Short communication

Identifying important species: Linking structure and function in ecological networks

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ABSTRACT

At least two different approaches have been used to quantitatively assess the importance of species in communities. One approach is to derive relatively simple, structural importance indices from network analysis. This assumes that well-connected species are more important. Another approach is to derive functional importance indices using dynamical simulations. We performed both kinds of analysis, and we ranked the species of the Prince William Sound food web based on 13 structural and 5 functional importance indices. We then compared the rank correlation between structural and functional indices. Our results show that different approaches to quantifying importance give different results; unweighted structural indices never correlate significantly with functional ones, but certain weighted structural indices correlate reasonably well with simulated function. This line of research could help in improving our understanding of the usefulness of structural approaches in quantifying the importance of species and understanding biological communities in general. The results strongly indicate the fundamental importance of indirect effects in governing ecosystem dynamics and the need to account for them in structural approaches. Conversely, it generally verifies the usefulness of functional approaches to the investigation of biological communities that account for indirect effects, whether they are modelling or direct empirical studies.

1. Introduction

There is an increasing need for quantitatively evaluating the importance of species and predicting the most important targets for conservation practice (e.g. keystone species, Paine, 1966; Power et al., 1996). Since species are involved in complex interaction networks in natural communities, one major aspect of importance is how the effects starting from a focal...
species reach the others, both directly and indirectly (Menge, 1995). Technically this means that functionally important species could be the ones in central positions in the interaction network. We might expect more central species to play relatively more important roles in the community either through many direct links or indirectly—mediated by only a few neighbours (Allesina and Bodini, 2004). There are several network indices for quantifying centrality and they estimate quite varied importance ranks for different species (Jordán et al., 2007). It is difficult to test the predictions of these network analytical techniques because experiments, time series analyses and microcosm studies are all problematic. Simulations using whole food web trophodynamic models might represent a useful basis for evaluating these network structural indices. These models include quantitative estimates of biomasses, flows, trophic and non-trophic mediation and functional dynamic relationships in addition to structural information about networks of interactions, and they are among the most useful and frequently applied models of ecosystems ecology (Christensen, 1998; Christensen and Walters, 2004). Moreover, indices for ranking relative functional importance based on these mass-balance modelling simulations are also emerging (Mills et al., 1993; Okey, 2004; Libralato et al., 2006). Despite the different meaning carried by each functional importance measure, their comparison with structural indices may provide fruitful insights. Until now, the comparison of structural and functional indices mainly regarded “ecosystem level” indicators (Finn, 1976; Christensen, 1995). Findings showed higher effects of food web representation (trophic aggregation) on structural indices than on functional ones (see for example, the comparison between the Connectance Index and the System Omnivory Index; Libralato, 2008). In this paper we calculate 13 structural and 5 functional importance indices for the trophic components of an ecosystem model and examine their relationships. If statistically significant correlations emerge, we may be able to find the most efficient approaches for ranking the relative importance of species or functional groups in a system, or at least gain insight into the specific usefulness of each index.

2. Materials and methods

2.1. Data

We further analyse a previously well studied ecosystem model of Prince William Sound, Alaska (Okey and Pauly, 1999; Okey, 2004; Okey and Wright, 2004). The trophic network contains 51 components, including 3 nonliving groups (Appendix A). Trophic links are weighted: flows are in tonnes wet weight km$^{-2}$ year$^{-1}$ (Figure 1 and Appendix B).

2.2. Quantifying importance

Mass-balance trophic models (Ecopath with Ecosim, Christensen and Walters, 2004) have been used to estimate functional importance either by simulating the removal of components from the interaction web (Okey, 2004; Okey et al., 2004; Libralato et al., 2006) or by examining network attributes such as mixed trophic impact matrices (Hannon, 1973; Ulanowicz and Puccia, 1990; Libralato et al., 2006).

We calculated five functional importance indices (Table 1): community importance (CI – Mills et al., 1993; Okey, 2004), community longevity support (CLS), interaction strength index (ISI), and keystoneness index (KI) (Okey, 2004) and another keystoneness index (KS), derived from the biomass-scaled measure of overall effect (Libralato et al., 2006). All of these indices quantify the importance of species in communities. Still, there are important differences between them: besides the original index of CI (community impact related to
Table 2 – Spearman rank correlation coefficients between 13 structural and 5 functional importance indices

<table>
<thead>
<tr>
<th></th>
<th>D</th>
<th>BC</th>
<th>wD</th>
<th>uBC</th>
<th>CC</th>
<th>TI1</th>
<th>WI1</th>
<th>TI2</th>
<th>WI2</th>
<th>TI3</th>
<th>WI3</th>
<th>TI4</th>
<th>WI4</th>
<th>Mean</th>
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</thead>
<tbody>
<tr>
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<td>0.16</td>
<td>0.28</td>
<td>0.22</td>
<td>0.17</td>
<td>0.24</td>
<td>0.28</td>
<td>0.21</td>
<td>0.29</td>
<td>0.21</td>
<td>0.30</td>
<td>0.18</td>
<td>0.30</td>
<td>0.23</td>
</tr>
<tr>
<td>CLS</td>
<td>0.02</td>
<td>−0.01</td>
<td>0.16</td>
<td>0.06</td>
<td>0.06</td>
<td>0.04</td>
<td>0.20</td>
<td>0.05</td>
<td>0.20</td>
<td>0.06</td>
<td>0.19</td>
<td>0.06</td>
<td>0.18</td>
<td>0.10</td>
</tr>
<tr>
<td>ISI</td>
<td>0.00</td>
<td>−0.08</td>
<td>0.44</td>
<td>0.08</td>
<td>0.01</td>
<td>0.07</td>
<td>0.55</td>
<td>0.04</td>
<td>0.54</td>
<td>0.03</td>
<td>0.53</td>
<td>0.00</td>
<td>0.49</td>
<td>0.22</td>
</tr>
<tr>
<td>KI</td>
<td>−0.11</td>
<td>−0.18</td>
<td>−0.75</td>
<td>−0.09</td>
<td>−0.06</td>
<td>−0.15</td>
<td>−0.54</td>
<td>−0.13</td>
<td>−0.63</td>
<td>−0.12</td>
<td>−0.66</td>
<td>−0.09</td>
<td>−0.71</td>
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<tr>
<td>KS</td>
<td>0.08</td>
<td>0.05</td>
<td>0.21</td>
<td>0.21</td>
<td>0.08</td>
<td>0.16</td>
<td>0.52</td>
<td>0.13</td>
<td>0.49</td>
<td>0.12</td>
<td>0.47</td>
<td>0.10</td>
<td>0.42</td>
<td>0.23</td>
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<tr>
<td>Mean</td>
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<td>0.09</td>
<td>0.37</td>
<td>0.13</td>
<td>0.08</td>
<td>0.13</td>
<td>0.42</td>
<td>0.11</td>
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<td>0.11</td>
<td>0.43</td>
<td>0.09</td>
<td>0.42</td>
<td></td>
</tr>
</tbody>
</table>

Bold is significant (>0.29 and <−0.29). “Mean” is average of absolute values.

Table 2 – Spearman rank correlation coefficients between 13 structural and 5 functional importance indices

3. Results

Different importance indices, whether structural or functional, give different ranks of importance for the species of the same food web (Fig. 1). Note, for example, that the importance rank of Porpoises (#7) ranges from 37 (BC) to 24 (CLS) to 3 (D and KI). Beyond following the ranks of a particular species, we were interested in the relationships between the studied structural and functional indices (Table 2). The overall score of each structural index (bottom row in Table 2) is the average of the absolute value of the Spearman correlation coefficients between the importance ranks of the given structural index and each of the functional ones. Conversely, the overall score of each functional index (right column in Table 2) is the average of the absolute value of the Spearman correlation coefficients between the importance ranks of the given functional index and each of the structural ones. By calculating the average values of the correlation coefficients, we have considered all the indices of the opposite type as equally important in each case.

Table 2 shows that no significant correlation was revealed between binary network indices (D, BC, uBC, CC, TI) and any of the functional indices. Direction of links is even less important; our directed index (BC) correlates with none of the functional indices. The direct index (D) is also a very weak predictor of species importance if our functional measures are realistic, indicating that consideration of indirect effects is essential. Indeed, indirect indices correlated with functional indices best out of all the structural indices; short indirect effects (TI) are the best correlates in the unweighted case, while interaction chain length matters little in the weighted case (WI). Weighted structural indices were most correlated with the functional attributes. KI was the best correlating functional index in terms of significant correlations with structural attributes; its correlations were significant (−0.75, −0.54) with weighted direct and short indirect measures of structure, but also particularly with weighted long indirect measures (−0.63, −0.66, −0.71). KS correlated significantly with indirect weighted structural measures (0.52, 0.49, 0.47, 0.42). CI correlated significantly with the longer, weighted structural indices (WI). ISI was significantly correlated with all the weighted direct and indirect structural measures, though it was most closely correlated with the indirect measures. Significant correlations were not detected between CLS and any of the structural indices. According to Table 2, the best correlating functional and structural indices are KI and WI (0.32, 0.42), respectively. If we consider only unweighted indices of community structure, overall correlation for uBC and TI (0.13 for both) are the highest. The strongest correlation is between KI and wD (−0.75). Table 3 shows that the structural indices used show significant (and always negative) rank correlation with fractional trophic level if and only if they are weighted (wD, WI). Functional indices may show positive (KI), negative (CLS) or no significant (CI, ISI, KS) correlation.

4. Discussion

The initial motivation of this exercise was to evaluate how structural indices might correlate with the importance rank of species estimated using some functional indices of species importance. Structural features of a system influence its dynamical behaviour, so the correlation of structure and function is not surprising: the real question was exactly which structural properties of a given network node make it functionally important in the system. The converse question also emerged during this exercise; which of the functional indices were most useful indicators of structural properties. Our primary finding is that unweighted indices of the interaction web structure of a community show no correlation with any of the

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Fig. 1 – The Prince William Sound food web of 48 living components (#1–#48) and 3 nonliving components (#49–#51). Names of components are given in Appendix A. Link width is proportional to interaction strength. Radius of nodes is proportional to particular importance indices (larger nodes represent more important species): (a) degree (D); (b) weighted topological importance index for two steps (WI²); (c) community longevity support (CLS); (d) keystone index (KI). In (e) radius is proportional to trophic level (TL): smallest nodes are producers, largest nodes are top predators. Drawn using UCINET (Borgatti et al., 2002).
were not detected between the CLS and any of the structural indices.

The present contribution highlights the role of network analysis in understanding how to link species to communities and how to quantify their relative importance. Structural and functional indices are more understandable and applicable if we can clarify their relationships and assess their strengths and weaknesses. This line of research is useful to better understand large networks where the use of dynamical analyses is sometimes limited. From a structural point of view, results of structural network analysis are useful only if they can be tested and verified as reliable in the context of functional approaches. Perhaps the combination of the two approaches reveals the most important mechanisms driving dynamics. Indirect effects, for example, play a large role in governing ecosystem dynamics. Observing only structure without taking into account the magnitude of flows was less informative. The present exercise provides a simple framework for evaluating these indices.

Acknowledgements

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Appendix A. Supplementary data


Table 3 – Spearman rank correlation coefficients between 18 importance indices (topological and functional) and trophic level (trophic height)

| Index | D   | BC  | wD  | uBC | CC  | TI1 | WI1 | TI2 | WI2 | TI3 | WI3 | TI4 | WI4 | CI  | CLS | ISI | KI  | KS  | wD  | BC  |
|-------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
|       | 0.21| 0.16| -0.85| 0.15| 0.21| 0.12| -0.41| 0.15| -0.52| 0.16| -0.56| 0.20| -0.63| -0.26| -0.32| -0.15| 0.66| 0.09| -0.85| 0.16|
| Bold is significant.

functional indices. This is especially true of degree (D), which is the most local (i.e. direct) unweighted index. This is an important message for network analysts focusing on degree in searching for key nodes in many kinds of networks (Albert et al., 2000), and is especially important for ecologists who would otherwise underestimate the importance of weighting links in food webs. As for the weighted structural indices, we found that indices that include indirect interactions correlate better with functional indices than those that include only direct ones. Empirical tests (Wootton, 1994; Menge, 1995) and theoretical studies (Higashi and Patten, 1989; Fath and Patten, 1999; Schramski et al., 2007) already highlighted the importance of indirect effects in communities, and our contribution agrees with their findings. This result is valuable for field and theoretical researchers, but also for resource managers and conservation professionals involved in debates about the role of indirect effects of human activities and management actions. No correlation was revealed between D and ISI (but see Bascompte et al., 2006). The negative correlation between KI and the weighted structural indices may be related to top-down effects emphasised by Ecosim models (Watters et al., 2003; Maury and Lehodey, 2005): species of high WI-values are more frequent at lower trophic levels and expected to have mostly bottom-up effects. The relatively strong positive correlation between KI and TL supports the traditional notion that keystone species tend to be high trophic level species. This manifests because the KI reflects that keystone species, by definition (sensu Power et al., 1996), have low biomasses (or abundances) and because species at the top of food webs usually have low biomasses (due to constraints of trophic transfer efficiencies, see Lindeman, 1942).

Community longevity support is more of a measure of the contribution of a species or functional group toward the support of community stability or resilience, directly or indirectly, rather than a measure of interaction strength or keystoneness. It is therefore not surprising that significant correlations


