Additivity of pairwise perturbations in food webs: Topological effects

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ABSTRACT

Food webs dynamically react to perturbations and it is an open question how additive are the effects of single-species perturbations. Network structure may have topological constraints on additivity and this influences community response. Better understanding the relationships between single-species and multi-species perturbations can be useful for systems-based conservation management. Here we study a single model food web by (1) characterising the positional importance of its nodes, (2) building a dynamical network simulation model and performing sensitivity analysis on it, (3) determining community response to each possible single-species perturbation, (4) determining community response to each possible pairwise species perturbation and (5) quantifying the additivity of effects for particular types of species pairs. We found that perturbing pairs of species that are either competitors or have high net status values in the network is less additive: their combined effect is dampened.

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1. Introduction

The complexity of ecosystems makes it very hard to predict the effects of various perturbations, in terms of both sign and size (Eklöf and Ebenman, 2006; Yodzis, 1988). It is even more difficult in case of multiple perturbations. In the context of a dynamical food web, it is a basic question how individual single-species perturbations are related, how additive are their effects in terms of community response.

It is an old problem to understand the effects of species deletions (perturbations) in food webs (Allesina and Bodini, 2004; Allesina et al., 2006; Pimm, 1980; Quince et al., 2005). Recent developments in network ecology generated a wide interest in the link between population dynamics and network position of nodes. Several topological characteristics have been proposed to be a useful proxy for understanding and predicting dynamics (Estrada, 2007; Jordán, 2009; Jordán et al., 2003; Pocock et al., 2011) with the help of dynamical models. Following Pimm (1980), a number of studies focused on better understanding this aspect of the pattern to process issue in both toy models (Jordán et al., 2002, 2003; Móréh et al., 2009) and realistically parameterized system models (Jordán et al., 2008; Livi et al., 2011). Importantly, network analysis cannot directly solve the problems of multi-species fisheries but it

can quantify the mathematical (topological) constraints on ecosystem dynamics. In order to separately analyse topological effects on the additivity of single-species perturbations in food webs, simple models should be used with the minimal number of factors complicating the evaluation of the structure to dynamics link.

In this paper, we present a dynamical sensitivity analysis of a model food web. Our goals are (1) to perform a topological analysis of the food web and determine key nodes (central trophic groups), (2) to build and run a simulation model for the same system, in order to perform sensitivity analysis, (3) to determine the community response generated by single-species perturbations, (4) to perform pairwise perturbations with the same conditions and (5) to compare the results of single-species and multi-species perturbations and determine the level of additivity. The key aim is to determine the topological position of species j and k such that their parallel perturbation has dampened effects on the ecosystem.

2. Data

We analyse a single food web, containing three producers (species #1, #2 and #8), one top predator (species #15) and 11 intermediate species (Fig. 1). The network is of intermediate size ($N = 15$ living trophic groups), so it is still manageable for dynamical simulations (using several population dynamical parameters) but already interesting enough for topological studies (focusing only on food web structure). The topology of the network is arbitrary but a similar study of 100 randomly generated, comparable networks is already in progress.
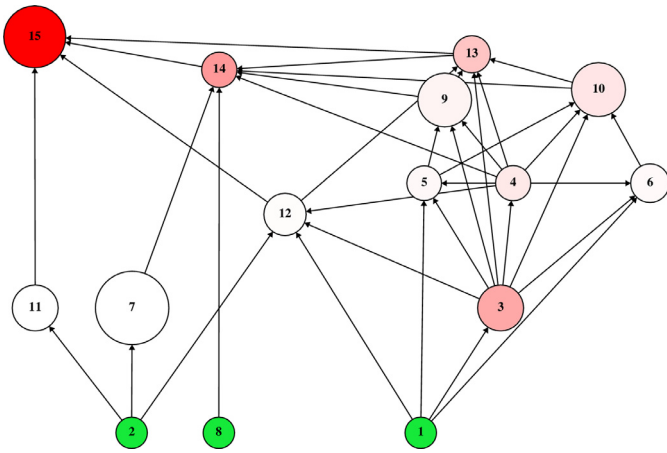
Fig. 1. The studied food web. Arrows show carbon flows from resources to consumers. Producers (species #1, #2 and #8) are marked green, these are not perturbed in our study. Their size is arbitrary but the size of other nodes is proportional to the community response generated by their single-species perturbations (CR_j; species #7 is the largest one). The red shading of nodes is proportional to their indirect keystone index (K_{indir}; species #15 is of the deepest red colour). See Table 1 for numerical results. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

3. Methods

3.1. Network structure

In order to quantify the structural importance of network nodes, first, we consider the food web as an undirected network where effects can spread in any direction (from prey to predator and from predator to prey). These are clearly not only energy flows but trophic interactions in a broader sense. A range of network indices can be used for quantifying the positional importance of nodes in undirected networks (note that some of these indices have versions adapted to directed networks too). Since we still do not understand the structure to dynamics relationship, it makes sense to test several structural indices and clarifying their relationship with dynamics. The structural indices are clearly not independent of each other but we study relationships between structural versus simulated metrics and investigate which structural indices are correlating best with simulated non-additive effects.

3.2. Degree and weighted degree (D, wD)

The most local network centrality index is the *degree* of a node (D). This is the number of other nodes connected directly to it. In a food web, the degree of a node i (D_i) is the sum of its preys and predators. In the case of weighted networks, the weighted degree of node i (wD_i) equals the sum of weights on links adjacent to node i (Wassermann and Faust, 1994). Degree and weighted degree can be calculated by the UCINET programme (Borgatti et al., 2002).

3.3. Betweenness centrality (BC)

This measure of positional importance quantifies how frequently a node i is on the shortest path between every pair of nodes j and k. This index is called "betweenness centrality" (BC), used routinely in social network analysis (Wassermann and Faust, 1994) and we calculated it using the UCINET programme (Borgatti et al., 2002). The standardised index for node i (BC_i) is:

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

where $i \neq j$ and k. g_{jk} is the number of equally shortest paths between nodes j and k, and $g_{jk}(i)$ is the number of these shortest paths to which node i is incident (of course, g_{jk} may equal one). The denominator is twice the number of pairs of nodes without node i. This index thus measures how central a node is, in the sense of being incident to many shortest paths in the network. If BC_i is large for trophic group i, it means that deleting this group will more affect many rapidly spreading effects in the web.

3.4. Closeness centrality (CC)

Closeness centrality (CC) is a measure quantifying how short are the minimal paths from a given node to all others (Wassermann and Faust, 1994) and is again calculated using UCINET (Borgatti et al., 2002). The standardised index for a node i (CC_i) is:

$$CC_i = \frac{N-1}{\sum_{j=1}^{N} d_{ij}} \tag{2}$$

where $i \neq j$ and d_{ij} is the length of the shortest path between nodes i and j in the network. This index thus measures how close a node is to others. The larger CC_i is for trophic group i, the more directly deleting this group will affect the majority of other groups.

3.5. Positional importance based on indirect chain effects (TI^n and WI^n)

We can assume a network with undirected links where trophic effects can spread in many directions without bias. Indirect effects do spread in both bottom-up and top-down directions through trophic links and, as a result, horizontally, too. We first consider an unweighted network. Here, we define $a_{n,ij}$ as the effect of j on i when i can be reached from j in n steps. The simplest mode of calculating $a_{n,ij}$ is when $n=1$ (i.e. the effect of j on i in 1 step): $a_{1,ij} = 1/D_i$, where D_i is the degree of node i (i.e. the number of its direct neighbours including both prey and predator species). We assume that indirect chain effects are multiplicative and additive. For instance, we wish to determine the effect of j on i in 2 steps, and there are two such 2-step pathways from j to i: one is through k and the other is through h. The effects of j on i through k is defined as the product of two direct effects (i.e. $a_{1,kj} \times a_{1,ik}$), this is why multiplicative. Similarly, the effect of j on i through h equals to $a_{1,hj,1} \times a_{1,ih}$. To determine the 2-step effect of j on i ($a_{2,ij}$), we simply sum up those two individual 2-step effects (i.e. $a_{2,ij} = a_{1,kj} \times a_{1,ik} + a_{1,hj} \times a_{1,ih}$) in an additive way (Jordán et al., 2003).

When the effect of step n is considered, we define the effect received by species i from all species in the same network as:

$$\varphi_{n,i} = \sum_{j=1}^{N} a_{n,ji} \tag{3}$$

which is equal to 1 (i.e. each species is affected by the same unit effect.). Furthermore, we define the n-step effect originated from a species i as:

$$\sigma_{n,i} = \sum_{j=1}^{N} a_{n,ji} \tag{4}$$

which may vary among different species (i.e. effects originated from different species may be different). Here, we define the topological importance of species i when effects "up to" n step are considered as:

$$TI_i^n = \frac{\sum_{m=1}^{n} \sigma_{m,i}}{n} = \frac{\sum_{m=1}^{n} \sum_{j=1}^{N} a_{m,ji}}{n} \tag{5}$$