Food web dynamics in trophic hierarchies

Anett Endrédi[a], Vera Senánszky[a], Simone Libralato[b], Ferenc Jordán[a,c,d,e,*]

[a] Danube Research Institute, MTA Centre for Ecological Research, Budapest, Hungary
[b] Istituto Nazionale di Oceanografia e di Geofisica Sperimentale, Trieste, Italy
[c] Evolutionary Systems Research Group, MTA Centre for Ecological Research, Budapest, Hungary
[d] Wissenschaftskolleg zu Berlin, Berlin, Germany
[e] Stazione Zoologica Anton Dohrn, Napoli, Italy

ARTICLE INFO

ABSTRACT

Using network analysis for making predictions about food web dynamics is one of the major challenges in systems ecology. Since there are several notoriously difficult methodological problems with food webs, only a comparative perspective can help. We study a standard database for trophic flow networks and analyse the correlation between structure and dynamics in strictly hierarchical food webs (directed acyclic graphs, DAGs). To characterize the structural information about trophic nodes in food webs (their positional importance), we use 8 topological indices that had been developed for quantifying DAGs (3 indices related to status, s, and 5 indices related to the keystone index, K). For dynamics, we use the KS (keystoneness) index that quantifies the importance of trophic nodes in the food web, considering also carbon flows and biomass. We statistically compare the structural and dynamical importance of each network node and find that the K indices are much better predictors of KS than the s indices. Based on these results, we suggest that functional studies have to consider both bottom-up and top-down effects as well as indirect effects that are dampening with distance. We suggest that this kind of study can be helpful to better understand the relevance and applicability of network analysis, an otherwise popular research methodology with continuously increasing predictive power.

© 2017 Published by Elsevier B.V.

1. Introduction

Food web models are helpful to integrate and represent a large amount of ecological data. They are potentially applicable in many areas from system-based conservation to sustainable fisheries management (Belgrano, 2005). Yet, being data demanding, their applicability critically depends on availability of large ecological datasets (e.g., Link et al., 2008), while their complexity usually result in their low predictive power (e.g., Harvey et al., 2003). Nevertheless, food web models represent tools increasingly used for integrating ecological data and quantifying ecosystem properties (Villasante et al., 2016; Tam et al., 2017).

In ecological network analysis, trophic links can be considered as either directed or undirected. If links are considered directed (and typically also weighted), the approach focuses on material flows from producers towards top predators and helps to understand, for example, the community biomagnification effects of pollution at

the basis of the food web (e.g. Kelly et al., 2007). If links are considered undirected, the approach is broader, also taking into account counter effects like trophic cascades (i.e. A affecting C by A eating B eating C; that spreads in top-down direction) or exploitative competition (i.e. A affecting B by A and B feeding on C; that spreads horizontally in the food web). This latter approach allows to address general issues like identifying keystone species (Paine, 1966; Mills et al., 1993) in food webs (e.g. Jordán, 2009).

Even if link direction is considered, loops may appear in food webs (A eats B eats C eats A). These directed loops represent challenges from the viewpoint of biological interpretation of food web data (e.g. the frequency of loops may depend on aggregation level, see also Fenchel 1988), it may cause complications from the viewpoint of dynamical consequences (by having demographic and life-history effects, e.g. Polis and Strong, 1996) and methodological difficulties from the viewpoint of network analysis (some methods simply cannot be used for networks containing loops, e.g. Jordán et al., 1999). If there is no directed loop in a food web (i.e. it is a directed acyclic graph, DAG), methods developed for the analysis of hierarchical networks can be applied. Methods for analysing strictly hierarchical food webs are traditionally rich, focusing on stability (probability of reliability, MacArthur, 1955), importance of species

---

(status, Harary, 1961), reliable networks (flow reliability, Jordán and Molnár, 1999), critical positions (dominator trees, Allesina and Bodini, 2004; Allesina et al., 2006), secondary extinction (keystone species, Quince et al., 2005) and trophic height (effective trophic level, Scotti et al., 2009). We may note that the attempt to quantify the relative importance of species in ecological communities (Harary, 1961), based on their network position was a pioneering effort not followed by biologists for decades (Mills et al., 1993); and even the qualitative discussion of importance came only years later (see Paine, 1966).

It is still an open question, how the typical structure of food web hierarchies emerge and how it is related to the functioning of ecological systems and their sensitivity to natural and anthropogenic sources of disturbance. After decades of research, how network topology (structure) is exactly related to dynamics (functioning), for instance, is not completely unravelled. A large body of work relates biodiversity to ecosystem functioning, this latter usually synthetized through the changes in the primary productivity (Loreau et al., 2001). Other works synthesize ecosystem functioning thorugh ecosystem-wide indicators (Link et al., 2015). However, much less is known on the contribution of food web components to the functioning of the ecosystem (e.g., D'Alelio et al., 2016), in particular to its complex dynamics. Thus, although the "structure to function" problem can be addressed at the level of the whole ecosystem ("global" perspective; Loreau et al., 2001), here we are interested at the "local" perspective, i.e., the contribution by species and/or functional groups to ecosystem functioning. Thus we study the relationship between the network position and the dynamical behaviour of individual network nodes in a range of high-quality network models.

We use only directed acyclic food webs developed using Ecopath with Ecosim (EwE, Christensen and Walters, 2004), and compare the topological properties of their nodes to their dynamics by applying eight hierarchical centrality indices (Harary, 1961; Jordán et al., 1999) and one index that can be considered as a good proxy for dynamical effects (Libralato et al., 2006a). The comparative analysis of sets of food webs is of high importance from a network analysis point of view (single networks can be highly sensitive to the methodology of network construction, while the differences between methodologically uniform, comparable networks may be more informative). Thus we perform statistical analyses on how structure (synthesized by topological indices) can predict functioning (estimated using a measure of dynamical effects) using a set of food web models. The statistical correlations performed may take us closer to better understanding the structure to dynamics relationship at the level of individual network nodes (see Jordán, 2009).

2. Data and methods

Before performing network analysis, we modified the studied trophic networks in two ways. First, we deleted the non-living components (e.g. detritus). Second, we filled the main diagonal of the trophic matrices by zeros (i.e. cannibalistic self-loops are not considered). Both modifications show that we focused less on energy pathways and more on interspecific interactions among living organisms (following the approach of, for example, MacArthur, 1955). Even having done so, networks might contain directed cycles but we have selected only the ones without them (DAGs).

We characterised the importance of nodes in food webs by topological (2.1.) and dynamical (2.2.) indices. While the former consider only "who eats whom" relations in binary networks, the latter consider also biomass and community response values. The key question is the statistical relationships (2.3.) between these

two groups. We only focused on directed, acyclic food webs, so we studied trophic hierarchies, a subset of trophic networks.

2.1. Topological analyses

2.1.1. Status index and its components (s, s', Δs)

In a hierarchy, it is clear which nodes are at the top and which nodes are at the bottom of the network. Yet, it is a matter of long interest how to quantify the relative positional importance of different nodes. The status index is one of the tools for this: it was introduced in sociometry (for quantifying the prestige of a certain person, Harary, 1959) and it was applied immediately in ecology (for quantifying the most important species in a forest community, Harary, 1961). The status of node i (s_i) is the sum of its distances to all other j nodes in the network. Its contrastatus (s'_i) is calculated in the same way —but after reversing the sign of all links in the graph. The net status of this node i (Δs_i) is their difference:

$$\Delta s_i = s_i - s'_i \qquad (1)$$

These indices can be calculated by the CoSBi Graph software (Valentini and Jordán, 2010).

2.1.2. Keystone index and its components (K, K_{bu}, K_{td}, K_{dir}, K_{indir})

The keystone index (K) (Jordán et al., 1999) is derived from the status index. Two modifications of the s index make the K index more adapted to ecology. First, according to the s index, the influence of node i on node j is larger with a larger d_{ij} distance in the network (as it counts the sum of distance values). On the contrary, distance makes effects smaller in the calculations according to the K index (as units effects are distributed, step by step, among more and more network nodes). Second, according to the s index, the bottom-up network neighbourhood weakens the top-down network neighbourhood (as it is calculated as the effect on inferiors of node i minus the effect by superiors on node i). On the contrary, K calculates the sum of effects in the two directions, i.e. the richness of the vertical network neighbourhood in the network. The keystone index of a species i (K_i) is defined as:

$$K_i = K_{bu,i} + K_{td,i} = K_{dir,i} + K_{indir,i} = \sum_{c=1}^{n} \frac{1}{d_c}(1 + K_{bc}) + \sum_{e=1}^{m} \frac{1}{f_e}(1 + K_{te}), \qquad (2)$$

where n is the number of predators eating species i, d_c is the number of prey species of its cth predator and K_{bc} is the bottom-up keystone index of the cth 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. For node i, the first sum in Eq. (2) (i.e. $\sum 1/d_c(1 + K_{bc})$) quantifies the bottom-up effect ($K_{bu,i}$) while the second sum (i.e. $\sum 1/f_e(1 + K_{te})$) quantifies the top-down effect ($K_{td,i}$). In Eq. (2), terms including K_{bc} and K_{te} (i.e. $\sum K_{bc}/d_c + \sum K_{te}/f_e$) refer to indirect effects for node i ($K_{indir,i}$), while terms not containing K_{bc} and K_{te} (i.e. $\sum 1/d_c + \sum 1/f_e$) refer to direct ones ($K_{dir,i}$). Both $K_{bu,i} + K_{td,i}$ and $K_{indir,i} + K_{dir,i}$ equals K_i, so the K index can be separated either into a bottom-up and a top-down component, or into a direct and an indirect component. The degree of a node in a network (D) characterises only the number of its connected (neighbour) points, while the keystone index gives information also on how these neighbours are connected to *their neighbours*. The K index, therefore, emphasises vertical over horizontal interactions (*e.g.* trophic cascades as opposed to apparent competition), but also characterises positional importance by separating indirect from direct, as well as bottom-up from top-down effects in food webs (Jordán, 2001). Its conceptual counterpart is the trophic field of a species and has been applied several times in network analysis (e.g. Ortiz and Wolff 2002; Quince et al., 2005). Its important feature is the sensitivity to both distance and degree: it