A new nestedness estimator in community networks

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Abstract

A recent problem in community ecology lies in defining structures behind matrices of species interactions. The interest in this area is to quantify the nestedness degree of the matrix after its maximal packing. In this work we evaluate nestedness using the sum of all distances of the occupied sites to the vertex of the matrix. We calculate the distance for two artificial matrices with the same size and occupancy: a random matrix and a perfect nested one. Using these two benchmarks we develop a nestedness estimator. The estimator is applied to a set of 23 real networks of insect-plant interactions.

Keywords: nestedness, networks, insect-plant interactions

1 Introduction

Networks have been widely used to describe systems in a multitude of disciplines, such as genetic networks, protein networks or the Internet. In ecology, networks are mainly used to visualize and describe food webs. But not only trophic interactions are the focus of attention. In the last years researchers show a growing interest in the study of other species interactions such as parasitism (Vzquez et al., 2005), scavenger species (Selva and Fortuna, 2007) and mostly mutualism (Bascompte and Jordano, 2007 and references therein). Studies on mutualistic food webs focus on specific pairwise interactions between a plant and an animal and how they are shaped by a community context, either in a single locality, or geographically (Bascompte and Jordano, 2007).

Pairwise interactions can be described in the form of a bipartite graph or an interaction matrix. These webs are characterized by nodes that represent species or species groups and observed interactions are drawn as links that, when not binary, can render their intensity or frequency in graded thicknesses. In the interaction matrix, links are represented as nonzero cells on the intersection of a row and column. According to Almeida-Neto et al., 2007,
bipartite webs do in fact offer several advantages of their own: first, they are often fully resolved, without the problems of uneven resolution which haunt the analysis of complete webs. Second, all links are of a single kind of ecological interaction (e.g. mutualism), which ensures structural integrity as well as similar ecological and evolutionary processes throughout the entire assemblage.

The most studied structure within a bipartite graph is the nested pattern of species interactions, although other structures are also possible (Prado et al. 2006; Almeida-Neto et al., 2007). In nested assemblages, plants with few interactions are related only with generalist animals; conversely, specialized animals are found related to plants with many links, that is, with large associated faunas. Moreover, generalists in one species set tend to interact with generalists in the other, forming a dense core of interactions (Prado et al., 2006; Bascompte and Jordano, 2007).

A nested structure is very cohesive and stable. The fact that few species are involved in many interactions (functional redundancy), poses the community with the possibility for alternative routes if some interactions disappear (Bascompte and Jordano, 2007). A nested structure is also quite robust: it is less prone to sampling bias than number of species and links (Nielsen and Bascompte, 2007) and not generated by the random combination of sets of plants and animals solely in proportion to their different abundances as previously thought (Prado et al., 2006).

Recently, a large series of mutualistic interaction assemblages have shown a significantly nested structure (Bascompte et al. 2003). Substantial effort has been done in developing various measures and forms of calculating nestedness (Atmar and Patterson, 1993; Guimaraes and Guimaraes, 2006; Rodriguez-Girons and Santamara, 2006; Almeida-Neto et al., submitted). The most commonly used nestedness metric is the Nestedness Temperature Calculator, or Nestcalc, used to calculate nestedness in binary matrices (Atmar and Patterson, 1993). The nestedness from this algorithm has a problem, though: the absolute value of the nestedness temperature is dependent on
matrix size and fill. Some studies show that the nestedness temperature of randomly assembled matrices increases with network size and attains its maximum value for intermediate fills (Rodrguez-Girons and Santamara, 2006; Almeida-Neto et al., submitted). So, smaller networks need lower temperature than larger ones do to be significantly nested (Nielsen and Bascompte, 2007).

From a mathematical point of view, the central object in the discussion about nestedness is a matrix of zeros and ones. The ecologist in the field interpret this matrix as a table where she (he) marks a cross at the $i$ column and $j$ row each time a species of group one $i$ (e.g. plant) is related to group two $j$ (e.g. insect). In order to visualize nestedness in the studied ecological community the ecologist has to rank rows and columns of the table. In fact, each time one row (or column) is permuted to another row (or to column), the interactions among species of groups one and two do not change. For a matrix of $L_1$ species in group one and $L_2$ species in group 2, there are $L_1 \times L_2$ possibilities to represent the matrix following different permutations of rows and columns. Each one of these possibilities is just a different visualization of the same network structure.

Ranking rows and columns is a very practical option to visualize nestedness in a interaction matrix. When we rank the elements of a matrix we choose one of the $L_1 \times L_2$ possibilities, that one where the elements of the matrix are the most packed. In other words, we choose the representations where the elements of the matrix are as closest as possible from the $i = 1$, $j = 1$ corner. In the literature. Packing procedure is a previous step before the evaluation of a nestedness index (Atmar and Patterson, 1993). In this article we also pack the matrix before the evaluation of our nestedness index.

We introduce here a new nestedness measure applied to digraphs originated from ecological data. However, the method is more general than its predecessor and can be naturally applied to graphs (networks) other than digraphs. In section 2 we describe the formal objects used in this article: adjacency matrix, Manhattan distance in a matrix, projection of a generic
matrix into the unit square lattice, packing process, random matrix, maximum nested matrix and nestedness estimator. In section 3 we apply the nestedness estimator to a set of insect-plant herbivory networks extracted from the community ecology literature. In section 4 we summarize the article, point out potential applications of the method and give the final words.

2 A measure of nestedness

In this section we introduce the concept of distance in a matrix to characterize the nestedness of digraphs. In order to fix the notation we call digraph an object \( D \) formed by two sets of vertices \( D_1 \) and \( D_2 \) and a set of links between these two sets. The digraph is completely described by the adjacency matrix, \( M \), of size \( L_1 \times L_2 \), where \( L_1 \) and \( L_2 \) are the number of elements of \( D_1 \) and \( D_2 \), respectively. By definition \( M_{i,j} = 1 \) if there is a link between vertices \( i \) of \( D_1 \) and \( j \) of \( D_2 \) and \( M_{i,j} = 0 \) if \( i \) and \( j \) are not linked. It is useful to visualize \( M \) as a \( L_1 \) versus \( L_2 \) lattice with empty (zero) or full (one) sites. Moreover, the number of links of a vertex \( l \) is \( k_l \) and the distribution of links of \( D_1 \) and \( D_2 \) is \( P_{l_1} \) and \( P_{l_2} \) respectively.

In Ecology, the field data corresponding to the digraph is composed by two sets of species and the corresponding links (interactions) between them. As we pointed out in the introduction, the standard procedure in this area consists in packing the adjacency matrix of the data. The packing is performed in the following way: the link distributions \( P_{l_1} \) and \( P_{l_2} \) are ordered such that the most connected species go to the first position of the matrix. In this way the matrix \( M \) shows more ones close to \( i = 1 \) and \( j = 1 \) corner and zeros at the opposite corner, \( i = L_1 \) and \( j = L_2 \). From the matrix point of view, the packing process consists in replacing lines and columns until \( P_{l_1} \) and \( P_{l_2} \) are ordered. We emphasize that since the packing process do not change the links between species it does not alter the phenomenology underlying the network.

The idea behind packing the matrix \( M \) is to better visualize network
nestedness. In addition, nestedness is related with the dispersion of ones and zeros after the packing process. A very nested matrix is one that, after packing, has a minimal mixing of ones and zeros. Using a lattice analogy, a very nested lattice shows a minimum of holes.

To introduce distance properties in the original matrix $M$ we map it into a Cartesian space. In order to avoid distortions we map the $L_1 \times L_2$ matrix to the unit square. To perform this task the cell elements $(i,j)$ assume the positions $x_i$ and $y_i$ that are done by:

\[
x_i = (i - 1)/L_1 + 1/(2L_1)
\]
\[
y_j = (j - 1)/L_2 + 1/(2L_2)
\]

(1)

In this article we use the Manhattan distance because it is broadly employed to measure matrix distances. Euclidean distance is used for estimating distance between elements apart in continuum space, which is not the case here. In fact, in the context of abstract metric spaces (Courant, R. and Hilbert, D., 1937) set of distances $d_\chi = (x^\chi + y^\chi)^{1/\chi}$ that depends on the parameter $\chi$, the case $\chi = 1$ corresponds to the Manhattan distance and the case $\chi = 2$ to the Euclidean distance.

We define the occupancy number $\rho$ as the fraction of occupied sites in the adjacency matrix. For $N$ the total number of ones in $M$ we have $\rho = \frac{N}{L_1L_2}$.

To quantify nestedness of a given matrix $M$ we use two matrix benchmarks with the same $L_1$, $L_2$ and $\rho$: the maximal nested matrix $\tilde{M}$ and the random matrix $M_{rand}$. The maximal nested matrix is constructed in such a way that it has no holes and its elements are as close as possible to the $(1,1)$ corner. We construct $\tilde{M}$ filling the elements along equidistant diagonals to $(1,1)$. In fact all elements along the same diagonal have the same distance to the $(1,1)$ corner. The construction of $\tilde{M}$ is the following: the first element occupied is $(1,1)$, after that it comes $(1,2)$ and $(2,1)$, followed by $(1,3)$, $(2,2)$ and $(3,1)$, etc. Figure 1 illustrates the optimal filling strategy to build $\tilde{M}$. In contrast, the random matrix is constructed in such a way that all its elements are uniformly occupied with the same probability $p = \rho$. The maximum packed matrix of the species interaction will be in-between these two.
We use the Manhattan distance to evaluate the distances of the filled elements \(x_i, y_j\) (the distances are defined for the matrix elements projected into the unit square in the cartesian plane). We call \(d\) the sum over the distances of all the elements of the matrix projected into the unit square, that means, \(d = \sum d_{i,j}\) for \(d_{i,j} = x_i + y_i\). In order to define the nestedness estimator we introduce two additional distances: the total distance of the artificial matrices \(\tilde{M}\) and \(M_{\text{rand}}\). We note that \(\tilde{M}\) has the smallest total distance among all the lattices with the same \(\rho\) and we call \(d_{\text{min}}\) its total distance, while the total distance of \(M_{\text{rand}}\) is \(d_{\text{rand}}\). Consider a sample of \(N\) points randomly distributed along the unit square, the expected value of the distance to the origin, \(\mu\), is the Manhattan distance from the origin to the center of the square of size 1, that means, \(\mu = 1\). Therefore:

\[
d_{\text{rand}} = \sum_{k=1}^{N} d_{i,j} = N\mu = N
\]  

(2)

To get an insight about distances in \(M\) we start exploring the behavior of \(d_{\text{min}}\) and \(d_{\text{rand}}\) against occupancy \(\rho\) in figure 2. We use in this picture \(L_1 = L_2 = 20\). As expected, the distances follow the relation \(d_{\text{min}} \leq d_{\text{rand}}\). The total distance \(d\) for any matrix, after the packing process, shows the property:

\[
d_{\text{min}} < d < d_{\text{rand}}.
\]  

(3)

In fact, \(d_{\text{min}} < d\) since \(d_{\text{min}}\) is derived from an artificial matrix whose components, by construction, have the minimal distance to the origin. Otherwise, \(d < d_{\text{rand}}\) because \(d\) is derived from a packed matrix, and in the packing process the matrix reduces the distances of their elements when compared with a similar random matrix.

The distance as defined above depends on the matrix size and the occupation. In fact, the total distance observes the relation \(d \propto L^2\) for a given \(\rho\) and the relation \(d \propto N^2\) for a constant \(L\). This behavior can be visualized in figures 2 and 3. In order to have a \(N\) free nestedness index of the system
we define the nestedness index $\eta$ as follows:

$$\eta = \frac{d - d_{\text{min}}}{d_{\text{rand}} - d_{\text{min}}}$$  \hspace{1cm} (4)

We emphasize that $d_{\text{min}}$ and $d_{\text{rand}}$ are computed over a artificial matrix with the same $L_1$, $L_2$ and $\rho$ of the original system. In the next section we test $\eta$ over a set of digraphs from the context of community ecology and discuss the results.

3 Results

In this chapter we select a set of 23 insect-plant herbivory networks in the literature and apply the nestedness index we develop in this article. In table 4 we enumerate the set of networks with its main properties: the occupancy $\rho$, size $L_1$ and $L_2$, the nestedness estimator $\eta$, the temperature $T$ (according to Atmar and Patterson, 1993) and the reference of the network. A visual inspection of the table does not reveal correlation between $\eta$ and $T$. In fact, a linear correlation analysis between the two variables reveals no significant correlation ($R = 0.19$ and $p = 0.18$).

The range of values of our estimator is $0.17 < \eta < 0.83$ and the average value is $\bar{\eta} = 0.45$. In contrast, the usual temperature estimator have the range $6.8 < T < 43$ and average value $\bar{\rho} = 18.6$. In order to improve the visual intuition about the problem we plot in figure 4 four lattices of insect-plant networks. It is clear in the figure that (a) and (b) are highly nested, and that on the contrary, (c) and (d) are not nested at all. This intuitive idea is corroborated by the $\eta$ estimator, but not by the temperature, the estimator of the two initial matrices are 0.18 and 0.23 (low values), and of the last two 0.79 and 0.76 (high values). The temperature estimator, on the other hand, shows an intermediary value in case (a), where our estimator shows a low value and a very high temperature in (c) where our estimator points for a very large value. In fact, figures (c) and (d) have a large number of specialists, and in consequence the matrix cannot be well nested. Our
estimator corroborates this observation. As a final remark concerning this set of figures, we point that all the matrices in this figure are well packed, that means, the number of elements of lines and columns are ordered. On the other hand, the nestedness calculator from Atmar and Patterson, 1993, usually fails in packing well the matrices.

From the observation of figure 4 we see that the variables are correlated, in fact, a linear correlation analysis reveals $R = -0.74$, $t = 5.0$ and $p = 5.9 \times 10^{-6}$. An exponential correlation regression results $R = -0.86$, $t = 6.3$ and $p = 2.9 \times 10^{-6}$. Therefore the adjust of the data to the exponential curve is slightly better than the linear one. The dependence of a nestedness index to occupancy was already pointed in the literature (Girons and Santamara, 2006). At first, a relation between $\rho$ and $\eta$ seems intuitive: once the number of sites increase, in the average, they will be more nested after the packing process. We let for a future work a more carefull analysis of this point.

4 Final Remarks

In this work we develop a new nestedness estimator $\eta$ based on distances over the adjacency matrix of the network. We think that this estimator will be useful in the methodological discussion involving nestedness in community ecology. To make the method clearer to the reader we summarize the algorithm to find $\eta$ in the following sequence of steps:

1. Evaluate the link distributions $P_{L_1}$ and $P_{L_2}$ of the adjascency matrix of the network.

2. Pack the matrix, that means, permute lines and columns of the matrix in order that $P_{L_1}$ and $P_{L_2}$ are ranked. This step defines a corner of nestedness.

3. Project the matrix into the unit square in order to avoid distortion due to the diferences between the sizes $L_1$ and $L_2$ of the matrix.
4. Find the manhatann distance \( d_{x,y} \) of all elements \( x_i, y_i \) of the matrix and sum to find the total distance of the elements of the matrix \( d \).

5. Determine analitically the distance of the associated random matrix with the same occupancy \( \rho \): \( d_{rand} = N \), for \( N \) the total number of occupied elements of the matrix.

6. Determine computationally the distance of the asociated maximally nested matrix with the same \( \rho \): \( d_{min} \).

7. Finally, calculate the estimator \( \eta = \frac{d - d_{min}}{d_{rand} - d_{min}} \).

As estimated above, \( 0 < \eta < 1 \). In the limit \( \eta \to 0 \) the network is completely nested and \( \eta \to 0 \) corresponds to the random limit. We tested our estimator for a set of 23 insect-plant networks and the data is summarized in table 4. An interesting result of our estimator is that it depends on the occupancy number. This result is in agreement with the intuitive idea that the matrix nestedness increases with its occupancy density.

The parameter \( T \) is a very used nestedness estimator in community ecology. This parameter, despite of its popularity, is not well defined and present several problems (Fischer and Lindenmayer, 2002; Rodriguez-Girons and Santamara, 2006; Almeida-Neto et al., submitted). We are perfectly aware that our estimator will be compared with the usual temperature estimator developed by Atmar and Patterson (1993). What we should do is to show the good points of our method and let the methodological discussion to the scientific community. In this way we stress the strong points of our method in the following:

1. Our algorithm is based on plain geometry and metric statements. In this way it is simple and can be calculated with help of a easy computer program.

2. We have two benchmarks clearly defined: the total distance of the random matrix and of the completely nested one.
3. We do not use any ad hoc parameter in the equation that defines the nestedness estimator.

4. Our estimator gives a number between zero and one.

5. The visual inspection criterion of nestedness of empirical matrices agrees with our estimator.

This paper opens a new perspective in the study of nestedness. We develop an original index to measure nestedness that is based on direct metric analysis of the matrix. Instead of considering the dispersion of elements around an artificial isocline, we estimate directly the distances of all the matrix elements from the packing corner. The nestedness of a matrix is a measure of how much the elements of the matrix are close to the corner where the matrix is packed. We hope this paper to be useful to improve the understanding of nestedness in the community ecology context.
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Table 1: Set of 23 insect-plant community networks. For each network we show: the occupancy \( \rho \), size \( L_1 \) and \( L_2 \), the nestedness estimator \( \eta \) (multiplied by 100), the temperature \( T \) and the reference in the literature.
Figure captions

Figure 1: Lattice representation of a particular lattice with \( L_1 = L_2 = 5 \) and \( N = 8 \) (empty circles). The filled diamonds show the maximal nested lattice for the same \( L_1, L_2 \) and \( N \). We remark that the circles represent the lattice after the packing process, both \( P_{L_1} \) and \( P_{L_2} \) are ranked.

Figure 2: The behavior of \( d_{\text{min}} \) and \( d_{\text{rand}} \) versus \( \rho \) for \( L_1 = L_2 = 20 \). The curves obey the rule \( d_{\text{min}} < d_{\text{rand}} \) except for \( \rho \to 1 \).

Figure 3: The behavior of \( d_{\text{min}} \) and \( d_{\text{rand}} \) versus \( L \) for a constant occupation \( \rho = 0.5 \). For both curves we have \( d \propto L^2 \).

Figure 4: Four examples of real community matrices referred to data files on table 1. In (a) the matrix corresponds to file 10, in (b) we use file 9, in (c) file 2 and in (d) file 12.

Figure 5: The curve of occupancy \( \rho \), versus nestedness index \( \eta \), for all the network tested in this work.
| File | Fill(%) | Size (Plant × Insect) | $T$ | $\eta \times 100$ | Reference |
|------|---------|-----------------------|-----|-------------------|-----------|
| 1    | 42.9    | 18 × 57               | 28.0| 17.2              | Futuyama and Gould 1979 |
| 2    | 10.5    | 10 × 18               | 43.2| 79.1              | Dawah et al. 1995 |
| 3    | 20.0    | 43 × 14               | 10.0| 24.3              | Buruga and Oleombo 1971 |
| 4    | 8.4     | 63 × 25               | 6.9 | 28.1              | Buruga and Oleombo 1971 |
| 5    | 8.6     | 33 × 55               | 13.5| 40.8              | Claridge and Wilason 1981 |
| 6    | 1.1     | 107 × 104             | 7.29| 83.5              | Flowers and Janzen 1997 |
| 7    | 16.0    | 52 × 22               | 20.7| 35.1              | Joern 1979 |
| 8    | 13.3    | 54 × 24               | 11.0| 32.3              | Joern 1979 |
| 9    | 34.7    | 11 × 11               | 9.4 | 23.0              | Pielou 1974 |
| 10   | 43.5    | 13 × 12               | 19.3| 18.1              | Pielou 1974 |
| 11   | 4.7     | 52 × 27               | 14.5| 62.7              | Jermy and Szentesi 2003 |
| 12   | 2.0     | 53 × 92               | 8.3 | 75.9              | Memmot et al. 1994 |
| 13   | 5.5     | 46 × 22               | 20.1| 62.8              | Neck 1976 |
| 14   | 14.7    | 08 × 11               | 42.1| 68.1              | Pipkin et al. 1966 |
| 15   | 4.4     | 55 × 43               | 8.3 | 53.5              | Podlussány et al. 2001 |
| 16   | 23.0    | 13 × 09               | 35.8| 42.3              | Ratchke 1976 |
| 17   | 52.3    | 15 × 08               | 17.2| 18.2              | Sheldon and Rogers 1978 |
| 18   | 15.9    | 18 × 15               | 26.3| 45.3              | Prado and Lewinsohn 1994 |
| 19   | 4.5     | 33 × 29               | 20.5| 69.7              | Valladares, Argentina (unpublished) |
| 20   | 8.9     | 27 × 22               | 17.8| 53.7              | Lewinsohn, Brazil (unpublished) |
| 21   | 8.0     | 30 × 34               | 14.1| 44.1              | Lewinsohn, Brazil (unpublished) |
| 22   | 12.8    | 33 × 21               | 17.7| 37.9              | Almeida, Brazil (unpublished) |
| 23   | 19.6    | 21 × 32               | 20.6| 29.3              | Kubota, Brazil (unpublished) |

Table 1
Figure 2
Figure 4a
Figure 4d
