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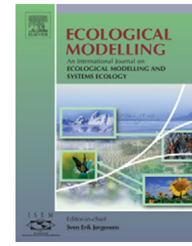

Short communication

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

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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

Table 1 – The functional and structural indices of community importance that are evaluated here

Index	Code	Citation
Functional		
Community importance	CI	Mills et al., 1993; Okey, 2004
Interaction strength index (trophic)	ISI	Okey, 2004
Keystoneness index (dynamic)	KI	
Community longevity support	CLS	
Keystoneness index (network)	KS	Libralato et al., 2006
Structural		
Degree (undirected, unweighted)	D	Wassermann and Faust, 1994
Weighted degree (undirected)	wD	
Betweenness centrality (directed, unweighted)	BC	
Undirected betweenness centrality (unweighted)	uBC	
Closeness centrality (undirected, unweighted)	CC	
Topological importance, max step number = 1	TI	Jordán et al., 2003
Topological importance, max step number = 2	T2	
Topological importance, max step number = 3	T3	
Topological importance, max step number = 8	T8	
Weighted topological importance, max step number = 1	W1	
Weighted topological importance, max step number = 2	W2	
Weighted topological importance, max step number = 3	W3	
Weighted topological importance, max step number = 8	W8	
Trophic level (fractional)	TL	Odum and Heald, 1975