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How interaction strength affects the role of functional and redundant connections in food webs

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ABSTRACT

Links in food webs can be classified as functional, which affect robustness, and redundant, which do not affect robustness. We explore whether this topologically based distinction may still be informative when interaction strength is considered. In 81 weighted food webs we identified functional and redundant links by exploiting the method of generalized dominators, and tested whether the two groups could be patterned according to link strength.

Overall, redundant connections are weaker than functional links. However this pattern does not hold for every food web. Also, the difference in strength between functional and redundant links seems to depend on food web topology. In fact the systems in which redundant connections are significantly weaker than functional ones show greater connectance than systems in which the difference in strength between the two groups is not significant.

We observed that redundant connections are fundamental in the formation of omnivory modules that have been described as being crucial for the stability/persistence of food webs. Although stability can be promoted by the specific arrangement of links magnitude within these modules, it does not necessarily imply that redundant links have to be weaker than functional connections at the whole web scale.

1. Introduction

The vast array of feeding interactions that make up a food web is an indicator of the complexity and organization of the community. Such complexity has been long discussed in its role of stabilizing factor (McCann and Hastings, 1997; Neutel et al., 2007) but also as a factor of risk. This latter concerns the possibility that external perturbations propagate through the various pathways and make impacts spreading well beyond the entry point of the perturbation (Bodini, 2000; Levins and Shultz, 1998; Wootton, 1994). An example is secondary extinction, the loss of species due to an initial extinction event (Allesina and Pascual, 2009; Dobson et al., 2009; Srinivasan et al., 2007). The bottom-up approach to secondary extinction exploits food web topologies to understand and forecast cascading effects of "resources" removal (Allesina and Bodini, 2004; Allesina et al., 2006; Dunne et al., 2002). The lack of dynamics weakens the entire construction; nonetheless as a minimum, best case scenario it provides a baseline to which dynamic effects can add further losses (Allesina et al., 2009; Curtsdotter et al., 2011). In a study that used a link rather than a node-oriented approach Allesina et al. (2009) showed that not all the connections in a food web contribute to robustness. Links differently affect this trait depending on whether they are redundant or functional. The former are somehow neutral, whereas the latter do affect this trait, and their loss would increase the risk of secondary extinction. Essentially, redundant connections do not affect robustness because they do not form independent pathways from resources to consumers.

However this distinction emerges from the condition imposed by the pure topological approach (presence-absence of links) which considers secondary extinction of a species as occurring only in case of complete resource loss. On the contrary, a species may go extinct even in the presence of its resources, if these latter do not guarantee enough energy income to it. In this respect information about link strength becomes crucial to understand bottom-up secondary extinction (Curtsdotter et al., 2011 Eklöf and Ebenman, 2006).

Our study has been inspired by the idea of testing whether redundant connections could be less important than functional

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[1] CB and AB designed the study and analyzed results; CB performed the numerical analysis; AB wrote the paper.

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links in terms of their energetic contribution and thus confirm their minor importance in food web bottom-up robustness. In this paper we show the outcomes of an exercise conducted over 81 weighted food webs. In particular these food webs have been analyzed searching for functional and redundant connections with the following objectives: (i) to highlight whether redundant and functional links can be patterned according to link strength and, in particular, whether redundant links are weaker than functional ones; (ii) to understand whether the way strength is distributed between functional and redundant links may depend on topological parameters such as connectance or linkage density; and (iii) to contribute clarifying the role of the two types of links in respect to bottom-up secondary extinction.

2. Material and methods

2.1. Food webs

The food webs of 81 ecosystems have been considered in this study. Data about their structure and link strength were obtained from previously published papers and reports. Table 1 provides the list of the selected ecosystems and their key references. This table also includes a minimal set of structural parameters, such as number of components, linkage density (number of links per species) and connectance (proportion of possible trophic links that are actually observed).

Some of the food webs refer to the same ecosystem. These ecosystems are the Everglade Gramminoids (2 food webs), Cypress Swamps (2), Mangrove estuary (2), Florida bay (2), Northern benguela (3), Crystal river (2), Chesapeake bay (4), Prince William sound (2), Peru Upwelling (2), Lake Victoria (2). This redundancy is only apparent because multiple webs for a given ecosystem refer to different conditions (i.e., seasonality, level of disturbance, different areas) that affected substantially the model by altering magnitude of flows (Florida ecosystems), connectance and overall number of links (Lake Victoria Crystal River, Benguela ecosystem). Because of the above features all food webs can be reasonably considered as independent data point for statistical analyses.

In all these ecosystems interaction strength is measured in weight/area/time (e.g., grC/m^2/year), which quantifies the amount of biomass that is passed from a prey item to its consumer population (e.g., the biomass loss of the prey item). No per capita effect is accounted for. We think this way to measure interaction strength is appropriate (Berlow et al., 2004) because the distinction between redundant vs. functional connections emerges in the bottom-up energetic approach to food web robustness.

2.2. Functional and redundant connections

Allesina et al. (2009) enriched food web topological analysis by suggesting that links are of two types: redundant and functional. To interpret the significance of this taxonomy, we start from considering that secondary extinctions in topological food web analysis occur with certainty when the disappearance of a given species leaves other species disconnected from their exploitable resources[1]. Robustness would accordingly express the tendency to secondarily loose species, and it is often measured as the fraction of nodes that have to be removed to result in a 50% loss of the original species in the food web (R_{50}; Coll et al., 2011; Chen et al., 2011). It might well happen that an extinction event does not cascade into secondary loss of species; nonetheless the risk of extinction for other nodes may increase. Consider the example food web in Fig. 1.

In this web node 5 has 3 preys. To drive it to extinction, that is disconnecting it from the web, node 2 and 3 must disappear. If, on the other hand, species 4 vanishes, still the same two species (2 and 3) must go extinct to drive 5 to extinction. Thus it can be said that species 4 is not essential for species 5 to survive, while 2 and 3 are. If only one of these two nodes vanishes, say 2, species 5 still remains connected to the web (through node 3) but its extinction risk increases because now only one further extinction is sufficient to make it disappear. In summary, links connecting species to their essential resources are said to be functional, whereas links whose removal leaves unaltered the number of extinctions required for a certain species to disappear are said to be redundant.

The redundant character of connection 4–5 can be appreciated considering that for each possible path connecting the root (R)[2] to node 5 that ends in 4–5 (say R-1-3-4-5), we can find a shorter path that contains a subset of its nodes and which does not contain species 4 (e.g., R-1-3-5): thus link 4–5 is redundant. The presence or absence of node 4 cannot determine the existence of an independent pathway connecting node 5 to the root; from the bottom-up perspective adopted in this work, the two networks in Fig. 1 behave exactly the same. Removing species 1 would cascade into the extinction of species 3 and 4 in both food webs, while the removal of 4 and 5 would not produce secondary extinctions. This illustrates that only functional connections do contribute to topological robustness. The distinction between functional and redundant connections extends the concept of robustness to include the risk of extinction (Allesina et al., 2009). In the context of food web robustness redundancy is not simply synonymous of multiplicity but, rather, it refers to the contribution a certain link gives to web robustness.

In search for functional and redundant connections in the selected webs we exploited the properties of generalized multiple dominators, a graph property originally introduced in control flow graph analysis (Alstrup et al., 1996, 2000; Gupta 1995) and extended to ecology in the form of an algorithm for single node dominators (Allesina and Bodini 2004; Allesina et al., 2006). The concept of single-node dominator is as follows: if all the pathways from the primary producers to a given species x contain another node y, then y is a dominator of x. If y goes extinct, so does x: y is a bottleneck in energy delivery, from the producers to x. The concept of domination can be extended to detect sets of nodes that collectively dominate a given species in a food web. It is the case of nodes 2 and 3 in the web of Fig. 1: they dominate species 5 because all the energy that reaches the top species resided once in either node 2 or node 3. Nodes like 2 and 3 are also called immediate dominators. The immediate dominator of a node is the dominator closest to that node. In Fig. 1 also species 1 dominates 5 but it is not an immediate dominator of it.

Functional and redundant links can be individuated searching for collective dominators for every food web nodes (Alstrup et al., 1996, 1999). A food web G(V,E,r) contains V species connected by E links (or edges) and is rooted in r (a virtual node in which we collapse the external environment as the ultimate source of energy for the ecosystem). Let us call imdom(v) the set of prey that collectively dominates a predator v (like 2 and 3 in the example of Fig. 1). This is the set of prey that connects v to the root by means of independent pathways. This set satisfies three properties: (i) it is contained in the set of prey of v; (ii) any path from r to v ($r \rightarrow \ldots \rightarrow v$) contains a species w that belongs to imdom(v): there is no way to connect v to primary producers bypassing the set

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[1] We are aware of the heavy criticism that was moved to this essential interpretation of secondary extinction. This phenomenon may occur in a variety of forms, but the most predictable case is when these species remain without connections to exploitable food (Allesina and Bodini, 2004).

[2] R is a virtual node in which we collapse the external environment as the ultimate source of energy to the food web.