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Topological keystone species in ecological interaction networks: Considering link quality and non-trophic effects

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ABSTRACT

There is increasing evidence that non-trophic interspecific interactions play an at least as important role in community dynamics as trophic relationships. More and more studies on pollination, mutualism and facilitation are published but these effects are interpreted more like alternative explanations than being synthesized with results of trophic analyses. Here, we construct and analyze the interaction web of the well-studied Chesapeake Bay mesohaline ecosystem. By interaction web we mean a food web completed by a carefully selected set of non-trophic links. We quantify the interaction structure of the web and the positional importance of nodes by different network indices. We perform the suitable analyses for different variants of the network: combinations of direction, sign and weights, as well as considering also non-trophic links result in a set of webs of different information content. We also create a semi-quantitative variant of the web, in which only the order of magnitude of the mass flows are considered. The appropriate network indices for each web variant are calculated and compared. Finally, however our paper is primarily of methodological nature, we present some findings about the fish community of the Bay. We suggest that the multiple techniques presented here, adapted even from social network analysis, can help field conservation efforts by suggesting optimal preferences for data collection.

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1. Introduction

The construction and analysis of food webs is a traditional approach to understanding the structure and functioning of ecological systems. Food webs depict the collection of pairwise prey–predator interactions between species or their suitably defined groups (Pimm, 1982, 1991; Pimm et al., 1991). Although the information food web analysis provides is probably essential, notorious methodological problems weaken the predictions appearing during all of the three basic phases of the work (sampling during field data collection, right aggregation process during network construction, choosing sensible graph properties during network analysis).

Apart of the methodological problems of how to construct a network showing who eats whom, a number of additional issues are frequently claimed for: (1) trophic interactions are very important but other pairwise (direct) non-trophic interspecific interaction types are also of high importance (e.g. pollination: Memmott, 1999; mutualism: Bronstein, 2001; facilitation: Turner, 1983; Callaway, 1995; see also Kareiva and Bertness, 1997 and subsequent papers), (2) interactions could be characterized not only binarily (yes or no) but also by their strength, sign and direction. The direction and sign structure of a direct trophic interaction (a negative feeding effect in top–down direction and a positive food supply in bottom–up direction) is evident but still can be complemented by informa-

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tion on the magnitude of energy flows (strength). Non-trophic interactions are variable also in sign (e.g. the effects in both directions are positive in a mutualism) and direction (e.g. facilitation is a one-way positive effect with no response). Thus, a complex interaction network, defined as a general extension of a food web (but see Paine, 1980 for a different meaning), contains trophic and non-trophic, directed, signed and weighted effects between pairs of species. The combinations of co-occurring pairwise effects give rise to indirect interaction modules (e.g. trophic cascade or apparent competition; see Menge, 1995, for a classification) embedded in community-wide interaction networks. Indirect chain effects do spread in both bottom–up and top–down directions through trophic links and, as a result, may act also horizontally (Wootton, 1994; Menge, 1995; Abrams et al., 1996). If non-trophic interactions are also considered, the network may also have direct horizontal links.

The role non-trophic interactions have in organizing a community has traditionally been considered more local, and their analysis mostly focused on species pairs. The current need for taking also non-trophic effects into account while thinking within the network perspective is parallel with the recognition of their less local nature (e.g. diffuse mutualism; Jordano, 1987; Bronstein, 2001). We already have plant–pollinator (Jordano, 1987) and competitive networks, even with weighted interactions (Paine, 1984). However, to our knowledge, there is no community-wide interaction network showing a variety of both trophic and non-trophic links between species. An evident problem with weighting such a network is that there is no common currency, i.e. it is not easy to define the common denominator of material transfers and a facilitation effect (it is no problem in case of binary webs). Another problem is that mass-balance can comfortably be assumed in case of trophic flow networks but there are lots of problems with assuming "interaction balance". This might be one reason for studying more intensively the trophic-dynamic aspect (Lindeman, 1942) in the past. We also have to note the problem of aggregation. It is frequently the case that trophic effects are less specific, so the aggregation process seriously affects how the two kinds of interactions will complement each other within a single graph (also, different interactions might suggest different aggregation procedures). Nevertheless, the dual nature of interaction networks could be helpful in better understanding, for example, the community-wide answers to stress and disturbance (Bertness and Shumway, 1993). An ultimate question to be addressed is whether to take into account non-trophic effects or to measure interaction strengths in a trophic network, if we want to optimize our efforts in improving a traditional, binary food web.

Both ecological research and conservation practice claim for quantitative, a priori approaches to characterizing the importance of different species in ecosystems. Keystone species have been defined variously and a number of studies report on their roles but their objective description is still immature. One of the very few quantitative approaches is their characterization based on the position they occupy within food webs: topological keystone species have been defined as being in key positions in trophic interaction networks (Jordán et al., 1999; Solé and Montoya, 2001; Montoya and Solé, 2002; Jordán and Scheuring, 2002). New graph theoretical techniques have also been suggested for their finer characterization (Allesina and Bodini, 2004; Jordán et al., 2006). Here, we wish to extend these techniques to directed, signed and weighted interaction networks including also non-trophic links. We have to note that the "keystone" term is strictly used only for in "importance/biomass" context (Power et al., 1996), thus we should not use the term in the strictest sense. The topological importance indices could be easily combined with biomass data but, in this paper, our primary task is to compare different variants of the same web (and outline the methodological background of this problem), and our intention is to keep everything else as simple as possible.

Our primary concern is to develop the methodology of ecological network analysis, in other words, we are more interested in how to analyze such an "ideal" network than in how to construct it. The aims of our present paper are: (1) to construct an interaction network as a combination of a published food web and a collection of published data on non-trophic effects, (2) to construct the variants of this web according to different but only sensible combinations of link direction, strength and sign, as well as whether including non-trophic links, (3) to apply several graph theoretical indices for (3) mapping the direct and indirect interaction structure of these variants, and (4) determining the topological keystone species in the networks, and finally (5) to compare the network variants from the perspective of the fish community. We present results concerning the organization of the studied community but emphasize that this is more like illustration, since our paper is primarily of methodological nature.

2. Data base

Energy flows between the trophic components of the Chesapeake Bay mesohaline community are well known (Baird and Ulanowicz, 1989; see Table 1 for carbon flow data and Table 2 for trophic groups) and have been analyzed extensively (see Baird et al., 1995 for nitrogen and Ulanowicz and Baird, 1999 for limiting nutrients). Since the Bay is well studied, there is a lot of information, even if more sporadic, about the functionally important and typical non-trophic effects between species inhabiting the Bay. We have collected a large number of non-trophic interspecific effects and selected the seemingly most characteristic and unambiguous links in order to complement our food web such that an interaction network can be constructed (Fig. 1). Table 3 shows the origin of non-trophic links considered in our study. Of course, our selection is subjective, but not intentionally biased, and we emphasize that the analysis of this interaction web is basically an illustration of our methodological investigation.

3. Methods

3.1. *Network construction*

Our task is to complete a food web by considering also the seemingly most important non-trophic relationships between

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