Stability of food webs to biodiversity loss: Comparing the roles of biomass and node degree

Huayong Zhang [a,*], Lei Zhao [a,b], Wang Tian [a], Hai Huang [a]

[a] Research Center for Ecological Engineering and Nonlinear Science, North China Electric Power University, Beijing 102206, China
[b] Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, Berkshire SL5 7PY, UK

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ABSTRACT

Population biomass, a key concept in traditional ecology, plays a vital role in assessing the consequences of biodiversity loss, in terms of community structure and ecosystem processes. Recent studies derived from network analysis assumed node degree, the number of trophic links of a focal node, as an indicator of node importance in maintaining stability, yet largely ignored the role of biomass. Here, we focus on this underappreciated concept and test if biomass can be used to identify node importance, and compare it with the more commonly applied indicator – node degree. The dynamical approaches were used to simulate secondary extinctions after sequential deletion of nodes in order of highest degree, biomass or random assignment. We showed that biomass-based deletions caused more collateral losses and thus led to lower stability than random removals in the dynamical analyses, i.e. biomass was an efficient indicator. However, the traditional indicator degree failed in identifying node importance. Our findings indicated the overstatement of the importance of node degree and emphasized the importance of population biomass in food webs, and supported a new view in analyzing the stability of food webs to species loss.

1. Introduction

Earth's ecosystems are experiencing an unprecedented rate of biodiversity loss (Dunne et al., 2002; Cardinale et al., 2012), as we enter what has been described as the Sixth Great Extinction (Barnosky et al., 2011). Species losses are unlikely to occur in isolation, with cascading secondary extinctions rippling through the food web, e.g. consumers are left without resources (Sahasrabudhe and Motter, 2011; Sanders et al., 2013). This causes a gradual change of conservation focus from a species-centered approach to preserving functional ecosystems (Heleno et al., 2012). The stability of a system could be dictated by the risk and extent of secondary extinctions (Dunne et al., 2002; Ives and Carpenter, 2007), and it is critical that we understand its drivers (i.e. what kind of species are likely to cause secondary extinctions when they go extinct) if we are to appreciate the true magnitude of the impending extinction crisis (Dunne and Williams, 2009).

Stability is typically studied by dealing with species interaction networks under particular deletion sequences, with the number of resulting secondary extinctions being recorded at each step

(Curtsdotter et al., 2011). To date, the trajectories of primary deletions have been determined by a range of autecological or synecological species traits, such as their connectivity or number of links (i.e. degree) in the network (Sole and Montoya, 2001; Dunne et al., 2002, 2004; Memmott et al., 2004; Dunne and Williams, 2009; Staniczenko et al., 2010; Torres-Alruiz and Rodríguez, 2013), trophic position (Staniczenko et al., 2010; Curtsdotter et al., 2011), generality and vulnerability (Curtsdotter et al., 2011), body mass (Berlow et al., 2009; Curtsdotter et al., 2011), and environmental optima (Srinivasan et al., 2007; Layer et al., 2010). Most research on this topic has focused on removing species based on their degree via topological approaches, assessing network tolerance to removal of the most connected species (Sole and Montoya, 2001; Dunne et al., 2002, 2004; Memmott et al., 2004; Staniczenko et al., 2010). In general, losing the most connected species (i.e. 'hubs') in these empirical webs caused more secondary extinctions than random removals (Sole and Montoya, 2001; Dunne et al., 2002; Curtsdotter et al., 2011).

This process showed clearly that node degree successfully indicated the importance of a node, but this might be misleading in ecological networks, particularly because degree weights all nodes and links equally in a binary matrix (Berlow et al., 2004; Jordán et al., 2006). This may have little influence in other kinds of networks because node strength (the sum of the weighted links

belonging to a node) is strongly related to node degree (Barrat et al., 2004; Aftabuddin and Kundu, 2006), which means a similar order is possibly achieved whether considering weight or not. However, in ecological networks, there is no evidence that the sum of link weights is related to the number of the links for a species, especially considering the highly uneven distribution of link weights (Ledger et al., 2012). Besides, degree is sensitive to sampling effort, and many empirical webs are undersampled (Woodward et al., 2005, 2010). Additionally, the results were mostly generated with a topological approach, which considers bottom-up effects only, and ignores top-down effects as well as link weights (Eklöf and Ebenman, 2006; Curtsdotter et al., 2011).

Biomass has been regarded as an indicator of species importance, with dominant species (with a large population size) playing a central role in the maintenance of ecosystem function (Smith and Knapp, 2003). Population biomass also plays a vital role in determining the stability of ecosystems to species extinctions (Schläpfer et al., 2005; Berlow et al., 2009; Davies et al., 2011). Therefore dominant species typically affect whole-system stability and key ecosystem processes because they provide the major flow of energy (Power et al., 1996). However, very little is known about the role of biomass in predicting food web resistance to species loss. Generally the biomass of a species is a consequence of the balance between the incoming flux of energy and matter from resource species and the outgoing flux to consumer species. It represents the combined influence of all other species directly, or indirectly, interacting with the focal species. Therefore, the strength of links between species is implied in the biomass distribution of a food web, and its investigation could give new insights into food web stability in natural communities.

In this study, we used dynamical approaches to analyze ecosystem flow and simulate secondary extinctions after sequential deletions ordered by degree, biomass or random assignment. This ecosystem flow analysis, or 'storage analysis', can be traced back approximately four decades, when models were proposed to analyze the structure of energy flow through an ecosystem (Barber, 1978a,b; Fath and Patten, 1999). An indicator should be efficient at identifying node importance if it leads to more collateral losses than random ordering (Dunne et al., 2002). Based on this criterion, we compared the effect on food web stability of removing nodes in order of their highest degree and biomass with random deletions. To increase the generality of our findings, we applied three commonly used functional response types: Holling type II, Holling type III and Beddington-De Angelis predator-interference (BDA). Our aim was to compare the performance of the two indicators (biomass and degree) in detecting node importance, and test if the conclusion was robust for different functional response types. Our expectation was to emphasize the importance of biomass as a centrality index in food webs, which may complement a deeper understanding of the relationship between biodiversity and food web stability.

2. Materials and methods

2.1. Food web data

We picked 20 aquatic food webs from a well analyzed database containing 50 food webs (Borrett and Salas, 2010; Borrett and Freeze, 2011; Salas and Borrett, 2011; Borrett, 2013). The chosen food webs contained no less than 15 taxa and each of them were collected from distinct water bodies to avoid using similar networks from the same location (e.g. we randomly chose one web from Florida Bay Wet Season and Florida Bay Dry Season). Each food web dataset contains a list of taxa, the biomass of each taxon (gCm^{-2}), the carbon per unit time of import, export and respiration of each taxon ($gCm^{-2} day^{-1}$), and the carbon flux between a pair of taxa ($gCm^{-2} day^{-1}$). Taxa here represent species, trophic guilds, functional groups, or non-living components of the system. For some taxa, the flows of matter entering and leaving the web are not equal. The initially unbalanced food webs were balanced following the AVG2 algorithm (Allesina and Bondavalli, 2003).

2.2. Food web dynamics

We employed an energy-budget model to simulate the carbon flux entering and leaving each taxon by feeding, respiration, egestion, and natural death. The imports and exports are considered to be in balance and not influence food web dynamics, as for many other dynamical models (Moore et al., 1993; Hudson and Reuman, 2013). The taxa in the system can be divided into four basic categories: producers, consumers, decomposers, and non-living compartments (i.e. detritus).

The biomass of a producer is increased by photosynthesis and decreased by inter-taxon competition, consumption, and non-predatory death. The changes in biomass of producers are described as:

$$\frac{dB_i}{dt} = r_i B_i \left(1 - \frac{1}{K}\sum_{j=res} B_j\right) - \sum_{j=herbi} \phi_{ij} y_j B_j - d_i B_i \tag{1}$$

Here, 'res' and 'herbi' indicate resources and herbivores, respectively; r is the maximum specific growth rate and can be calculated from $(GPP_i - R_i)/B_i(1 - \sum_{j=res} B_j/K)$, where GPP is gross primary production and R is respiration; K is the carrying capacity, ranging three orders of magnitude above and below the total biomass of producers; Φ_{ij} is the functional response when taxon j consumes taxon i; y is the maximum consumption rate; and d is the specific death rate, which can be obtained from $\sum_{j=det} F_{ij}/B_i$, where 'det' refers to detrital taxa.

The biomass of a consumer taxon (including herbivores and predators) is increased by assimilation of consumed resources and decreased by predation and respiration. Its change can be depicted as:

$$\frac{dB_i}{dt} = \sum_{j=res} a_i \phi_{ji} y_i B_i - \sum_{j=pred} \phi_{ij} y_j B_j - x_i B_i \tag{2}$$

Here, 'pred' refers to predatory taxa; a is the assimilation efficiency which can be calculated from $1 - (\sum_{j=det} F_{ij}/\sum_{j=res} F_{ij})$; and x is the respiration rate, calculated from R_i/B_i.

The biomass of a decomposer taxon is increased by assimilation of consumed detritus and decreased by predation and respiration. Its change can be depicted as:

$$\frac{dB_i}{dt} = \sum_{j=det} a_i \phi_{ji} y_i B_i - \sum_{j=pred} \phi_{ij} y_j B_j - x_i B_i \tag{3}$$

The biomass stored in a detritus is increased by the dead body of producer taxa, the feces of consumer taxa, and the conversion from other detritus, and decreased by consumption of decomposer taxa and conversion to other detritus. Its change can be described as:

$$\frac{dB_i}{dt} = \sum_{j=pro} p_{ji} d_j B_j + \sum_{j=con} (p_{ji} e_j y_j B_j \sum_{k=res} \phi_{kj}) + \sum_{j=det} c_{ji} B_j - \sum_{j=dec} \phi_{ij} y_j B_j$$
$$- \sum_{j=det} c_{ij} B_i \tag{4}$$

Here, 'pro', 'con' and 'dec' are producer, consumer, and decomposer taxa, respectively; p_{ji} is the proportion of converted detritus i to the