

The ghost of nestedness in ecological networks

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Ecologists are fascinated by the prevalence of nestedness in biogeographic and community data, where it is thought to promote biodiversity in mutualistic systems. Traditionally, nestedness has been treated in a binary sense: species and their interactions are either present or absent, neglecting information on abundances and interaction frequencies. Extending nestedness to quantitative data facilitates the study of species preferences, and we propose a new detection method that follows from a basic property of bipartite networks: large dominant eigenvalues are associated with highly nested configurations. We show that complex ecological networks are binary nested, but quantitative preferences are non-nested, indicating limited consumer overlap of favoured resources. The spectral graph approach provides a formal link to local dynamical stability analysis, where we demonstrate that nested mutualistic structures are minimally stable. We conclude that, within the binary constraint of interaction plausibility, species preferences are partitioned to avoid competition, thereby benefiting system-wide resource allocation.

Nestedness has been studied in a wide range of ecological systems. The concept was first proposed in the early Twentieth Century but only became popular among ecologists with its application to the biogeographic pattern of species occurrence in islands and other fragmented

landscapes^{1,2}. More recently, nestedness in species interaction networks has received significant attention^{3–7}, where it has been suggested that a nested pattern of interactions leads to greater biodiversity in mutualistic systems such as plant-pollinator networks^{8,9}. In a nested bipartite network or graph, interactions are organised such that specialists (e.g., pollinators that visit few plants) interact with subsets of the species with whom generalists (e.g., pollinators that visit many plants) interact. A nested structure corresponds to a systematic arrangement of non-zero entries in the binary matrix used to represent a network, and existing detection methods are based on distinguishing the nested pattern from other possible arrangements of matrix elements^{10,11}. However, these methods are often computationally expensive for large matrices and are not applicable to quantitative networks (binary metrics extended to work with quantitative data, such as WNODF¹², do not make full use of the available quantitative information).

Quantitative networks contain the number or frequency of pairwise interactions between species, and we show how empirical data can be rescaled to permit investigation of feeding or visitation preferences in addition to basic presence-absence structure. If preferences are quantitatively nested then the most generalist resources are preferred by all consumers—most strongly by generalist consumers, closely followed by specialist consumers—and specialist resources are neglected. We formally extend the definition of nestedness to include quantitative networks and propose a new and robust detection method based on the eigenvalue spectrum of a graph’s adjacency matrix. The spectral properties of perfectly nested graphs were first discussed in the mathematical literature, where they are known as Double Nested Graphs (DNGs)¹³ or chain graphs¹⁴, and we show that large dominant eigenvalues are associated with highly nested structures (for both binary

and quantitative matrices). A spectral method has the advantage that the eigenvalues of a matrix can be computed extremely quickly—even for large matrices—and results are invariant to matrix permutation¹⁵.

Of 52 bipartite ecological networks from the literature, including plant-pollinator, parasitoid-host, and seed dispersal types, 51 (98%) were binary nested, however, only 3 (6%) had preference structures that were quantitatively nested. These results agree with our analysis of the dynamical (local) stability of nested graphs, where we demonstrate that perfectly nested configurations are minimally stable. Within the restriction of interaction plausibility—whether an interaction is forbidden or not, and identifiable with binary structure¹⁶—species preferences are partitioned to avoid competition. Thus, ecological systems are organised such that niches are exploited and the efficient use of available resources is promoted.

Results

Before explicitly considering ecological systems and empirical data, we begin by formally defining nestedness for both binary and quantitative bipartite networks, and present a general detection method that follows naturally from the matrix properties of nested graphs.

A bipartite network or graph contains S nodes (species) that can be partitioned into two disjoint sets A (animals in pollination networks) and P (plants) such that each of the E undirected edges (an animal-plant interaction) connects a node in the set A with one in the set P . For the binary case, the adjacency matrix \mathcal{A} is a square matrix in which $\mathcal{A}_{ij} = 1$ if i and j are connected

and is zero otherwise; for quantitative networks \mathcal{A}_{ij} can take positive non-zero values other than 1. The set of eigenvalues are an invariant property of a matrix (they do not change if rows or columns are permuted). Because \mathcal{A} is a symmetric matrix all of its eigenvalues are real, and because the graph is bipartite the eigenvalues are distributed symmetrically about zero. The largest eigenvalue of \mathcal{A} is known as its spectral radius $\rho(\mathcal{A})$, and for binary matrices its value is bounded from above by $\sqrt{|E|}$ ^{13,15}.

Since matrix \mathcal{A} is symmetric and the graph bipartite, we need draw only the $|P| \times |A|$ incidence matrix \mathcal{B} (e.g., Figure 1). Nestedness can be defined as a property of the matrix \mathcal{B} . If \mathcal{B} is a perfectly nested binary matrix then there exists a permutation of rows and columns such that the set of edges in each row i contains the edges in row $i + 1$, while the set of edges in each column j contains those in column $j + 1$. More formally, the rows and columns of \mathcal{B} can be sorted (with $\mathcal{B}_{1,j} > 0 \forall j$ and $\mathcal{B}_{i,1} > 0 \forall i$) such that $\mathcal{B}_{i,j} \leq \min(\mathcal{B}_{i,j-1}, \mathcal{B}_{i-1,j})$.

This definition of perfect nestedness extends to quantitative as well as binary matrices. Matrices A , C , D , I , K and N in Figure 1 are perfectly nested, as is matrix C in Figure 2, while the others are not.

In the mathematical literature regarding DNGs, Bell *et al.*¹⁷ provide a theorem that states: among all the connected bipartite graphs with $|S|$ nodes and $|E|$ edges, the one yielding the largest spectral radius $\rho(\mathcal{A})$ is a perfectly nested graph. It was subsequently proved that the same holds if the number of nodes in each set P and A are fixed¹⁸, rather than choosing among all possible sizes such that $|P| + |A| = |S|$ as in the original theorem. We confirm numerically that among all the

81 bipartite graphs with $|P|$ plants, $|A|$ animals and $|E|$ edges, the configuration leading to the largest
 82 spectral radius is a perfectly nested graph, with all other perfectly nested graphs have spectral
 83 radii close to this maximum value (Figure 1). This finding extends to quantitative matrices and
 84 quantitative nestedness (Figure 2). The right tail of the spectral radius distribution contains either
 85 perfectly nested graphs—of which there can be many configurations (SI)—or graphs that are very
 86 close to being perfectly nested, while the left tail contains graphs that are far from being perfectly
 87 nested. The spectral radius therefore represents a natural scale for nestedness, with larger $\rho(\mathcal{A})$
 88 obtained for more nested matrices, and we have developed a set of statistical tests to determine the
 89 significance of nestedness for matrices that are not necessarily perfectly nested.

90 Remarkably, matrices that are significantly non-nested in their binary form become signif-
 91 icantly nested when a nested quantitative pattern is overlaid. This suggests that the quantitative
 92 structure of a network is likely to dominate any underlying binary pattern (SI).

93 The eigenvector associated with the spectral radius measures the contribution of each node
 94 in the graph to nestedness, which besides being of interest in its own right¹⁹, provides a natural
 95 way of ordering nodes that best illustrates matrix nestedness. This follows from the standard
 96 eigenvalue equation $\mathcal{A}\vec{x} = \lambda\vec{x}$: Because any eigenvector \vec{x} multiplied by the original adjacency
 97 matrix \mathcal{A} yields a vector parallel to the original adjacency matrix, the spectral radius (dominant
 98 eigenvalue) represents a scale factor λ for the dominant eigenvector. Conversely, if the spectral
 99 radius is understood to be a measure of nestedness, then the entries of the dominant eigenvector
 100 (of size the number of species) represent the weighting of each species with respect to nestedness.

We now turn our attention to the specific case of ecological systems. In general, interactions among species can be described by a set of dynamical equations: $\frac{dx_i}{dt} = f(x_i) + g(x_i, \vec{x})$, where x_i is the density of a given species i , $f(x_i)$ describes the effect of its density on population growth, and $g(x_i, \vec{x})$ is the contribution to growth from interactions with other species in the system^{20–22}. We can divide the interaction term between two species, $g(x_i, \vec{x})$, into two parts: the frequency of interactions $\gamma_{i,j}x_ix_j$, and the effect of each interaction $h(x_i, \vec{x})$, and so $g(x_i, \vec{x}) = \sum_j \gamma_{i,j}x_ix_jh(x_i, \vec{x})$. Typically, $h(x_i, \vec{x})$ takes the form of a functional response that captures the effect of an interaction between i and all of its partners \vec{x} (e.g., Holling’s Type II²³). For each pair of species, x_ix_j is a mass action term, and $\gamma_{i,j}$ indicates the relative frequency or probability of interaction compared to mass action. Under the mass action hypothesis the basic affinity between two species—the expected magnitude of encounters—is directly proportional to the product of their densities, and factors such as the spatial layout of the environment, consumer search efficiency or handling time are not accounted for. These additional factors are aggregated in $\gamma_{i,j}$. For each plausible ($\gamma_{i,j} \neq 0$) interaction, $\gamma_{i,j}$ can be thought of as a preference parameter: if $\gamma_{i,j} > 1$ then the interaction is more likely to occur than expected and is therefore favoured, $\gamma_{i,j} < 1$ indicates that the interaction is less favorable, and $\gamma_{i,j} = 1$ is exactly the expectation based on mass action. When we record ecological data such as the number of pollinator-plant visits—data that can be organised in the form of a quantitative incidence matrix \mathcal{B} —we implicitly record $\mathcal{B}_{i,j} = \gamma_{i,j}x_ix_j$. So in practice, empirical data must be adjusted for mass action (x_ix_j) to isolate species preference $\gamma_{i,j}$.

We are particularly interested in whether the pattern of nestedness observed in binary bipartite ecological networks⁴ is maintained in the quantitative preference structure represented by the

γ -matrix. In a nested quantitative network, generalist-generalist species interactions are strongest, followed by generalist-specialist interactions, whereas specialist-specialist interactions are much weaker (and may be absent altogether).

Before applying the tests for nestedness to empirical data, we first remove the effect of mass action in order to isolate species preferences. Since interaction data are rarely accompanied by independent measures of species density, we use a method based on solving overdetermined sets of equations²⁴ to infer effective species abundances from quantitative interaction networks. These effective abundances should not be interpreted as field-measurable equivalents, rather, they are best-fit abundances under the mass action hypothesis. In some regards their use is more appropriate than raw abundance data because they incorporate confounding factors such as life-cycle turnover, partner co-occurrence overlap, and unevenness in spatial distribution.

To obtain effective abundances recall that we can write empirical count data $\mathcal{B}_{i,j} = \gamma_{i,j}x_i x_j$. If no interaction is recorded $\mathcal{B}_{i,j} = 0$ and we set the estimate for species preference $\hat{\gamma}_{i,j} = 0$. For the remaining set of recorded counts with $\mathcal{B}_{i,j} > 0$, we take logarithms $\log \mathcal{B}_{i,j} = \log \gamma_{i,j} + \log x_i + \log x_j$ and perform a linear regression. However, rather than regressing “y” against “x” as is more commonly done, we do the opposite such that we infer the log-transformed effective abundances \hat{x}_i and \hat{x}_j from the log-transformed (non-zero) counts (SI). The preference γ -term then represents errors or residuals, and since $\log \gamma_{i,j}$ ’s are minimised during regression the estimated $\hat{\gamma}_{i,j}$ ’s are constrained to be as close to 1 as possible. In this way, binary matrices can be seen as a special case in which interaction magnitude is completely explained by mass action. And as required,

preferences are scaled relative to mass action—based on the inferred effective abundances—with $\hat{\gamma}_{i,j} = \mathcal{B}_{i,j}/(\hat{x}_i\hat{x}_j)$. This quantitative $\hat{\gamma}$ -matrix can be assessed for nested patterns.

We tested 52 bipartite empirical networks for binary and quantitative nestedness (Table 1). For each network and test, we computed the probability p that a randomly constructed matrix \mathcal{A}' , which preserves some of the properties of the empirical matrix \mathcal{A} , is associated with spectral radius $\rho(\mathcal{A}') \geq \rho(\mathcal{A})$ (SI). All but one of the networks were binary nested ($p < 0.05$), in agreement with earlier studies⁴. However, nestedness was not observed in species preferences: for the vast majority of networks, the quantitative structure of the $\hat{\gamma}$ -matrix was indistinguishable from random configurations, and in some cases, anti-nestedness became apparent ($p > 0.95$) (Table 1, Figure 3). The lack of nestedness in the dominant quantitative structure of empirical networks is consistent with our mathematical treatment of the local stability of nested structures. Although capturing only one aspect of ecological system dynamics, the mathematical tractability of local stability analysis provides a good starting point for assessing the dynamical consequences of network structure in its most simplistic form²⁵.

Local stability analysis is concerned with how a dynamical system resting at equilibrium responds to perturbations. If an equilibrium point is stable, then the system returns to that point following small perturbations. For unstable equilibrium points, small perturbations will move the system away from the original resting state. Mathematically, the stability of an equilibrium point is completely defined by the sign of the real parts of the eigenvalues of the so-called community matrix M^{25-27} (these eigenvalues are distinct from the adjacency matrix eigenvalues we have been

considering so far). If all of the signs are negative then the equilibrium point is stable. Contemporary work has shown that nested mutualistic networks are less likely to be stable than their random counterparts²⁵. We now demonstrate that a nested structure within M minimises local stability.

A community matrix can be written as the sum of a matrix with zeros on its diagonal, M' , and a corresponding diagonal matrix, D , i.e., $M = M' - D$. For very large systems, the spectral radius of M is $\rho(M) \approx \rho(M') - \bar{D}$, where \bar{D} is the average value of the diagonal²⁵. Stability is therefore achieved whenever $\rho(M') < \bar{D}$. Analogous to arranging coefficients in an adjacency or incidence matrix (as we did above), among all possible ways of arranging the coefficients of M' the configuration yielding the largest spectral radius is perfect nestedness (binary or quantitative). (Note that the community matrix is often considered non-symmetric, i.e., the effect of an animal on a plant is often assumed to be different from that of the plant on the animal. However, the maximum spectral radius is obtained for symmetric matrices.) Hence, for a given diagonal and set of coefficients, nestedness minimises local stability.

This is seemingly at odds with the prevailing view that nestedness promotes the persistence of species in mutualistic systems^{8,9} (although recent work has begun to question this proposition²⁸). As an approach to assessing system robustness, persistence encompasses local stability analysis— in many models of mutualism, local stability guarantees species persistence but locally unstable states may yet display persistence. Repeating precisely the analysis of Thébault & Fontaine⁹ we show that many dynamical models inadvertently build-in trivial local stability and hence guarantee persistence: the diagonal elements of the community matrix are always large enough to compen-

sate for the potential destabilising effect of nestedness, thereby precluding nestedness—or, indeed, any other configuration of interactions—from having a significant contribution to local stability or persistence in such models (SI). The claimed positive relationship between nestedness and persistence actually reflects a trivial positive relationship between connectance and persistence in obligate mutualistic systems; Trivial because species without partners immediately go extinct (a feature not considered by Thébault & Fontaine⁹), and species with initial densities close to zero will quickly go extinct unless they have sufficient (binary) mutualistic partners to “pull” them to larger densities, after which, they are guaranteed to persist²⁹.

Discussion

Traditionally, nestedness has been associated with the plausibility of interaction: if the length of a pollinator’s proboscis is sufficient to obtain nectar from plants with deep corolla tubes, then it can also obtain nectar from species with shallower tubes, otherwise its visitation partners are restricted—for a community with many pollinator species, each with a different proboscis length, a nested binary interaction pattern emerges. Quantitative data allow us to investigate whether pollinators interact with particular plants more or less frequently than would be expected through random encounter, and whether they do so in any systematic fashion. With a nested preference structure, almost all consumers disproportionately interact with a common subset of the most generalist resources, while ignoring more specialist resources.

While we found empirical networks to be binary nested, after adjusting for uneven species abundances according to mass action, their quantitative preference structures were distinctly non-

nested. The need to account for abundances has been highlighted using synthetic networks, where heterogeneous abundance distributions combined with random species associations was sufficient to produce significantly nested binary patterns, leading to the conclusion that complex trait-based models were not necessary to explain nestedness³⁰. Our results extend this argument to quantitative networks: The vast majority of empirical networks analysed had quantitative preference structures indistinguishable from random graphs, meaning that no systematic process is required to promote or constrain observed levels of nestedness.

The lack of quantitative nestedness also finds support from mathematical analysis, where we showed that nested configurations of mutualistic interactions are minimally stable from the perspective of local stability analysis. How other types of interaction—such as antagonistic or facilitative pairings⁸—formally combine with mutualism to determine the overall stability and persistence of a network requires further work. At the community level, compared to quantitatively nested preference structures, non-nested structures suggest that species preferences are partitioned to avoid competition. Species rarely forgo abundant and accessible resources, rather, less abundant resources are disproportionately favoured by different sets of consumers—niches naturally arise. It would be instructive to see whether this kind of niche partitioning is also apparent at the level of individuals within a single species population³¹.

Much like the constituent elements of our sun can be inferred by studying the solar spectrum of light, we used a spectral approach—spectrum derived from the Latin for ghost—to detect nestedness in complex ecological networks. And like a ghost, nestedness, which was strongly ap-

parent in binary structures (although the ecological significance of this observation is debatable³⁰), disappeared when quantitative preference structures were analysed. As the size of ecological data grows, the advantages of a spectral approach will become more pronounced; here we considered only the dominant eigenvalue of a network's adjacency matrix, the relationship between other spectral properties and ecological phenomena warrants further investigation. Nestedness may not be the preeminent structure once thought, but spectral analysis may yet offer clues as to what structural features influence the function of large complex ecological networks.

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294 wrote the code. J.C.K. obtained data and performed simulations. All authors wrote the manuscript.

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Figure Captions

Figure 1. Binary nestedness and eigenvalues. Spectral radius (ρ , largest eigenvalue) distribution for all connected graphs with $|P| = 6$, $|A| = 4$ and $|E| = 17$. There are 346,104 possible incidence matrices with this parameter combination, and of these, 339,192 are connected (shown in figure). Among the connected graphs, 7,560 are perfectly nested (coloured orange), and have higher spectral radii than most other matrices (all perfectly nested matrices are contained in the top 4.59% of the distribution). The maximum spectral radius is found for matrix N , and all matrices with spectral radius greater than that of matrix A are either perfectly nested or very close to being perfectly nested (bottom series): matrices B , E , F , G , H , J , L and M would become perfectly nested if we were to move just one edge. Matrices with the lowest spectral radii depart most severely from perfect nestedness (top series).

Figure 2. Quantitative nestedness and eigenvalues. Spectral radius (ρ , largest eigenvalue) distribution for a perfectly nested binary structure (matrix A from Figure 1) with randomised quantitative overlay. A single set of $|E| = 17$ coefficient values are shuffled within the binary structure 10,000 times, and each time the spectral radius is computed. High spectral radius is associated with a highly-nested quantitative configuration (e.g., matrix C , where darker colours indicate higher relative element values), medium spectral radius with a non-specific quantitative configuration (e.g., matrix B), and low spectral radius with an anti-nested quantitative configuration (e.g., matrix A). Thus, the positive relationship between spectral radius and nestedness found for binary matrices extends to quantitative matrices.

Figure 3. Empirical nestedness.

Three versions of a seed-dispersal mutualistic network with $|P| = 19$, $|A| = 29$ and $|E| = 211$ (web 37 in SI). In each incidence matrix darker colours indicate higher relative element values, p -values are for 10,000 null model randomisations: a) binary network is nested with $p < 0.001$; b) empirical count quantitative interaction network is nested with $p < 0.05$; and c) quantitative preference structure, $\hat{\gamma}$ -matrix, is anti-nested, $p > 0.95$. Within the restriction of interaction plausibility, i.e., not forbidden interactions (matrix a) and after rescaling the raw data (matrix b) according to mass action, species preferences are found to be distributed in an anti-nested manner (matrix c).

Table 1: Nestedness of ecological networks using quantitative null model iv
(maintain binary structure and shuffle non-zero coefficients)

Structure	nested	no pattern	anti-nested	Total
Binary	51 (98%)	1 (2%)	0 (0%)	52
Preference	3 (6%)	45 (86%)	4 (8%)	52

325 **Figure 1. Binary nestedness and eigenvalues.**

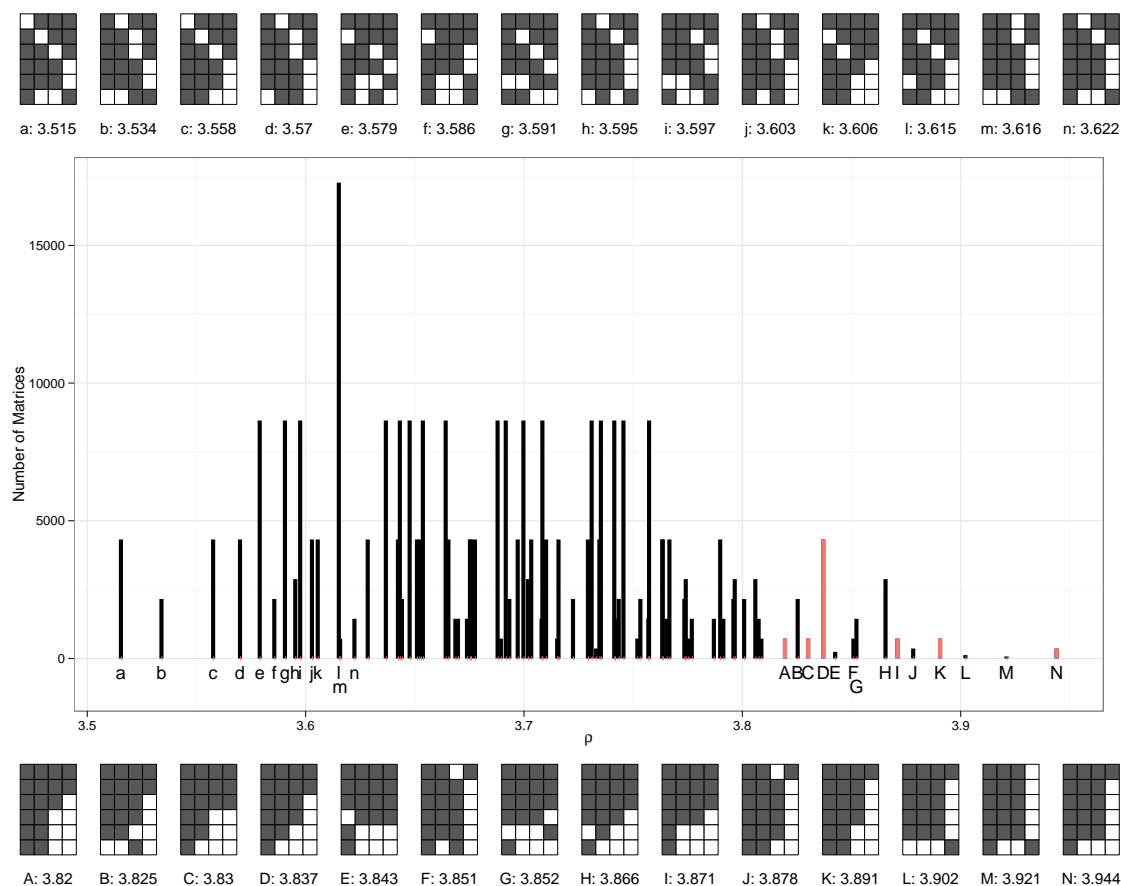


Figure 2. Quantitative nestedness and eigenvalues.

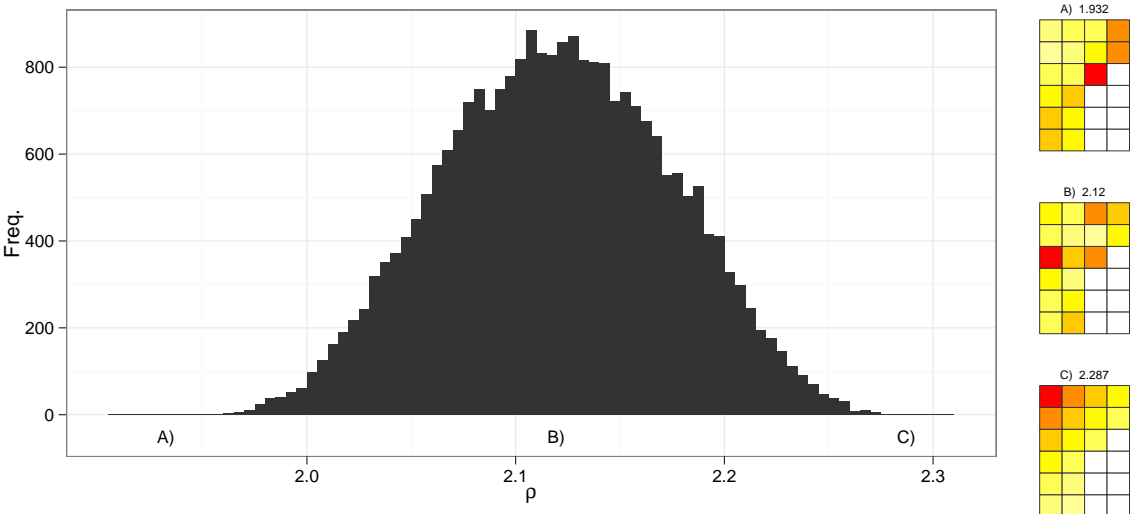


Figure 3. Empirical nestedness.

