

# Food webs robustness to biodiversity loss: The roles of connectance, expansibility and degree distribution

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## Abstract

We analyse the robustness of food webs against species loss by considering the influence of several structural factors of the networks, such as connectance, degree distribution and expansibility. The last concept refers to the absence of structural bottlenecks in the food web, whose removal separate the network into large isolate clusters. In theory networks with identical connectance can display different expansibility characteristics. Using the spectral scaling method we studied 17 food networks and classified them as good expansion (GE) and not-GE networks. The combination of GE properties and degree distribution of species permitted the classification of food webs into six different classes. These classes characterize the differences in robustness of food webs to species loss. While the webs having uniform degree distributions and displaying GE properties are the most robust to species loss, the presence of bottlenecks and skewed distribution of the number of links per species make food webs very vulnerable to primary removal of species.

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## 1. Introduction

A way to consider the interrelationship between several aspects of an ecosystem—species interactions, ecosystem structure and function—is by analysing the structure of food webs (Green et al., 2005). These are complex networks describing trophic relationships between species in an ecological system. In a network representation of a food web, nodes represent species and links represent who eats whom in the ecosystem (Proulx et al., 2005). This kind of representation permits to analyse the similarities and differences between complex systems of very different nature, ranging from technological to biological and social systems (Strogatz, 2001; Albert and Barabási, 2002; Newman, 2003). For instance, it was concluded from empirical analysis that several real-world systems, such as Internet, World Wide Web, power grids, metabolic and neural networks, are very vulnerable to loss of the most connected nodes due to their “scale-free” nature (Albert

et al., 2000). “Scale-free” networks are those showing a power-law distribution of the number of links per nodes, the so-called degree distribution (DD). Most food webs have less-skewed uniform or exponential DDs (Dunne et al., 2002a). However, they also display high fragility to intentional removal of the most connected nodes (Dunne et al., 2002b). According to Dunne et al. (2002b), robustness in food webs increase with connectance (links/species<sup>2</sup>) but it is independent of species richness and omnivory. Low connectance webs display extreme sensitivity to loss of the most connected nodes, but this sensitivity decreases as the connectance of the web increases. The connectance of a web is a global topological characteristic of the system, which accounts for the organization of these links across the web. Such link organization can give rise to the existence of certain topologies that can affect the robustness of a food web to species loss. In this work, we have analysed some of these organizational characteristics in food webs, such as the web expansibility, which accounts for the lack of structural bottlenecks in the network. We have shown that food webs with good expansion (GE) characteristics and displaying

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uniform DD are the most robust to species loss. On the other side, food webs with skewed DDs and lacking GE properties are very vulnerable to the loss of the most connected species as well as to certain key species connecting large communities in the web. The role of connectance for the appearance of such topological characteristics is also investigated and we determined that webs with high connectance display GE and uniform DD with higher probability than networks with low connectance.

## 2. Theoretical motivation

Connectance,  $C$ , is a global topological measure of the complexity of food webs which is defined as the fraction of observed links ( $E$ ) divided by the squared number of species ( $N^2$ ) in the web (Dunne et al., 2002b). This quantity measures the “interaction richness” of a network and it has been found to be relevant in explaining food web robustness. According to Dunne et al. (2002b) food webs with high connectance are significantly more robust to removals of the most connected species than low connectance webs, which display extreme sensitivity from the outset. They found that the removal of less than 25% of species produces the complete collapse of the lowest connectance webs ( $0.07 < C$ ). In webs with intermediate values of connectance,  $0.06 < C < 0.14$ , it is necessary that 20–30% of species be removed to collapse the network. However, this threshold is increased up to 40–50% of primary species removals for food webs with high connectance, e.g.  $C > 0.15$ . Thus, it is interesting to investigate how connectance influences the organization of nodes and links in a food web in such a way that might determine its robustness in a significant way. In order to explore this relationship we have selected an “artificial” web formed by 18 nodes and 33 links, which gives an intermediate value of connectance,  $C = 0.102$ . This web is illustrated in Fig. 1 where we have marked in blue the four most connected nodes. Removing these four nodes, which represent 22% of the total number of nodes, makes that the network collapses forming four isolated clusters, the largest ones having only 5 nodes. This experiment confirms the observations of Dunne et al. (2002b) that 20–30% of species removals are necessary to collapse networks with intermediate connectance. In addition, we have created another network with identical connectance obtained by a random rewiring of the original network. This new web not only has the same connectance but also the same distribution of links per nodes than the original network. In this case (see Fig. 1) the removal of the most connected nodes does not produce the collapse of the web but only divided it into two clusters, the larger one still having 72% of the nodes in the original web. To make that this web collapses completely it is necessary to remove 50% of the nodes in the original network, which is characteristic of high connectance networks according to the findings of Dunne et al. (2002b). However, we have

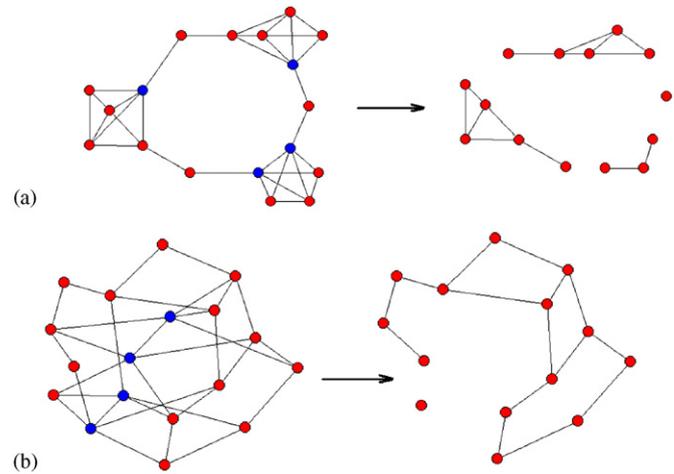


Fig. 1. Schematic illustration of node removal in two networks with identical connectance and node degree distribution (DD). (a) Network formed by three main clusters connected by few links. The four most connected nodes coincide with the bottlenecks, thus their removal collapses the web to several small isolated clusters (right network). (b) Random rewiring of network shown in A, which improves the GE properties keeping constant the connectance and DD. The removal of the same four hubs does not produce the collapse of the web, which remains as a main cluster containing 72% of original nodes.

seen that this web has identical connectance,  $C = 0.102$ , and links per node distribution than the original one. Consequently, the question does not appear to be how much interaction richness a network has but how are these links distributed across the network. In network A of Fig. 1 it is evident that there are three clusters having large internal connectances ( $C_{int} > 0.32$ ) but displaying low number of inter-clusters connections. The three nodes connecting these clusters are simply *bottlenecks*. This situation changes in the second network where these clusters do not exist and there are not bottlenecks. The topological characteristics displayed by a network lacking these structural bottlenecks are studied by means of the *network expansibility* properties.

## 3. Network expansibility

We start by defining informally the concept of network expansibility. A food web having “good expansion” properties is the one that cannot be divided in at least two isolated “large” parts by disconnecting a “small” number of nodes or links (Sarnak, 2004; Gkantsidis et al., 2006). These nodes or links, which make the function of bridges between these parts, are known as *bottlenecks*. Consequently, a “Good Expansion Network” (GEN) is a network without bottlenecks (Gkantsidis et al., 2006). Formally, a network is considered to have GE if every subset  $S$  of nodes ( $S \leq 50\%$  of the nodes) has a neighbourhood that is larger than some “expansion factor”  $\phi$  multiplied by the number of nodes in  $S$ . A neighbourhood of  $S$  is the set of nodes, which are linked to the nodes in  $S$ . For each vertex  $v \in V$  (where  $V$  is the set of nodes in the network), the neighbourhood of  $v$ , denoted as  $\Gamma(v)$  is

defined as:  $\Gamma(v) = \{u \in V | (u, v) \in E\}$  (where  $E$  is the set of links in the network). Then, the neighbourhood of a subset  $S \subseteq V$  is defined as the union of the neighbourhoods of the nodes in  $S$ :  $\Gamma(S) = \bigcup_{v \in S} \Gamma(v)$  and the network has GE if  $\Gamma(v) \geq \phi |S| \forall S \subseteq V$ .

In a GEN there is the same possibilities for going from one node to another located at any part of the network. However, non-GENs are formed by at least two main clusters having large density of intra-cluster connections, but low connectivity between nodes in the different clusters. Consequently, the possibilities for visiting neighbours of a node inside a cluster are different than the ones for visiting a node located into the other cluster. The high density of intra-cluster links permits the existence of many different ways for travelling from one node to another inside a cluster. On the contrary, for going from one cluster to another it is necessary to transverse the bottleneck, which are the very few connections between the different chunks of the network.

Based on this fundamental difference between GENs and non-GENs it is possible to design a method for identifying expansibility properties in a food web. Our approach consists in measuring the probability that an “information” emitted at an arbitrary node of the web travels to any other node by visiting an infinitely large number of (not necessarily different) links of the network. In networks with GE properties this probability should be proportional to the probability that this information returns to this node after visiting the (not necessarily different) links in the neighbourhood of this point. Of course, this proportionality is lost in networks lacking expansibility. This is a consequence of the difference in the large number of ways that exist for visiting the neighbourhood of a node and the reduced number of ways in going from it to another node located in a different cluster.

Let  $W_L(i)$  designate the number of walks of length  $L$  starting at node  $i$  and let  $W_L(G)$  be the total number of walks of this length existing in the network. We will consider walks of extremely large lengths, in such a way that we can consider  $L \rightarrow \infty$ . The probability that a “long-range” walk selected at random in the network has started at node  $i$  is simply

$$P_L(i) = \frac{W_L(i)}{W_L(G)}. \quad (1)$$

This probably increases with the density as well as with the regularity of the network. In the first case, in a network having a large proportion of links to nodes there is a high probability that a walk selected at random has started in an arbitrary node  $i$ . This probability is equal to one when all nodes are interconnected to each other. On the other hand, this probability is also equal to one when all nodes have the same number of links. In these cases every walk of infinite length starting at any node of the network will visit necessarily at least one of the other nodes, but because all nodes are equivalent, it guarantees that the walk will necessarily visit node  $i$ .

This probability can be obtained from the graph spectral properties of a network. The “spectrum” of a network is a listing of the *eigenvalues* of the adjacency matrix of such network. Let  $\vec{\gamma}$  be an  $n$ -dim real vector;  $\vec{\gamma}$  can be thought as a function on the nodes of the network. We say that  $\vec{\gamma}$  is an *eigenvector* of the matrix  $\mathbf{A}$  with *eigenvalue*  $\lambda$  if and only if  $\vec{\gamma} \mathbf{A} = \lambda \vec{\gamma}$ . It is well known that every  $n \times n$  real symmetric matrix  $\mathbf{A}$  has a spectrum of  $n$  orthonormal eigenvectors  $\vec{\gamma}_1, \vec{\gamma}_2, \dots, \vec{\gamma}_n$  with eigenvalues  $\lambda_1 \geq \lambda_2 \geq \dots \geq \lambda_n$ .

It is known that for non-bipartite connected network such as those studied in this work, with nodes  $1, 2, \dots, n$ , for  $L \rightarrow \infty$ , the vector  $[P_L(1) \ P_L(2) \ \dots \ P_L(n)]$  tends toward the eigenvector corresponding to the largest eigenvalue of the adjacency matrix of the network (Cvetković et al., 1997). Consequently, if  $\lambda_1$  designates the largest eigenvalue of the network and  $\gamma_1$  is the eigenvector corresponding to  $\lambda_1$ , then the elements of  $\gamma_1$  represent the probabilities of selecting at random a walk of length  $L$  starting at node  $i$  when  $L \rightarrow \infty$ :  $\gamma_1(i) = P_L(i)$ .

In a similar way we can account for the probability that a “short-range” walk selected at random in the network has started and ended at node  $i$ . This probability can be written as follows:

$$P_S(i) = \frac{SC_{odd}(i)}{SC_{odd}(G)}, \quad (2)$$

where the term  $SC_{odd}$  refers to the *odd subgraph centrality*, which accounts for the participation of a node in all subgraphs containing at least one odd cycle but giving more weight to closest neighbours (Estrada and Rodríguez-Velázquez, 2005a, b). This weighting scheme guarantees the “short-range” nature of this parameter because walks visiting very distant nodes receive a very small weight in the sum (Estrada and Rodríguez-Velázquez, 2005a).

We have previously shown that  $SC_{odd}(i)$  can be calculated by using the graph spectrum in the following form (Estrada and Rodríguez-Velázquez, 2005a, b):

$$SC_{odd}(i) = \sum_{j=1}^N [v_j(i)]^2 \sinh(\lambda_j). \quad (3)$$

Because  $SC_{odd}(G)$  is simply the sum of  $SC_{odd}(i)$  for all nodes in the network we can use the values of  $SC_{odd}(i)$  directly instead of using  $P_S(i)$ . The approach that study the existence of a correlation between  $P_L(i)$  and  $SC_{odd}(i)$  is designated as *spectral scaling method* (Estrada, 2006).

#### 4. Spectral scaling method

The relationship between expansibility and graph spectrum has been known from some time. For instance, it is known that for a network to be a *good expander*, the second eigenvalue,  $\lambda_2$ , of the adjacency matrix must, compared to the index  $\lambda_1$ , should be as small as possible

(Sarnak, 2004; Gkantsidis et al., 2006). However, the main question for the analysis of GE properties of real-world networks is the problem of determining how large the spectral gap must be for the network has GE properties. We tackle this problem by the following way. First we write  $SC_{odd}(i)$  in the following form:

$$SC_{odd}(i) = [\gamma_1(i)]^2 \sinh(\lambda_1) + \sum_{j=2} [\gamma_j(i)]^2 \sinh(\lambda_j), \quad (4)$$

where  $\gamma_1(i)$  is the  $i$ th component of the principal eigenvector and  $\lambda_1$  is the principal eigenvalue of the network.

If we consider the extreme case of a network consisting of two separated (identical) components we obtain that the difference between the largest and second largest eigenvalues (spectral gap) is zero:  $\Delta\lambda = 0$ . The inclusion of a “small” number of links joining together these two components will change the values of the first two eigenvalues but the spectral gap remains close to zero. However, when the number of links connecting both clusters increases, the spectral gap also increases, reaching its maximum when every pair of nodes is connected to each other. Consequently, it is known that when a network has bottlenecks:  $\lambda_1 \approx \lambda_2$ . On the contrary, in cases where the network is a GEN  $\lambda_1 \gg \lambda_2$ . In these cases it is evident that the first term of (3) will be much larger than the second one,  $[\gamma_1(i)]^2 \sinh(\lambda_1) \gg \sum_{j=2} [\gamma_j(i)]^2 \sinh(\lambda_j)$ . Thus, for food webs with expansibility properties we will have that

$$SC_{odd}(i) \approx [\gamma_1(i)]^2 \sinh(\lambda_1) \quad (5)$$

and the principal eigenvector of the network will be directly related to the subgraph centrality in GENs according to the following expression:

$$\gamma_1(i) \propto A [SC_{odd}(i)]^\eta, \quad (6)$$

where  $A \approx [\sinh(\lambda_1)]^{-0.5}$  and  $\eta \approx 0.5$ . This means that a linear correlation exists between the  $\gamma_1(i)$  and  $SC_{odd}(i)$  for GENs, which in a log–log scale can be written as (Estrada, 2006):

$$\log[\gamma_1(i)] = \log A + \eta \log[SC_{odd}(i)]. \quad (7)$$

Consequently, a log–log plot of  $\gamma_1(i)$  vs.  $SC_{odd}(i)$  has to show a linear fit with slope  $\eta \approx 0.5$  and intercept  $\log A$  for GENs. This scaling is simply a confirmation of the expansibility of this network due to the lack of bottlenecks as we have previously analysed by means of the existence of proportionality between  $P_L(i)$  and  $P_S(i)$  or  $SC_{odd}(i)$ .

A criterion of the “good expansion character” of a food web is given by the deviation from this scaling plot

$$\xi(G) = \sqrt{\frac{1}{N} \sum_{i=1}^N \{\log[\gamma_1(i)] - [\log A + \eta \log[SC_{odd}(i)]]\}^2}. \quad (8)$$

Food webs with perfect GE will have  $\xi(G) = 0$ . On the other hand, the higher the value of  $\xi(G)$  the larger the departure of the web from GE properties.

### 5. Food webs data sets

The following are the names and description of the food webs studied here, including the number of species (network nodes),  $N$ , and trophic relationships (network links),  $E$ . Benguela ( $N = 29$ ,  $E = 191$ ) represents a marine ecosystem of Benguela off the southwest coast of South Africa (Yodzis, 1998). Bridge Brook Lake ( $N = 75$ ,  $E = 542$ ) represents pelagic species from the largest of a set of 50 New York Adirondack lake food webs (Havens, 1992). Canton Creek ( $N = 108$ ,  $E = 707$ ) is formed primarily by invertebrates and algae in a tributary of the Taieri River, surrounded by pasture, in the South Island of New Zealand (Townsend et al., 1998). Chesapeake Bay ( $N = 33$ ,  $E = 71$ ) represents the pelagic portion of an eastern US estuary, with an emphasis on larger fishes (Baird and Ulanowicz, 1989). Coachella Valley ( $N = 30$ ,  $E = 241$ ) is formed by a wide range of highly aggregated taxa from the Coachella Valley desert in southern California (Polis, 1991). El Verde ( $N = 156$ ,  $E = 1439$ ) represents insects, spiders, birds, reptiles and amphibians in a rainforest in Puerto Rico (Waide and Reagan, 1996). Grassland ( $N = 75$ ,  $E = 113$ ) represents all vascular plants and all insects and trophic interactions found inside stems of plants collected from 24 sites distributed within England and Wales (Martinez et al., 1999). Little Rock Lake ( $N = 181$ ,  $E = 2318$ ) is formed by pelagic and benthic species, particularly fishes, zooplankton, macroinvertebrates, and algae of the Little Rock Lake, Wisconsin, US (Martinez, 1991). Reef Small ( $N = 50$ ,  $E = 503$ ) is a Caribbean coral reef ecosystem from the Puerto Rico-Virgin Island shelf complex (Opitz, 1996). Scotch Broom ( $N = 154$ ,  $E = 366$ ) contains trophic interactions between the herbivores, parasitoids, predators and pathogens associated with broom, *Cytisus scoparius*, collected in Silwood Park, Berkshire, England, UK (Memmott et al., 2000). Shelf ( $N = 81$ ,  $E = 1451$ ), is a marine ecosystem on the northeast US shelf (Link, 2002). Skipwith Pond ( $N = 35$ ,  $E = 353$ ) represents invertebrates in an English pond (Warren, 1989). St. Marks Seagrass ( $N = 48$ ,  $E = 218$ ) is formed mostly by macroinvertebrates, fishes, and birds associated with an estuarine seagrass community, *Halodule wrightii*, at St. Marks Refuge in Florida (Christian and Luczkovich, 1999). St. Martin Island ( $N = 44$ ,  $E = 218$ ) represents interactions between birds and predators and arthropod prey of *Anolis* lizards on the island of St. Martin, which is located in the northern Lesser Antilles (Goldwasser and Roughgarden, 1993). Stony Stream ( $N = 112$ ,  $E = 830$ ) is similar to Canton Creek but in native tussock habitat (Townsend et al., 1998). Ythan1 ( $N = 134$ ,  $E = 593$ ) is formed mostly by birds, fishes, invertebrates, and metazoan parasites in a Scottish Estuary (Huxham et al., 1996) and Ythan2 ( $N = 92$ ,

$E = 416$ ) is a reduced version of Ythan1 with no parasites (Hall and Raffaelli, 1991).

## 6. Expansibility in food webs

We have used the spectral scaling method (Estrada, 2006) to determine the GE properties of the 17 food webs studied here. We consider that a food web has GE properties if it has simultaneously  $\zeta(G) < 0.01$ , slope = 0.500 and  $r > 0.999$ . Based on these criteria we found that 70% of food webs can be clearly classified as GENs and 5 networks display departure from good expansibility, which classify them as non-GEN. In Table 1 we give the values of all these parameters for the 17 food webs.

The five food webs lacking GE properties are Scotch Broom, Grassland, Chesapeake, Canton and Stony. There are significant differences in the topological organization of these webs, which are only partially manifested in the parameters compiled in Table 1. These differences are better seen in Figs. 1 and 2 where we have plotted the spectral scaling for all food webs studied. In Fig. 2 we plot this scaling for webs with uniform DD and in Fig. 3 we plotted those having exponential or power-law DDs. As can be seen in these figures the plots for Scotch Broom, Chesapeake and Grassland display dispersions of points at both sides of the “ideal” scaling—in a very low degree for Scotch Broom and very large for the other two. The ideal scaling corresponds to the line  $\log[\gamma_1(i)] = \log A + 0.5 \cdot \log[SC_{\text{odd}}(i)]$ , with intercept  $\log A = \log\{\sinh(\lambda_1)\}^{-0.5}$ . On the contrary, Stony and Canton webs only display

“positive” deviations from the ideal scaling. We call “positive” (negative) deviations from the ideal scaling when the points of the plot stand over (under) the straight line of ideal scaling.

We have further investigated the possible structural causes of these positive deviations from ideality in the case of Stony and Canton food webs. This situation can occur when the probability that a “short-range” walk selected at random in the network has started (and ended) at node  $i$ ,  $P_S(i)$ , is lower than expected compared with the probability that a “long-range” walk selected at random in the network has started at node  $i$ ,  $P_L(i)$ . In other words, when there is a group of nodes, which are “well-communicated” with all other nodes in the web but having a very low cliquishness, compared with the rest. The simplest model for this situation is conceived by a network formed by a central core of highly interconnected nodes, some of them having at least one cluster connected to them. For the sake of simplicity we selected clusters of only one node, i.e. pendant nodes. We illustrate this type of network in Fig. 4 together with its spectral scaling plot.

The nodes in the central core are in red and those in the periphery, which are all pendant nodes, are in blue. As can be seen the spectral scaling only shows positive deviations from the ideal plot, which is the situation observed for Canton and Stony food webs. These two networks can also be partitioned into two parts, one consisting of highly interconnected nodes forming a “central core” and a series of nodes in the “periphery”. In the case of Canton web these two series are formed by 54 species. The central core

Table 1  
Topological characteristics of food webs grouped according to their degree distribution (DD) and expansibility characteristics

Network	DD	$\lambda_1$	$\Delta\lambda$	$r$	Slope	$\zeta(G)$
<i>GENs with uniform degree distribution</i>						
Benguela	U	15.228	11.147	0.9998	0.50	$6.30 \times 10^{-3}$
Coachella	U	18.147	13.058	1.0000	0.50	$7.18 \times 10^{-5}$
Skipwith	U	22.076	18.648	1.0000	0.50	$6.16 \times 10^{-5}$
St. Marks	U	11.865	6.934	0.9999	0.50	$2.90 \times 10^{-3}$
Reef Small	U	23.756	15.174	1.0000	0.50	$4.31 \times 10^{-5}$
Bridge Brook	U	20.639	7.943	1.0000	0.50	$9.00 \times 10^{-3}$
Shelf	U	41.916	30.193	1.0000	0.50	$6.75 \times 10^{-5}$
<i>GENs with exponential or power-law degree distribution</i>						
St. Martin	E	12.531	5.559	0.9999	0.50	$1.50 \times 10^{-3}$
Ythan2	E	15.771	9.635	0.9999	0.50	$2.92 \times 10^{-3}$
Ythan1	E	16.737	9.272	0.9999	0.50	$1.50 \times 10^{-3}$
Little Rock	E	40.816	14.643	1.0000	0.50	$3.72 \times 10^{-5}$
El Verde	E	31.494	22.082	1.0000	0.50	$4.50 \times 10^{-5}$
<i>Non-GENs</i>						
Chesapeake	U	5.745	1.215	0.9824	0.48	0.094
Stony	U	22.702	16.423	0.9905	0.50	0.219
Grassland	P	5.524	1.274	0.6150	0.31	0.518
Canton	E	19.559	12.524	0.9930	0.49	0.183
Scotch Broom	P–E	14.714	8.714	0.9997	0.50	0.020

The principal eigenvalue,  $\lambda_1$ , of the adjacency matrix representing the network and the spectral gaps,  $\Delta\lambda$ , are provided together with the parameters of the spectral scaling method: correlation coefficient,  $r$ , slope and expansion character,  $\zeta(G)$ .

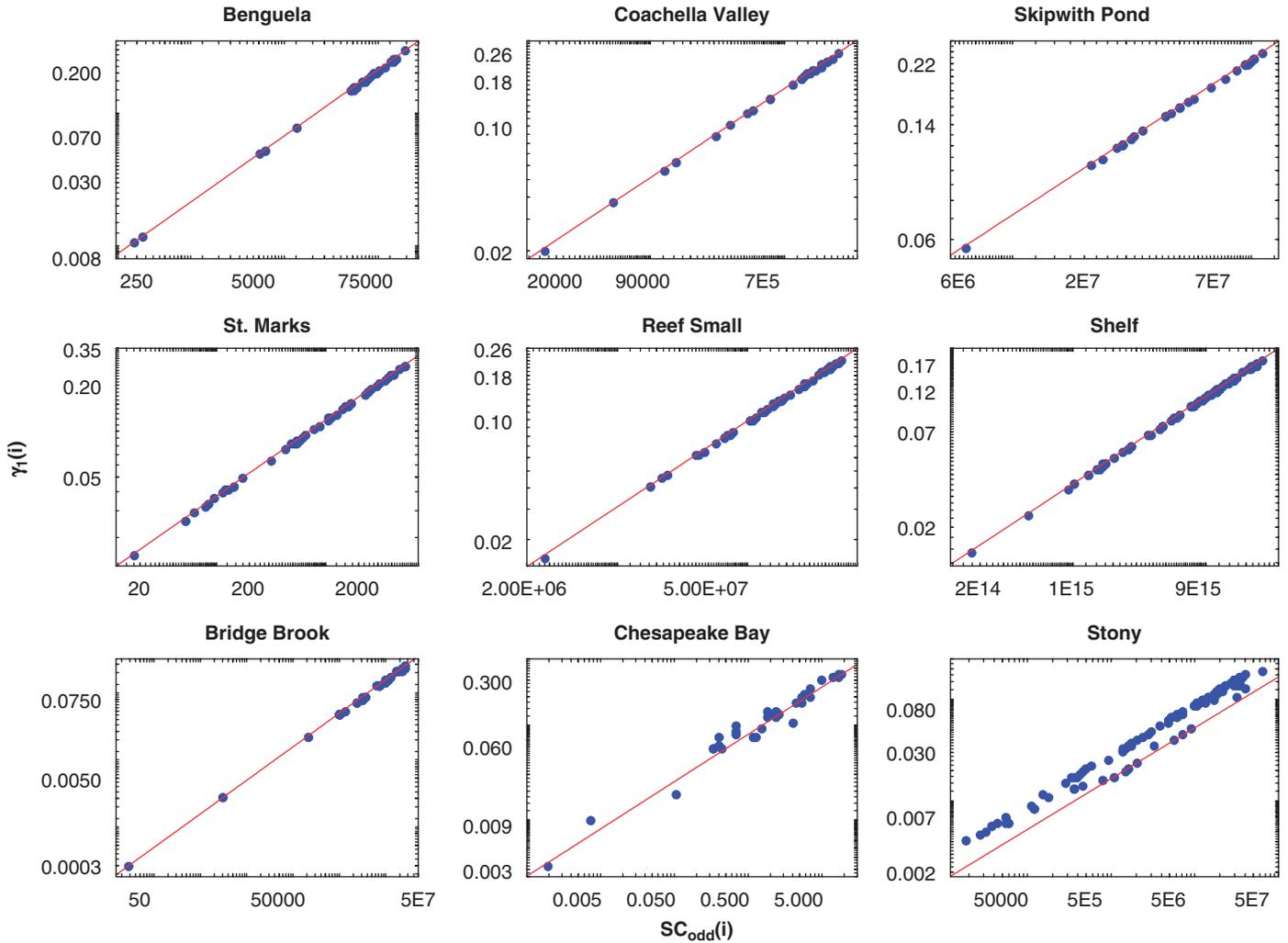


Fig. 2. Spectral scaling plots of food webs displaying uniform degree distributions. The abscissa represents the odd subgraph centrality of each species—a weighted sum of the number of odd closed walks starting at this node—and the ordinate represent the entry of the principal eigenvector of the adjacency matrix of the web corresponding to this species, which is also known as the eigenvector centrality. The straight line illustrated in every plot corresponds to the ideal scaling (see text for explanation).

has 454 trophic links and the periphery has only 30 links. There are 223 links between species in the central core and those in the periphery. This means that 64% of all links in this network are between species in the central core, while only 31% of trophic interactions occur between this core and the periphery. In the case of Stony web there are 51 nodes in the central core, which share 60% of all trophic links in this web. The other 61 species are in the periphery and share only 27 links between them. The number of connections between the central core and the periphery represents only 36.4% of all trophic interactions in the network. In both cases the core-periphery links represent the bottleneck, which produce the lack of GE in these food webs.

The situation in the other three food webs is more “classical” (Estrada, 2006). They consist of a series of highly interconnected clusters which share only very few links between them. In Chesapeake Bay food web there are two main clusters, which are connected through 10 trophic

links representing 14% of the total links in the web. There are only four species whose removal separate the web into two isolated clusters. In Grassland food web there are at least 5 main clusters interconnected only by 10% of the links in the web. There are several bottleneck nodes but the disconnection of only two of them separate the network into five isolated clusters. In Scotch Broom the clusters are interconnected only by 6% of the trophic links in the web and the removal of seven bottleneck nodes, which represents 4.5% of the total number of species in the web, makes the network collapses into several disconnected chunks. In Fig. 5 we illustrate the five food webs lacking GE properties: Chesapeake, Grassland, Scotch Broom, Canton and Stony. In the first two webs, we illustrate the bottleneck nodes in different sizes and shapes and for the last two webs we represent the core-periphery structure. The consequences of these structures for the robustness of food webs to loss of biodiversity is analysed in the following paragraphs.

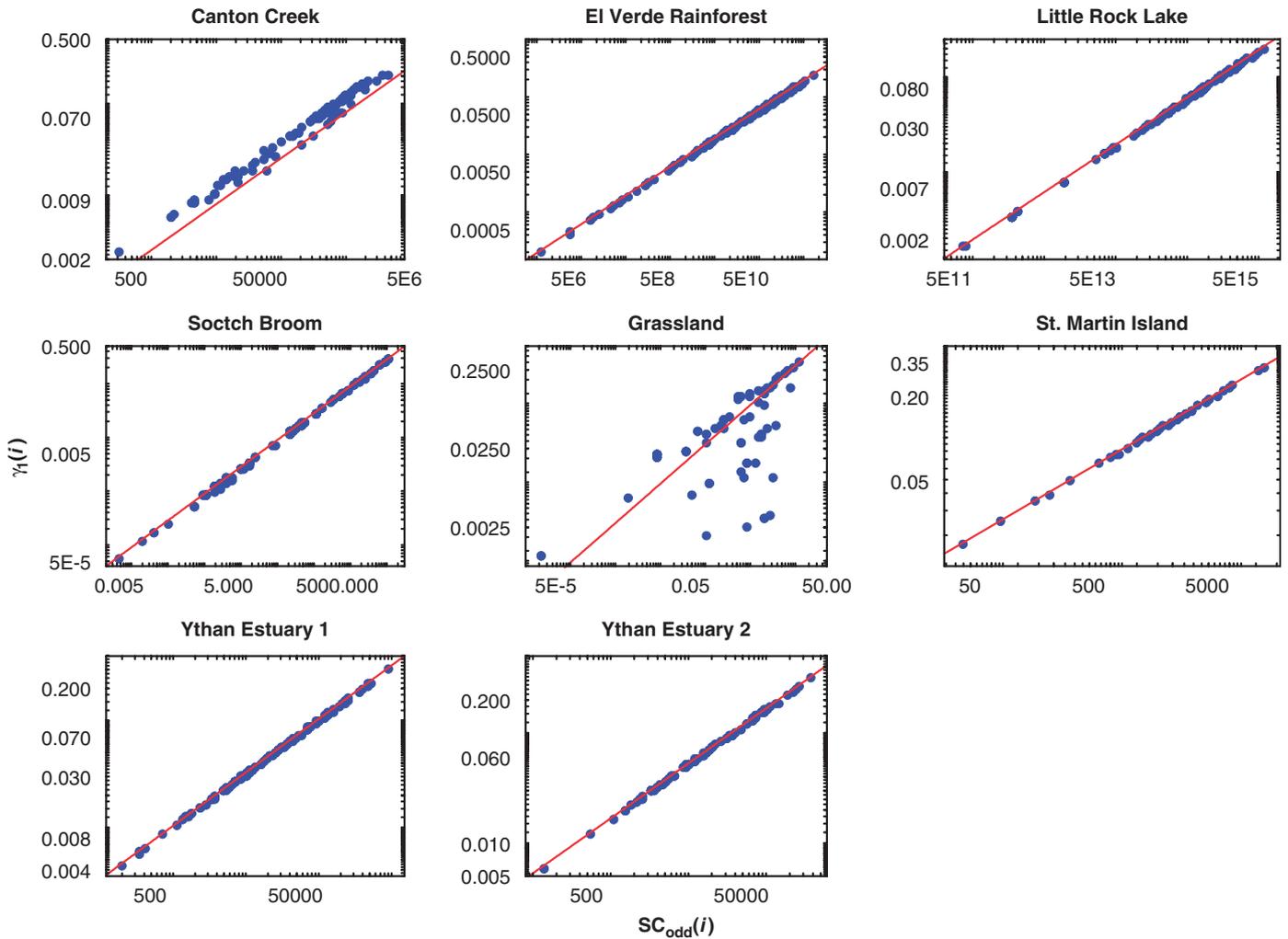


Fig. 3. Spectral scaling plots of food webs displaying skewed degree distributions—power-law or exponential (see caption of Fig. 1 for explanation).

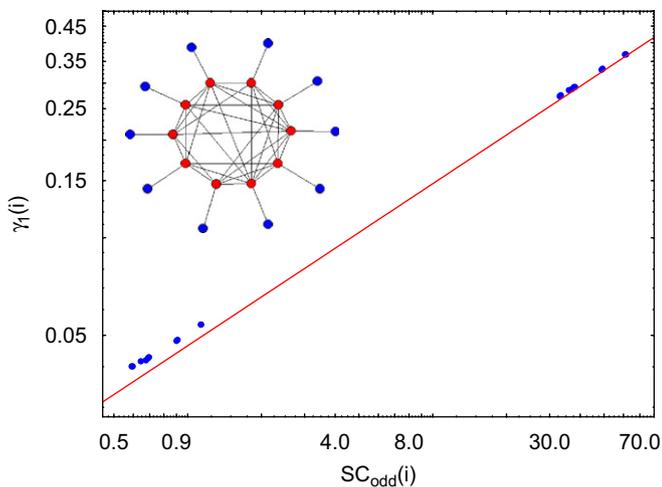


Fig. 4. Spectral scaling plot of an artificial network showing a core-periphery structure. The core, represented by red nodes, corresponds to a number of highly interconnected nodes. The periphery, illustrated by blue nodes, are nodes connected to the core through few links. The spectral scaling of these networks is characterized by positive deviations of points (see text for explanation).

## 7. Food web robustness

The analysis of link distributions of nodes has received great attention in the literature related to complex networks (Barabási and Albert, 1999; Albert and Barabási, 2002; Newman, 2003; Mitzenmacher, 2004; Keller, 2005; Sollow, 2005). This analysis is concerned with the question of how many nodes are characterized by different numbers of neighbour nodes in the network, which is known as the DD of the web. The influence that the DD has on the resilience of complex networks against random failures and intentional attacks is well-known since the publication of the seminal paper of Albert et al. (2000). They showed that networks displaying power-law DD—the so-called “scale-free” networks—are very vulnerable to the removal of the most connected nodes, which produces a catastrophic fragmentation of the network. However, most food webs have less-skewed exponential or uniform DDs (Dunne et al., 2002a). Exponential networks are also very vulnerable to the removal of the most connected nodes but in a least pronounced way than for power-law networks (Albert

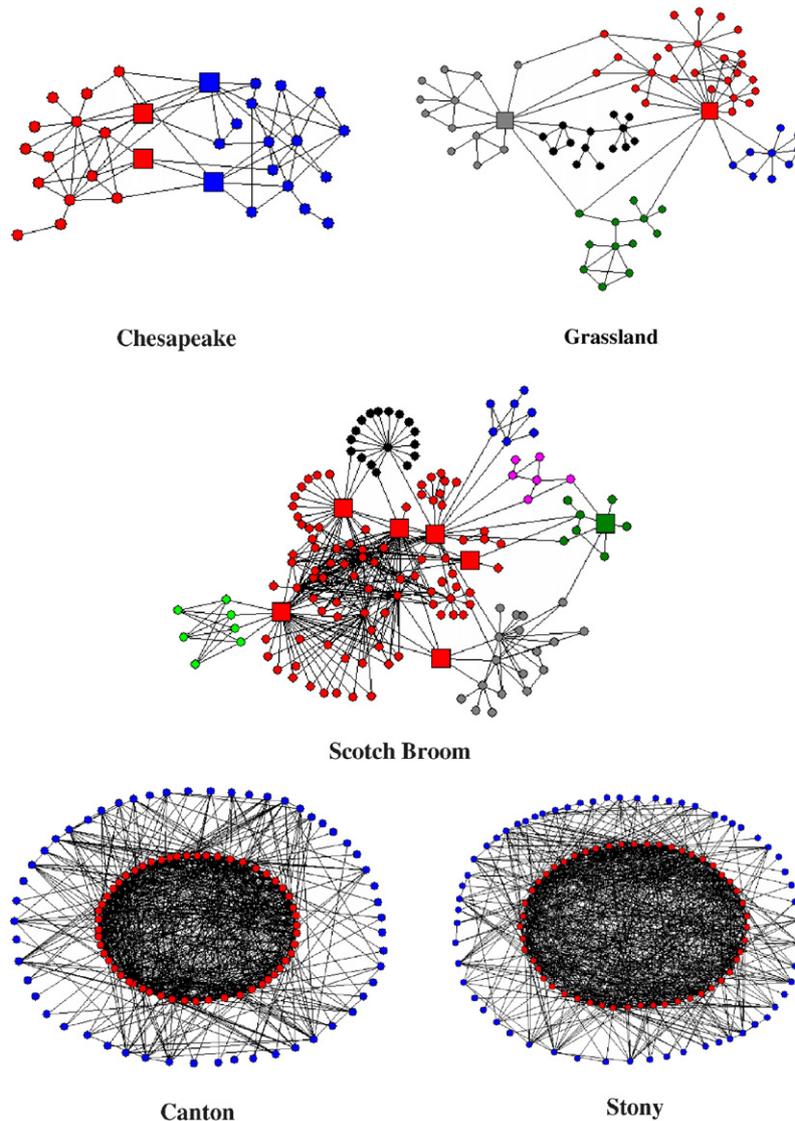


Fig. 5. Representation of the topological structure of the five food webs lacking good expansion properties. The first three webs represent “classical” non-GENs in which several highly connected clusters are linked by very few links. Bottleneck nodes are illustrated as large squares. The last two networks correspond to webs with core-periphery structure. Cores are represented as central nodes in red and periphery as external nodes in blue.

et al., 2000). However, exponential networks are catastrophically fragmented by random removal of nodes while in scale-free networks no threshold for fragmentation is observed for random failures. On the contrary, networks with a uniform DD are expected to be more robust against intentional removal of the most connected nodes than networks with more skewed DD.

Considering the relevance of DD in network robustness we have considered this parameter in our analysis of food webs vulnerability to species loss. In particular we are interested in the intentional removal of certain species in the food web more than in the random extinction of species. As Dunne et al. (2002b) have correctly pointed out the anthropogenically caused species and population extinctions are far from being random as human have historically tended to impact higher trophic levels in the ecosystems. In addition to species DD we also consider the

food web expansibility as an important topological parameter related to network robustness. Food webs lacking GE properties are very vulnerable to the removal of bottleneck species and trophic relations. In these food webs the extinction of very few species connecting two or more separated clusters will produce the collapse of the ecosystem to several isolated groups of species. Similarly, the removal of trophic links between these bottleneck species will have catastrophic consequences on the web structure.

Considering these two factors—DD and expansibility—we have classified food webs into six different groups:

- *Group I*: Food webs displaying uniform DD and GE properties.
- *Group II*: Food webs with uniform DD without GE properties due to a core-periphery organization.

- *Group III*: Food webs with uniform DD but lacking GE properties due to the presence of bottleneck nodes.
- *Group IV*: Food webs with skewed (power-law or exponential) DD and GE properties;
- *Group V*: Food webs with skewed (power-law or exponential) DD without GE properties due to a core-periphery organization.
- *Group VI*: Food webs with skewed (power-law or exponential) DD without GE properties due to the presence bottleneck nodes.

nodes/links that when removed separate the network in at least two isolated parts. However, food webs with uniform DD but having bottlenecks are very vulnerable to both removal of most connected species and removal of bottleneck nodes. In Fig. 6a we illustrate the effects of species removal on the cumulative secondary extinctions of species. It can be seen in this figure that food webs in group III are significantly more vulnerable than networks in group I to biodiversity loss. The food webs displaying skewed DD and GE properties (group IV) are as vulnerable as networks in group III to the removal of the most connected species. However, in this group the presence of a few bottleneck nodes makes the network very vulnerable to their removal. As observed in Fig. 6a removing these bottleneck nodes produces a catastrophic

Food webs in the group I are expected to be more robust to intentional removal of species. In these networks all species have approximately the same number of trophic links and due to lack of bottlenecks there are not a few

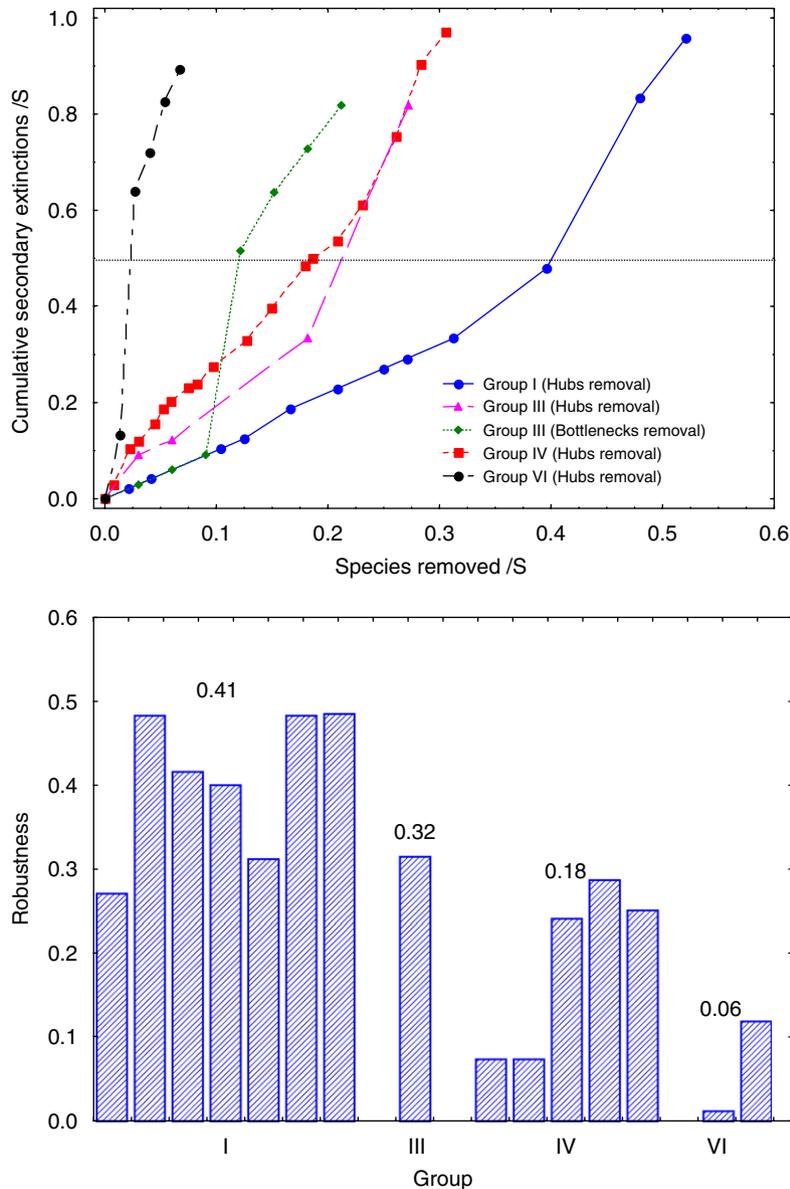


Fig. 6. Secondary extinctions resulting from primary species removal in food webs of different groups according to the classification introduced in this work (see text for explanation). The network of group I corresponds to St. Marks food web, that of group II corresponds to Chesapeake Bay, and the ones of groups IV and V correspond to Ythan Estuary 1 and Grassland, respectively.

collapse of the web in a more sensitive way than removing the most connected species. In consonance with this observation, food webs of group VI are the most vulnerable ones to species loss because they have a very sensible combination of hubs and bottlenecks whose elimination produce a catastrophic collapse of these webs. In Fig. 6a, we show the effects of hubs removals in the Grassland food web, which is in group VI. The removal of bottleneck species has the same effect because in this case there is a coincidence between hubs and bottlenecks (see also Fig. 5). In Fig. 6b, we illustrate the robustness of food webs to species loss for the different groups identified in this work (groups II and V are excluded, see further). The robustness of food webs to species loss was taken from Dunne et al. (2002b, 2004) who measured it as the fraction of species that had to be removed in order to result in a total loss of  $\geq 50\%$  of the species. At the top of each group we give the average robustness for the group calculated as the average value for all webs in the group. We can clearly observe that the trend of robustness predicted in this work due to the classification of networks in different groups coincides with the robustness obtained by Dunne et al. (2002b, 2004) by removing the most connected species in the web.

Groups II and V of food webs correspond to networks displaying a core-periphery organization as illustrated for Canton and Stony in Fig. 5. They have not been represented in Fig. 6 because their vulnerability is not related to species loss (as analysed in this figure) but they are extremely vulnerable to the loss of trophic links. For instance, the elimination of the trophic links connecting the core to the periphery make these networks collapse retaining only the species, which are interconnected in the core of the web. In the Stony food web, which has this structure and a uniform DD, the removal of 36.4% of links—those connecting the core and periphery species—produces the extinction of 54.5% of species. In the case of Canton food web, which has a core-periphery structure and an exponential DD, the removal of only 31% of (core-periphery) trophic links produces the extinction of 50% of species in the web.

Trophic link removals can arise as a consequence of human activity on ecological systems. Well-known examples are the isolation of species and habitat fragmentation due to the intensified agricultural utilization of land, mining activities, transport and urban infrastructures, etc. For instance, Forman (2000) has estimated that about one-fifth of the land area in US is directly affected ecologically by the system of public roads. The effect of link removal has not been previously studied in ecological networks but as we have illustrated here at least for networks having a core-periphery structure they represent a real thread to real-world ecosystems. A simplified summary of food web robustness based on the distribution of trophic links per species and the expansibility character of such webs is provided by the “robustness triangle” represented in Fig. 7.

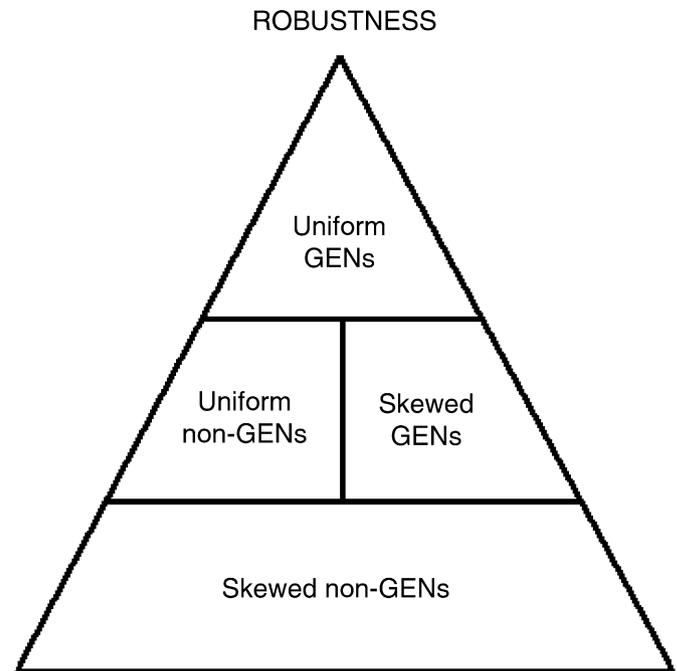


Fig. 7. A simplified representation of the triangle of robustness in food webs. At the bottom are the networks with power-law or exponential degree distributions (DD), which are non-GENs. They are the most vulnerable food webs to biodiversity loss. In the middle we place the networks with intermediate resilience to species removal and at the top the most robust food webs found in this work, those showing simultaneously uniform DD and GE properties.

## 8. The role of connectance

It has been shown by Dunne et al. (2002b) that connectance plays an important role in food web robustness beyond any doubt. These authors obtained a logarithmic correlation between connectance and robustness, which shows a significant correlation coefficient of  $r^2 = 0.76$  for the robustness against removal of the most connected species ( $r^2 = 0.81$  when marine food webs are considered) (Dunne et al., 2004). On the other hand, we have shown here that networks with the same connectance and identical DDs can display different resilience to species loss. We have shown that this different robustness is mainly due to the lack of GE properties in some food webs, which make them more vulnerable to the loss of certain key species connecting large communities in the web. If we combine these two results we can see that they are intimately connected. The webs having GE properties coincide with those having the highest connectance. On the contrary, food webs lacking GE properties have, in general very low connectance.

The largest possible connectance is obtained for a network in which every pair of species are connected by a trophic link giving rise to a complete graph,  $K_N$ . In this case  $C = E(E - 1)/2E^2$ , where  $E$  is the number of trophic links, which tends to  $\frac{1}{2}$  when  $N$  tends to infinite. The spectral gap for these networks is also the maximum possible because  $\lambda_1 = N - 1$  and  $\lambda_2 = -1$ , which gives

$\Delta\lambda = N$ . We have previously shown that a necessary condition for a network be a GEN is that the spectral gap needs to be “sufficiently large” as for guaranties that  $[\gamma_1(i)]^2 \sinh(\lambda_1) \gg \sum_{j=2}^N [\gamma_j(i)]^2 \sinh(\lambda_j)$ . Then, it is obvious that  $K_N$  will obey the spectral scaling. Consequently, the probability that a network with high connectance displays GE properties is larger than the same probability for a network with low connectance. This is, in fact, what we observe for the food webs studied here where high connectance networks in general display GE properties. However, we have to say that high connectance is not sufficient for a web displays GE properties and we can find networks with large connectance, which are not GENs despite the fact that this is not observed for any of the food webs studied here. On the other hand, for food webs with intermediate or low values of connectance we can find different resilience to species loss for networks with the same connectance. This case is well illustrated in Fig. 8 where we give the response of Scotch Broom and Ythan 1 to species removal. Both networks have approximately the same connectance (Ythan 1  $C = 0.038$  and Scotch Broom  $C = 0.031$ ) and display exponential DDs. However, Ythan 1 is significantly more robust than Scotch Broom due to the existence of GE properties in the first web.

It is also observed in the data sets studied here that food webs with high connectance, which are GENs frequently, display uniform DDs. For instance, the food webs in group I have an average connectance of 0.25, which is 10 times larger than the average connectance of webs in group VI. Uniform distribution of node degree is not necessary for the existence of GE properties. We have shown here and in

previous works that network with skewed DDs can display GE properties. These are the cases of St. Martin, Ythan 1 and 2, Little Rock and El Verde, which are GENs and display exponential DDs. These webs, however, have intermediate values of connectance, e.g. the average connectance is 0.078. Thus, it could be possible that the combination of high connectance and GE properties in food webs increases the probability that a network displays uniform DD as observed here in 7 of the networks studied.

## 9. Conclusions

The analysis of network robustness is a multifactor problem. We have shown here that not only node degree distribution (DD) but also the structural organization of these nodes in the network is significant for understanding the robustness of a food web to species loss. The distribution of species in the food web determines in a great measure the vulnerability of the system to the loss of the most connected species. It is well known that networks with skewed DDs, in particular power-law distributions, are very vulnerable to the removal of the hubs. About the half of the networks studied here display exponential or power-law DDs of species, which make them vulnerable to the loss of the most connected species. The other half of food webs displays uniform DDs, which are less vulnerable to the loss of the most connected species. However, the existence of bottlenecks in some of these networks can change dramatically this situation. The removal of bottleneck species produces the collapse of the network separating it into isolated clusters, which in general contain large number of species. One example is provided by

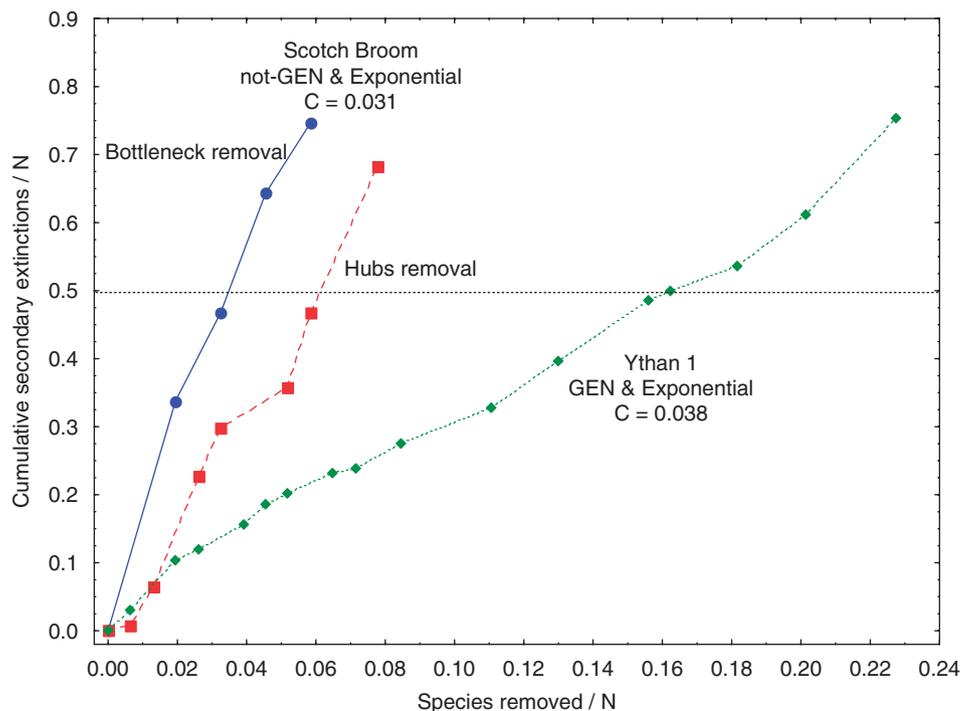


Fig. 8. Comparison of network robustness against removal of most connected and bottleneck species for two food webs with approximately the same connectance and degree distribution but having different expansibility characteristics.

the food web of Chesapeake Bay, which has a uniform DD but lacks GE properties, which makes it very vulnerable to the loss of bottleneck species. In the case of webs with skewed DDs it can be possible that the most connected species coincides with the bottlenecks making the network vulnerable to removal of the hubs. However, in other cases where this coincidence does not exist the webs are more vulnerable to the removal of the bottlenecks than to the removal of the most connected species. Connectance is intimately related to the organization of species in the web. For instance, food webs with the highest connectance display uniform DD and GE properties, which make them the most robust networks to species loss. On the contrary, the food webs with the lowest connectance are not GENs and can display uniform or skewed DDs, making them the most vulnerable networks to loss of species.

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