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Robustness of empirical food webs with varying consumer's sensitivities to loss of resources



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H I G H L I G H T S

- We study the robustness to random node loss of 10 food webs with empirical weightings.
- We use extinction threshold ν as an energetic criterion to define species extinction.
- Robustness of food webs increases linearly with ν .
- Among food webs, sensitivity of robustness to ν varies with complexity.

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A B S T R A C T

Food web responses to species loss have been mostly studied in binary food webs, thus without accounting for the amount of energy transferred in consumer–resource interactions.

We introduce an energetic criterion, called extinction threshold, for which a species goes secondarily extinct when a certain fraction of its incoming energy is lost. We study the robustness to random node loss of 10 food webs based on empirically-derived weightings. We use different extinction scenarios (random removal and from most- to least-connected species), and we simulate 10^5 replicates for each extinction threshold to account for stochasticity of extinction dynamics.

We quantified robustness on the basis of how many additional species (i.e. secondary extinctions) were lost after the direct removal of species (i.e. primary extinctions). For all food webs, the expected robustness linearly decreases with extinction threshold, although a large variance in robustness is observed. The sensitivity of robustness to variations in extinction threshold increases with food web species richness and quantitative unweighted link density, while we observed a nonlinear relationship when the predictor is food web connectance and no relationship with the proportion of autotrophs.

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1. Introduction

The response of food webs to species loss and how food web properties affect extinction patterns have been thoroughly investigated in recent years (Dunne et al., 2002, 2004; Memmott et al., 2004; Estrada, 2007; Allesina et al., 2009; Allesina and Bodini, 2004; Bellingeri et al. 2013). Several removal criteria can be used to attack networks, such as removing the most-connected nodes (Dunne et al., 2002, 2004; Allesina et al., 2009; Solé and Montoya, 2001), bottlenecks (Allesina and Bodini, 2004), topologically

important species (Jordán et al., 2007) or nodes responsible for network expansibility (Estrada, 2007).

Ecological networks are generally considered error resistant, but vulnerable to attack. The concepts of “error resistance” and “attack vulnerability” have been first developed in physics (Albert et al., 2000; Albert and Barabasi, 2002; Newman, 2003), and have then been largely applied to the analysis of ecological networks (Albert et al., 2000; Albert and Barabasi, 2002; Newman, 2003; Allesina et al., 2006). A network is error resistant (or error tolerant) when the removal of nodes taken at random is unlikely to damage the networks, while it is vulnerable to attack when it can be damaged by removal or “disconnection” of few important nodes (Albert et al., 2000). Food webs are typically considered vulnerable to attack, since a great proportion of species may go extinct after the removal of key nodes (Allesina and Bodini, 2004; Jordán et al., 2002). On the other hand, the general result emerging

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from the ecological literature is that food webs are highly resistant to random removal of species (Dunne et al., 2002; Montoya and Sol, 2002; Allesina et al., 2009; Allesina and Bodini, 2004).

The analyses of secondary extinctions in food webs are carried out using either binary, quantitative, or dynamical networks. The vast majority of the studies cited above were carried out using binary (i.e. based on presence/absence of trophic interactions) food webs, but it is now clear that trophic interactions of varying intensity may have substantially different effects on food web properties (Banašek-Richter et al., 2009; Allesina and Pascual, 2009). The description and analysis of food webs with non-binary (i.e. quantitative or weighted) links among species started in the 70s with the seminal paper of Hannon (1973), who drew novel parallels between the structure of economy and the structure of ecosystems, and was later followed by further investigation of energy flows in weighted food webs (Finn, 1976; Patten, 1978, 1986; Herendeen, 1981; Higashi and Patten, 1989).

The disregard of potentially huge variation in trophic relationships within a food web in favor of simple binary food webs has been described as “an approach similar to analyzing traffic without differentiating between highways and side roads” (Banašek-Richter et al., 2009). The stability of ecological communities also largely depends on the distribution of strong trophic interactions between predators and their prey. Berlow et al. (2004) suggested that non-random patterning of strong and weak links can be critical for the stability or persistence of food webs. Bascompte and Meliá (2005) showed that the magnitude of these interactions are non-randomly distributed in a large Caribbean marine food web, and the co-occurrence of strong interactions on two consecutive levels of food chains occurs less frequently than expected by chance. This may reduce the likelihood of trophic cascades after the overfishing of top predators.

The evidence and insight provided by analysis on weighted food webs cast doubts on the generality of predictions of secondary extinction obtained with binary food webs, in which even the weakest remaining incoming link is able to support the consumer. In fact, with a pure topological (i.e. binary) approach, secondary extinctions occur when a species is left without any exploitable resources. From an energetic point of view, this means that a species faces extinction when its inflow energy is 0, but it is intuitive that species extinction may occur well before all incoming energy disappears (Bodini et al., 2009), and this largely affects the estimation of food web robustness.

In a study on food webs including population dynamics, Borrvall et al. (2000) showed how a generalist could go extinct after losing just one of its prey while still having others available. An example of secondary extinction following a reduction in energy intake is the “local extinction” of the harp seal (*Phoca groenlandica*) in the Barents Sea in 1986–1988 (Huag and Nilssen, 1995). The harp seal underwent a mass migration (hundreds of thousands of individuals) from the Barents Sea to Northern Norwegian waters after the collapse of one of its preys: the capelin (*Mallotus villosus*) (Huag and Nilssen, 1995). The capelin covered only a fraction of the energy intake of the harp seal, although it is the main resource in some parts of the year in the Barents Sea (Nilssen et al., 1995), but the energy provided by the remaining preys (e.g. polar cod, amphipods) was not sufficient to sustain the predator, thus causing the “local secondary extinction” of the harp seal (Bodini et al., 2009). Another interesting case is the decline in numbers of black-legged kittiwakes (*Rissa tridactyla*) living in colonies in the Shetland Isles (UK) in the last decades, and extinctions have been recently observed (Heubeck et al., 1999; Frederiksen et al., 2005). The declines have been caused by the collapse of the sandeel (*Ammodytes marinus*), a high-lipid fish and main prey for breeding kittiwakes, caused by the combined effect of overfishing and climate change (Poloczanska et al., 2004).

Breeding kittiwakes and chicks living in colonies in the Northern European seas can also feed on other species, including clupeids, waste from trawlers and snake pipefish *Enterus aequoreous* (Harris and Wanless, 1997; Harris et al., 2007). However, these other species are probably not sufficient to sustain kittiwake colonies; for instance, the main resource for kittiwakes in the Shetland Isles when sandeel is not present is the snake pipefish, which has been increasing in Northern European seas since 2003 (Harris et al., 2010). Unfortunately, snake pipefish has low energy value and is particularly difficult to swallow for kittiwake chicks, and any increase in snake pipefish seems unlikely to compensate for a reduction in sandeels and other high-lipid fish species (Harris et al., 2007; Grémillet and Boulinier, 2009).

Thierry et al. (2011) explored the effects on robustness of model food webs of the use of a secondary extinction criterion based on a threshold of energy loss, where a species may go extinct when it loses less than 100% of its incoming energy. Using a random removal approach for food webs of 40 species constructed with the Allometric Diet Breadth Model, they showed that a higher susceptibility of species to loss of incoming energy decreases robustness of food webs. For conservation biology, they thus suggested it is necessary to understand how network robustness is dependent on species sensitivity to resource loss. Despite this recent investigation of model food webs, how species' sensitivity to loss of resources along with food web structural properties affects food web robustness and extinction dynamics is still a largely unexplored question in empirical food webs (Bellingeri and Bodini, 2013). However, the development of a quantitative ecological network, including the estimation of the strength of the trophic links between species, requires vastly more data than those needed to characterize network structure (Pascual and Dunne, 2006). The collection of the necessary data can be limited by logistic, monetary and time constraints, and in addition energy flows between species may vary through space and time and it may be difficult to characterize “average” and at the same time ecologically-meaningful energy flows. More recently, ecologists started to integrate ecological dynamics (e.g., functional responses, fluctuations in abundances, density-dependent processes) in complex food web structure, aspiring to strike a balance between simplifying and including aspects of the complexity of natural systems in order to better model and understand the stability of ecosystems (Curtsdotter et al., 2011). For example, empirical observations have shown that extinction cascades may occur after the removal of a top-predator, e.g. when this causes the release of a meso-predator that can thus over-exploit its preys (Elmhagen and Rushton, 2007). Dynamical approaches to the study of food web properties and dynamics have shown to be able to capture both bottom-up and top-down effects (Curtsdotter et al., 2011).

Here, we explore how predicted patterns of secondary extinctions resulting from random loss of species may change when species sensitivity and interaction strength are accounted for in the analyses. We selected for this study 10 food webs previously published as ecological flow networks, in which empirically-estimated link strengths represent energy (or matter) flows from resources to consumers (Scotti et al., 2009). We start our analysis from the well-known binary extinction scenario where a species goes extinct when it has no resources left to exploit (Dunne et al., 2002; Solé and Montoya, 2001). In the binary scenario, we analyze the robustness of food webs by removing species as a function of their degree (i.e. the number of links of the species) and by random deletion (Dunne et al., 2002, 2004). Then, we test food webs' robustness to random removal with increasing species sensitivity to loss of resources. Finally, we estimate the relationship between the sensitivity of secondary extinction to variation in extinction thresholds and five descriptors related to food web

complexity, namely species richness, fraction of autotrophs in the food web, connectance, link density and quantitative link density (Banašek-Richter et al., 2009; Bersier et al., 2002).

2. Methods

2.1. Weighted food webs

A quantitative (or weighted) food web is a weighted directed graph that represents relationships of ecological energy transfer (Banašek-Richter et al., 2009; Hannon, 1973, 1979; Scotti et al., 2009). A weighted food web is described by a type of adjacency matrix called flux matrix **A** (Bersier et al., 2002). Each non-zero element **A**[*i*,*j*] represents the magnitude of a flow of energy (or matter) from resource *i* to consumer *j*. Column *j* represents the diet spectrum of species *j*, and each non-zero element **A**[*i*,*j*] is an inflow from a resource of *j*. It is straightforward that the column sum is the total amount of energy incoming to consumer *j*. For simplicity, we assume that consumers cannot switch from one type of prey to another after prey extinction (i.e. no food web “rewiring”) (Staniczenko et al., 2010).

2.2. Data set

We analyzed the food webs of 10 ecosystems of various size, with species richness varying from $S=31$ to $S=123$ (Table 1). We chose only webs with species richness $S > 30$ to avoid bias due to small web size (Bersier and Sugihara, 1997). The food webs were previously investigated as ecological flow networks, i.e. graphical representations of ecosystems for which the magnitude of trophic transfers from prey to predators is known (Ulanowicz, 1986; refer to the ATLSS website <http://www.cbl.umces.edu/~atlss/> for a detailed description of the networks). We excluded “non-living nodes” (i.e. detrital and particulate compartments) from the food webs. We preserved mass balance by considering flows from living to non-living species as output of the system. On the other hand, we considered flows from non-living to living compartments as input of the system (Allesina and Bondavalli, 2003). In our analysis, we divided each element *i* of column *j* by the sum of column *j* to obtain the proportion of energy provided by each resource in the consumer diet. From now on, we write $e(j)$ to indicate the normalized column sum.

2.3. Simulations of extinction dynamics

In the classic binary extinction scenario, a species *j* goes extinct when

$$e(j) = 0 \quad (1)$$

Table 1

Main features of food webs used in the present study. S =number of species; A =number of autotrophs; L =number of links, LD =link density; C =connectance; LDq =quantitative unweighted link density. *Dry* and *Wet* refers to food webs for dry and wet season, respectively.

Food web	<i>S</i>	<i>A</i>	<i>L</i>	<i>LD</i>	<i>C</i>	<i>LDq</i>
Narragansett Bay	31	5	113	3.65	0.12	2.68
Cheasepeake Lower	31	12	57	1.84	0.06	1.72
Cheasepeake Bay Mesohaline	33	5	72	2.18	0.07	1.63
Lake Michigan	35	6	130	3.71	0.11	2.47
Mondego	42	12	279	6.64	0.16	2.98
St. Mark River	48	7	219	4.56	0.09	2.8
Everglades Graminoids (Dry)	63	5	617	9.79	0.15	3.78
Cypress Wetland (Wet)	65	13	439	6.75	0.10	2.84
Mangrove (Dry)	91	7	1149	12.63	0.14	4.72
Florida Bay (Wet)	123	15	1767	14.48	0.12	5.92

that is, species *j* goes extinct when it is left with no exploitable resources (Dunne et al., 2002, 2004; Allesina et al., 2009; Solé and Montoya, 2001). More realistically, a species can go extinct when the incoming energy is reduced below a critical level. Let ν be the fraction of the initial (i.e. before any species has been removed from the food web) inflow energy below which the species goes extinct. In a binary extinction scenario, ν is equal to 0. We can also refer to ν as the extinction threshold, and we can interpret the parameter ν as the sensitivity of a species to the loss of its prey items.

We generalize condition (1), and assume that a species goes extinct when:

$$e(j) \leq \nu \quad (2)$$

By increasing or decreasing ν in Eq. (2), we can investigate food webs robustness to species loss under various extinction thresholds. When $\nu=0.1$, a species goes extinct in the case its inflow energy goes below 10% of the starting energy inflow, while for $\nu=0.2$ a species goes extinct in the case its inflow energy falls below the 20% of the starting energy inflow. Therefore, the higher the extinction threshold, the more sensitive the species to the decrease in energy intake. In our analysis, we used values of ν from 0 to 0.9, with a step size of 0.1. The extinction threshold equal to 1 represents the trivial extinction scenario for which all species in the food web go extinct after the first removal. This scenario does not provide any valuable information and was not used in our study.

We performed simulations in which a single species is randomly removed at each step and the number of secondary extinctions is recorded. A species is considered extinct according to condition (2). Secondary extinctions can be direct (i.e. consumers go extinct after the removal of a species to which they are directly connected) or indirect (i.e., consumers go extinct after the removal of a species to which they are not directly connected). The procedure is repeated until all the species have gone extinct. For each extinction sequence, we recorded the “secondary extinction area” (SEA), a measure of robustness with a clear geometric interpretation (Fig. 1). To calculate SEA, we generated a response curve describing the total fraction of original species lost as a function of the fraction of species previously removed. If secondary extinctions never occur following any of the primary extinctions, the fraction extinct will always match the fraction removed (1:1 line). However, if species removal leads to subsequent secondary extinctions, the resulting fraction lost will exceed the fraction removed, and the response curve will lie above the 1:1 line. We calculated SEA as the area below the response curve but above the 1:1 line, so SEA is equal to 0.5 when all species go extinct after the first removal, whereas it is equal to 0 when no secondary extinction is ever observed (Fig. 1) (Allesina et al., 2009). It follows that the larger the SEA, the less robust the food web under species removal.

We first computed SEA by systematic removal of nodes from the most- to the least-connected for $\nu=0$ (binary degree removal, BDR), that is removing species in decreasing order of species' number of links (Dunne et al., 2002; Solé and Montoya, 2001; Dunne and Williams, 2009). BDR usually drives higher secondary extinctions than random removal of species (Dunne et al., 2002, 2004; Dunne and Williams, 2009). Since different species may have the same number of links, the SEA of BDR scenario that we used is the mean of 100 simulations.

Any random removal extinction scenarios occurring under the same constraint (i.e. in our case equal ν) can theoretically display very different patterns of secondary extinction, as any combination of nodes removal is possible when selecting species at random. To account for the random outcome of any single replicate with random removal, for each combination of food

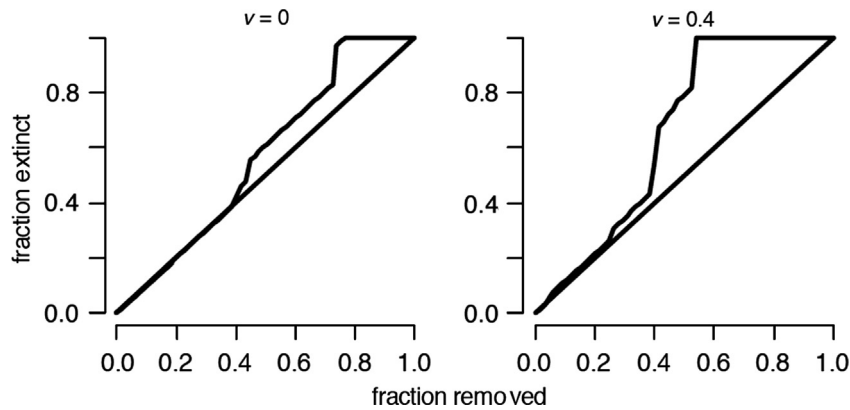


Fig. 1. Secondary extinction area (SEA). Examples of an extinction scenario in Cypress wet food web ($S=65$). Fraction of nodes removed (x axis) and cumulative fraction of nodes extinct (y axis), i.e. nodes removed (primary extinctions) plus secondary extinction. The bisector line indicates no secondary extinctions. The secondary extinction area (SEA) is the area between the two lines and is bounded between 0 (no secondary extinctions) and 0.5 (all species go extinct after the first removal). The two panels indicate examples for $\nu=0$ and for $\nu=0.4$.

web and ν we carried out 10^5 simulations. For each set of 10^5 SEAs, we: (1) computed the expected SEA; (2) computed the fraction of SEAs greater than the value of SEA obtained with the BDR criterion. Then, for each food web we estimated the parameters of a linear regression model for the relationship between the expected value of the SEA (response variable) and ν . Finally, we investigated whether the complexity of the food web decreases the sensitivity of robustness to increasing extinction thresholds, i.e. decrease the slope of the functional relationship, with regressions on either linear and log scales, using AIC to discriminate between models (we modified the log-likelihood when the response variable was on the log scale). We visually inspected residuals for strong violations of assumptions of linear models.

We tested the slope of the functional relationship with size S of the food web (i.e. the number of species), number of autotrophs (A , i.e. organism capable of synthesizing its own food from inorganic substances) divided by the total number of species (A/S), link density (LD , average number of binary links per species) and food web connectance (C , the fraction of all possible links that are realized in a food web). Finally, to investigate how the quantitative structure of the food web flows affects the robustness of the system, we analyzed the relationships between the slope of the functional relationship and quantitative unweighted link density (LDq) (Banašek-Richter et al., 2009). The quantitative link density represents the number of “effective” links in a quantitative food web. To compute LDq , for each species we first apply Shannon's formula to the quantitative diet, as follows. With b_{ij} the fractional amount of energy passing from species i to species j , and b_j the total amount of energy flowing to species j , we calculate the species-specific Shannon index for the inflows $H_j = -\sum_{i=1}^S b_{ij}/b_j \log b_{ij}/b_j$ and for the outflows $H_i = -\sum_{j=1}^S (b_{ij}/b_i) \log (b_{ij}/b_i)$. Then, we compute $N_j^* = \exp(H_j)$ and $N_i^* = \exp(H_i)$. N_j corresponds to the effective number of prey and N_i the effective number of predators for the species. The average number per species of these effective links is the quantitative unweighted link density LDq , that is $LDq = 1/(2S)(\sum_{i=1}^S N_i^* + \sum_{j=1}^S N_j^*)$, where S is number of species in the food web (Banašek-Richter et al., 2009).

3. Results

With random removal, the expected value of the set of SEAs linearly increases with ν for all the food webs ($p < 0.01$) (Fig. 2 and Table A3.2). For almost all the food webs, an extinction threshold ν greater than 0.4 provided a mean SEA comparable to the SEA

obtained with the BDR scenario (Table A3.1). Only in two food webs (Mangrove dry and Florida wet food webs), was the mean SEA with random removal in the neighborhood of the SEA obtained with BDR with a very low extinction threshold ($\nu < 0.1$) (Table A3.1). In the Appendix, we provide mean SEAs for each ν for all 10 food webs (Table A3.1).

The distribution of 10^5 SEAs obtained by randomly removing nodes shows that even with very low extinction thresholds ($\nu=0$ and $\nu=0.1$) large damage may occur, although rarely (Figs. A1.1–A1.10), and in some food webs a small fraction of SEAs is greater than the SEA obtained with the BDR scenario (Table A3.3). For example, in the Everglades dry food web the SEA with the BDR scenario is 0.24 and for $\nu=0$ the 0.4% of random removal replicates provide a SEA greater than 0.24. In the same food web, with $\nu=0.2$, 20% of events have SEA greater than that obtained with the binary degree removal criterion (Figs. 3 and 4). The fraction of SEAs with random removal greater than SEA obtained with BDR increases in all food webs with the extinction threshold, although with different patterns of increase (Fig. 3).

The change of the distribution of SEA with increasing extinction threshold is consistent across food webs. As shown in Fig. 4 for the Everglades dry food web, the mode of the distribution of SEAs moves to higher SEA for increasing ν . With values of ν between 0.1 and 0.6, the distribution flattens and the probability of obtaining a large SEA increases. For $\nu > 0.7$, the variance of the distribution of SEAs decreases and the mode of the distribution is close to maximum SEA. We provide in Appendix the distribution of SEAs for all the food webs (Figs. A1.1–A1.10). Since SEAs were approximately beta-distributed, we provide in the Appendix the parameter estimates of scaled beta distributions fitted on the set of SEAs for each ν (Table A2.1), which will allow future parametric comparison with the results coming from other empirical or model food webs. Linear regression models obtained with distribution medians are not qualitatively different than those obtained with means (data in Table A3.4 and regression models in Fig. A3.1).

For each food web F , the slope of the straight line describing the increase of mean SEA with ν ($\beta_{s,F}$) represents the sensitivity of food web robustness to ν (Fig. 2). We found a positive linear relationship between $\beta_{s,F}$ and food web size ($p < 0.05$), binary link density LD ($p < 0.05$) and quantitative link density LDq ($p < 0.05$) (Fig. 5). A regression of $\beta_{s,F}$ on food web connectance was significant when including a linear and a (negative) quadratic term ($p < 0.01$), while linear regression of $\beta_{s,F}$ on fraction of autotrophs in the food web was not significant ($p=0.16$ for the fraction of the autotroph species) (Fig. 5).

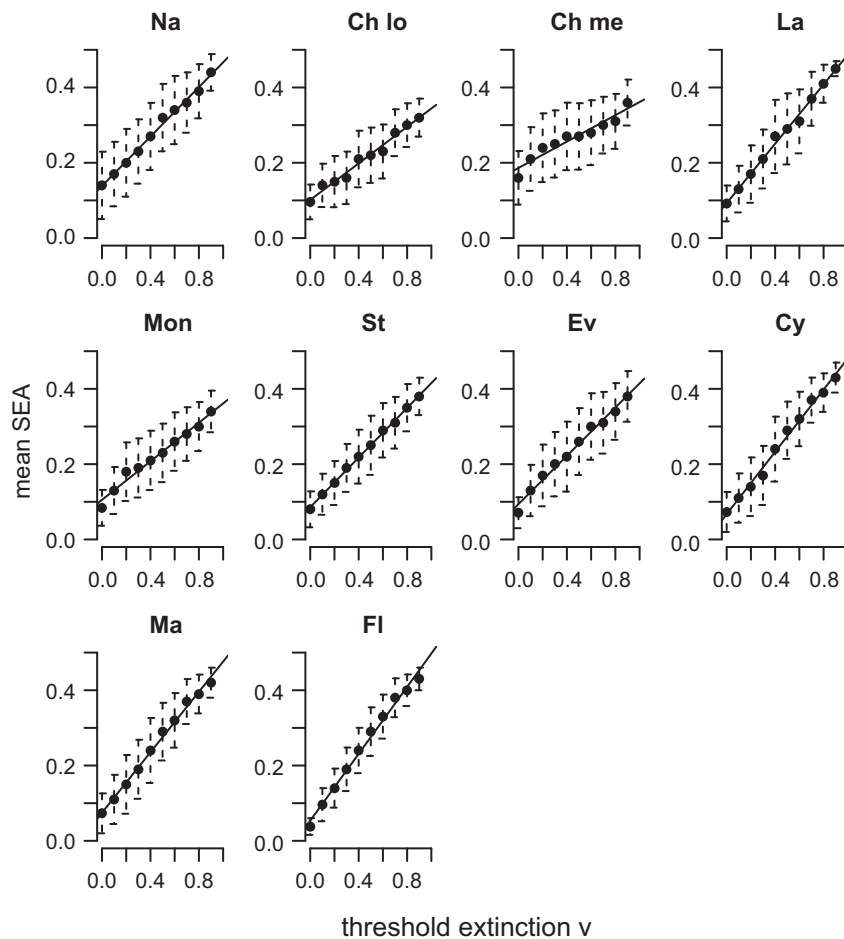


Fig. 2. Linear model of SEA. Linear model of mean secondary extinction area (SEA, y axis) with random removal as a function of extinction threshold ν (x axis) for all the 10 food webs we analyzed. SEA is bounded between 0 (no secondary extinctions) and 0.5. We also report the standard deviation of the distribution of SEA for each ν . Mean SEA increases linearly in all food webs ($p < 0.01$ for all). Narragansett Bay food web (Na), species richness $S=31$ (intercept of the linear model \pm se $\alpha_{Na}=0.138 \pm 0.005$, slope of the linear model \pm se $\beta_{s,Na}=0.328 \pm 0.01$); Cheasapeake Bay lower food web (Ch lo), $S=31$ ($\alpha_{Ch\ lo}=0.10 \pm 0.0064$, $\beta_{s,Ch\ lo}=0.24 \pm 0.012$); Cheasapeake Bay mesohaline food web (Ch me), $S=33$ ($\alpha_{Ch\ me}=0.186 \pm 0.01$, $\beta_{s,Ch\ me}=0.175 \pm 0.001$); Lake Michigan (La), $S=36$ ($\alpha_{La}=0.09 \pm 0.0057$, $\beta_{s,La}=0.39 \pm 0.012$); Mondego Estuary (Mo), $S=42$ ($\alpha_{Mo}=0.25 \pm 0.0014$, $\beta_{s,Mo}=0.10 \pm 0.078$); St. Marks (St), $S=48$ ($\alpha_{St}=0.086 \pm 0.003$, $\beta_{s,St}=0.330 \pm 0.005$); Everglades dry food web (Ev), $S=63$ ($\alpha_{Ev}=0.094 \pm 0.007$, $\beta_{s,Ev}=0.321 \pm 0.001$); Cypress wet food web (Cy), $S=65$ ($\alpha_{Cy}=0.070 \pm 0.007$, $\beta_{s,Cy}=0.413 \pm 0.014$); Mangrove dry food web (Ma), $S=91$ ($\alpha_{Ma}=0.075 \pm 0.006$, $\beta_{s,Ma}=0.401 \pm 0.011$); Florida Bay wet food web (FI), $S=123$ ($\alpha_{FI}=0.053 \pm 0.008$, $\beta_{s,FI}=0.444 \pm 0.015$).

4. Discussion

Our results show how food web robustness to random loss of species decreases with increasing species sensitivity to reduction of incoming energy. Using the mean of the SEAs obtained with random removal of species as a measure of robustness, we observed a linear increase with increasing extinction threshold. Our results show that the introduction of an energetic extinction criterion substantially affects estimates of robustness of food webs. This suggests that a detailed knowledge of species' susceptibility to a decrease in energy intake is necessary to realistically predict food web responses to species loss, as also found by Thierry et al. (2011) for model food webs and reported by Brose (2011). An interesting empirical example is provided by the consequences of community reorganization in the Bering Sea and Gulf of Alaska. Since the late 1970s, the numbers of Steller sea lions *Eumatopias jubatus* and Pacific kittiwakes in some parts of the Bering Sea and Gulf of Alaska sharply declined. It was hypothesized that the decline of bird and marine mammal predators was caused by a reduction in forage fish species such as herring, capelin, sand lance and increases in demersal fish species (e.g. pollock and halibut) ("junk-food hypothesis" (Österblom et al., 2008)) caused by a regime shift from cold to warm conditions that started in the

late 1970s (Hunt et al., 2011). Demersal fish species have lower energy densities than fatty forage fish, and this largely seems to have determined the decline and in some cases extinction of predator populations or colonies (Anderson and Piatt, 1999; Hatch, 2013).

The need for information about the species susceptibility to the loss of prey is corroborated by other analyses carried out on model food webs. For instance, Binzer et al. (2011) showed that in order to survive a species must be able to obtain enough energy, since it is a high energy supply through the food web that minimizes the species' risk of extinction, whereas other factors play only a minor role. Ingram and Steel (2010) have recently shown how incorporating ecological dependencies in models of extinction substantially inflates prediction variance. In addition, they showed that the uncertainty in the prediction of future biodiversity is considerably higher when species interactions are included in the model. We found a similar uncertainty in the prediction of extinction dynamics. Although the mean expected value of SEA increases linearly with extinction threshold, we found a substantial variability in SEA for thresholds greater than 0. In the context of how accurately we can predict future biodiversity loss, this high variability suggests that the prediction of the response of ecological communities to species loss may be intrinsically challenging.

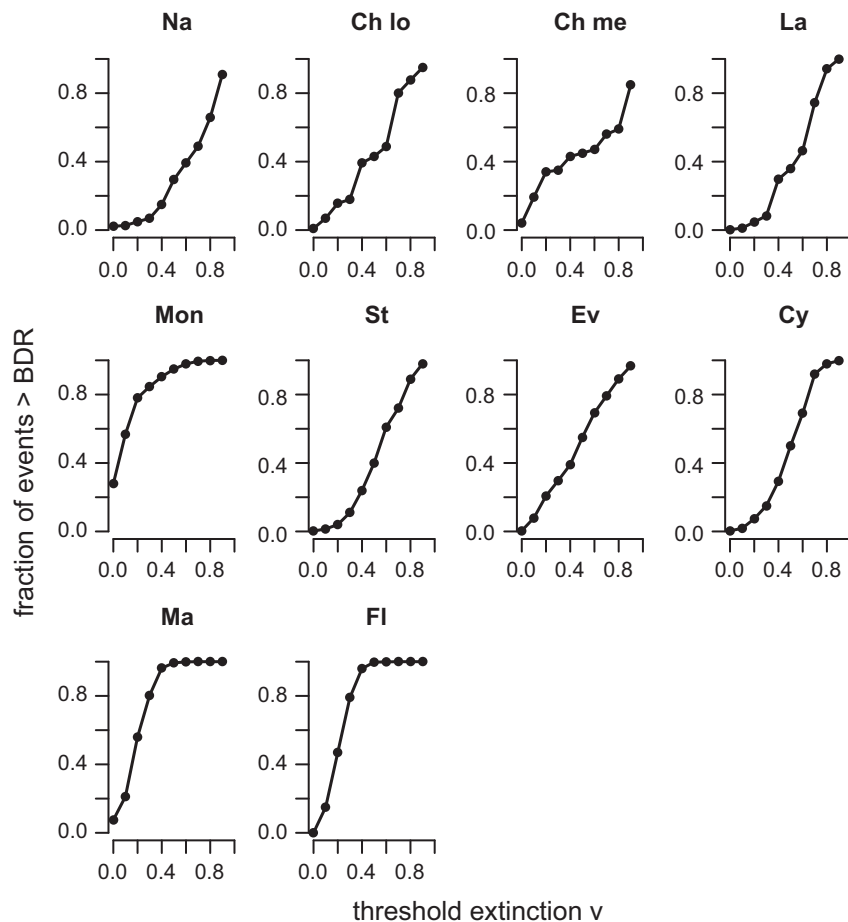


Fig. 3. Comparison of SEA with random or BDR removal. Fraction of the 10^5 simulations with secondary extinction area (SEA) with random removal of nodes greater than SEA obtained with the binary degree removal (BDR), i.e. from most to least connected criterion (y axis) as a function of extinction threshold ν (x axis) for all food webs analyzed. Since different species may have the same number of links, the SEA of BDR scenario that we used is the mean of 100 simulations. Narragansett Bay food web (Na); Cheesepeake Bay lower food web (Ch lo); Cheesepeake Bay mesohaline food web (Ch me); Lake Michigan food web (La); Mondego Estuary food web (Mo); St. Marks (St); Everglades dry food web (Ev); Cypress wet food web (Cy); Mangrove dry food web (Ma); Florida Bay wet food web (FI).

Our results show that even in the binary case, some replicates with random removal may have SEA area greater than that obtained when species are removed from the most- to the least-connected. This result, although interesting, was not unexpected, since it has been previously shown with simulation analyses that even after removing the most connected species, secondary extinctions may not occur (Dunne et al., 2002; Allesina and Bodini, 2004). In fact, connectedness is not synonymous with functional dependence or control, but only accounts for the number of links, and this may explain the absence of secondary extinctions after the primary extinction of highly connected species. A crucial area of investigation in food web theory concerns the complexity–robustness relationship, i.e. the relationship between the robustness and parameters describing food web complexity (e.g. connectance, species richness) (Dunne et al., 2002; May, 1972; McCann, 2000). Investigations using binary empirical webs did not show a clear relationship between food web robustness and species richness, whereas more connected networks were found to be more robust to primary species removal (Dunne et al., 2002, 2004). In binary models of food webs, the same positive relationship between robustness and connectance along with a positive relationship of robustness with the size of the food web have been found: larger networks would be more robust to species removal (Dunne and Williams, 2009).

When robustness of model food webs is analyzed with species extinction defined by energetic criteria (i.e. a species go extinct

before all of its prey are lost) rather than with a binary approach, it emerges that with a higher extinction threshold (higher ν), less complex webs are those that are more robust (Thierry et al., 2011). This finding suggests that the complexity–robustness relationship of model food webs may depend on the sensitivity of consumers to loss of prey.

Our analyses provided further results for empirical food webs. We found a positive relationship between the slope of the secondary extinction increase with extinction threshold and link densities (binary and quantitative) of the food webs. The quantitative unweighted link density is a measure of the complexity of the trophic flow structure in the food web and describes the average number of effective links per species in a quantitative food web (Banašek-Richter et al., 2009). We observed a faster increase of secondary extinction with an increasing extinction threshold in food webs with larger quantitative link densities. Both the positive relationships between link densities and the sensitivity of robustness to increasing extinction threshold may be explained as follows. In a food web with a greater mean number links per species, either binary or effective, each species is on average more likely to be directly affected by the removal or extinction of another species. However, when the extinction threshold is 0, each trophic interaction of a species acts as insurance against extinction—since all connections need to be lost for the species to go extinct—thus increasing the network's robustness (Dunne et al., 2002; Thierry et al., 2011). In quantitative food webs, the negative

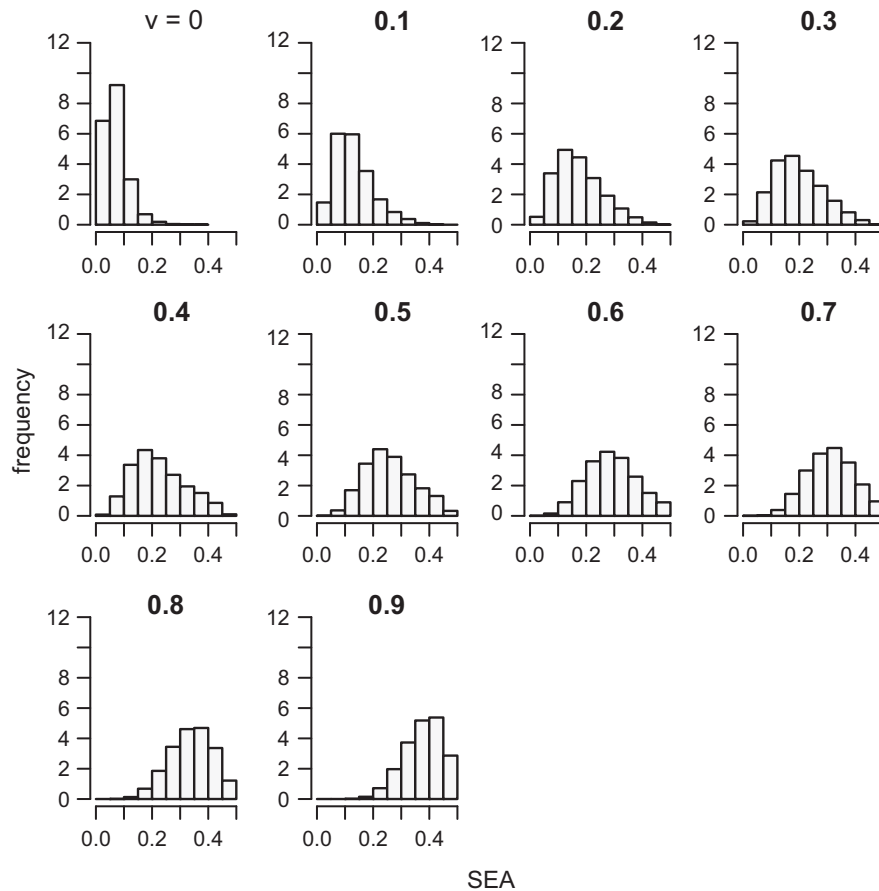


Fig. 4. SEA as a function of extinction threshold. Secondary extinction area (SEA) with random removal of nodes as a function of extinction threshold ν in Everglades dry food web (10^5 simulations). SEA ranges from 0 (i.e. no secondary extinctions following primary extinctions) to 0.5 (i.e. all species in the food web go extinct at the first removal). With increasing ν , the mode of the distribution of SEA moves to the right. With low ν , high damage (SEA close to 0.5) can occur, albeit with low probability. In the Appendix, we provide the same panels for the other food webs and parameters of a scaled beta distribution fitted on the set of 10^5 replicates for each food web.

effects of primary species extinctions propagate faster in more complex food webs. This happens because, on average, with a large energy threshold the extinction of even a single link can push a species to extinction (Herendeen, 1981).

We found an interesting pattern when we explored the sensitivity of SEA increase to increasing extinction threshold (i.e., the regression slope) as a function of connectance (i.e. the fraction of all possible links that are realized in a food web). The sensitivity of robustness had a peak for intermediate values of connectance, and this means that both low and (relatively) high connectance decrease the sensitivity of robustness to increasing energy threshold. Since larger values of connectance can be found in real food webs, further investigations with datasets providing a greater range of connectance values are necessary to confirm and interpret the processes generating the quadratic pattern.

The robustness of species-rich food webs seems to be even more sensitive to energy threshold. In a recent analysis on the size and structure of the energy flows among species, Banašek-Richter et al. (2009) found that larger webs are more richly endowed with the weak trophic interactions that recent theories have shown to be responsible for network stability, due to the role they play in dampening population oscillation (McCann et al., 1998; Neutel et al., 2002, 2007).

We found no relationship between the fraction of autotrophs and the increase in secondary extinction. This result differs from those from analyses carried out on model and real food webs, which showed that robustness of the network increases with the number of autotrophs (Dunne et al., 2002). Targeting basal species when relative few of them are present in the food web often

triggers cascading extinctions, since they tend to be more connected (i.e. have more consumers) than in webs with a larger basal species list (Dunne et al., 2002). For example, Dunne et al. (2002) showed using simulations that the removal of Scotch broom, the only autotroph species as well as one of the two highest connected species in the Scotch terrestrial food web, make the entire food web disappear. Using model food webs of 20–60 species and both topological or dynamical approaches, Curtsdotter et al., 2011 have shown that the sequential removal of basal species quickly disintegrates the food web. In our study, we deleted food web nodes at random, and a sequence in which all the autotrophs are deleted sequentially is unlikely (Dunne et al., 2002). In addition, at least 5 autotroph species are present in each of the food webs we included in our study; in a random removal scenario, the number might be sufficient to avoid extinction cascades when one autotroph, even when highly connected, is removed. The food web-specific role of autotrophs in contributing to robustness clearly deserves further investigation.

Although quantitative food webs should theoretically present a more realistic description of ecological networks, a few caveats should be noted. First, the estimation of flows among species or trophic levels is typically difficult, mainly because way more data are needed to characterize and quantify energy flows, especially in species-rich food webs, than to just characterize the network structure (Berlow et al., 2004; Pascual and Dunne, 2006). Quantitative food webs can be built starting from binary food webs, which may be constructed with gut content of individuals from each species without taking into account the relative proportion of preys in the gut. For instance, diet proportion webs are

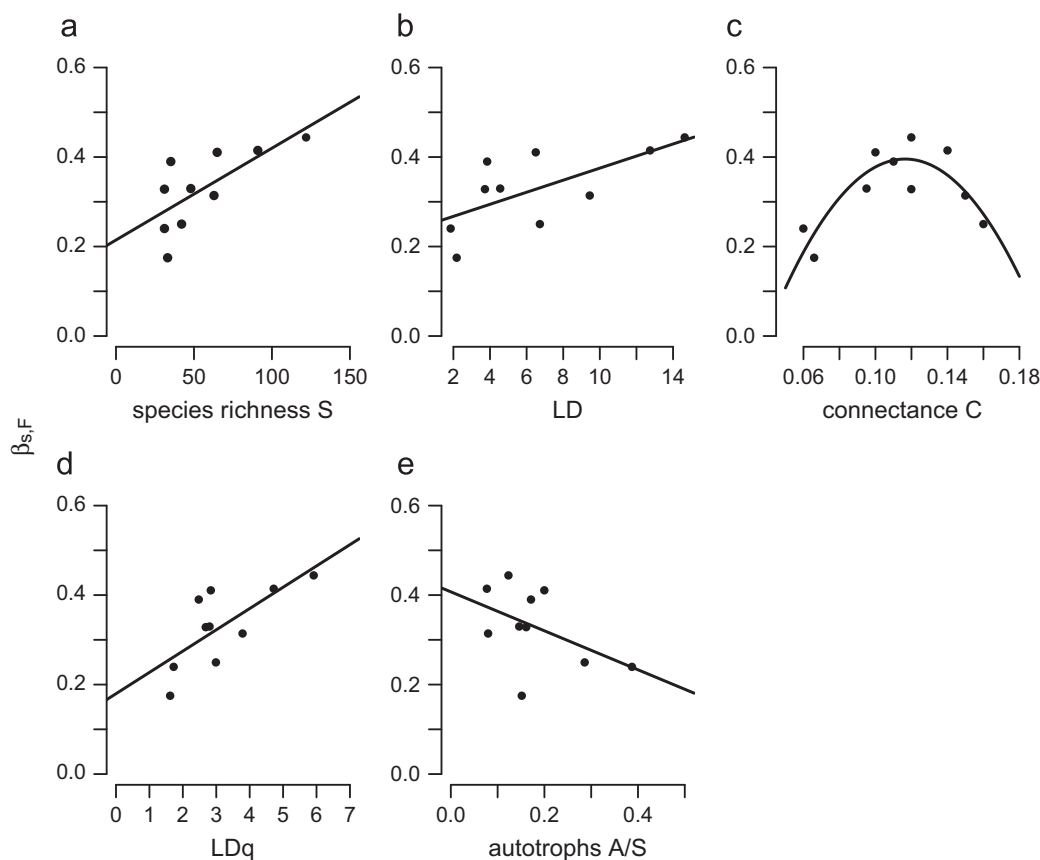


Fig. 5. Regression of $\beta_{S,F}$ on food web complexity. Linear regression of $\beta_{S,F}$ (slope of the linear model of Fig. 1) on five descriptors food web complexity: (a) species richness S (intercept \pm se $\alpha=0.21 \pm 0.05$, slope \pm se $\beta=0.002 \pm 0.0007$, $R_{adj}^2=0.44$, $p < 0.05$); (b) binary link density ($\alpha=0.24 \pm 0.04$, $\beta=0.014 \pm 0.05$, $R_{adj}^2=0.39$, $p < 0.05$); (c) connectance C (i.e. the fraction of all possible links that are realized in a food web) ($\alpha=0.4882 \pm 0.19$, marginal term $\beta_1=15.17 \pm 3.63$, quadratic term $\beta_2=-6.09 \pm 16.44$, $R_{adj}^2=0.66$, $p < 0.01$); (d) quantitative link density LDq ($\alpha=0.18 \pm 0.055$, $\beta=0.05 \pm 0.016$, $R_{adj}^2=0.46$, $p < 0.05$); (e) fraction of autotrophs A/S ($\alpha=0.41 \pm 0.05$, $\beta=-0.43 \pm 0.29$, $R_{adj}^2=0.12$, $p=0.16$).

quantitative food webs that can be built by including information on the relative proportion of food resources in the consumer diet (Woodward et al., 2005). Assimilation food webs add another layer of complexity by taking into account how much of the food resource is assimilated (thus going beyond simple ingestion of the resource) by the consumer (Benke et al., 2001).

More complex food webs can be constructed including ecological dynamics (i.e., “dynamical food webs”), that is by including functional responses, species abundances, density-dependent processes, spatial heterogeneity, meta-population dynamics, age-class structure (Dunne et al., 2005) and/or the possibility for consumers to switch preys (food web “rewiring”) (Thierry et al., 2011). In addition, there are different mechanisms driving secondary extinction cascades that can only be captured using a dynamical approach, such as top-down effects (Curtsdotter et al., 2011).

However, while several studies approached the estimation of food web robustness in dynamical models after the deletion of a single species (Ebenman et al., 2004; Eklöf and Ebenman, 2006; Petchey et al., 2008; Sahasrabudhe and Motter, 2011), only a few studies estimated robustness in (species-poor) dynamical models after sequential deletion of species (Curtsdotter et al., 2011). It remains to be seen whether the insights coming from the study of dynamical models can give rise to generalities, novel predictions, or new theory.

In our work we did not include dynamics and we assumed that consumers cannot switch from one type of prey to another (i.e. no food web “rewiring”). Exploring how our results may change when modification of trophic interaction may occur, as well as when dynamics are included, is thus encouraged (Section A.4 in the Appendix).

We are confident that our work will encourage the inclusion of energetic criteria in the analysis of responses of real ecological networks to species loss.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.jtbi.2013.04.033>.

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