



The robustness of keystone indices in food webs

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ABSTRACT

Species that have outstanding importance in the functioning of a community are called keystone species. Network indices are increasingly used to identify them, e.g. for conservation biological purposes. The problem is that the calculation of these indices is based on the particular network model of the studied food web, which can include network construction errors. For example, additional, unnecessary trophic links can be built in, or, to the contrary, functional links can be left out. What is the effect of such errors on the result of network analysis, e.g. the centrality values of species? Can you rely on the importance rank of species that you calculated? We developed a robustness measure (R) for network indices to answer these questions. R is proportional to the likeliness that the importance rank of nodes in the given network according to a given index would not change due to possible errors in network construction. For calculating R , first the maximum expected error (P) has to be computed which represents the potential range of error in estimating the keystone index in question. Basically, R is calculated by comparing P to the keystone indices of species to assess the reliability of the importance rank of species based on the network model. We calculated the robustness of 13 different structural indices in 26 food webs of different size to test the P and R values. We found that fragmentation indices and the number of dominated nodes can be characterized by quite low R values, while betweenness, topological importance, keystone index and mixed trophic impact have high R values, which means that they are relatively more reliable for assessing the importance rank of species in an uncertain network model. However, as R was found to be very variable, depending on the topology of a given network, a detailed description is provided for performing the actual calculations case-by-case.

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1. Introduction

Species are not equally important in maintaining the integrity of ecosystems—there are some whose perturbation would have large (and undesired) effects on the community. Such species are called keystones (Power et al., 1996). It is of primary importance for conservation biological purposes to have quantitative methods for their identification: the classical view of protecting rare species might be shifted towards protecting the most important species (Jordán and Scheuring, 2004). Analyzing the structure of interaction networks is an important tool for studying the key problems of community ecology, but there is an embarrassingly wide arsenal of network indices to choose from (Jordán and Scheuring, 2004). Matching the adequate indices to the particular problems is a difficult task and it can turn out that several indices would be suitable. For assessing the importance of species within

a community, centrality indices are increasingly used (Proulx et al., 2005), the ultimate objective being the ‘a priori’ identification of keystone species (Jordán et al., 2006a); furthermore, indices derived from centrality measures are used to study e.g. centrality distributions (Dunne et al., 2002a; Jordán et al., 2006b; Proulx et al., 2005).

Apart from the difficulty of choosing the appropriate index, the network model itself also involves serious uncertainties. The construction of a trophic network is far from trivial and the definition of nodes and links largely rely on the author’s possibilities and opinion. Apart from problems with the definition of nodes that we do not discuss here, the existence of trophic links in the network is usually based on the biomass and feeding habits of species (e.g., the Ecopath approach, Christensen et al., 2004) rather than actual measurements on the strength of effects (Paine, 1992). Due to these difficulties, more than one network can be constructed for describing the same community, and these could be different from each other in the number of links that connect species. If there is a link in the model which connects species that in fact, are not in trophic interaction with each other (false positive link), this counts as an error in the model. Likewise, it is also possible that the author is not aware of a real trophic

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interaction and does not represent it in the model (false negative link). In the following, we will refer to these discrepancies (deficit or surplus of links) simply as errors in the model.

What is the effect of such errors on the keystone indices of species? Can you rely on the importance rank of species that you calculated? We would like to answer these questions in this study and to provide some guidance for deciding which index to choose, if the network model might include construction errors. Although these questions have already arisen in sociometry (Borgatti et al., 2006; Costenbader and Valente, 2003; Frantz and Carley, 2005) and, most recently, in connection with animal social networks (Wey et al., 2008), the findings could not be directly used in food web analysis. This is because topology, that may be substantially different in sociometric and trophic networks, affects robustness profiles of centrality measures (Frantz and Carley, 2005). Moreover, these studies are not problem-oriented, in the sense that apart from providing a global measure of robustness, they do not offer guidance to decide what difference in node centrality can be considered significant. Ecological network analysis has already developed diverse methods to test the sensitivity of results to flow uncertainty (for a recent application, see Borrett and Osidele, 2007), while topological food web analyses still lack such systematic methods.

To fill this gap, we developed a robustness measure for network indices against construction errors. We investigated the role of error quantity and error type in the robustness of indices and compared the robustness of different structural indices. Our purpose was to assess how robust keystone indices are for errors in network construction and to provide some guidance for deciding whether a calculated difference in species importance is significant or not.

2. Data

We analyzed 26 food webs (Table 1) of different size. The source of our data is the predator–prey dataset from the NCEAS (National Center for Ecological Analysis and Synthesis) Interaction Web Database (<http://www.nceas.ucsb.edu>). All food webs are provided in binary adjacency matrices, in a directed and unweighted form. There were few unconnected species in some of the food webs which were excluded from the analysis as they are not part of the food web by definition, and they are not expected to affect or be affected by other species. All food webs contain abiotic components, such as detritus, plant material and other organic material.

3. Methods

3.1. Indices

We calculated the robustness of 13 different topological indices in the 26 food webs mentioned above. The description of indices is only given as a reminder; for a detailed explanation, see the cited literature. N refers to the number of nodes in the network throughout the section. The following indices handle binary and undirected webs:

Node degree (ND) is the most widely used index that quantifies the number of adjacent nodes (in a food web this means the sum of prey and predator species) (Wassermann and Faust, 1994).

Betweenness centrality (BC) quantifies how frequently a node i is on the shortest paths between every pair of nodes j and k . The standardized index for node i is

Table 1
Food webs analyzed.

Name of food web	No. of nodes	No. of links
AkatoreA	84	227
AkatoreB	54	117
Berwick	77	240
Blackrock	86	375
Broad	94	564
Canton	108	707
Catlins	48	110
Coweeta1	58	126
Coweeta17	71	148
DempstersAu	83	414
DempstersSp	93	538
DempstersSu	107	965
German	84	352
Healy	96	634
Kyeburn	98	629
LilKyeburn	78	375
Martins	105	343
Narrowdale	71	154
NorthCol	78	241
Powder	78	268
Stony	112	830
SuttonAu	80	335
SuttonSp	74	391
SuttonSu	86	423
Troy	77	181
Venlaw	66	187

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$$BC_i = \frac{\sum_{j < k} g_{jk}(i) / g_{jk}}{(1/2)(N-1)(N-2)},$$

where $i \neq j$ and k . g_{jk} is the number of the shortest paths with the same length between nodes j and k , and $g_{jk}(i)$ is the number of these shortest paths to which node i is incident (Wassermann and Faust, 1994).

Information centrality (IC) differs from BC in that it considers all paths (including the shortest), weighted by path length (for detailed explanation, see Wassermann and Faust, 1994).

Closeness centrality (CC) quantifies how long the shortest path is from a given node to all others. The standardized index for node i is

$$CC_i = \frac{N-1}{\sum_{j=1}^N d_{ij}},$$

where $i \neq j$, and d_{ij} is the length of the shortest path between nodes i and j (Wassermann and Faust, 1994).

Fragmentation measure (F) quantifies the importance of a given node based on network fragmentation after its deletion. It is calculated as

$$F_i = 1 - \frac{\sum_k s_k(s_k - 1)}{N(N-1)},$$

where s_k is the number of nodes in the k th component (i.e. disconnected subgraph) (Borgatti, 2003).

Distance-based fragmentation (FD) can be used when the deletion of a node does not increase the number of components, but modifies the average distance between nodes. This is expressed as

$$FD_i = 1 - \frac{2 \sum_{i > j} \frac{1}{d_{ij}}}{N(N-1)},$$

where d_{ij} is the distance between nodes i and j (Borgatti, 2003).

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