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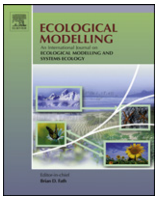

Increasing the extinction risk of highly connected species causes a sharp robust-to-fragile transition in empirical food webs

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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.

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 $W(k)\tilde{}k^{\alpha}$ 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 an 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):

$$R_{\alpha} = \frac{E}{S} \tag{1}$$

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 web), while the minimum is 1/*S* (i.e. the extinction of one species leads to the extinction of half of the species in the food web). For R_{100}, maximum and minimum values of robustness are 1 and 1/*S*, respectively.

2.3. Attack strategies

The total number of trophic interactions *k* of a species in a food web (i.e. degree of the node/species) is the sum of the number of the ingoing links (resources or prey) and the number of the outgoings links (consumers or predators).

We used two different probability mass functions to define the removal probability of species in a food web, namely the exponential and the power-law probability mass functions.

In the first case, the probability of removing a species with *k* trophic interactions with intentionality *I*, P_E $(K = k|I)$, is defined by the family of exponential probability mass functions:

$$P_E(K = k|I) = \frac{(1-I)^{(k_{\max}-k)} N_k}{\sum_{i=k_{\min}}^{k_{\max}} (1-I)^{(k_{\max}-i)} N_i} \quad 0 \le I < 1 \tag{2}$$

where $k_{\max}$ is the maximum number of trophic interactions for a species, $k_{\min}$ the minimum number, N_k the number of species with degree *k*. The subscript *E* in P_E specifies the exponential probability mass function. From now on, we simply use P_E $(k|I)$ in order to simplify notation. When $I \to 1$, we tend to sequentially remove the most connected species (intentional attack), where:

$$P_E(k|1) \equiv \lim_{I\to 1} P(k|I) = \delta k,\, k_{\max} \tag{3}$$

When $I = 0$, species are randomly removed, i.e. all nodes share the same probability of being removed:

$$P_E(k|0) = \frac{N_k}{N_{\text{tot}}} \tag{4}$$

where N_{tot} indicates the total number of nodes in the network. In the second case, the removal probability P_P $(k|I)$ of nodes is defined by the power-law probability mass function:

$$P_P(k|I) = \frac{k_i^I}{\sum_{i=1}^{N_{\text{tot}}} k_i^I} \quad 0 \le I < \infty \tag{5}$$

where k_i indicates the degree of node *i*, the exponent *I* is the intentionality parameter (corresponding to parameter α in Gallos et al., 2006) and the subscript *P* in P_P indicates the power law. With the power-law formulation, the probability of removing highly connected species increases with *I*, where for $I = 0$ species are randomly removed, and with $I \to \infty$ nodes are removed from most- to least-connected. We chose the power-law probability mass function in order to compare robustness of food webs to that of scale-free networks in Gallos et al. (2006). Examples of removal probability for three values of the intentionality parameter in (Fig. 1).

In addition, as a third scenario we removed species from the most- to the least-connected (i.e. intentional attack). The degree *k* is recalculated with each new primary extinction. In the case of ties, i.e. nodes with the same degree, we randomly ordered those nodes.

Since the result of simulations using Eq. (2), Eq. (5) and with the intentional attack are stochastic realizations, for each value of *I* and each food web we carried out 1000 simulations. We used the mean across replicates as our measure of robustness for both R_{50} $(\bar{R}_{50})$ and R_{100} $(\bar{R}_{100})$. We could not directly compare the results obtained with the two family of functions as we had to use different sets of values of *I* for the power-law and exponential probability mass functions. For the exponential removal probability function (Eq. (2)), we used *I* values obtained by bisections from $I \sim 1$ to $I = 0$ ($I = 0, 0.00098, 0.00196, 0.00390625, 0.0078125, 0.015625, 0.03125,$

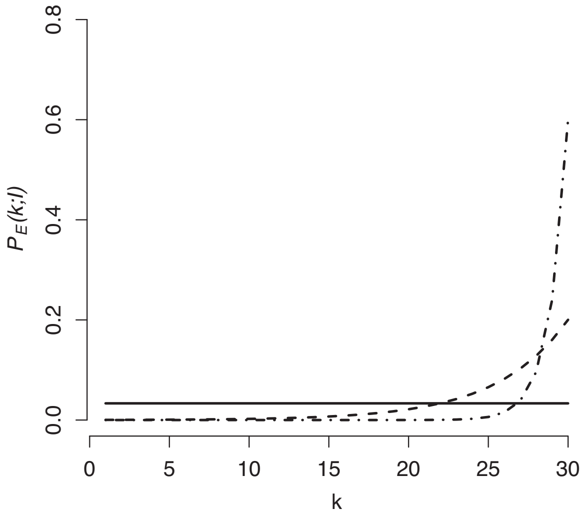

Fig. 1. Removal probability P_E $(k|I)$ of a species with *k* trophic interactions for three value of intentionality *I* (solid line, $I = 0$; dashed line, $I = 0.1$; point-dashed line, $I = 0.2$) in Eq. (2) (exponential probability mass function) for St Marks food web. The solid horizontal line represents the random removal extinction scenario. The probability of removing highly connected species increases with *I*.

$0.0625, 0.125, 0.25, 0.5, 0.9999$). We used the following bisections in order to analyse in greater details the increase of the removal probability in the highest degrees region.

For the power-law removal probability function (Eq. (5)), we used the same set of *I* values used by Gallos et al. (2006) ($I = 0, 0.25, 0.5, 1, 2, 4$) in order to directly compare the response of scale-free networks presented in Gallos et al. (2006) to that of food webs.

A visual inspection of plots of robustness *R* ($\bar{R}_{50}$ and $\bar{R}_{100}$) vs. *I* when using the exponential function in Eq. (2) showed that *R* was fairly constant for increasing *I* up to a threshold value after which it sharply declined with further increases of *I*. To fit these trajectories, we used two-phase regression models, that is regression models in which two straight lines are connected at a breakpoint I_t, in the form:

$$\begin{cases} R = \alpha_1 + \beta_1 I & \text{for} \quad I < I_t \\ R = \alpha_2 + \beta_2 I & \text{for} \quad I \ge I_t \end{cases}$$

with the restriction for continuity $\alpha_1 + b_1 I_t = \alpha_2 + \beta_2 I_t$. We fitted the two-phase regressions using the library *segmented* available for *R* (R Development Core Team, 2011). Parameters estimation proceeds in two parts: a generalized linear model (GLM) is first fitted to the data, then a broken-line relationship (estimation of slopes and breakpoint) is added by re-fitting the model. We used Davies test for significant difference-in-slope (Davies, 1987). We set statistical significance at the 0.05 level. We carried out all simulations and statistical analyses using *R* 2.14.0 (R Development Core Team, 2011).

2.4. Robustness–complexity relationship

We used linear regressions on both linear and log–log scales to explore the relationship between I_t and two parameters describing food web complexity, namely species richness (*S*) and connectance ($C = L/S^2$) (Table 1). We used AIC to select the best model (we corrected the likelihood when the response variable was log-transformed).

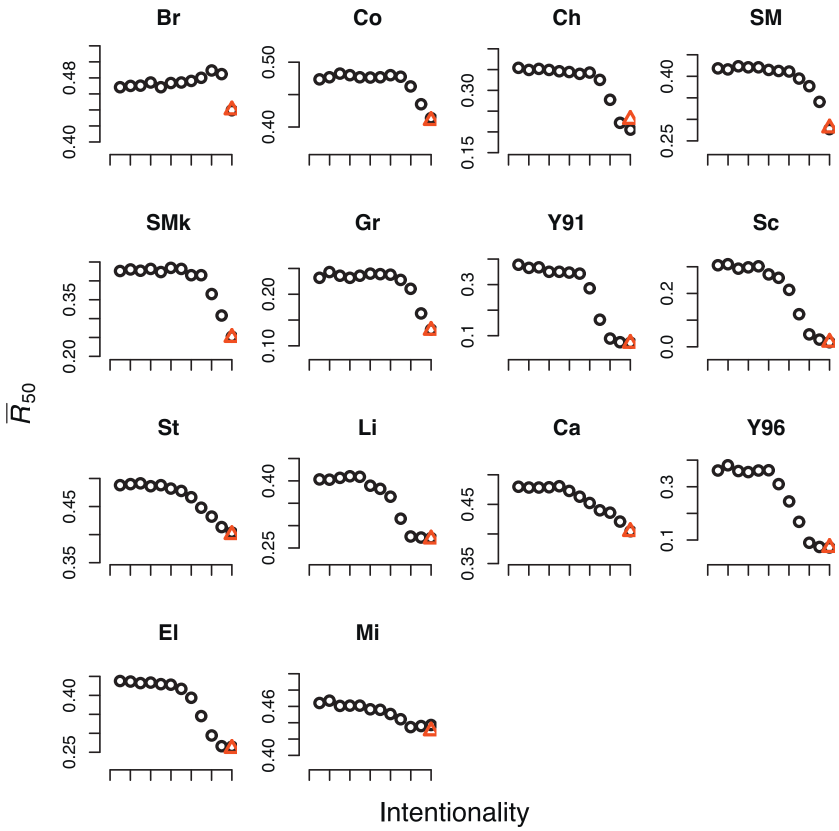

Fig. 2. Robustness $\bar{R}_{50}$ as a function of intentionality I when using the exponential function in Eq. (2) for each of the 14 food webs we analysed. Note that the y axis is different for each food web in order to facilitate the visual analysis of patterns. ○ represents results using the exponential probability function; △ (in red) indicates $\bar{R}_{50}$ for the intentional attack, from most- to least-connected species. Almost food webs show a slow decrease of $\bar{R}_{50}$ when I increases (Bridge, Coachella, Little Rock and Canton Creek food webs show a little increase) and then a sharp decrease after a critical value of I. The key on each panel identifies the food web as reported in Table 1. Left to right $I = 0$, 0.00098, 0.00196, 0.00390625, 0.0078125, 0.015625, 0.03125, 0.0625, 0.125, 0.25, 0.5, 0.9999. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

3. Results

3.1. Exponential

Using the exponential probability mass function, a value of intentionality close to 1 (i.e. close to the maximum value allowed by the probability mass function) was necessary across food webs to obtain robustness values for both $\bar{R}_{50}$ and $\bar{R}_{100}$ comparable to those obtained with the intentional attack (Figs. 2 and 3).

For increasing I, we observed a slow-to-fast decrease in robustness after reaching a threshold value (Figs. A1 and A2). The Davies test for difference-in-slope was significant for each food web and for both $\bar{R}_{50}$ and $\bar{R}_{100}$ (Table 2). For all the food webs, the slope of the regression line for values of intentionality $I > I_t$ was on average an order of magnitude greater than the slope of the regression line for $I < I_t$ (Table 2). Only in Mirror lake food web (for $\bar{R}_{50}$) a sharp decrease in robustness was not observed. Interestingly, some food webs showed an increase in robustness with increasing intentionality before the sharp decline in robustness for values of I greater than I_t.

3.2. Power-law

For both measures of robustness, increasing intentionality generally decreased robustness, although for two food webs (Bridge for $\bar{R}_{50}$ and Coachella for $\bar{R}_{100}$) robustness tended to increase for values of I up to 2. Across food webs, robustness for $I = 1$ in Eq. (5) was substantially greater than robustness obtained with the intentional attack for both $\bar{R}_{50}$ and $\bar{R}_{100}$ (Figs. 4 and 5). Table A.1 shows the ratio between robustness obtained with $I = 1$ in Eq. (5) and robustness obtained with the intentional attack. Only when setting $I = 4$ in Eq. (5), and only for some food webs, we obtained values of robustness similar to the one given by the intentional attack.

3.3. Relationship between breakpoint and complexity

Food web connectance C showed no statistically significant relationship with breakpoint I_t for $\bar{R}_{50}$ with variables either on either linear or log–log scale, while we found a negative relationship between C and I_t for $\bar{R}_{100}$ on both scales ($p < 0.01$, Table A2 and Fig. A3). We found a negative linear relationship between species richness and I_t on both linear and log-log scales ($p < 0.01$, Table A2 and Fig. A3). AIC strongly indicated the model on the linear scale as the best one. We found a negative linear relationship between S and the breakpoint of the two-phase regression I_t for $\bar{R}_{100}$ ($p < 0.01$), and also in this case AIC was lower for the model on the linear scale (Table A2 and Fig. A3).

4. Discussion

Our study shows that when increasing the probability of deleting highly connected species there is a sharp transition in system behaviour, from a region where food webs show high resistance to species loss ('*random removal regime*') to a region where robustness decreases rapidly and quickly reaches the robustness obtained with the sequential attack from most- to least-connected species ('*intentional attack regime*'). This pattern was particularly clear when using the exponential probability removal function, although a fast

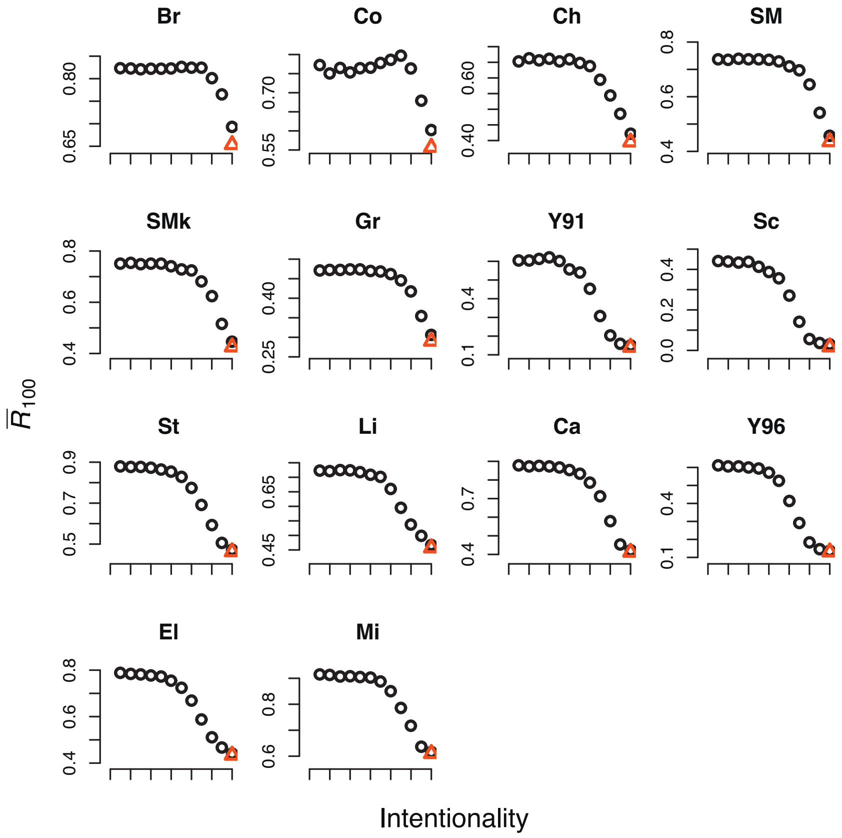

Fig. 3. Robustness $\bar{R}_{100}$ as a function of intentionality I when using the exponential function in Eq. (2) for each of the 14 food webs we analysed. Note that the y axis is different for each food web in order to facilitate the visual analysis of patterns. △ (in red) indicates $\bar{R}_{100}$ for the intentional attack, from most- to least-connected species. For the exponential function, almost all food webs show a slow decrease of $\bar{R}_{100}$ when the intentionality of the removal criterion is increased (Bridge, Coachella and YThan Estuary 91 food webs show a slight increase of robustness with increasing I) and then a sharp decrease after a critical value of intentionality is reached. The key on each panel identifies the food web as reported in Table 1. Left to right $I = 0$, 0.00098, 0.00196, 0.00390625, 0.0078125, 0.015625, 0.03125, 0.0625, 0.125, 0.25, 0.5, 0.9999. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

decrease in robustness with increasing intentionality was observed in the majority of food webs when using the power-law probability mass function, in particular for $\bar{R}_{100}$.

For $\bar{R}_{100}$, we found that connectance increased the value of intentionality at which the transition between the two regimes of robustness occurred (i.e. breakpoint of the two-phase regression) (Table A2). This result suggests that food webs with greater connectance are less affected than low-connectance food webs by an increase of the extinction risk of highly connected species. This result is in agreement with previously investigations showing an increase of food web robustness with connectance (Dunne et al., 2002a, 2004; Dunne and Williams, 2009). The regime transition at a larger value of intentionality that we found in our analyses for food webs with higher connectance may have two different explanations. First, it may be related to the buffer provided by an high number of trophic connections against further extinctions in the event of species loss (Dunne et al., 2002a). Second, it may be explained by the degree-distribution of food webs, which typically changes from distributions similar to power-law to exponential or uniform with increasing connectance (Dunne, 2006; Dunne et al., 2002b; Montoya and Sole, 2003). In fact, in food webs with highly skewed degree-distribution, highly connected species are more likely to function as “hubs” and their extinction may have dramatic effects on the stability of ecosystems, while in food webs with a more uniform degree-distribution the extinction of highly connected species leads to a lower number of secondary extinction, thus preserving food web stability.

However, when using $\bar{R}_{50}$ as a measure of robustness, we did not observe a significant relationship between connectance and robustness, even after removing a clear outlier.

On the contrary, for both robustness measures we observed a negative linear relationship between the breakpoint of the two-phase regression and species richness (S). In empirical food webs, no relationship is typically found between robustness and species richness (Dunne et al., 2002a, 2004), whereas in model food webs species richness increases robustness (Dunne and Williams, 2009). In our extinction scenarios, larger food webs seem to be more sensitive to the increase of intentionality (i.e. to the preferential targeting of highly connected species). Also this pattern may be explained by variations in the shape of the degree-distribution, as its skewness tends to increase with species richness (Montoya and Sole, 2003). In terms of conservation ecology, this result suggests that protecting highly connected species may be more important in larger ecosystems. In fact, a smaller value of the breakpoint of the two-phase regression of robustness on intentionality (i.e. the transition from ‘random removal’ to ‘intentional attack’ regime) increases the probability of falling in the intentional attack regime in the case highly connected are preferentially targeted. Since in larger food webs the transition in system behaviour occurred for lower values of intentionality, it follows that the preservation of highly connected species may be particularly important for the stability of larger ecosystems.

In addition, this threshold effect strongly suggests that when modelling extinction dynamics to carefully assign or estimate a risk of primary extinction to species as a function of their

Table 2
Two-phase linear regression of the robustness measures ($\bar{R}_{50}$ and $\bar{R}_{100}$) on intentionality I for the exponential probability function. The breakpoint I_t indicates the value of the intentionality at which the transition of system response occurred (i.e. slow-to-fast decrease in robustness). β_1 and β_2 are the slopes of the straight lines on the left and on the right of I_t, respectively, while α_1 and α_2 are the respective intercepts. We present standard errors for all parameters estimates except for α_2, since it was calculated and not estimated in the two-phase regression. p-Values of the Davies test for difference-in-slope are all smaller than 0.01 except for $\bar{R}_{50}$ for Mirror ($p = 0.078$).

Food web	Breakpoint I_t	β_1	β_2	α_1	α_2
$\bar{R}_{50}$					
Bridge Brook Lake	0.9 ± 0.01	0.0021 ± 0.00034	−0.03 ± 0.0009	0.463 ± 0.011	0.8
Coachella Valley	0.163 ± 0.002	0.00017 ± 0.0003	−0.0244 ± 0.002	0.4769 ± 0.002	0.7055
Cheasepeake Bay	0.095 ± 0.002	−0.0018 ± 0.001	−0.04168 ± 0.003	0.3551 ± 0.006	0.6949
St Martin Island	0.194 ± 0.03	−0.0023 ± 0.0009	−0.0499 ± 0.0049	0.4263 ± 0.005	0.8807
St Marks Seagrass	0.1175 ± 0.004	−0.000716 ± 0.0008	−0.05483 ± 0.003	0.4306 ± 0.005	0.911
Grassland	0.17 ± 0.05	−0.000301 ± 0.0007	−0.0398 ± 0.004	0.2377 ± 0.004	0.606
Ythan Estuary 91	0.025 ± 0.003	−0.00618 ± 0.008	−0.0587 ± 0.012	0.3812 ± 0.003	0.7289
Scotch Broom	0.022 ± 0.0002	−0.00553 ± 0.006	−0.0527 ± 0.008	0.3158 ± 0.02	0.6153
Stony Stream	0.027 ± 0.001	−0.0012 ± 0.001	−0.0156 ± 0.001	0.4918 ± 0.003	0.5883
Little Rock Lake	0.011 ± 0.002	0.00186 ± 0.0043	−0.0236 ± 0.005	0.4006 ± 0.014	0.537
Canton Creek	0.0115 ± 0.013	0.00014 ± 0.001	−0.01081 ± 0.001	0.4787 ± 0.003	0.5386
Ythan Estuary 96	0.015 ± 0.002	−0.0029 ± 0.008	−0.0534 ± 0.01	0.3717 ± 0.03	0.6695
El Verde Rainforest	0.026 ± 0.003	−0.00187 ± 0.002	−0.03421 ± 0.002	0.4394 ± 0.01	0.6551
Mirror Lake	0.011 ± 0.006	−0.00124 ± 0.001	−0.00408 ± 0.001	0.4665 ± 0.004	0.4818
$\bar{R}_{100}$					
Bridge Brook Lake	0.34 ± 0.008	0.0004 ± 0.0007	−0.054 ± 0.00375	0.8213 ± 0.004	1.345
Coachella Valley	0.18 ± 0.001	0.0041 ± 0.0013	−0.081 ± 0.0074	0.7501 ± 0.008	1.571
Cheasepeake Bay	0.072 ± 0.0002	−0.0009 ± 0.0012	−0.053 ± 0.0023	0.660 ± 0.0053	1.078
St Martin Island	0.17 ± 0.0009	−0.0042 ± 0.0012	−0.094 ± 0.007	0.7496 ± 0.007	1.578
St Marks Seagrass	0.096 ± 0.001	−0.003977 ± 0.002	−0.0816 ± 0.0042	0.761 ± 0.007	1.424
Grassland	0.11 ± 0.009	−0.00113 ± 0.001	−0.0483 ± 0.003	0.4754 ± 0.005	0.8879
Ythan Estuary 91	0.0122 ± 0.03	0.0011 ± 0.012	−0.0794 ± 0.014	0.6058 ± 0.039	1.054
Scotch Broom	0.0123 ± 0.002	−0.0059 ± 0.011	−0.0688 ± 0.013	0.4500 ± 0.037	0.8009
Stony Stream	0.027 ± 0.01	−0.004848 ± 0.0034	−0.0765 ± 0.0048	0.888 ± 0.013	1.37
Little Rock Lake	0.026 ± 0.009	−0.00245 ± 0.0021	−0.049 ± 0.003	0.7283 ± 0.008	1.042
Canton Creek	0.045 ± 0.04	−0.0066 ± 0.0038	−0.0986 ± 0.008	0.8913 ± 0.017	1.576
Ythan Estuary 96	0.0135 ± 0.01	−0.0043 ± 0.011	−0.082 ± 0.013	0.6168 ± 0.036	1.062
El Verde Rainforest	0.02 ± 0.0003	−0.0059 ± 0.004	−0.0598 ± 0.0051	0.7963 ± 0.014	1.134
Mirror Lake	0.038 ± 0.004	−0.0038 ± 0.0022	−0.0619 ± 0.0041	0.9202 ± 0.001	1.34

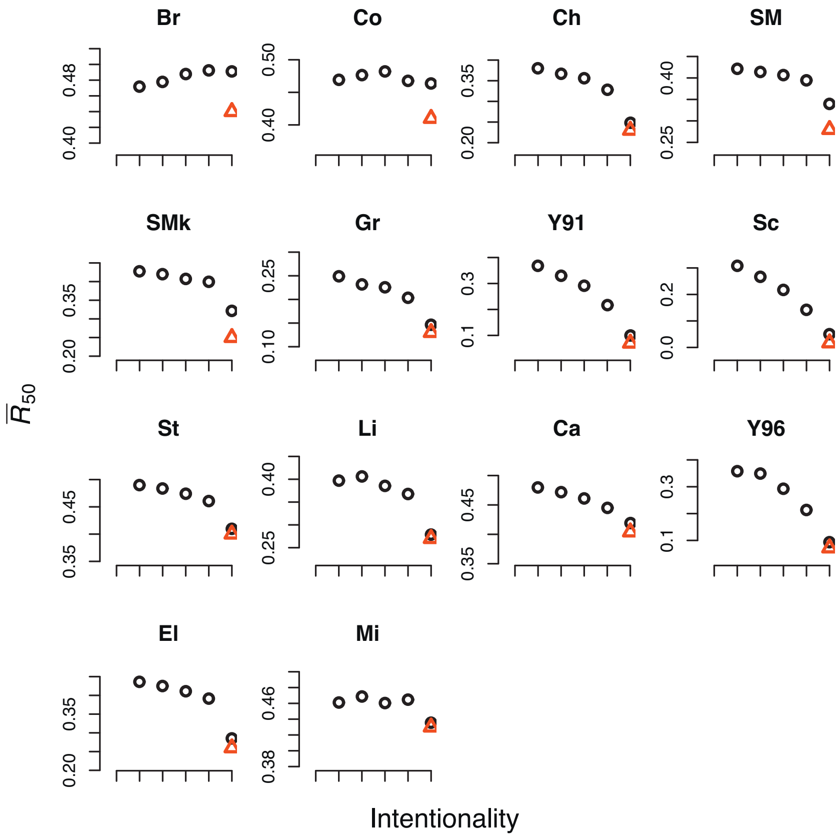

Fig. 4. Robustness $\bar{R}_{50}$ as a function of intentionality I when using the power law function in Eq. (5) for each of the 14 food webs we analysed. △ (in red) indicates $\bar{R}_{50}$ for the intentional attack, that is with sequential primary extinctions from the most- to the least-connected species. Left to right $I = 0, 0.25, 0.5, 1, 2, 4$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

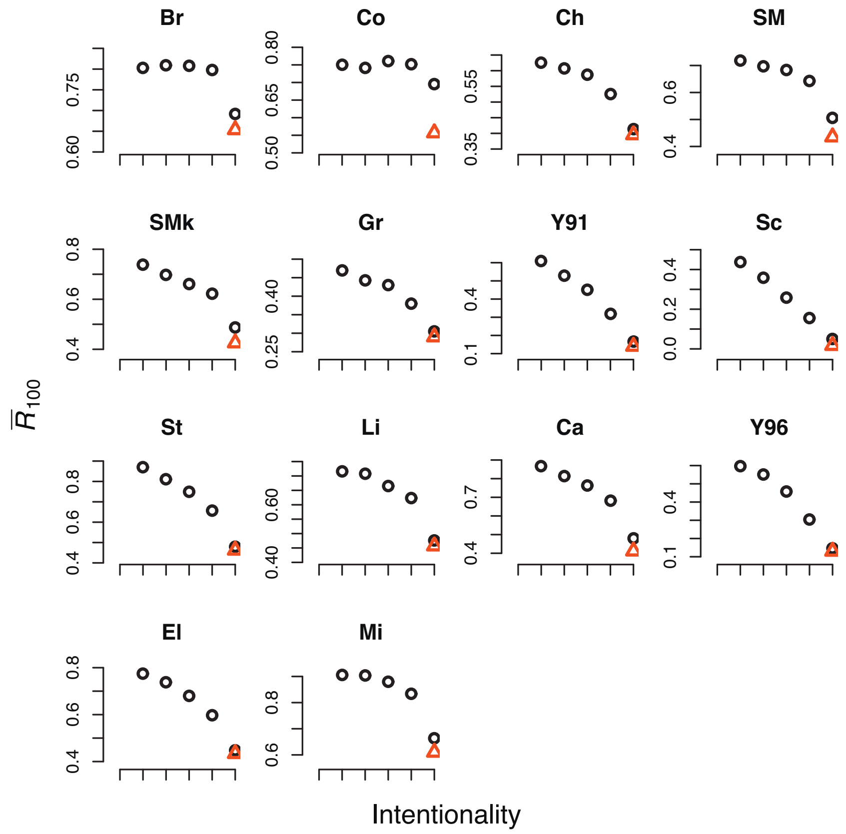

Fig. 5. Robustness $\bar{R}_{100}$ as a function of intentionality I for the power law function in Eq. (5) for each of the 14 food webs we analysed. △ (in red) indicates $\bar{R}_{100}$ for the intentional attack, that is with sequential primary extinctions from the most- to the least-connected species. Left to right $I = 0$, 0.25, 0.5, 1, 2, 4.

number of trophic links. In fact, intentionality values slightly smaller or bigger than the breakpoint of the two-phase regression may lead to substantially different patterns of secondary extinction, as well as largely different estimates of food web robustness.

When using the power-law function to define the extinction probability of highly connected species, patterns of robustness of food webs differed from those showed by Gallos et al. (2006) for scale-free networks. Scale-free networks are typically highly robust to random removal of nodes, but become fragile when highly connected nodes are removed. In scale-free networks, the attack with $I = 1$ in Eq. (5) can reduce the percolation threshold in scale free network to $p_c = 0.25$, from $p_c = 1$ when nodes are randomly removed ($I = 0$) (Gallos et al., 2006). Contrary to what found for scale-free networks, a small increase in the extinction risk of highly connected species does not strongly reduce the robustness of food webs. This is likely to be ascribed to the structural differences between scale-free networks and food webs. First, the number of nodes N is much smaller in food webs (typically <200, in our study $9 < N < 140$) than in scale-free networks (>1000) (Camacho et al., 2002; Dunne, 2006). Second, food webs exhibit smaller maximum node degree, and the degree-distribution in food webs is in general less skewed than a power-law (Camacho et al., 2002; Dunne, 2006). Clearly, with respect to a scale-free network, a smaller maximum degree of the food web along with a less skewed degree-distribution would reduce the probability of attacking highly connected nodes with an increase of intentionality. Since scale free networks did not show a threshold response to the increase in the intentionality parameter (Gallos et al., 2006), the emergence of the breakpoint does not seem to be a general occurrence in all networks.

An interesting question is how the addition of ecological dynamics may modify the results presented here. In addition, the food webs we analysed in this work are binary, i.e. they describe only the presence of trophic interaction and do not describe the amount of energy passing from resource to consumer (i.e. interaction strength). Thus, it would be interesting to use our methodology with weighted food webs, that is food webs including information about the amount of the energy and matter passing along a trophic interaction (Bellingeri and Bodini, 2012; Bodini et al., 2009; Thierry et al., 2011). Finally, the same approach we used in the present work could be applied to food webs where rewiring (i.e. modification of trophic interactions) may occur. Rewiring in the food web may simply occur when a predator consumes prey species not included in the trophic data. However, in modern data sets it is unlikely that potential resources resulting from switching prey go unregistered (Allesina and Pascual, 2009). Alternatively, food web rewiring may occur when following the extinction of one of its competitors (competitive release), a consumer might expand its diet to include a prey that it had previously been not available (Staniczenko et al., 2010, Thierry et al., 2011). Finally, a consumer species forages on the subset of possible prey items that provides it with the highest net energy intake per unit effort (optimal foraging strategy). Following the loss of its preferred prey item(s), a predator may expand its diet to include novel resources (Thierry et al., 2011). All the above processes can thus be potentially included in the analysis of food webs and exploring how food web robustness changes with increasing intentionality when modification of trophic interaction may occur is thus encouraged.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2012.12.011.

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