent, although, admittedly, it struggles with low-degree nodes (for which the excess degree cannot be compensated), and it exhibits minor deviations for high-degree nodes. Noteworthy, EE and FF models are not included in this figure—their scatter plots would render a trivial picture.

The same figures for other nested configurations are available in Figs. S2–S6 of the Supplemental Material [33]. Also, similar comparisons for matrices with planted modular and in-block nested structures are available in Fig. S7 of the Supplemental Material. In those, the only evident degree fluctuations stem from the probabilistic model.

IV. RESULTS

In the following, we examine different aspects of the five null models in relation to the three architectural patterns of interest. For a systematic exploration we exploit the synthetic generative model introduced in Sec. II.

In Secs. IV A and IV B, the presence of modular, nested or in-block nested arrangements is quantified using specific measures. Regarding modularity Q , we use Barber's formulation [53] for bipartite networks. In-block nestedness quality score $\mathcal{I}$ is measured as in Solé-Ribalta *et al.* [24]. Both quantities are maximized via an extremal optimization algorithm [54], followed by the Kernighan-Lin refinement of the resulting

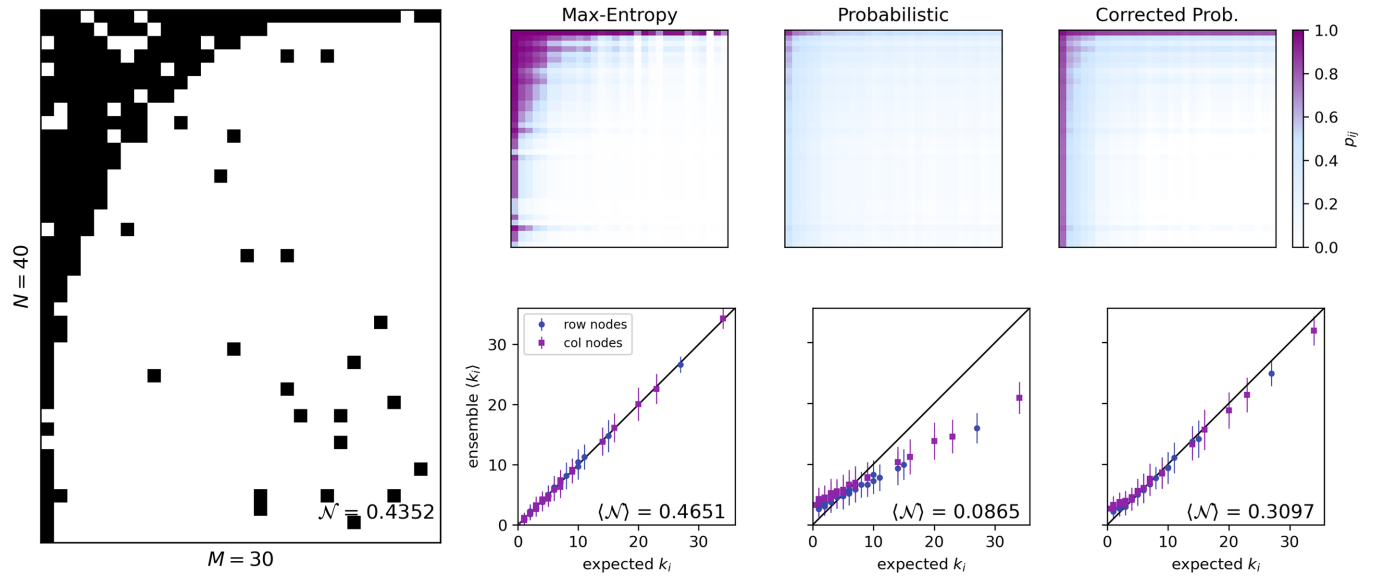


FIG. 3. Left: a 40×30 bipartite graph realization of the generative model with planted nested structure ($\xi = 2.1$ and $p = 0.1$). Its nestedness score $\mathcal{N}$ is reported. Top right row: for that network, the corresponding matrices of interaction probabilities p_{ij} produced by the three PP models: max-entropy, probabilistic, and corrected probabilistic are generated. Bottom right row: scatter plots in the lower panel show the fit between the obtained average degree sequences by each model (ensemble $\langle k_i \rangle$) and the real degrees of the matrix (expected k_i). The plot is obtained from 100 randomized realizations. Error bars correspond to one standard deviation above and below the average. The average nestedness $\langle \mathcal{N} \rangle$ for each of the model ensembles is reported as well, as an indirect proxy of the amount of shuffling that has occurred in the randomization process. The same exercise has been repeated for multiple size, density, and intrablock noise configurations; see Figs. S2–S6 in the Supplemental Material [33].

partition. For nested networks, we explore the behavior of the null models under the $\mathcal{N}$ nestedness metric [24], which is a degree overlap expectation corrected version of the NODF [55], and highly correlated with yet another nestedness measure, i.e., the spectral radius $\tilde{\rho}$ [13,56], normalized with respect to the square root of the number of links in the matrices, $\sqrt{L}$, as in [57]. More details are given in Sec. S1B of the Supplemental Material [33].

A. Resemblance of original versus randomized networks

We first analyze how closely the original network resembles its null-model ensembles. Figure 3 already provided some hints: in it, nestedness $\mathcal{N}$ is reported for the reference matrix (left panel), as well as the average $\langle \mathcal{N} \rangle$ for the ensemble of randomizations in each of the PP models. Interestingly, $\langle \mathcal{N} \rangle$ for the exponential random graph's random networks is very similar, and most often *higher* than $\mathcal{N}$ in the original network. This is consistent for the whole range of sizes (20–300 nodes), densities ($\xi \in [1.0, 2.6]$), and noise ($p \in [0.05, 0.25]$) tested (see Figs. S2–S6 in the Supplemental Material [33]). These results cast some doubt on the capacity of the models to actually provide truly randomized ensembles.

For this reason, that is, to test the capacity of the null models to actually deliver random ensembles of a network, we now study the similarity between the random matrices and the original synthetic ones over the range of parameters of the synthetic network generator model introduced in Sec. II. To quantify such resemblance, we employ the Jaccard distance J_d , i.e., the complementary of the Jaccard similarity J_s ,

between two matrices $A, B \in 0, 1^{N \times M}$:

$$J_d = 1 - J_s = 1 - \frac{\sum_{i,j} a_{i,j} b_{i,j}}{\sum_{i,j} a_{i,j} + b_{i,j} - a_{i,j} b_{i,j}}, \quad (15)$$

which accounts for the level of dissimilarity between two binary arrays—the original and its random counterparts, in this case. In the case of binary arrays, $J_d = 0$ indicates that the matrices are identical.

Top row in Fig. 4 shows the average Jaccard distance $\langle J_d \rangle$ over the nested $\xi - p$ parameter space for each null model scheme. Similar results for the modular and in-block nested matrices are shown in Fig. S8 of the Supplemental Material [33]. As expected, the results for the EE and the probabilistic models show high values of the $\langle J_d \rangle$ over the entire $\xi - p$ parameter space, confirming that the randomized matrices generated by these models are substantially different from the original one. This is in good agreement with the extremely low $\langle \mathcal{N} \rangle$ reported in Fig. 3, suggesting that, compared to these models' outcomes, many networks might incorrectly be identified as significantly nested—Type I error. Turning to the FF (represented by the Curveball algorithm) and max-entropy models, we observe a wide region of the $\xi - p$ parameter space in which $\langle J_d \rangle$ drops to intermediate and low values—specially for networks with small noise p , regardless of the slimness of the nested structure dictated by ξ . These results for FF and max-entropy confirm that, at least for nested networks, the resulting null matrices are very similar to the original one, since the models only allow for a very little deviation on the degree sequences—none in the FF model. This is consistent with the intuitions that resulted from Fig. 3. Hence, these

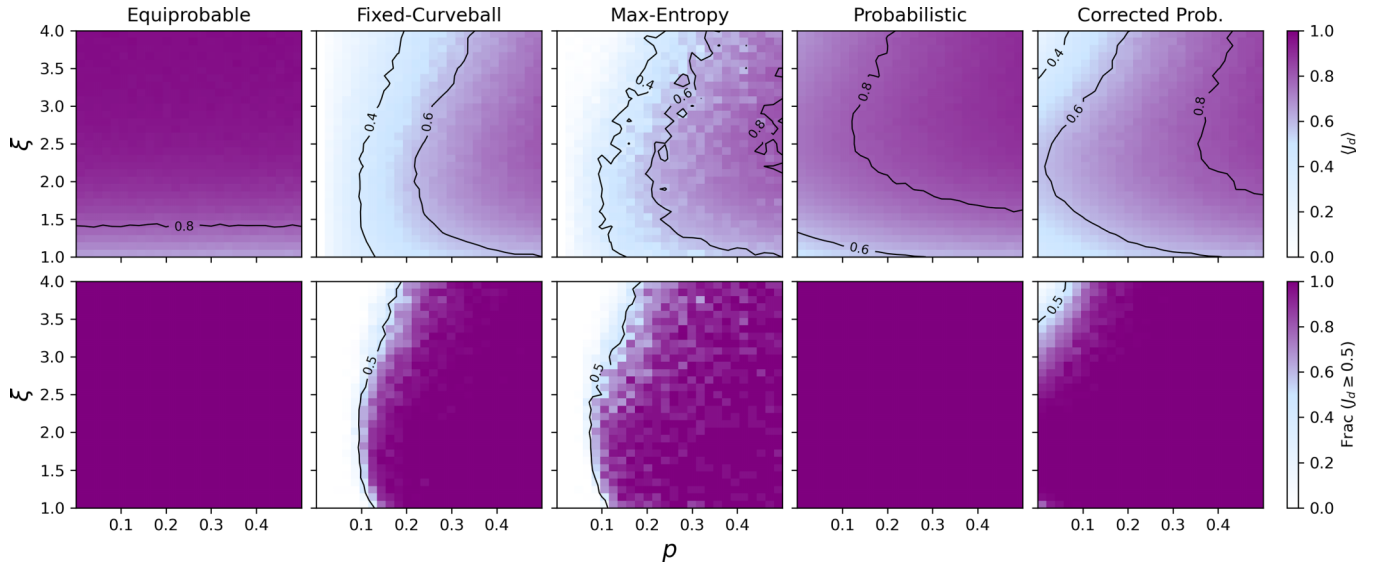


FIG. 4. Synthetic nested networks: two-dimensional plot in the $\xi - p$ parameter space showing, on top, the average Jaccard distance $\langle J_d \rangle$ with of the null model ensembles with respect to the original nested synthetic matrix, and (bottom panel) the percentage of matrices in the null model ensembles for which the Jaccard distance with respect to the original synthetic matrix was above a threshold of $J_d \geq 0.5$, for the five models studied in this work.

models might easily fall into Type II errors. The corrected probabilistic model, instead, provides a good trade-off, offering a better fit of the degree sequences (compared to EE and probabilistic), while generating null matrices less similar to the original one (compared to FF and max-entropy), as evinced by the overall intermediate values of the $\langle J_d \rangle$ over the nested $\xi - p$ parameter space.

Complementarily, the bottom panel of Fig. 4 shows the percentage of matrices in the null model ensembles for which $J_d \geq 0.5$ in the nested $\xi - p$ parameter space. Clearly, there are relevant regions for which the FF and the max-entropy models cannot generate true variants of the original matrix, even with such moderate threshold. Of course, when imposing a more rigid threshold this region becomes wider. In the other extreme, the EE and probabilistic schemes prove to have ample room to generate largely different networks, no matter the parameter values under study. Somewhere in between, the corrected probabilistic model is flexible enough to produce different networks, except in some extreme cases (very sparse networks with low p). These insights are all in good agreement with the work by Strona *et al.* [17], in which they proved that slightly relaxing the restrictiveness in the preservation of the rows and column totals—quasi-FF matrices—can reduce the tendency to underestimate significant nestedness.

B. Statistical significance of structural patterns

We now analyze how consistent the five null models described above are in assessing the statistical significance of nested, modular, and in-block nested patterns, for different sets of generated synthetic matrices. This rich set of networks span sizes from ~ 30 to 400 nodes, including varied configurations up to an eccentricity $1 \leq N/M \leq 2.5$: The smallest synthetic network is 20×16 , and the largest one 200×200 . In each case, we assessed the significance of the three patterns of

interest by means of z scores, as obtained from the average and standard deviations of an ensemble of randomized networks.

In the remainder of this section, to evaluate how well the null models sample networks that can help in detecting the structural arrangements, we adopt a proof-by-contradiction perspective. The idea is that, when analyzing planted structures with clearly recognizable features (e.g., nested or modular organization), a suitable null model should preserve the statistical detectability of those features. If, instead, the randomizations produced by a null model consistently lead to classifications that contradict the planted structure (e.g., identifying clearly nested networks as non-nested), this indicates that the model is prone to systematic Type I (false positives) or Type II (false negatives) errors. The results of the analysis are summarized in Table I, which accounts the percentage of networks with $z \geq 2$, i.e., an associated $\alpha/2$ confidence limit around 0.025.

For networks with planted nested structure ($B = 1$, $\xi \in [1.0, 4.0]$, $p \in [0, 0.5]$), the EE and probabilistic models systematically overestimate the statistical significance for nestedness, with 100% of the networks exhibiting $z \geq 2$ —no matter the amount of noise p . In the other extreme, both the FF and max-entropy restrictive schemes deliver a severe underestimation (0%) of the amount of truly nested networks. Thus, confirming their proneness to Type I and Type II errors, respectively. Only the corrected probabilistic model renders a balanced assessment, consistent with the parameters used in the generation of this set of nested synthetic matrices. The assessment of the significance for in-block nestedness is generally consistent with the one observed for nestedness, as $\mathcal{I}$ reduces to $\mathcal{N}$ when $B = 1$ (see Ref. [24]). Finally, all models wrongly identify a very small fraction of nested-by-construction networks as being significantly modular. This corresponds to the low- p nested matrices in the generated collection, in which the densest part of the network is (wrongly) identify as a block [24].

TABLE I. Percentage of networks with $z \geq 2$ for three sets of synthetic networks with nested, modular, and in-block nested structure. The over- and underestimation values mentioned in the text are marked with (1) and (2) superscripts, respectively.

Planted structure		EE	FF	PP		
		Equiprobable	Fixed curveball	Max-entropy	Probabilistic	Prob. corrected
Nested	$\mathcal{N}$	100 ⁽¹⁾	0.0 ⁽²⁾	0.0 ⁽²⁾	100.00 ⁽¹⁾	36.97
	Q	0.12	1.11	0.12	0.86	
	$\mathcal{I}$	42.67 ⁽¹⁾	0.0 ⁽²⁾	0.0 ⁽²⁾	43.92 ⁽¹⁾	22.58
Modular	$\mathcal{N}$	0.0	0.0	0.0	0.0	0.0
	Q	37.57	34.02	40.82	56.80	
	$\mathcal{I}$	0.0	0.0	0.0	0.0	0.0
In-block nested	$\mathcal{N}$	94.67 ⁽¹⁾	81.95 ⁽¹⁾	30.76	79.28 ⁽¹⁾	30.02
	Q	51.48	51.47	55.32	73.07	
	$\mathcal{I}$	24.11	16.71	30.62	22.18	19.97

Turning to modular-by-construction networks ($B > 1$, $\xi = 1.5$, $p = 1$, $\mu \in [0, 0.5]$), we observe that—unlike the previous case—all models produce results consistent with expectations: these networks are unanimously assessed as non-nested and non-in-block nested, and assessed as modular with different proportions. The largest differences (e.g., 34% for the Curveball algorithm against 65% for max-entropy) are difficult to analyze, and have to do with the sensitivity of these models against μ . That is, at which level of interblock noise the null model ceases to discriminate between an existing block structure and a nonexistent one.

Finally, inconsistencies also arise for networks with planted in-block nestedness ($B = 4$, $\xi = 1.5$, $p \in [0, 0.5]$, $\mu \in [0, 0.5]$). All randomization strategies assess a notable amount of networks as being nested. While this is expectable to some extent (the overall amount of connectivity overlap is large, provided that B is kept to four blocks only), clearly, EE, Curveball, and probabilistic schemes overshoot the assessment. On the other hand, the consideration of a large fraction of networks as modular cannot be considered an error: indeed, an in-block nested structure is, strictly speaking, a modular network—except that it has an extra constraint. Finally, it makes sense that the fraction of networks with $z_Q \geq 2$ is larger than the one with $z_{\mathcal{I}} \geq 2$: they add to the networks with a clear in-block nested structure (low p , low-to-mild μ), the ones with modular structure, those with high p .

The most intriguing results from Table I are better grasped in a visual way, which we present in Figs. 5–7. Starting with nested structures—the most puzzling in Table I—Fig. 5 focuses on the subset of nested-by-construction synthetic networks. The figure shows the averaged z -score values for nestedness $z_{\mathcal{N}}$ (top) and modularity z_Q (bottom) over the ξ – p parameter space, considering the three PP models. Thumbnails of the resulting generated matrices over the parameter space are shown on the left part of the figure as a visual aid.

The results of Fig. 5 for the probabilistic model confirm the tendency for overestimating the statistical significance of nested patterns, i.e., Type I error. The model yields values of $z_{\mathcal{N}} \geq 2$ over the whole parameter space, including the regions where the planted nested structure becomes hardly identifiable (high p). The max-entropy model, conversely, is not able to confirm the significance of nestedness, even in regions where the networks have a clearly defined nested pattern. In fact,

it deems a large amount of networks as, indeed, antinested, i.e., $z_{\mathcal{N}} \leq 0$. The corrected probabilistic model is capable of confirming the significance of the nested pattern over a wide region of the parameter space, for intermediate to low values of noise p —as expected—and different shape values ξ . Note, however, that the higher the value of ξ is, the less noise p is necessary for the model to reach $z_{\mathcal{N}} \leq 2$. This is not surprising, since ξ affects the network connectance, and sparser networks will require a lower level of noise to distort the planted nested structure.

Focusing on the bottom row of Fig. 5, the assessment of significance for modularity $z_Q < 2$ for the three models, except for extremely small regions. In these few cases, one can assume that networks are dense enough, such that the optimization algorithm employed for modularity is able to find a partition with $B > 1$, resulting in values of Q larger than expected [24].

Results for the assessment of modularity and in-block nestedness from Table I are complemented with Fig. 6. The figure shows the average z -score values for modularity z_Q (top) and in-block nestedness $z_{\mathcal{I}}$ (bottom) over the μ – B parameter space, as obtained under the three PP models. Each point corresponds to the mean z score computed across ensembles of more than 100 000 synthetic bipartite networks of various sizes (see caption), with planted modular structure. Thumbnails of the resulting matrices across the parameter space are displayed on the left part of the figure. Both top and bottom panels reflect exactly the results reported in Table I. On top, an unanimous assessment of modularity across the displayed models, both regarding the significance of modularity for all the range of B and up to a certain level of μ . Noteworthy, the probabilistic model appears to be more sensitive to the level interblock noise μ . Results for the assessment of in-block nestedness also show consistent results: all models rule out the significant presence of in-block nestedness—as they should.

Finally, we move on to examine the results for the last set of synthetic networks, with planted in-block nested structure. Figure 7 complements the results reported in Table I, showing the averaged z -score values for in-block nestedness $z_{\mathcal{I}}$ (top) and nestedness $z_{\mathcal{N}}$ (bottom) over the μ – p parameter space. The three models illustrated here show similar (and expected) results for $z_{\mathcal{I}}$: In-block nestedness becomes less significant

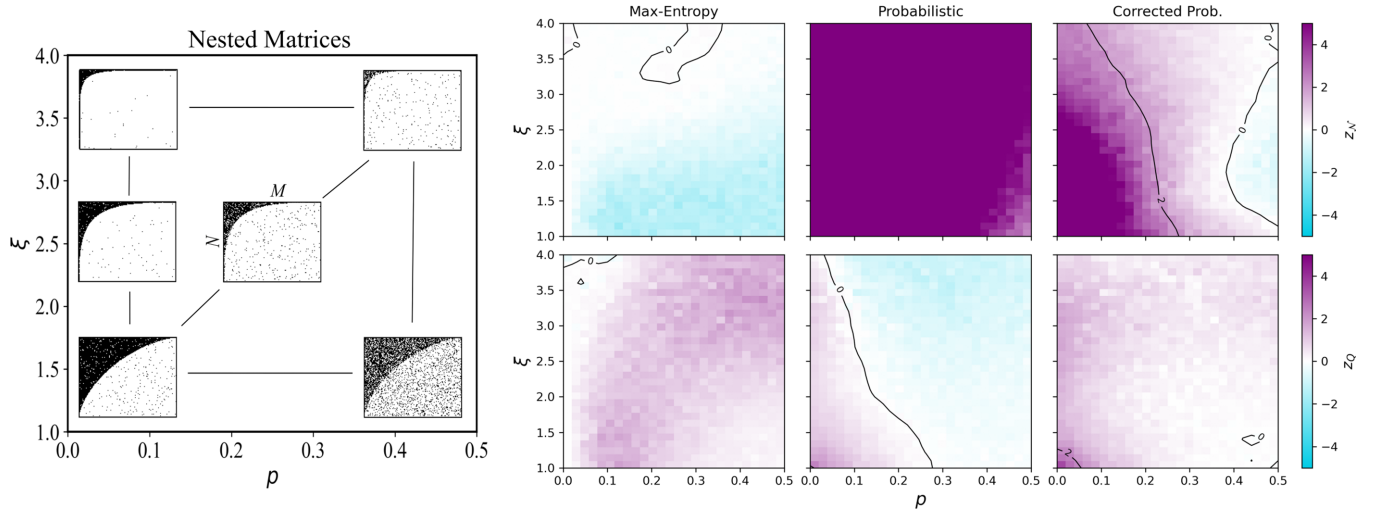


FIG. 5. Synthetic nested networks: Heatmaps in the ξ - p parameter plane showing the average z_N (top) and z_Q (bottom) scores obtained under the max-entropy, probabilistic, and corrected probabilistic models. Each point represents the mean value computed over ensembles of synthetic bipartite networks with planted nested structure ($B = 1$, $\xi \in [1, 4]$, $p \in [0, 0.5]$) and different sizes, with $N + M \in [36, 400]$. For each network size, z scores were first computed across 100 realizations and then across sizes. Overall, more than 2.2×10^5 networks were built and analyzed for this figure (three models). Examples of generated adjacency matrices across the parameter space are shown on the left.

when the structure is distorted within (higher p) or among (higher μ) blocks. The bottom row of the figure (i.e., the assessment of significance for $\mathcal{N}$ in in-block nested networks) strongly resembles the top one: The three models identify as nested a large fraction of in-block nested networks, with decreasing values of z as p and μ grow. In some sense this is expectable: global nestedness decreases with the number of blocks in a network [58], and the number of blocks is relatively low here ($B = 4$). On the other hand, the result leaves a worrying conclusion—even when the baseline models behave as expected, the two patterns are hard to distinguish.

C. Empirical networks

Finally, we analyze how consistent the five null models are in assessing the statistical significance of nested, modular, and in-block nested patterns over a set of 192 empirical networks, which correspond to mutualistic ecological communities [59]. It is worth noting that the literature has consistently identified nestedness as the landmark signature of these types of ecological interactions [1,3,4,11] (with exceptions, see Ref. [52]).

All networks are treated as binary and have between 20 and 300 nodes (see Sec. S3 and Fig. S10 in the Supplemental Material for details [33]). We report the percentage of networks

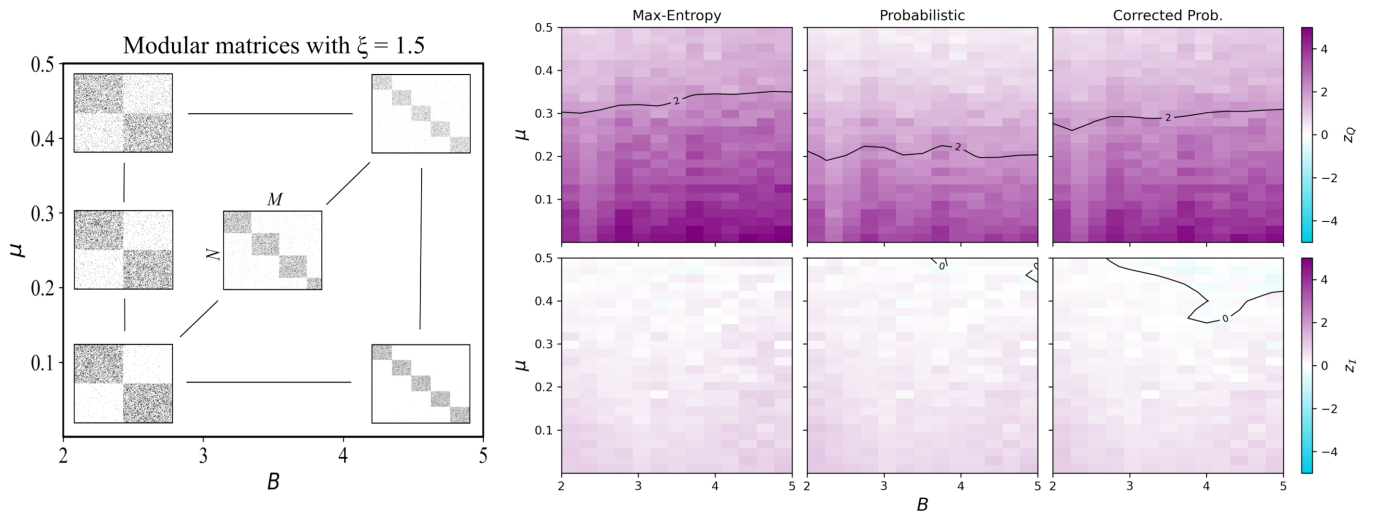


FIG. 6. Synthetic modular networks: Heatmaps in the μ - B parameter plane showing the average z_Q (top) and z_I (bottom) scores under the max-entropy, probabilistic, and corrected probabilistic models. The results correspond to ensembles of synthetic bipartite networks (over 10^5 networks) with planted modular structure ($p = 1$, $\xi = 1.5$, $\mu \in [0, 0.5]$, $B \in [2, 5]$) and various sizes (from 20×16 up to 200×200). The provided z scores are obtained by first averaging over 100 realizations and then across network sizes. Thumbnails on the left illustrate examples of generated matrices across the parameter space.

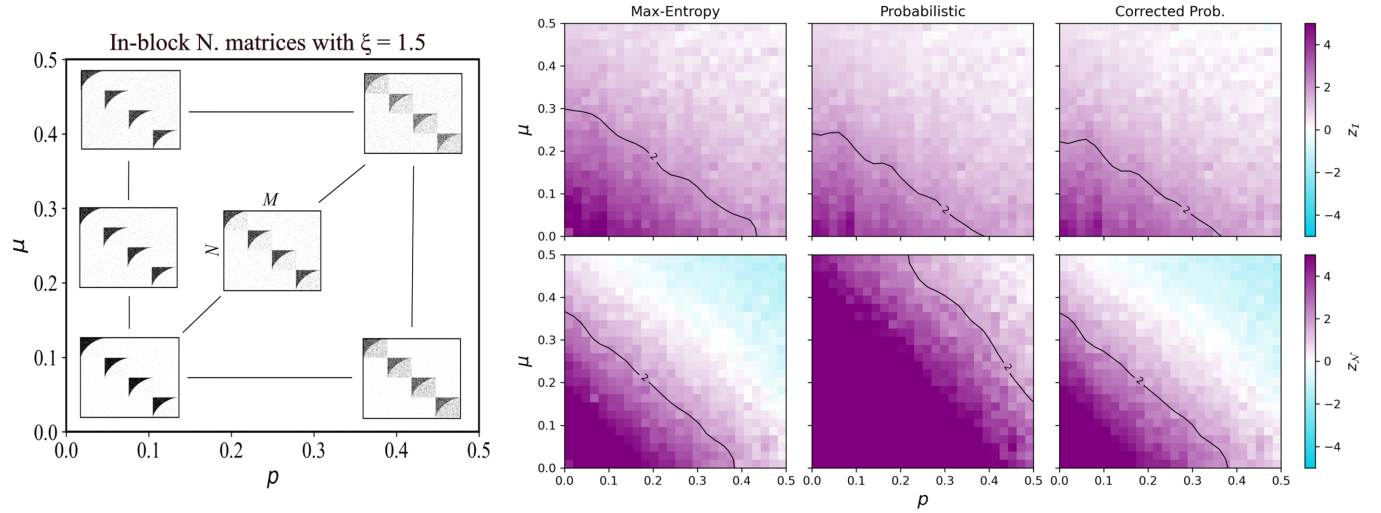


FIG. 7. Synthetic in-block nested Networks: Heatmaps in the μ - p parameter plane showing the average z_I (top) and z_N (bottom) scores obtained under the max-entropy, probabilistic, and corrected probabilistic models. Each point corresponds to the mean value over ensembles of networks with planted in-block nested structure ($B = 4$, $\xi = 1.5$, $\mu, p \in [0, 0.5]$) of multiple sizes (from 20×16 up to 200×200). Overall, $\sim 1.8 \times 10^5$ networks were built and analyzed for this figure (three models). For each network size, z scores were computed over 100 random realizations, and then averaged across all sizes. Examples of the generated adjacency matrices across the parameter space are displayed on the left.

with $z \geq 2$ ($\alpha/2 \sim 0.025$) for each one of our five structural metrics in Table II.

Assessment of nestedness in the empirical data for the EE and the probabilistic model is consistent with the findings in Fig. 5, yielding $z_N \geq 2$ for a large proportion of the analyzed networks (99.13% and 93.86%, respectively). Results for the strictest schemes—FF and max-entropy models—show as well, in the case of nestedness, a good agreement with the results in the synthetic matrices (and the literature [52]), yielding nonsignificant z scores for a large majority of the networks. Once again, the corrected probabilistic model seems to provide a more balanced assessment of nested patterns. The small variations in the preservation of the node's degrees in the corrected probabilistic model allow nestedness to re-emerge as significant in a fair proportion of the networks.

On the other hand, only a small fraction of the networks is significantly modular ($z_Q \geq 2$) under the EE and probabilistic schemes, followed closely by FF. The large percentage of significant modularity rendered by the max-entropy model suggests, in accordance with our previous results, its tendency toward positive assessments of modular patterns.

Notably, in-block nestedness appears to reconcile four of the null models (with the exception of FF), showing significant $z_I \geq 2$ for a similar (and notable) percentage of the networks, in agreement with recent studies suggesting the

presence of in-block nestedness as a frequent pattern in ecological communities [26,28,29].

Similar to our final comments in the previous section, Table II reveals an inconclusive scenario: in the hypothesis-testing framework, there is not a principled way to make strong claims on which model is over- or underestimating the presence (absence) of a given pattern. Furthermore, each null model presents at least one instance in which nested and modular patterns are simultaneously assessed as significant (despite analytical evidence of their difficult coexistence [58]), and even some cases in which $z \geq 2$ for the three patterns at the same time.

V. DISCUSSION

The overwhelming evidence that real ecological networks are highly structured, rather than randomly assembled, has sparked much research to explain the emergence and dynamical effects of those interaction patterns. In parallel, efforts have been devoted at determining the statistical significance of such patterns. As a result, the use and design of specialized null models to assess the statistical significance of selected architectures has become a widespread approach within the ecological community. However, to this day, there is still no agreement on which is the most suitable procedure to perform this kind of analysis. The discussion regarding the

TABLE II. Percentage of networks with score $z \geq 2$ for a collection of 192 empirical ecological networks.

	EE Equiprobable	FF Fixed Curveball	PP Max-entropy	Probabilistic	Corrected Prob.
$\mathcal{N}$	99.13	6.96	13.04	93.86	42.11
$\mathcal{Q}$	12.17	26.09	72.17	19.30	47.37
$\mathcal{I}$	35.65	12.17	38.26	35.09	29.82

selection on the level of constraints to build the null matrices, the construction of synthetic benchmarks, or the appropriate null model-metric combination remains an open issue among scholars. Furthermore, there is already abundant evidence suggesting that networks often exhibit hybrid structures and/or at different scales of organization, yet the concurrent assessment of the statistical significance of such complex patterns has not been extensively studied.

In this work, we have first addressed the need to build synthetic networks with total control over their dominant structure. Our generative benchmark allows for the construction of networks with clear defined architectural patterns, transitioning from structured (nested, modular, in-block nested) to random networks in a smooth way. Only then we can generate a rich sample to systematically study of the performance of five null models.

With several thousand networks of varying size, connectance and planted internal structure, we have observed the existence of ambiguities and biases in the concurrent assessment of network patterns, either over- or underestimating their significance. In particular, our use of an extensive ensemble of networks uncovers the weaknesses of both too restrictive (FF, max-entropy) and too permissive (EE, probabilistic) randomizing procedures. In light of such results, we propose a variation of the probabilistic model, that mitigates some of the limitations exhibited by the current models—in close agreement with recent research, regarding the convenience of quasi-FF approaches [17].

Our extensive analysis of synthetic ensembles offers a retrospective explanation for the long-standing inconsistencies in the literature regarding the prevalence of nested and/or modular architectures in ecological networks. By systematically revisiting empirical datasets under the most commonly used null model schemes, we reproduce those contradictions and identify their origin in the methodological biases of the different randomization strategies. The same empirical network may appear significantly nested, modular, both, or neither—depending on how randomness and constraints are introduced. This observation clarifies why previous studies have reached diverging conclusions despite analyzing comparable data.

At present, our results and tools provide a practical way to navigate this complexity. The framework introduced here—combining a controlled synthetic generator, structural descriptors, optimization algorithms, and a suite of null models—enables researchers to perform consistent and reproducible analyses of bipartite structure. Through this unified implementation, users can better assess the statistical significance of multiple patterns across scales, from macrolevel nestedness to mesolevel modularity and in-block nestedness. While no framework can yet provide a fully definitive assessment of ecological structure, our proposal represents a balanced, transparent, and immediately applicable approach for current research.

Looking forward, our findings highlight the limitations of the prevailing practice. Structural measures based on optimization heuristics and hypothesis-testing significance levels, though useful, are ultimately descriptive and can produce ambiguous or contradictory results when applied in isolation. We believe that future progress will come from adopting a genuinely inferential perspective—for instance, through Bayesian or likelihood-based approaches capable of quantitatively comparing competing generative hypotheses. In that sense, the generative model introduced here constitutes a promising step in that direction: It bridges descriptive pattern analysis with probabilistic modeling, opening a path toward a more theoretically grounded understanding of the architectures observed in real-world bipartite systems.

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DATA AVAILABILITY

The data that support the findings of this article are openly available [59–61].

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