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, keystoneness 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 kth 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).

The m-reach (R2) simply measures the number of nodes reachable within m steps (here $m = 2$) from node i (Borgatti, 2003).

Distance-weighted reach (RD) is a more sensitive measure that can be defined as the sum of the reciprocals of distances from node i to all nodes. It is calculated as

$$\mathrm{RD}_i = \frac{\sum_j \frac{1}{d_{ij}}}{N},$$

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

Topological importance (TI) is for characterizing long indirect effects. The effects of i on j in m steps is given as $a_{m,ij}$. The direct effects ($m = 1$) of a node are defined as

$$a_{1,ij} = 1/ND_j,$$

where ND_j is the degree of node j. Indirect effects of m step are calculated as the mth power of the matrix that contains all direct effects. Finally, topological importance up to n step equals

$$\mathrm{TI}_i^n = \frac{\sum_{m=1}^{n} \sum_{j=1}^{N} a_{m,ij}}{n}.$$

We have calculated TI1 and TI10, i.e. TI for $n = 1$ and 10 steps, respectively (Jordán et al., 2003).

The following three indices take into account the direction of trophic interactions as well:

The number of *dominated nodes* (DM) quantifies bottom-up influences. Node i is a dominator of node j if every path from the external environment to j contains i (Allesina and Bodini, 2004).

The *keystoneness index* (K) emphasizes vertical (bottom-up and top-down) over horizontal interactions.

$$K_i = \sum_{j=1}^{n} \frac{1}{d_j}(1 + K_{bj}) + \sum_{e=1}^{m} \frac{1}{f_e}(1 + K_{te}),$$

where n is the number of predators consuming species i, d_j is the number of prey species of its jth predator and K_{bj} is the bottom-up keystone index of the jth predator. Symmetrically, m is the number of prey eaten by species i, f_e is the number of predators of its eth prey and K_{te} is the top-down keystone index of the eth prey (Jordán et al., 1999).

The *mixed trophic impact* (IMA) distinguishes between the negative effects of predators and the positive effects of prey. Assuming that the effects are additive and multiplicative, it calculates the total (direct plus indirect) impact of a given species. When applied to unweighted networks, the positive effect of prey i on predator j is calculated as $g_{ij} = 1/D_{j,in}$, where $D_{j,in}$ is the number of prey of j. Similarly, the negative effect of predator i on its prey j is measured as $f_{ij} = 1/D_{j,out}$ where $D_{j,out}$ is the number of predators of j. The net impact of i upon j equals $g_{ij} - f_{ji}$ and is defined as the one-step (direct) effect of i on j. Its values range from -1 to $+1$. Taking every pair of N nodes, we calculate the above-defined direct net impacts and constitute the $N \times N$ net impact matrix, $[Q]$. The total (direct and indirect) effects are calculated by summarizing the all integer powers of $[Q]$, using the following equation known from input–output theory:

$$[M] = \{[I] - [Q]\}^{-1} - [I],$$

where $[I]$ is the identity matrix. We use the summed absolute values of effects (IMA) to measure the importance of species (Ulanowicz and Puccia, 1990; Vasas and Jordán, 2006).

3.2. Measuring robustness

We used a Monte Carlo method to calculate the robustness of indices. For each web, links were manipulated to simulate the effect of construction errors. The quantity of manipulated links is given with respect to network size (the number of links deleted were 1–10%, 20% and 30% of the number of nodes). Each index was recalculated for each species in the modified networks. The differences between original and modified centralities were then compared to the differences between centrality values of different species in the original networks.

Manipulation of links means either the deletion of existing links from the network or the addition of new links to the network. The deletion of existing links simulates the possible effect of false positive links, while the addition of links simulates the effect of false negative links in the network. Note that the probability of these two types of errors is different and depends mainly on the methods of network building.

We constructed two measures: P, the maximum expected error in the calculated centrality values, and R, the robustness of the calculated centrality rank. The calculations of P and R can be easily reproduced by following the pseudocode below. The code is also available at request from the corresponding author in R programming language (we calculated both measures for link deletion and link addition separately, and since the algorithm was essentially the same the pseudocode applies to both).

- For the number of possible false positive/negative links in the network
  {
  - Calculate the index of every node
  - Delete/add one link from/to the network
  - Recalculate the index of every node
  - Subtract the original index of every node from its new index
  - Save the absolute value of the differences (this measures how much a deleted/added link changes the index of species)
  - Replace the link that was deleted/remove the link that was added
  }
- P = the upper 95% boundary of the distribution of the merged absolute differences
- Order nodes according to their original index
- Calculate the difference between indices of nodes following each other
- R = the % of these differences greater than P

In the pseudocode above, these values are calculated against the deletion/addition of one link. The number of possible false positive links in the network is the number of links, i.e. each link is deleted one by one. The number of possible false negative links equals the number of links in a fully connected network minus the number of existing links in the network (possible false negative links are all links that are not present in the model).

For calculating robustness against more link deletions/additions, we manipulated several links at a time. For smaller food webs, we did it in all combinations of possible false positive/negative links, while for larger food webs, we manipulated links in a random way in 1000 combinations to shorten running time. Care was taken to leave out modified networks from the calculations where a deleted link resulted in a disjoint network, since some of the indices cannot be calculated for networks of more than one component. In the case of link addition, some of the resulted networks contained cycles (a cycle is a path such that the start vertex and the end vertex are the same). We did not include these networks in the analysis in the case of two indices, namely DM and K, since these cannot be calculated in such networks.

P, the maximum expected error, represents the potential range of errors in estimating an index, meaning that the difference

between the index of a given node calculated from two different network models of the same food web is smaller than or equal to P with minimum 95% of certainty. In other words, this is the maximum expected error in the index of a given node, if there is an error in the model.

Unfortunately, the distribution of the errors does not follow any known distribution (data not shown), hence the significance of the difference between centrality values cannot be directly evaluated; however, it will be a multiple of P. Therefore, we suggest that if the difference between the centrality values of two nodes is smaller than P, it should not be considered significant, since this difference is smaller than the possible error for one node. In this case, we cannot say for sure that one of the nodes is more important than the other, even if only one of them would be affected by the errors in network construction.

R, the robustness, ranges from 0% to 100%. It is proportional to the likeliness that the importance rank of nodes in the given network according to the given index would not change due to possible errors in network construction. We calculated the percentage of differences that are greater than P, and used this to measure the robustness of the given index against errors in constructing links.

4. Case study

We would like to demonstrate the calculations of P and R on an example. For simplicity, we chose a small food web from Baird and Ulanowicz (1993), the Ythan Estuary food web, the simplest index, node degree (ND) and we measure its robustness against the deletion of one link.

If we have the model of the network (Fig. 1) we can simply count the links to and from a certain node to have its ND. This is the ND of the node according to the model (Table 2). Then, to simulate possible errors in the model, we delete the links one by one and recalculate the ND of every node (Table 3). Note that the deletion of links d, f and g are not considered here, because they would result in a separated node.

Then, we take the absolute difference of the values before and after the deletion to have the distribution of the effect of a possible error. In this case, this distribution consists of 22 ones, and 88 zeros (of course, in the case of other indices, different values are possible). P value (the 95% percentiles) of this distribution is 1. It means that the effect of a possible error on the index of a node is smaller than or equal to 1 with the probability of 95% (at least).

Then, to calculate robustness of ND in this network, first we take the importance rank of nodes according to their original index, and then calculate the difference between the indices of nodes following each other (Table 2). To compare the possible error with the difference between the index of nodes, we calculate R, which is the percentage of these differences greater than P. In
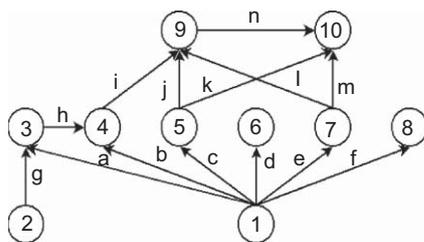

Fig. 1. The model of the Ythan Estuary food web. Nodes: 1—pelagic producers, 2—benthic producers, 3—microzooplankton, 4—mesozooplankton, 5—benthic suspension feeders, 6—meiofauna, 7—deposit feeders, 8—herbivorous birds, 9—fish, and 10—carnivorous birds.

Table 2
The importance rank of trophic groups according to their ND in the Ythan Estuary food web, and the differences between them.

Nodes	ND	Difference
Pelagic producers	6	–
Benthic producers	4	2
Microzooplankton	3	1
Mesozooplankton	3	0
Benthic suspension feeders	3	0
Meiofauna	3	0
Deposit feeders	3	0
Herbivorous birds	1	2
Fish	1	0
Carnivorous birds	1	0

Table 3
Recalculated ND of nodes in the Ythan Estuary food web after the deletion of links.

Deleted link\nodes	1	2	3	4	5	6	7	8	9	10
a	5	4	2	3	3	3	3	1	1	1
b	5	4	3	2	3	3	3	1	1	1
c	5	4	3	3	2	3	3	1	1	1
e	5	4	3	3	3	3	2	1	1	1
h	6	4	2	2	3	3	3	1	1	1
i	6	4	3	2	3	3	3	1	0	1
j	6	4	3	3	2	3	3	1	0	1
k	6	4	3	3	2	3	3	1	1	0
l	6	4	3	3	3	3	2	1	0	1
m	6	4	3	3	3	3	2	1	1	0
n	6	4	3	3	3	3	3	1	0	0

For the names of the trophic groups, represented here as numbered nodes, see Fig. 1.

this case, we have only two values greater than 1 among the differences, which is 22% of the values ($R = 22\%$). This means that a possible error would change the importance rank of nodes with the probability of 78% at least. This is a quite high value if we wanted to know the complete importance rank of species. On the contrary, if we have the humbler aim to select the single most important species only, we can be quite confident. No error would confuse us, since the difference between the index of the most important species and the index of other species is always greater than 1, irrespectively of the errors. As we can see, robustness heavily depends on the particular problem. For this reason, it is very important to compare the P value to the importance values of species in order to make valid assertions when errors are probable in the network model.

5. Results

We expect a robustness measure to be intuitive: it should decrease as the quantity of errors increase, because more errors supposedly cause larger changes in the indices of nodes. Our results show that R is mainly in accordance with this expectation. Robustness usually decreases with more links manipulated (Figs. 2–4), i.e. the less precise our network is, the less reliable our importance ranks are.

Generally, average robustness of importance ranks was rather low (Fig. 2). For 5% link manipulation, it rarely reached $R = 20\%$; and for 30% link manipulation, it approximated zero for most indices. Note that 30% means that the number of manipulated links is 30% of the number of nodes in the network. This quantity is only 3–14% of the links in the network (depending on the network's connectance), which implies a very low reliability for the importance ranks. Robustness of indices against link deletions was usually higher than against link additions. This is not
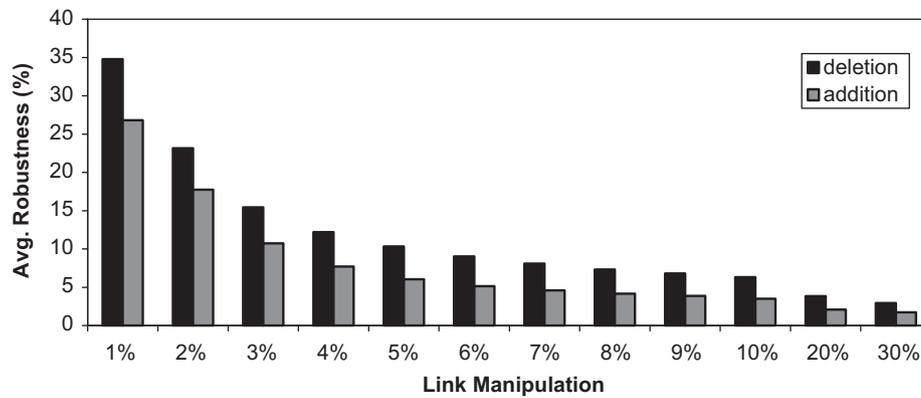
Fig. 2. Average robustness of indices (averaged over all food webs analyzed) against link deletions and link additions as the function of manipulated links. The quantity of manipulated links is given compared to the number of nodes in the network (network size).
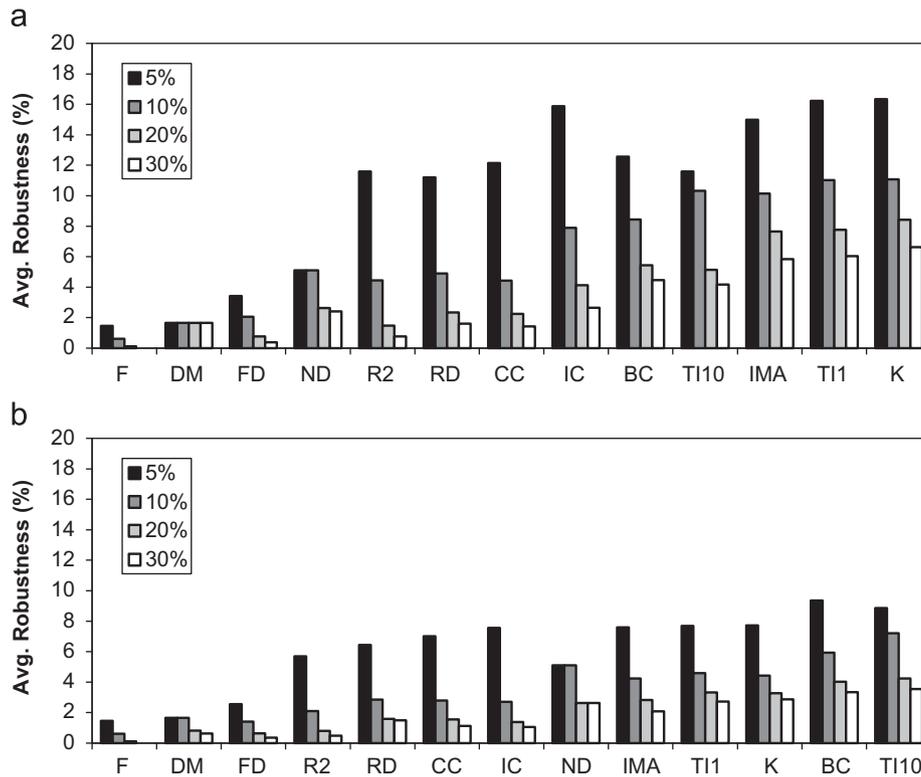

Fig. 3. Average robustness of indices (averaged over all food webs analyzed). (a) The number of links deleted is 5%, 10%, 20% and 30% of the number of nodes. (b) The number of links added is 5%, 10%, 20% and 30% of the number of nodes. BC: betweenness centrality, CC: closeness centrality, DM: number of dominated nodes, *F*: fragmentation measure, FD: distance-based fragmentation, IC: information centrality, IMA: mixed trophic impact, *K*: keystoness, ND: node degree, R2: *m-reach* in 2 steps, RD: distance-weighted reach, TI1, TI10: topological importance in 1 and 10 steps, respectively.

surprising given that we added links randomly without any selection, hence link additions caused a bigger structural change in the networks than link deletions and altered the indices of nodes to a greater extent.

Interestingly, the robustness of indices has a somewhat similar order in different food webs (Fig. 3): typically, fragmentation indices and the number of dominated nodes seem to be the least robust indices, while betweenness, topological importance, keystoneness and mixed trophic impact are more robust.

It can be the case that we would like to know the complete importance rank of species; however, it is not a very common task. Usually, the first few most important species are in the focus of our interest. We can have very different values of robustness if only the first few most important species (approximately 10% of the species, but minimum three species) according to the

importance rank of the given index are taken into consideration. First of all, it is very reassuring that the robustness of indices is much higher when it is calculated only for the first few most important species, thus our predictions can be more reliable when we just want to select the few most important species (Fig. 4). This happens because centrality distributions are mostly unimodal (sometimes with a right skew; Bauer et al., submitted) which implies that there are few important species and many of average importance. The order of indices remains approximately the same.

6. Discussion

We constructed a robustness measure, *R*, to assess the possible effect of network construction errors on the importance rank of
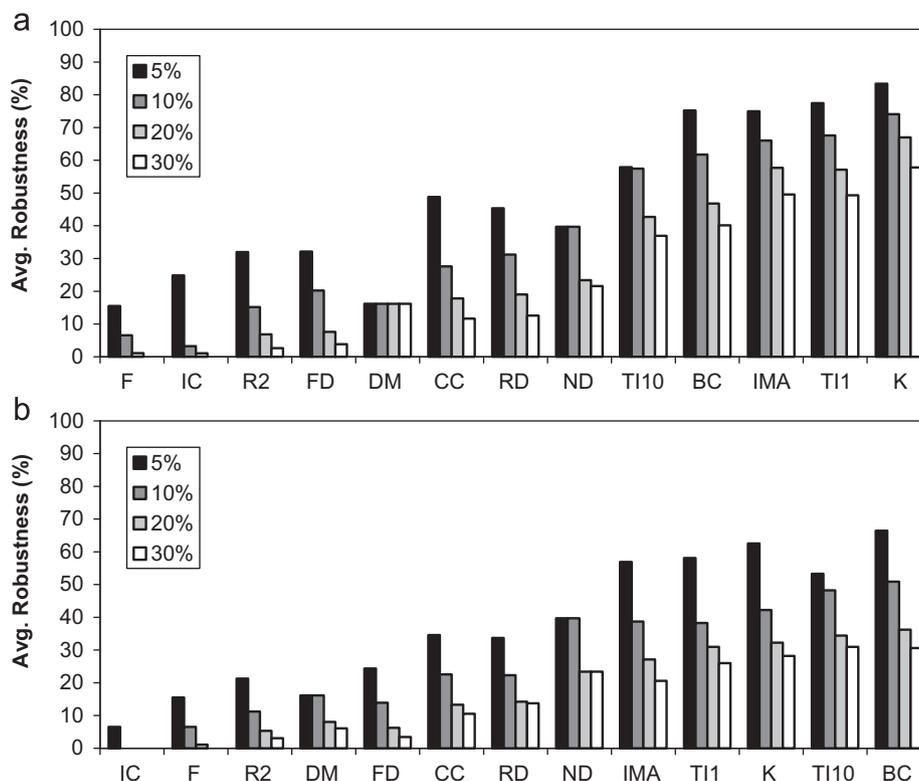
Fig. 4. Average robustness of indices calculated only for the first few most important species (averaged over all food webs analyzed). The first few most important species (approximately 10% of the species, but minimum three species) were selected according to the importance rank of the given index. (a) The number of links deleted is 5%, 10%, 20% and 30% of the number of nodes. (b) The number of links added is 5%, 10%, 20% and 30% of the number of nodes. BC: betweenness centrality, CC: closeness centrality, DM: number of dominated nodes, F: fragmentation measure, FD: distance-based fragmentation, IC: information centrality, IMA: mixed trophic impact, K: keystoness, ND: node degree, R2: m-reach in 2 steps, RD: distance–weighted reach, TI1, TI10: topological importance in 1 and 10 steps, respectively.

species according to various keystone indices. After the analysis of 26 food webs of different size by 13 keystone indices, we can conclude that R conforms quite well to our intuitions. Some indices can be characterized by quite low R values, which means that they are usually quite unreliable if there are possible errors in the network model. On the contrary, others have higher R values, which means that it is better to choose one of them if we want to know the importance rank of species in a less well-known food web. However, the patterns of robustness are quite complex and largely vary among the different food webs, because they can be heavily influenced by the topology of the network: and thus we suggest to use the robustness values in our study only as a guidance and recalculate the exact values for the networks to be analyzed whenever it is possible.

Before the calculations, the possible type and number of errors has to be assessed. Two types of errors occurring during network construction are false positive and false negative links and their probability can be estimated from input data, if the model building has been accurately documented (Cohen et al., 1993). The total number of links can be deduced from the asymptotic maximum of the yield–effort curve for links as a function of cumulative sampling effort (Cohen et al., 1993), and thus the number of likely missing links can be estimated. This in turn, can be used in calculating robustness as the number of randomly added links to estimate the effect of errors in the model caused by false negative links. False positive links can appear either when a feeding relationship has not been observed in the field, but was deduced from similar studies; or when the relationship has been confirmed to exist, but it is irrelevant for the interacting species. The number of probable false positive links gives the number of link deletions in the calculations of robustness.

These calculations are not only important if one wants to set up the importance rank of species. They are also essential when one just wants to compare the importance of few species, or even just two species. It is advised to always compare the possible error (the P value) to the difference between the indices of species before concluding that one of them is more important than the other.

Note that there is another way to interpret our results. Link manipulation in our model can be viewed not only as an artifact during network construction, but also as the disappearance of species interactions or appearance of new species interactions as a behavioral response to environmental changes (e.g. altered turbidity may modulate predation levels for fish, Gadomski and Parsley, 2005). It can also happen that diminishing populations change their feeding habits (e.g. group size affects prey selection, Gese et al., 1988). Consequences of species extinction represented as deletion of nodes from the network has been more widely studied (Dunne et al., 2002b). In this sense, the robustness measure is an indicator of the changes in the keystone structure after such an event. Changes in the importance rank, or in the indirect interactions that are behind the rank, may result in an altered dynamical functioning of the ecosystem. This may make the responses of the ecosystem less predictable, and the generally low robustness measures that we calculated suggest that this scenario may be a veritable threat.

In the present study, only binary webs were analyzed, and the indices were selected accordingly. On the other hand, several functional indices exist that are able to handle weighted networks, such as the weighted mixed trophic impact (Ulanowicz and Puccia, 1990; Vasas and Jordán, 2006), the relative and absolute environ system control (Schramski et al., 2006) and others. While these functional indices are indeed more advanced,

we claim that the simplest indices still can provide valuable information, when applied with knowing their limitations. Topological keystone indices are increasingly used in ecological studies, but their verification is still missing, and this flaw greatly hinders their practical application. Our study provides a quantitative method to evaluate—at least one aspect of—their reliability. Such a critical approach is essential if conservational issues are supposed to be based on structural analyses, since the future of many other species could depend on the species chosen for protection.

Acknowledgments

References

Allesina, S., Bodini, A., 2004. Who dominates whom in the ecosystem? Energy flow bottlenecks and cascading extinctions. J. Theor. Biol. 230, 351–358.

Baird, D., Ulanowicz, R.E., 1993. Comparative study on the trophic structure, cycling and ecosystem properties of four tidal estuaries. Mar. Ecol. Prog. Ser. 99, 221–237.

Bauer, B., Jordán, F., Podani J., Submitted. Node centrality indices in food webs: rank orders versus distributions. Ecological Complexity.

Borgatti, S.P., 2003. The key player problem. In: Breiger, R., Carley, K., Pattison, P. (Eds.), Dynamic Social Network Modeling and Analysis: Workshop Summary and Papers, Committee on Human Factors. National Academies Press, Washington, DC, pp. 241–252.

Borgatti, S.P., Carley, K.M., Krackhardt, D., 2006. On the robustness of centrality measures under conditions of imperfect data. Social Network 28, 124–136, doi:10.1016/j.socnet.2005.05.001.

Borrett, S.T., Osidele, O.O., 2007. Environ indicator sensitivity to flux uncertainty in a phosphorus model of Lake Sidney Lanier. USA Ecol. Model. 200, 371–383, doi:10.1016/j.ecolmodel.2006.08.011.

Christensen, V., Walters, C.J., Pauly, D., 2004. Ecopath with ecosim: a user's guide. Fisheries Centre Research Reports, University of British Columbia, Vancouver, Canada, p. 12.

Cohen, J.E., Beaver, R.A., Cousins, S.H., DeAngelis, D.L., Goldwasser, L., Heong, K.L., Holt, R.D., Kohn, A.J., Lawton, J.H. Improving food webs. Ecology 74, 252–258.

Costenbader, E., Valente, T.W., 2003. The stability of centrality measures when networks are sampled. Social Network 25, 283–307, doi:10.1016/S0378-8733(03)00012-1.

Dunne, J.A., Williams, R.J., Martinez, N.D., 2002a. Food-web structure and network theory: the role of connectance and size. Proc. Natl. Acad. Sci. 99, 12917–12922.

Dunne, J.A., Williams, R.J., Martinez, N.D., 2002b. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecol. Lett. 5, 558–567.

Frantz, T.L., Carley, K.M., 2005. Relating network topology to the robustness of centrality measures. Technical Report CMU-ISRI-05-117, Carnegie Mellon University.

Gadomski, D.M., Parsley, M.J., 2005. Effects of turbidity, light level, and cover on predation of white sturgeon larvae by prickly sculpins. Trans. Am. Fish. Soc. 134, 369–374.

Gese, E.M., Rongstad, O.J., Mytton, W.R., 1988. Relationship between coyote group size and diet in southeastern Colorado. J. Wildl. Manage. 52, 647–753.

⟨http://www.nceas.ucsb.edu/interactionweb/html/thomps_towns.html⟩.

Jordán, F., Liu, W.C., Davis, A.J., 2006a. Topological keystone species: measures of positional importance in food webs. Oikos 112, 535–546.

Jordán, F., Liu, W.C., van Veen, F., 2003. Quantifying the importance of species and their interactions in a host-parasitoid community. Commun. Ecol. 4, 79–88.

Jordán, F., Scheuring, I., 2004. Network ecology: topological constraints on ecosystem dynamics. Phys. Life Rev. 1, 139–172, doi:10.1016/j.plrev.2004.08.001.

Jordán, F., Scheuring, I., Vasas, V., Podani, J., 2006b. Architectural classes of aquatic food webs based on link distribution. Commun. Ecol. 7, 81–90.

Jordán, F., Takács-Sánta, A., Molnár, I., 1999. A reliability theoretical quest for keystones. Oikos 86, 453–462.

Paine, R.T., 1992. Food-web analysis through field measurement of per capita interaction strength. Nature 355, 73–75.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T., 1996. Challenges in the quest for keystones. Bioscience 46, 609–620.

Proulx, S.R., Promislow, D.E.L., Phillips, P.C., 2005. Network thinking in ecology and evolution. Trends Ecol. Evol. 20, 345–353, doi:10.1016/j.tree.2005.04.004.

Schramski, J.R., Gattie, D.K., Patten, B.C., Borrett, S.R., Fath, B.D., Thomas, C.R., Whipple, S.J., 2006. Indirect effects and distributed control in ecosystems: distributed control in the environ networks of a seven-compartment model of nitrogen flow in the Neuse River Estuary, USA; steady-state analysis. Ecol. Model. 194, 189–201.

Ulanowicz, R.E., Puccia, C.J., 1990. Mixed trophic impacts in ecosystems. Coenoses 5, 7–16.

Vasas, V., Jordán, F., 2006. Topological keystone species in ecological interaction networks: considering link quality and non-trophic effects. Ecol. Model. 196, 365–378, doi:10.1016/j.ecolmodel.2006.02.024.

Wassermann, S., Faust, K., 1994. Social Network Analysis: Methods and Applications. Cambridge University Press, Cambridge.

Wey, T., Blumstein, D.T., Shen, W., Jordán, F., 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. Anim. Behav. 75, 333–344, doi:10.1016/j.anbehav.2007.06.020.