



Increasing the extinction risk of highly connected species causes a sharp robust-to-fragile transition in empirical food webs

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ARTICLE INFO

Article history:

Received 8 October 2012

Received in revised form

30 November 2012

Accepted 4 December 2012

Available online 8 January 2013

Keywords:

Complex biological networks

Food web robustness

Scale-free networks

Extinction risk

ABSTRACT

Random removal and the attack from most- to least-connected node (i.e. species) are the two limit criteria for sequential extinction of species in food webs, but a continuum of possibilities exists between them.

We use simulations to test the robustness of 14 empirical food webs to species loss by varying a parameter I (intentionality) that defines the removal probability (extinction risk) of species with high number of trophic connections. The removal probability of highly connected species increases with I . We found that food web robustness decreases slowly when the extinction risk of highly connected species increases (we call this region *random removal regime*), until a threshold value of I is reached. For greater values of the threshold, we found a dramatic reduction in robustness with increasing intentionality in almost all the food webs (*intentional attack regime*).

Link-dense networks were more robust to an increase of I . Larger food webs (i.e. higher species richness) were more sensitive (i.e. robustness decreased faster) to the increase of extinction risk of highly connected species. The existence of a clear transition in system behaviour has relevant consequences for the interpretation of extinction patterns in ecosystems and prioritizing species for conservation planning.

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1. Introduction

Food webs have been central to ecological research for decades (Cattin et al., 2004; Jordán et al., 2003; May, 1972; McCann, 2000; Montoya and Sole, 2003), and the study of the robustness of food webs to species loss is increasingly relevant for species and ecosystem conservation (Montoya et al., 2006; Raffaelli, 2004; Zavaleta, 2004).

The loss of a species in ecosystems (primary extinction) can cascade into further extinctions (secondary extinctions), as consumers' persistence depends on the persistence of their resources. Many theoretical and empirical studies have investigated how food web properties, such as modularity, degree-distribution (i.e. the probability distribution of the number of trophic connections of species), presence and distribution of keystone species may influence the pattern of secondary extinctions in ecosystems as well as food web robustness (Allesina and Pascual, 2009; Bascompte et al., 2005; Dunne et al., 2002a; Jordán et al., 2003; Solé and Montoya, 2001). In the vast majority of studies on extinction patterns in food webs, a species is assumed to go extinct after a primary extinction when is left without any resources to exploit (Allesina and Bodini,

2004; Allesina and Pascual, 2009; Dunne et al., 2002a; Solé and Montoya, 2001). This is clearly the best-case scenario (Allesina and Pascual, 2009; Dunne, 2006), as the occurrence of other common effects, such as size-dependent-dynamics, top-down cascades or energetic thresholds, would result in additional losses (Bellingeri and Bodini, 2012; Curtsdotter et al., 2011; Dunne, 2006).

Simulation studies have shown that the extinction of highly connected species is likely to generate a greater number of secondary extinctions than when species are randomly removed from the food web (Allesina and Bodini, 2004; Dunne et al., 2002a; Dunne and Williams, 2009; Solé and Montoya, 2001). Notions of error and attack sensitivity were first introduced in the physical literature and then successfully applied to the study of food webs (Albert and Barabasi, 2002; Dunne et al., 2002a; Solé and Montoya, 2001; Strogatz, 2001). A network is error resistant (or resistant to failure) when it is unlikely to be damaged by random removal of nodes. On the other hand, a network is sensitive to attack when it can be either highly damaged or destroyed by a targeted attack, such as the selective removal of highly connected nodes (Albert and Barabasi, 2002; Dunne et al., 2002a).

The sequential removal from most- to least-connected species (intentional attack) and random extinction of species (random removal) are two limit criteria for determining primary extinctions in food webs (least- to most-connected should be the other limit criterion, but it is rarely used in practice), and both approaches

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Table 1
Main features of food webs used in this study. L , total number of links in the food web; S , number of species; C , food web connectance (L/S^2). Refs: Literature reference for the food web. Keys: Short id of food web.

Food web	S	$C = L/S^2$	L/S	Refs	Key
Bridge Brook Lake	25	0.171	4.28	Havens (1992)	Br
Coachella Valley	29	0.312	9.03	Polis (1991)	Co
Cheasepeake Bay	31	0.071	2.19	Baird and Ulanowicz (1989)	Ch
St Martin Island	42	0.116	4.88	Goldwasser and Roughgarden (1993)	SM
St Marks Seagrass	48	0.096	4.60	Christian and Luczkovich (1999)	SMk
Grassland	61	0.026	1.59	Martinez et al. (1999)	Gr
Ythan Estuary 91	83	0.057	4.76	Hall and Raffaelli (1991)	Y91
Scotch Broom	85	0.031	2.62	Memmott et al. (2000)	Sc
Stony Stream	109	0.07	2.19	Townsend et al. (1998)	St
Little Rock Lake	92	0.118	10.84	Martinez, 1999	Li
Canton Creek	102	0.067	6.83	Townsend et al. (1998)	Ca
Ythan Estuary 96	124	0.038	4.76	Huxham et al. (1996)	Y96
El Verde Rainforest	155	0.063	9.74	Waide and Reagan (1996)	El
Mirror Lake	172	0.146	25.13	Dunne et al. (2002a,b)	Mi

have been widely used to study patterns of secondary extinctions in ecosystems as well as to measure food web robustness. However, it is possible to introduce other removal criteria along the continuum from the random removal of species to the intentional attack.

Across ecosystems, certain species – not necessarily the most connected – can be more prone to extinction, either because preferentially targeted by natural or human agents (e.g. pollution, species invasion, overexploitation, weather extremes) or for internal dynamics or properties of the biological community (e.g. size-dependent dynamics). Other factors can decrease the species risk of extinction, e.g. the ability of consumers to use or prey on other resources in the case of resource loss (i.e. “rewiring of the food web”), or the human conservation efforts. In this context, a valuable approach to primary species extinction in food webs is to introduce non-uniform and non-deterministic criteria for species extinction. The introduction of probabilistic approaches to species extinction may offer more realistic predictions of both primary and secondary extinction dynamics in food webs as well as insights on possible transitions in system behaviour (e.g. from robustness to fragility). Further, a probabilistic approach can help understand how changes in the primary extinction risk of species affect secondary extinctions in ecosystem.

In a recent work, Gallos et al. (2006) studied the robustness of scale-free networks, i.e. networks whose degree-distribution follows a power law. They used the probability $W(k) \sim k^\alpha$ for a node of degree k (i.e. number of links of the node) to become inactive, where for: (i) $\alpha = 0$ the removal is random; (ii) $\alpha < 0$ low-degree nodes are more vulnerable; (iii) $\alpha > 0$ high-degree nodes are more likely to be removed than low-degree nodes. Gallos et al. (2006) showed that a little increase of α strongly reduces the percolation p_c . In other words, with a moderate increase of the probability of removing highly connected nodes, the scale-free network is quickly destroyed following the inactivation of a small number of nodes.

So far, how network robustness changes when increasing the probability of removing highly connected nodes has not been studied either in model or empirical food webs. Here, we analyse the robustness of 14 empirical food webs to node loss by introducing a parameter I (intentionality) that defines the probability of removing highly connected species. When I increases, so does the extinction risk of highly connected species.

2. Material and methods

2.1. Data set

A food web can be described as a directed network with S species (nodes) and L trophic interactions among them (links), describing

who eats whom (Dunne, 2006; Montoya et al., 2006). In this work, we used food webs that represent a wide range of species numbers, link densities, taxa, habitat types (terrestrial, aquatic and transition ecosystems). In Table 1, we report the basic properties of each food web, such as number of species (S), average number of links per species (L/S), and connectance ($C = L/S^2$). Since S^2 is the maximum possible number of trophic interactions in a $S \times S$ matrix, food web connectance describes the realized fraction of trophic interactions in the food web.

2.2. Robustness

Food web robustness is usually tested with simulations in which a single species is removed at each step (i.e. primary extinction), and the number of secondary extinctions (i.e. extinctions following the primary extinction) is recorded (Allesina and Pascual, 2009; Dunne et al., 2002a; Dunne and Williams, 2009; Solé and Montoya, 2001). Species going primarily extinct may be selected according to a particular criterion (i.e. random removal, decreasing or increasing number of connections, etc.), and primary extinctions are repeated until all the species have gone extinct. With a topological approach (i.e. based on presence/absence or links, with no information on interaction strength), a network node goes extinct when it loses all incoming connections. In food webs, that means a species goes extinct when it is left without any exploitable resources.

Here, we test the robustness of 14 empirical food webs (Table 1) by introducing a novel criterion for primary extinctions. We assume that consumers cannot switch from one type of prey to another (i.e. no food web “rewiring”). Several measures of food web robustness have been proposed, such as secondary extinction area (Allesina and Pascual, 2009), error and attack sensitivity (Allesina and Bodini, 2004; Allesina et al., 2006), R_{25} (Srinivasan et al., 2007). In this work, we use ‘structural robustness’ (R), that is the proportion of primary extinctions leading to a particular proportion of total extinctions (Curtsdotter et al., 2011; Dunne et al., 2002a; Dunne and Williams, 2009; Dunne, 2006):

$$R_\alpha = \frac{E}{S} \quad (1)$$

where E is the number of primary extinctions that produces a percentage α of total extinctions (primary + secondary) out of the total number of species S in the food web. We used two measures of R : (i) the proportion of primary extinctions triggering the loss of half of the species (R_{50}) (Curtsdotter et al., 2011; Dunne et al., 2002a; Dunne and Williams, 2009; Dunne, 2006) and (ii) the proportion of primary extinctions causing food web collapse (i.e. extinction of all species, R_{100}) (Dunne, 2006; Ebenman, 2011). The maximum possible value of robustness when using R_{50} is 0.5 (i.e. half of the species must be removed to trigger the loss of half of the species in the food

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