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Nestedness and τ -temperature in ecological networks

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Abstract

The τ -temperature is a measure of disorder of bipartite networks that is based on the total Manhattan distance of the adjacency matrix. Two properties of this measure are that it does not depend on permutations of lines or columns that have the same connectivity and it is completely determined by connectivities of lines and columns. The normalisation of τ is done by an uniform random matrix whose elements were previously sorted. τ shows no bias against uniform random matrices of several occupations, ρ , sizes, L , and shapes. The scaling of the total Manhattan distance of a random matrix is $D_{rand} \propto L^3 \rho$ while the same scaling for a full nested matrix is $D_{nest} \propto L^3 \rho^{3/2}$. We test τ for a large set of empirical matrices to verify these scalings. The index τ correlates better with the temperature of Atmar than with the *NODF* index of nestedness. We conclude this work by discussing differences between nestedness indices and order/disorder indices.

Keywords: bipartite interaction networks, nestedness, order/disorder, ecology of communities, biogeography, NODF

1. Introduction

The concept of nestedness was initially proposed in biogeography to describe a pattern of species composition within sets of islands and was later extended to species distribution along landscape fragments (Boecklen 1997; Darlington 1957; Whittaker and Fernández-Palacios 2007). A nested pattern has a species composition such that small assemblages are formed by subsets of species of large assemblages. The same nestedness concept originating in biogeography studies was imported to the context of species interaction networks (Bascompte et al.

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2003). In this new area nestedness is used to characterise how much generalist species are subsets of specialist species (Bascompte 2009). This measure has been so successful to characterise interaction networks that today the two most used tools to unveil their architectures are modularity and nestedness (Fontaine et al. 2011; Fortuna et al. 2011).

In both contexts, biogeography and ecology of communities, the main mathematical object of study is a bipartite network **BN**. If we use the example of island composition, the **BN** consists of a set of species and a set of islands, where the links between the two sets are established by species belonging to islands. In the context of ecology of communities the two sets are group of species and links are established by interactions between species. The **BN** is a versatile object that can be represented by a graph, an adjacency matrix, or, in the case of a qualitative binary network, a lattice of empty or occupied sites.

Ironically the nestedness concept became popular among ecologists after the theoretical work of Patterson and Atmar (Patterson and Atmar 1986), who introduced a temperature T which is supposed to be an indirect measure of nestedness. In that article the temperature is variously presented as an order/disorder, a pattern structure or an anti-nestedness measure. The index T is a measure of dispersion (temperature) of lattice elements relatively to the state of complete order (zero temperature). The zero temperature corresponds to the most organised possible state where all lattice elements are perfectly nested, an increase in the disorder (temperature) will create holes in the perfect nested structure and nestedness decreases. To quantify T the adjacency matrix is previously packed and a median line separating occupied from empty sites is drawn. The index T is a normalised measure of the standard deviation of sites respect to the median. We cite a further development of this algorithm (Rodríguez-Gironés and Santamaria 2006) that has improved the estimation of the median line and the bias that arises with the packing procedure.

A proper index to quantify nestedness of a **BN** is the *NODF* which is an acronym for nestedness metric based on overlap and decreasing fill (Almeida-Neto et al. 2008; Ulrich et al. 2009). Decreasing the fill of a matrix, or packing the matrix, means ranking it according to its connectivities. *NODF* estimates how much lines (or columns) with lower connectivities are actually subsets of lines (or columns) of higher connectivities. To be a subset means to overlap elements, and *NODF* is computed by counting overlapping elements among all pairs of columns (and lines) of the matrix. By construction *NODF* estimates independently nestedness along lines and columns and the normalisation of the index is always performed for all pairs of lines (or columns) of the matrix.

The indices *NODF* and T follow different strategies, the first quantifies overlapping subsets, while the second is an order/disorder measure. In a wider context we call an order/disorder (temperature) index any one that is based on three statements: (i) it presents a state of maximal order, or zero temperature; (ii) it quantifies deviance relative to the state of maximal order using a metric procedure; (iii) it has an adequate normalization of this deviation. We cite three indices that fulfill these conditions: the Temperature of Atmar as presented in the previous paragraph, the τ -temperature that is the main subject of this

paper and the discrepancy of Brualdi (Brualdi and Sanderson 1999). Indeed, the discrepancy has a state of maximal order that corresponds to the case of all occupied sites of the matrix placed at the most to the left and to the top as possible; the discrepancy quantifies how many switches are necessary to drive the occupied matrix elements to this state of zero temperature.

In this work we focus on the τ -temperature which is an estimator of order/disorder in the matrix (Araujo et al. 2010a,b). This index is closely related to T but it is simpler and has clearer mathematical properties (Corso et al. 2011) because it does not use a median line that is a cumbersome quantity. We will compare the τ -temperature with T and $NODF$ index. We remark that the original work of Atmar (Patterson and Atmar 1986) as well as the article that introduced $NODF$ (Almeida-Neto et al. 2008) assume that the temperature index is a measure of anti-nestedness, and, as a consequence, that it is valid to define a generic nestedness index ν in association with a temperature index T in the following way:

$$\nu = 1 - T \tag{1}$$

This complementary relation between temperature and nestedness, as if they were alternative measures of the same phenomenon, is not proved. We shall not assume this hypothesis; we consider that $NODF$ is indeed a measure of nestedness, because it counts overlapping of subsets, in opposition to the τ -temperature and the T that are temperature-like indices.

There is an epistemologic ambiguity connecting the concepts of nestedness and order/disorder in the literature of ecology. It is well accepted that it is ecologically relevant to quantify how much sets of decreasing diversity are subsets of sets of larger diversity - the idea behind nestedness. But at the same time it is also reasonable to question how much communities of increasing diversity are ranked according to size (or other criterion), which is a concept related to order/disorder in the rank. Indeed, the concept of nestedness, in its simplest form, is a rank concept: a series of sets A_k are perfectly nested if $A_1 \subset A_2 \subset \dots \subset A_N$. If some A_l do not fulfill this condition they are out of order and we could, in principle, quantify how much the complete set deviate of the state of perfect order (or perfect nestedness). However, despite the close semantic connection between these two ideas, we prefer not to identify them; we return to this point in the last section of the manuscript.

Today there are two indices largely used in the characterisation of nestedness: the $NODF$ using the algorithm of ANINHADO (Almeida-Neto et al. 2008) and T in the version of algorithms BINMATNEST (Rodríguez-Gironés and Santamaria 2006) and ANINHADO. There are concerns about the mathematical foundations of these measures as well as their extension to quantitative networks (Araujo et al. 2010a; Galeano et al. 2009; Podani and Schmera 2012), and also (Almeida-Neto and Ulrich 2011). Therefore we believe in the necessity of deeper investigation about nestedness and order/disorder measures, in particular because it is necessary to clarify the differences between these two concepts.

The τ -temperature was introduced previously in (Araujo et al. 2010a), but

in this article we improve the previous index in two points: the normalisation procedure no longer uses the nested pattern as a benchmark, and the random matrix used in the normalisation has a more realistic statistical distribution. In addition, in this paper we interpret the τ -temperature as a measure of order instead of (Araujo et al. 2010a) where it is regarded as an anti-nestedness index. Mainly, this paper discusses the mathematics behind τ -temperature and tests this index against null models. In section 2 we present in some detail the main properties of τ -temperature and discuss its best normalisation strategy. In section 3 we compare τ -temperature for an ensemble of networks with variable occupation, size and shape. Also we estimate τ -temperature for 288 matrices obtained in the literature and compare it with T and $NODF$ indices. In section 4 we present the most important properties of the τ -temperature and discuss differences between temperature-like and nestedness-like indices.

2. Methodology

We start the methodology presenting the adjacency matrix, the mathematical object that resumes information of the **BN**. The adjacency matrix has a dimension $L_1 \times L_2$ for L_1 and L_2 the number of elements in the two sets. The data of the **BN** is summarised in the matrix elements $a_{i,j} = 1$ or 0 for the case of a binary (presence-absence or qualitative) networks, and $a_{i,j} = w_{i,j}$ for a quantitative network. In the case of binary network, $a_{i,j} = 1$ indicates the presence of a link between an element of the first set i and an element j of the other set, while the zero indicates the absence of a link. Otherwise, for quantitative networks $w_{i,j}$ is the frequency of the interaction between elements i and j . In addition, in both cases, we can project the information of the matrix into connectivities of S^1 , γ^1 , or S^2 , γ^2 , that means:

$$\gamma_i^1 = \sum_{j=1}^{L_2} a_{i,j} \quad \text{and} \quad \gamma_j^2 = \sum_{i=1}^{L_1} a_{i,j} \quad (2)$$

The quantity γ_i^1 gives the number of interactions of S^1 elements i and γ_j^2 the equivalent information for S^2 species.

The most simple measure of the matrix is its occupation, which is defined by

$$\rho = \frac{N}{L_1 L_2}, \quad (3)$$

for N the total number of interactions of **BN**, or equivalently, using a lattice representation in the case of qualitative **BN**, the number of occupied sites in the lattice. From now on we shall direct our attention to binary networks due to their mathematical simplicity. An extension of the result of the present paper to quantitative networks should not lead to substantial differences since the adjacency matrix is a linear object.

2.1. The distances in the matrix

The main ingredients of the mathematical description of the τ -temperature are shown in figure 1. In this sketch is presented an adjacency matrix, with a couple of occupied sites that indicate the interactions between sets S^1 and S^2 . The first step in the determination of the distances of the matrix consists in packing the matrix, a process that is done by an adequate permutations of line and columns of the matrix. In this process we rank columns and lines of the matrix according to γ . In figure 1 the adjacency matrix is represented in a packed form, in addition we highlight the distances of two arbitrary sites. For any site $a_{i,j}$, the Manhattan distance is done by $d_{i,j} = i + j$, this quantity is the simplest way to measure the distance of any site to the upper corner of the matrix.

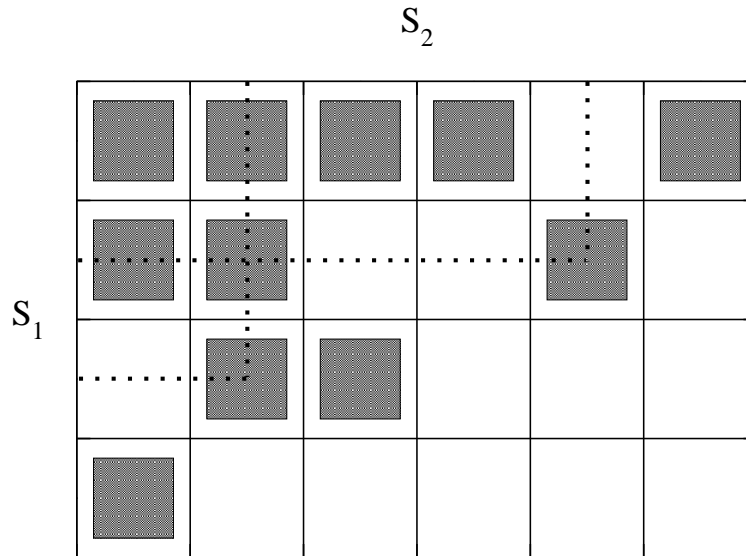


Figure 1: Sketch of a packed adjacency matrix of $S_1 = 4$ and $S_2 = 6$, the actual interactions correspond to the occupied sites of a lattice. We compute distances after the packing of the adjacency matrix; the Manhattan distances of sites $a_{2,5}$, ($d_{2,5} = 2 + 5$), and $a_{3,2}$, ($d_{3,2} = 3 + 2$), are highlighted in the figure. The main idea behind τ -temperature consists in summing all $d_{i,j}$ of the matrix.

The τ -index is estimated using the total distance D corresponding to all

occupied sites of the adjacency matrix:

$$D = \sum_{l=1}^N d_{i,j} = \sum_{i,j} a_{i,j}(i+j) \quad (4)$$

where index l runs over occupied sites. The temperature τ follows directly from a normalisation of the total distance:

$$\tau = D/D_{rand} \quad (5)$$

i.e. D_{rand} is the total distance computed for an adequate random matrix. A detailed description of D_{rand} is given in the next section. Before that we shall stress a mathematical property of D . For the sake of clarity we rewrite equation (4) in the following form:

$$D = \sum_{i,j} a_{i,j}i + \sum_{i,j} a_{i,j}j = \sum_i i\gamma_i^1 + \sum_j j\gamma_j^2 = D^1 + D^2, \quad (6)$$

where D^X stands for the total distance of sets S^1 and S^2 .

Equation (6) is interesting in two aspects. The first is that D can be split in two components that are related to sums over columns and lines. Indeed the Manhattan distance of each element has a horizontal (line) and a vertical (column) component. The expression of D as the sum of D^1 and D^2 stresses that it is possible to estimate independently distances along lines or columns. A similar property of independence measure over lines and columns is shared by the *NODF* index.

The second point we might highlight is that equation (6) assures that the computed τ -index depends linearly on γ^1 and γ^2 . Therefore, the estimation of τ -index can be performed directly from network connectivities γ^1 and γ^2 . This property of the τ -index, which was first pointed out in (Corso et al. 2011), is not shared with any other nestedness index. In the discussion we shall return to this issue.

The distance D is unique in the sense that it does not depend on the packing process. Indeed, D is not influenced by permutations of lines and columns that have the same γ . This fact can be verified with help of figure 2 where we plot the same matrix packed in two different ways, M^a and M^b , these two representations permute columns 3 and 4 that have the same connectivities. To compute D of M^a and M^b we can the sum of elements belonging to columns 1 and 2 and columns 3 and 4. The parcel corresponding to columns 1 and 2 is the same for D of M^a and M^b , for the other two columns we have: $(1+3) + (2+4) = 10$ in case of M^a and $(2+3) + (1+4) = 10$, for M^b . A decrease in D computed along lines corresponds to an increase in D along columns. This rule implies that as long as connectivities are ranked any alternative packing has the same total Manhattan distance.

2.2. The normalisation of D

To define an adequate normalisation of the total distance D for τ -index is not a straightforward task, indeed several possible normalisations may be used and

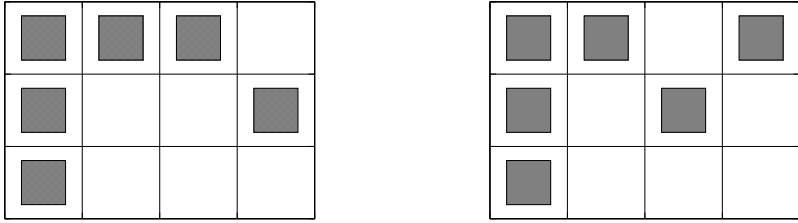


Figure 2: Two representations of the same interaction matrix: the only difference is in the permutation of columns 3 and 4 that have equal connectivities. The total distance D is the same for both matrices which guarantees that measures based in D are unique and do not depend on the packing process.

the choice for the best one should be considered with attention. In a previous work (Araujo et al. 2010a,b) they use a different normalised $\bar{\tau}$ from this article. The normalisation used there was

$$\bar{\tau} = \frac{D - D_{nest}}{D - D_{rand}}, \quad (7)$$

where D_{nest} accounts for the distance of a completely nested matrix. In this article we will define, in the following, a normalization τ different from $\bar{\tau}$. The problem of normalisation (7) is that the completely nested matrix as defined in (Araujo et al. 2010a) does not take into account size differences, indeed the nest pattern is just a triangular pattern with equal sizes. In the case of accentuated size differences ($L_1 \gg L_2$ or $L_1 \ll L_2$) the results for the normalisations are not realistic. In the same article the authors try to bypass this problem by using another metric that is not the Manhattan, but such approach loses the best properties of the Manhattan distance that is expressed by equation (6).

The random network used in the normalisation of the $\bar{\tau}$ index is an ordinary homogeneous random matrix with uniform distribution. In (Araujo et al. 2010a) D_{rand} is computed using the expected values of occupation along lines, $\mu_1 = N/L_1$, and columns, $\mu_2 = N/L_2$. However, the computation of a realistic D_{rand} should take into account the packing procedure of the matrix which is a preliminary step in the estimation of D . Indeed, the distribution resulting after the packing, and D_{rand} , depends on occupation and shape of the matrix.

To illustrate differences between the uniform distribution and the same uniform distribution after packing we show in figure 3 the distribution of occupation along lines. We use in this example a square matrix of size $L = 50$ of a matrix and $\rho = 0.05$. Three distributions are depicted: the uniform distribution model that represent the situation before the packing (dot points), a Monte Carlo distribution after packing (open squares) and the distribution that follow the binomial model (filled circles).

The uniform distribution is done by a constant line of $\mu = N/L = \rho L =$

2.5, this distribution corresponds to the expected result without packing of the matrix. The Monte Carlo approximation of the data is generated using 50000 random samples of a uniform distribution, but the statistic is performed after the packing. The result depicted in figure 3 corresponds to the ranked distribution of occupied sites in lines. As expected, the average value of this distribution fits to the uniform distribution. A similar analysis using columns instead of lines produces a similar result.

In this work we use the binomial model to perform our statistical estimations. To compute the distribution of elements along lines (or columns) of a matrix we assume that the distribution of occupied elements of the random matrix follows a binomial distribution. The probability of having k occupied elements in a line (or a column) of size L is given by

$$p_k = C_k^L \rho^k (1 - \rho)^{(L-k)}, \quad (8)$$

where C_k^L is the binomial coefficient L choose k . With the help of equation (8) and a randomisation technique we compute D_{rand} for the packed uniform distribution. The process of computing the actual D_{rand} is done by running a large number of vectors of size L with probability ρ and sorting the result. The D_{rand} is computed in the following way:

$$D_{rand} = \langle D^1 + D^2 \rangle_{sort}, \quad (9)$$

where $\langle \rangle_{sort}$ represents an average of the distances over a large ensemble of matrices that have previously being sorted.

3. Results

In this section we explore the statistical proprieties of τ -temperature as defined by equations (6) and (9). We use two data sets to test the τ -temperature, the first is a set of uniformly random matrices and the second is a set of 288 empirical matrices available at the site (Atmar and Patterson 2012). We focus our analysis on three major factors that may bias the interpretation of ecological results: lattice occupation, size and shape.

3.1. Test on uniform random matrices

The simplest test of a statistical index is against an ensemble of random matrices with uniform distribution what is known as the $R0$ null model (Gotelli and Graves 1996). We test the τ -temperature for random matrices with variable size, occupancy and shape, the results are shown in figure 4. In figures (a) to (c) we test shape, in this set we keep constant ρ and L_1 and change L_2 ; we use $L_1 = 50$ and $20 \leq L_2 \leq 200$, three distinct ρ are shown inside the figures. In figures (d) to (f) we employ a square matrix of constant occupation and increase size; ρ is indicated in the graphic. In figures (g) to (i) we test matrix occupation; we use again a square lattice with three different lattice sizes as indicated in the figure. Each point in the graphic corresponds to the τ of a single random matrix.

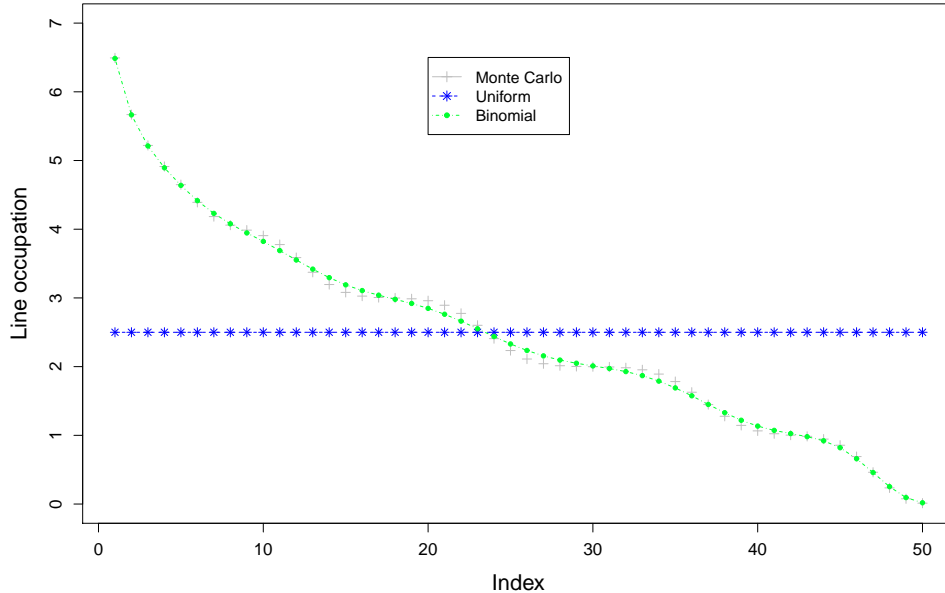


Figure 3: The ranked number of elements in a line for a random matrix. The vertical axis shows the average number of occupied sites in lines and the horizontal corresponds to line index; the position 1 goes for the most occupied and while L for the less one. We plot the Monte Carlo result over 50000 random matrices, it is also shown the uniform distribution and the binomial model.

To estimate D_{rand} we use the procedure indicated in equation (9) employing 5000 samples in the average.

This pictures indicate that the index has no appreciable bias for occupation, size or shape. The values of τ oscillate around 1 as expected and fluctuations are larger for small N , the number of occupied lattices, which correspond to the sample size in our statistical experiment. The simplest prediction for deviation in τ is $\Delta(\tau) \propto \frac{1}{\sqrt{N}}$. Indeed, fluctuations of τ diminish with increasing ρ , L and L_1 , the parameters that enlarge N . We can also increase sample size enlarging the number of matrices. A statistical analysis of these cases show that $\Delta(\tau) \rightarrow 0$ increasing the number of matrices in all these situations.

3.2. Test on empirical matrices

We perform an empirical test of the τ -temperature, evaluating it for the set of 288 matrices of presence-absence of species in metacommunities. We choose all the matrices that satisfy the condition $L_1, L_2 > 3$. As in the previous section

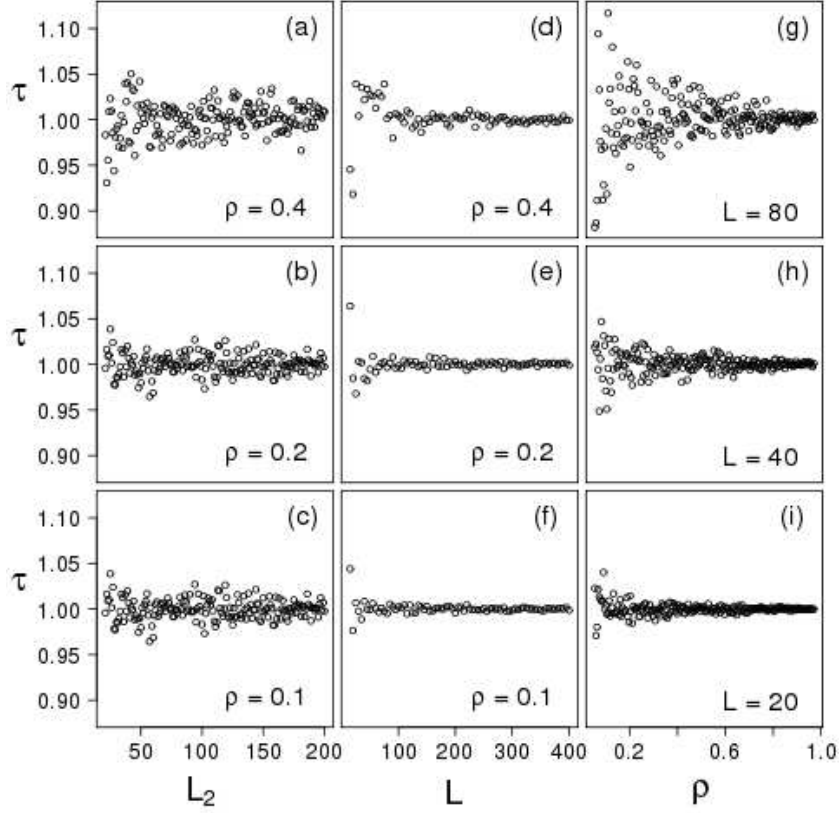


Figure 4: The behaviour of τ for an ensemble of uniform random matrices with variable shape (a) - (c), $L_1 = 50$; size (d) to (f) and occupation (g) to (i). Each point correspond to a single random simulation. The results oscillate around 1 indicating a good performance of the τ -temperature.

we explore occupation ρ , matrix size and matrix shape. To quantify matrix size s we take the geometrical mean between the number of species:

$$s = \sqrt{L_1 L_2}, \quad (10)$$

we use this definition because it resembles the square root of the area of the lattice which is an intuitive indicator of its size. The shape, δ , of the matrix is a measure of its size asymmetry, we employ the following normalised definition:

$$\delta = \frac{|L_1 - L_2|}{L_1 + L_2}. \quad (11)$$

In figure 5 we depict our results. In (a) we show matrix shape, in (b) occupation and in (c) size. We notice that τ shows no bias on matrix shape in

opposition to occupation and size. These figures show as well that τ increases with occupation and decreases with size. To clarify this point we plot in figures 5 (b) and (c) the curves of τ_{nest} that corresponds to the τ -temperature of a matrix with same occupation but all elements packed in the corner of minimal distance. By construction τ_{nest} corresponds to the lower bound value of τ , that means:

$$\tau_{nest} = D_{nest}/D_{rand}, \quad (12)$$

where D_{rand} is a non-packed uniform random matrix approximation given by $D_{rand} = N(L_1 + L_2)/2$ and D_{nest} is a distance of the full packed matrix. For a square matrix the expression of D_{rand} as a function of occupancy is given by

$$D_{rand} = N(\mu_x + \mu_y) = N(L + L)/2 = \rho L^2 L = \rho L^3, \quad (13)$$

where we have used equation (3). To estimate D_{nest} we construct the pattern that is maximally packed which corresponds to an isosceles triangle of side L_o placed at the corner of the matrix. The artificial full nested pattern we use in this work consists of a matrix where all occupied sites are inside a triangle whose right angle is at the $a_{1,1}$ matrix element. The area of this triangle is given by the total number of occupied sites:

$$N = L_o^2/2 \quad (14)$$

Using equation (3) we can write $L_o = L\sqrt{2\rho}$. The calculus of D_{nest} follow from the computation of the distance on this triangle:

$$D_{nest} = \int_0^{L_o} \int_0^{L_o-x} (x+y) dx dy = \frac{1}{3} L_o^3 = \frac{2}{3} L^3 \rho \sqrt{2\rho}. \quad (15)$$

Finally, putting together equations (12) and (15) we have

$$\tau_{nest} = \frac{2\sqrt{2\rho}}{3}, \quad (16)$$

which is the equation shown in figure 5 (b).

To compute a curve for the dependency of τ_{nest} versus s we use equations (12), (13) and (15):

$$\tau_{nest} = D_{nest}/D_{rand} = \frac{2L^3\rho\sqrt{2\rho}}{3\rho L^3} = \frac{2}{3}\sqrt{2\rho} = \frac{2}{3}\sqrt{2\frac{N}{L^2}}. \quad (17)$$

This equation expresses τ_{nest} as a function of N and L ; as the size is the geometrical mean of L_1 and L_2 we take for simplicity $s \propto L$. To write equation (17) exclusively as function of size L we perform a log-regression over the empirical matrices to obtain a relation of the form $N \propto L^\gamma$ that is a expression of how the number of links scales with nodes. We obtained $\gamma = 1.67$ and a regression coefficient $R = 0.875$. In this way relation (17) become:

$$\tau_{nest} = \frac{2}{3}\sqrt{2}L^{-0.167} \quad (18)$$

that is the relation plotted in 5 (c). Despite the crude estimations of D_{rand} and D_{nest} , they reveal the scaling of D for size and occupation. In addition, relations (16) and (18) give a good estimation of the lower bound of τ versus occupation and size.

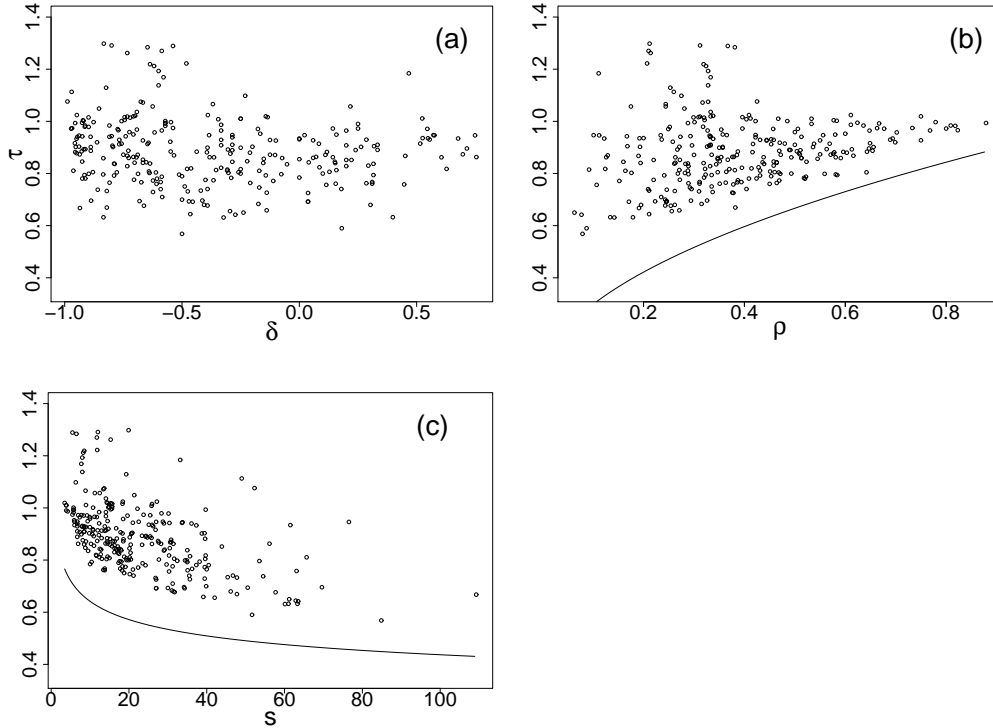


Figure 5: The τ -temperature for matrix shape (a), occupation (b) and size (c); the data correspond to empirical bipartite networks. The theoretical curves in (b) and (c) correspond to τ of a completely nested pattern, the lower bound τ .

In figure 6 we explore the correlation between τ -temperature and two other indices: the temperature of Atmar in the matrix (a) and the $NODF$ in (b). To compute these two indices we employ the algorithm present in the reference (Guimarães Jr. and Guimarães 2007). As expected the two temperatures correlated positively while $NODF$ is anticorrelated. The Pearson correlation test gives $R = 0.577$ for T and $R = -0.330$ for $NODF$; the result for T and $NODF$ is $R = -0.499$. Therefore τ correlates better with T than with $NODF$. We perform a similar analysis using the BITMATNEST algorithm (Rodríguez-Gironés and Santamaria 2006) and found $R = 0.409$ for the correlation between τ and T and $R = -0.454$ between T and $NODF$. These results suggest that τ -temperature is a measure of disorder, $NODF$ of nestedness and T an intermediate measure, in the discussion we return to this point.

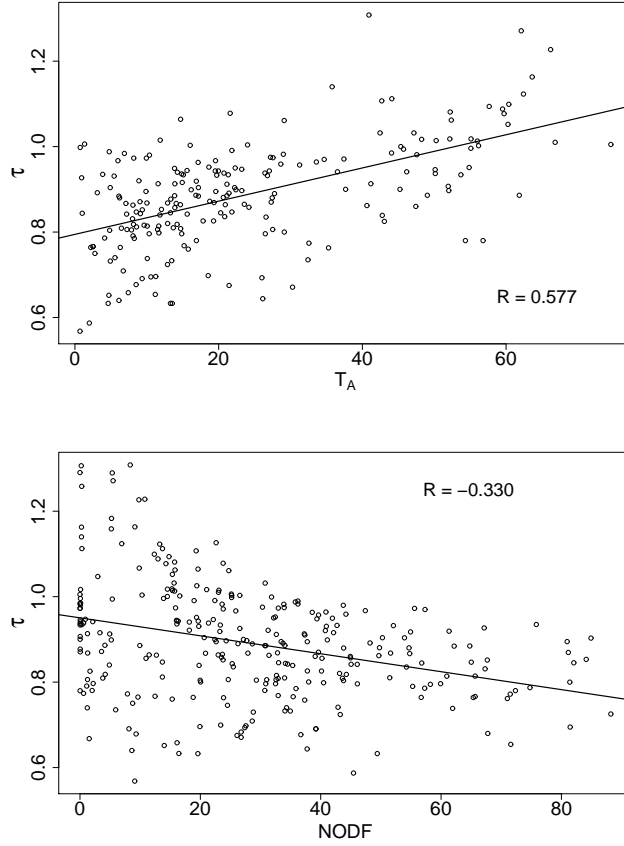


Figure 6: The τ -temperature versus the T and $NODF$ indices. The values inside the graphic correspond to the Pearson correlation coefficient. It is worth to note that τ correlates better with T than with $NODF$ index.

4. Discussion and Final Remarks

The τ -temperature is an order/disorder index of bipartite networks, that has an intuitive appeal because it is based on elementary geometrical assumptions. This index is based on counting distances on the adjacency matrix, the most ordered pattern correspond to the occupied sites at the closest positions to $a_{1,1}$ corner. This index share two remarkable characteristics, the first is that, despite it requires that the matrix has to be packed before counting the total Manhattan distance, τ -temperature does not depend on the packing procedure. In this way we claim that τ does not depend of permutation of lines or columns. The second aspect is that the τ -index depends only on the total marginals to be completely defined, equation (6). There is no information in connectivities γ_i^1 and γ_j^2 that is not in the τ -index. The metric statement of τ -temperature allows the derivation

of exact scaling expressions for occupation and size, equations (16) and (18).

In this paper we perform a statistical analysis of τ -temperature for a set of uniform random matrices and a set of empirical matrices. As τ -temperature is normalised by random matrices it is not unexpected that there is no bias in the behaviour of τ against matrix size, shape or occupancy. On the other hand τ shows a marked influence on matrix occupation and size. This phenomenon is related to scaling differences for D of random and perfectly nested matrices. The scaling for a random matrix is $D_{rand} \propto L^3 \rho$, equation (13), while for a full nested matrix is $D_{nest} \propto L^3 \rho^{3/2}$, equation (15). As these two distances do not scale in the same way, and empirical matrices, are nested to some extent, this fact explains the dependency of τ with occupancy and size.

A couple of works have explored the connectivity distribution in **BN** (Montoya et al. 2006; Saiz and Alados 2011). In the work (Montoya et al. 2006) was explored the truncated power-law behaviour of the distribution of γ in connection with dynamical network models. However, a further work (Okuyama 2008) did not find tangible power-law or truncated power-law distributions in the same data set. This discussion is marked by difficulties of obtained a best fitting curve of γ which is not the focus of this manuscript. The point we stress here is that there is no attempt in the literature to put in a common framework nestedness and connectivity distribution. The τ -temperature, by its turn, has a clear answer to this issue: these two quantities are intimately related, the τ -temperature, following equation (6), is completely determined by the connectivity distribution. This result is roughly intuitive since steeper distributions of γ should imply in nested patterns while flat distributions do not.

The temperature of Atmar is not defined analytically as the τ -temperature, neither has a clear algorithm as *NODF*. In this way it is easier to do theoretical inferences about *NODF* and τ -temperature. A comparison between *NODF* and τ -temperature shows that these two quantities do not follow equation (1), that means, $NODF \rightarrow 1$ does not imply $\tau \rightarrow 0$ or vice-versa. We take as an example the pattern of minimal filling which is composed by one filled row and one filled column. For this pattern *NODF* is almost zero because lines (or columns) are not sub-sets of other lines (or columns) since they have the same connectivity. Otherwise τ -temperature is the minimal possible for this matrix. The pattern of minimal filling shows clearly that low temperature does not imply in nested structure.

An analysis of the correlation among a set of empirical matrices shows that τ -temperature is more related to T than to *NODF* index. This result brings new light to the seminal paper of Atmar and Patterson that used an order/disorder approach to quantify nestedness (Patterson and Atmar 1986). Perhaps the confusion in the literature that follows that paper and goes to the development of several nestedness indices is rooted in the fact that nestedness is not properly an order/disorder-like phenomenon and, in this way, an equation like (1) is not valid. However, the Atmar temperature has been largely used in ecology of communities and metapopulation studies as a valuable index. Nestedness indices have proved to be usefull in the characterisation of pollinator networks (Bascompte et al. 2003; Guimarães Jr. et al. 2006), but it is not conclusive

if pollinator networks are really nested (in the sense of *NODF*) or if they are more ordered (as an order/disorder approach would suggest). To conclude, nestedness is a fruitful and problematic idea that arises in biogeography studies and ecology of communities, and we hope this paper will contribute to clarify a concept which is one of the major points in theoretical ecology (Loehle 2011).

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