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DEGREE DISTRIBUTION AND NESTEDNESS IN BIPARTITE NETWORKS FROM COMMUNITY ECOLOGY

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Community ecology history intermingles with island biogeography studies [1]. Given a set I_i of islands ad a set S_j of species, every time a species i is found on an island j a link between these two sets is established, originating an adjacency matrix and a bipartite network. In general, larger islands will support more species. But one can pose the question: species present in small islands will always be present in larger ones? The rough answer to this question is yes. This problem was studied for many archipelagos and several taxa (birds, lizards, beetles, etc) [2]. This pattern of species poor sites composing a subset of species-rich sites is called a nested structure. Since forest remnants can be considered islands in a sea of anthropogenic disturbed landscape, conservation studies have revived some aspects of island biogeography in last three decades [3].

Bipartite networks have also been used in community ecology to describe interspecific species interactions. Plants and their pollinators or animals and their parasites are examples of interaction networks in community ecology. Nestedness can be investigated in such networks characterizing the generalist-specialist balance in communities [4]. In nested interaction matrices, generalist species interact with many species, while a specialist interacts with few ones. In nested matrices, species are organized in such a way that specialist species only interact with more generalist ones. Ecologists suggest that nestedness patterns can distinguish between mutualist (eg. pollinator and plants) and antagonist (animals and parasites) networks [4]. In addition, the nestedness degree is important in the study of species coevolution [5].

Nestedness is not a straightforward concept, and this fact leads to misunderstandings in the literature as well as a proliferation of estimators [6] (this situation is similar to the definition of diversity, another key concept in community ecology that also shows several conflicting definitions and estimators [7]). The oldest and most popular estimator of nestedness is the "temperature" of Atmar and Patterson [8]. This index is constructed using a median line in the ranked adjacency matrix. This line equally separates holes and full cells in the matrix (zeros and ones). The "temperature" index t is a measure of the dispersion of holes in respect to the median. There are other indexes [9, 10] that basically count the number of vacancies in the matrix. The difficult point of these indexes is that they are defined by cumbersome algorithms that impede further analytical developments. We investigate nestedness using a nestedness index υ developed in [11]. This estimator is based on distances on the adjacency matrix of the network. The intuitive idea behind this nestedness index is based on the dispersion of ones and zeros through the adjacency matrix. First we pack the matrix ranking the degree distributions of ones (observed interactions) along lines and columns. A highly nested matrix is the one that, after packing, present a minimal mixing of ones and zeros. We estimate nestedness using the average distance d of the matrix:

$$d = \frac{1}{N}\sum_{k=1}^{N} d_{i,j} \qquad (1)$$

for N the number of ones in the matrix and $d_{i,j} = i + j$ the Manhattan distance. To normalize the nestedness index υ, two artificial matrices are used: the perfectly nested matrix and the equiprobable random matrix. These two matrices have the same sizes L_1, L_2 and occupancy υ of the adjacency matrix, and they work as benchmarks to properly define the nestedness index. In other words, we parametrize υ with help of the distance d of d_{nest} and d_{rand}. The first is the average distance related to a completely nested matrix and the second to the random matrix. υ is defined as follows:

$$\upsilon = \frac{\mathrm{d} - \mathrm{d}_{\mathrm{nest}}}{\mathrm{d}_{\mathrm{rand}} - \mathrm{d}_{\mathrm{nest}}} \qquad (2)$$

A zero υ corresponds to a state of minimal disorder, where all elements are perfectly nested. Conversely, $\upsilon = 1$ corresponds to a state of equiprobable randomly dispersed matrix elements. The main advantage of υ is that it is posed in an analytical way. Because of that we have already discussed the relation between nestedness and abundance [12] and now we intend to work the connection between nestedness and degree distribution.

A puzzling question when studying the nestedness pattern is the following: is it possible that nestedness can be defined only by the degree distribution of lines and columns in the matrix? An answer to this question will strongly help to demystify the nestedness concept. Using our index expressed in (1) and (2) we answer positively this question. We give here a sketch of the proof in three steps. First we find the group of permutations of elements among lines (or columns) in the matrix that keeps the degree distribution constant. Second we show that these group operations do not change the distance as defined in equation (1). Third, as a consequence the set of all matrices that share the same degree distribution has the same nestedness index υ.

We believe that a well defined nestedness estimator can be useful to investigate order and structure in bipartite networks such as the metabolic network of a cell or social webs like actors bipartite network [13]. To conclude, nestedness is a subject of high current interest in biogeography, community ecology and conservation biology. The *Web of Science* shows more than 300 papers on the subject in the last 14 years. We believe this work will be of interest to researchers in a great multitude of areas, as well as to physicists working with patterns in networks.

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