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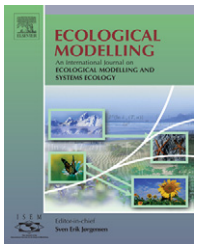

Short communication

Quantifying positional importance in food webs: A comparison of centrality indices

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ABSTRACT

Conservation biology should focus more on the importance rather than the rarity of species, although the definition and quantification of importance are not easy. One approach involves measuring the positional importance (e.g. centrality) of species in ecological interaction networks to provide a basis for species ranking. However, there are many centrality indices, each reflecting a particular aspect of positional importance and therefore giving a rank order of species different from those provided by alternative formulations. Thus, there is a strong need for comparing the available indices and for examining their relative merits in network analysis. In this paper, we apply 13 centrality indices to the "species" (trophic components) of methodologically comparable trophic flow networks, in order to answer the following questions: (1) What is the disagreement between different indices regarding the rank of a given species in a given network? (2) How is this disagreement in performance influenced by the choice of the network? (3) What is the overall relationship among these indices and, in particular, which are the most similar to degree (the simplest index of all, being equal to the number of links pertaining to a given node)? We compare the 13 indices based on the data of nine networks using metric and rank statistics and multivariate analysis procedures. We conclude that (1) different centrality ranks differ in each network; (2) different webs can be characterized by different relationships between ranks but there is a robust pattern of relationships among the indices, some index pairs behaving very similarly in all networks; and (3) it is the index of closeness centrality which provides a rank most similar to that based on degree.

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1. Introduction

Future conservation biology needs to be more functional and should be outlined within a multispecies context. For example, the conservation of rare species should be gradually replaced by conserving the most important species that play key role in maintaining ecosystem functions (Wilson, 1987). A fundamental requirement in such an approach is the more quantitative, less subjective and, hopefully, more predictive study on keystone species (Paine, 1969; Mills et al., 1993; Power et al., 1996).

The importance of species in a community is not easy to define and is even more complicated to quantify. The problem is discussed within a community ecology framework: we

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suppose that cascading indirect effects of extinctions spread only through the interspecific interaction network (see also Abrams et al., 1996). Doing so, we may define a type of important species ("topological keystone species") as species being in key positions of the topological space of interactions. A number of studies already suggested to use different network indices for characterizing the role species play in communities (Harary, 1961; Jordán et al., 1999, 2006a; Solé and Montoya, 2001; Dunne et al., 2002; Jordán and Scheuring, 2002; Luczkovich et al., 2003; Brose et al., 2005; Quince et al., 2005; Allesina and Bodini, 2005; Ebenman and Jonsson, 2005; Libralato et al., 2006; Eklöf and Ebenman, 2006). We believe that this kind of approach should be developed further (Jordán and Scheuring, 2004; Dunne, 2006; Jordán et al., 2006b).

Our main interests in the present paper are (1) how different centrality indices express the positional importance of trophic groups in nine trophic networks, (2) how similar are the centrality ranks of trophic groups in these networks provided by different indices, (3) how similar are the indices in performance over the nine-network data base, and in particular, which indices are the most similar to degree, the simplest possible index of positional importance of nodes in networks.

2. Data

Nine trophic flow networks have been selected for the present study. These describe the carbon flow among trophic components in the Baltic Sea (Baird et al., 1991), the Chesapeake Bay (Baird and Ulanowicz, 1989), the Crystal River (Ulanowicz, 1996), the Kromme estuary (Baird and Ulanowicz, 1993), Lake Ontario (Christensen, 1995), the Peruvian upwelling system (Baird et al., 1991), the Swartkops estuary (Baird et al., 1991), the Tongoy Bay (Ortiz and Wolff, 2002) and in the Ythan estuary (Baird and Ulanowicz, 1993). All of these networks have been described in a methodologically uniform way, thus, the data sets are comparable. Furthermore, these networks contain roughly the same number of trophic groups in order to reduce the possible size effects on results.

We have modified slightly the original data bases for our purposes. Only biotic compartments are considered here because of biological and technical reasons. The biological reason is that biotic–biotic interactions are characteristically different from biotic–abiotic ones: prey–predator and prey–detritus transitions have quite different dynamics, the first is a real interaction, while the second is material transfer. From a mass-balance perspective these are equally important but if we are interested in the complex web of indirect interspecific effects, we believe it is better not to consider these. The technical reason is that connecting "detritus" to every other graph node would greatly distort the analysis. Since basically every living components have a link to detritus, the latter would be suggested as a structural keystone species in each network (again, from a trophic perspective it is correct but does not help in better understanding the key players in the web of interspecific interactions). Since the networks studied are weighted graphs (showing the amount of carbon flow), we were able to use indices that consider weighted links as well in addition to "purely" topological indices.

3. Methods

3.1. Centrality indices

We calculated 13 indices to quantify the positional importance of every species (node) in each of the nine networks studied (see Supplementary Appendix A). These indices range from very simple measures dependent only on local characteristics of the given node to those considering information on wider web features. Each reflects a particular aspect of positional importance within networks and therefore the indices are not expected to provide identical importance ranks for nodes. Some indices had been introduced in social network analysis as centrality indices (like degree, closeness, betweenness and information centrality, *D*, CC, BC and IC, respectively, see Wassermann and Faust, 1994, see also Friedkin, 1991). We also used the *K* keystone index and its four components (Jordán et al., 1999) and the unweighted (TI) and weighted (WI) index for general topological importance, both for 1 and 10 steps long effects (see Jordán et al., 2003). Our present work is an extension of a former one discussing only a single food web (Jordán et al., 2006a, see Supplementary Appendix E for more explanation).

3.2. Comparison of indices

The performance of the 13 indices and index components (hereafter, "indices") was evaluated by a complex multivariate study. For each web *k*, we constructed an $M_k \times 13$ data matrix, with M_k as the number of nodes in the web, to summarize the 13 indices. Then, two basic types of analyses were made, (1) a metric study in which actual differences between index values were considered and (2) an ordinal study in which only the rank order of index values was meaningful. This double strategy allows the evaluation of the importance of the metric component in the data. The metric analysis used a matrix of product moment correlations between indices for each web. Correlations for indices *i* and *j* were calculated in dissimilarity form obtained using the formula $d_{ij} = 2 - r_{ij}$. UPGMA classification of the nine matrices thus obtained was used to reveal clustering tendency among the indices, to find the closest relative of *D* and to examine whether more complex and hard to compute formulae may be replaced by simpler ones without much loss of information. The ordinal analysis differed from this in that the starting matrix was calculated using Goodman and Kruskal (1954) gamma function which relies on the rank order of values within each column of the data matrix. Then, in accordance with the requirement that the subsequent analysis should also be rank-based, the indices were classified by ordinal clustering as described by Podani (2005). For both series of results, each containing nine dendrograms, a majority rule consensus dendrogram was constructed to emphasize agreements among the different webs (see e.g., Podani, 2000; for details of clustering and consensus generation). In this consensus dendrogram, only those clusters are present which appear in more than 50% of the competing results, i.e., at least in five dendrograms in the present study.

An alternative way of expressing between-index relationships is to merge all the nine data matrices and do the

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