THE ROYAL SOCIETY

Complexity and fragility in ecological networks

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A detailed analysis of three species-rich ecosystem food webs has shown that they display skewed distributions of connections. Such graphs of interaction are, in fact, shared by a number of biological and technological networks, which have been shown to display a very high homeostasis against random removals of nodes. Here, we analyse the responses of these ecological graphs to both random and selective perturbations (directed against the most-connected species). Our results suggest that ecological networks are very robust against random removals but can be extremely fragile when selective attacks are used. These observations have important consequences for biodiversity dynamics and conservation issues, current estimations of extinction rates and the relevance and definition of keystone species.

Keywords: food webs; scaling; fragility; stability; keystone species; extinction

1. INTRODUCTION

Ecological research has widely demonstrated that community fragility is far from being understood. Issues such as which species might be considered to be especially relevant because of their strong effects on the community have led to a heated debate since Paine's definition of keystone species (Paine 1966; Bond 1993). It is commonly accepted that community fragility and persistence are related to the way in which ecological communities are structured, and specifically to the distribution of trophic links throughout the community (May 1974; Pimm 1991; McCann 2000). But both the scarcity of high-quality data (Polis 1991; Cohen *et al.* 1993; Williams & Martinez 2000) and the lack of methods suitable for a detailed analysis of the complexity of food-web organization (Cohen *et al.* 1993) lead to the lack of a unified picture of community fragility and persistence.

Recently, there has been an increasing interest in the organization of complex networks (for a review, see Strogatz 2001); examples include technological (Watts & Strogatz 1998; Albert *et al.* 2000), neural (Watts & Strogatz 1998; Amaral *et al.* 2000) and metabolic (Jeong *et al.* 2000; Fell & Wagner 2000) networks. Each of these networks can be represented as a graph constituting a set of nodes and the links connecting them.

These complex networks share some topological features, the so-called 'small world' (SW) behaviour (Watts & Strogatz 1998; Newman 2000; Strogatz 2001). Some of these webs also exhibit scale-free (SF) distributions of links. Specifically, the frequency of nodes, P_k, with k connections follows a power-law distribution, $P_k \approx k^{-\gamma}$, where most units are connected with few nodes, and very few nodes are highly connected.

Networks exhibiting SW properties and SF distributions of connections present a characteristic response to the successive removal of their nodes, related to the way in which removals occur (Albert *et al.* 2000; Jeong *et al.* 2000). When nodes are removed at random the network exhibits high homeostasis. By contrast, if the most-connected nodes are successively eliminated, an intrinsic fragility of the structure of the network is revealed, which eventually leads to fragmentation into many small subgraphs. This behaviour is not shared with other networks, such as purely random ones, where P_k is Poissonian. It has been demonstrated that random networks are equally fragile whether nodes are removed at random or in order of connectedness (Strogatz 2001).

The surprising and general nature of these results immediately suggests their application to ecological networks (figure 1), which have been recently shown to display SW behaviour (Montoya & Solé 2001). The main question is: how dependent are ecosystem fragility and persistence (two types of stability; Pimm 1991) on graph architecture? In order to answer this question, we examine the ecosystem stability against different types of species loss in three species-rich food webs. As we will see, these networks display the robustness expected of long-tailed distributions of connections, but also a high fragility against selective species removals in terms of, first, food-web fragmentation into disconnected sub-webs, and second, secondary extinctions (i.e. species that become extinct due to the removal of other species; Pimm 1991). Our results might apply to other food webs that share common structural properties with those studied here (Pimm *et al.* 1991; Williams & Martinez 2000).

2. FOOD WEBS ANALYSED

As a result of the limitations of available data in terms of both taxonomic resolution and size (Polis 1991; Cohen *et al.* 1993; Williams & Martinez 2000), our study is limited to the three richest and best-described food webs available in the ecological literature (figure 2). These are the Ythan Estuary food web (Huxham *et al.* 1996), the Silwood Park food web (Memmott *et al.* 2000) and the Little Rock Lake food web (Martinez 1991).

The Ythan Estuary food web has $N_s = 134$ species. It is the second largest documented food web in the UK. Most nodes correspond to real species (88%), while the rest involve lower taxonomic resolution (all the species of Acarina and all the species of brown algae are combined in single nodes). It is one of the most reviewed food webs
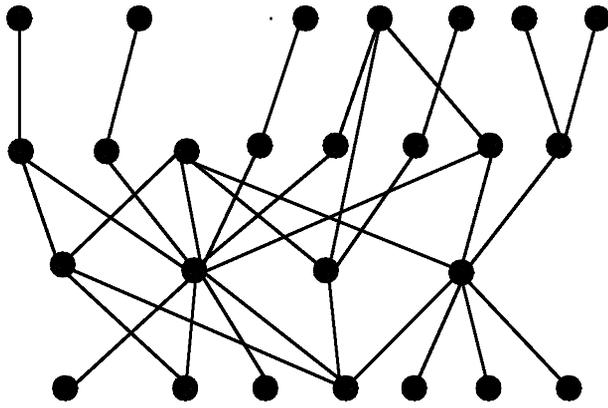
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Figure 1. Schematic representation of an ecological graph. Few species have many links and many have just one or two links (links are both predator–prey and prey–predator). This leads to a fat-tailed (scale-free) distribution of connections. This picture reflects the most common features observed in webs such as those reported here.

in the ecological literature and the average number of links per species is $\langle k \rangle = 8.7$. The Silwood Park food web is a very detailed food web (all nodes except one are real species) of those species associated with the Scotch broom, *Cytisus scoparius*, in a field site of 97 ha. Here, $\langle k \rangle = 4.75$. It includes 154 species: 60 predators, 66 parasitoids, five omnivores, 19 herbivores, three pathogens and one plant. Finally, the Little Rock Lake food web corresponds to a small lake. It is the largest of the three food webs analysed here ($\mathcal{N}_s = 182$), although it has a much lower taxonomic resolution. Only 31% of nodes are real species, with 63% representing genera and the rest corresponding to higher taxa. Here, $\langle k \rangle = 26.05$.

By using these webs, we have studied a diverse range of habitats: one food web is from a terrestrial habitat (Silwood Park), one is from a freshwater habitat (Little Rock Lake) and one is an interface environment (Ythan Estuary). The Ythan Estuary and Little Rock Lake food webs are both community food webs, while the Silwood Park web is a source food web (Cohen *et al.* 1990). Despite these differences in habitat and food-web type (source or community), the three food webs have some features in common. In a previous study, we have shown that these networks display SW properties (Montoya & Solé 2001). In a graph with a SW topology, nodes are highly clustered, yet the path length between them is small. In this sense, a SW stands for a network whose topology is somewhere between a regular and a totally random distribution of connections. These networks display a number of surprising features and have been suggested to be of great relevance in various biological contexts (Watts & Strogatz 1998; Jeong *et al.* 2000; Lago-Fernández *et al.* 2000).

In general, SW nets have been shown to provide fast responses to perturbations and, thus, a great source of homeostasis. Two of the food webs analysed also display power-law distributions (figure 2), and thus belong to the SF class of networks. The Little Rock Lake food web is also fat-tailed, but it displays deviations from the power law, possibly due to low taxonomic resolution (Montoya & Solé 2001). For food webs displaying fat-tailed

distributions, perturbations can have unexpected consequences, which are explored in § 3.

3. RESPONSE TO SPECIES REMOVAL

We have simulated two types of species removal: random and selective. These correspond to the removal of an arbitrary or the most-connected node, respectively. To establish the number of connections for each species in each web we have considered two kinds of ecological graphs: non-directed and prey-directed. In the former, we measured the global connectance for each species, i; that is, the sum of inward links (the number of prey species consumed by i) and outward links (the number of predator species that feed on i). In prey-directed graphs, only the outward links for species i are considered. Thus, under selective removal, for the non-directed graph we delete successively the most-globally-connected species, whereas for the prey-directed graph the deletion starts with the species with the most outward connections. Previous studies on non-directed and directed graphs have shown that the eventual effect of removal is network fragmentation, which takes place in very different ways depending on the type of removal used (Albert *et al.* 2000; Jeong *et al.* 2000).

The removal of the most-connected species has been shown to have large effects on community stability (Pimm 1980, 1991; Fagan 1997; Jórdan *et al.* 1999). There are several human-driven disturbances that mainly threaten the most-connected species in the ecosystems. For example, intensive hunting, and habitat loss and fragmentation are especially harmful to large herbivores and predators with a wide range of prey, respectively. In the former case, the extinction of large herbivores can lead to vegetation re-patterning and the co-extinction of many other species (Owen-Smith 1987). In the latter case, a change in competition among predator-free grazers often leads to population explosions, which can result in further extinctions and a modification in seed dispersal by some tree species (Wilson 1992).

We focus not only on network fragmentation but also on extinction patterns when species deletion takes place. Thus, community fragility and persistence are measured in different ways in relation to the fraction of species, f, that have been removed from each food web. First, we measured the topological changes of the food webs (figure 3) through the fraction of species contained in the largest species cluster, S, for each f; and the average size of the rest of the species clusters, $\langle s \rangle$, as the food web is fragmented. Here, f_c indicates the fraction of removed species at which the web becomes fragmented into many small sub-webs. Second, we calculated the fraction of secondary extinctions as f increases (figure 4), which can be used as a measure of the extinction rate (Pimm 1991). Secondary extinctions occur when a non-basal species (without inward links) has no prey to feed upon.

The nature of the behaviours of the three food webs is very similar, despite their differing in f_c, S and s. The threshold value, f_c, is very similar for both directed and non-directed webs, with the exception of the Ythan Estuary web, in which it is larger for the directed graph (figure 3*d*). These webs exhibit high homeostasis when random species removals occur, showing a slow linear
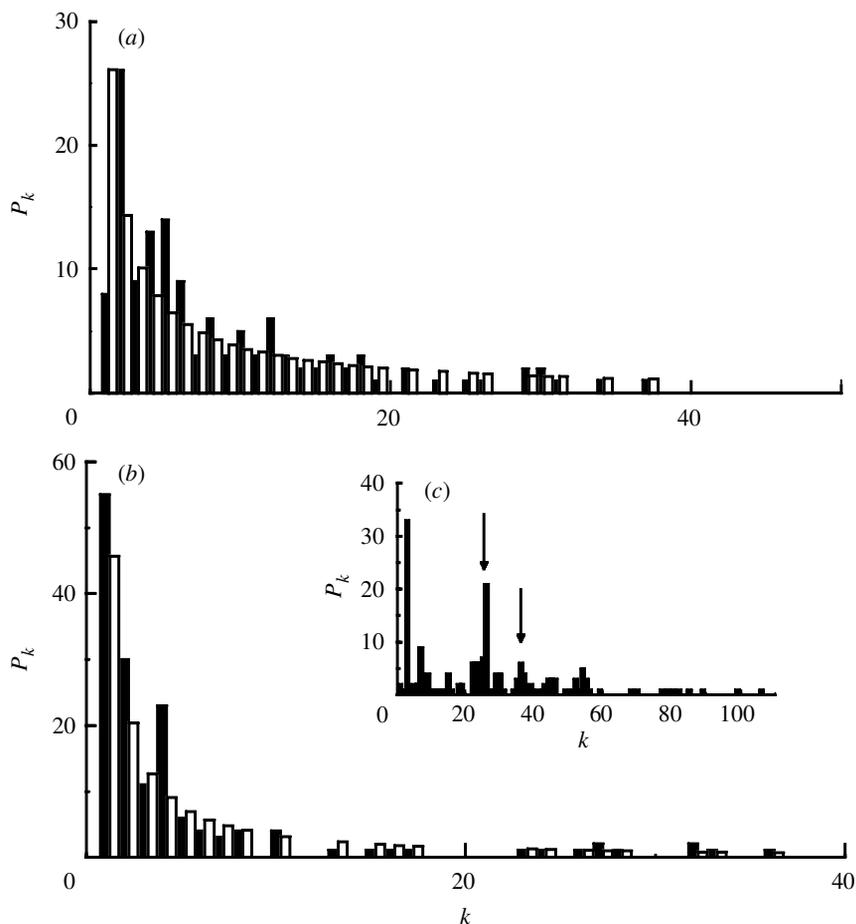
Figure 2. Histograms showing the distribution of the total number of links (inward plus outward) (k) per number of species (P_k) (black bars) for (*a*) Ythan Estuary, (*b*) Silwood Park and (*c*) Little Rock Lake. The Ythan Estuary and Silwood Park webs are shown together with their best power-law fit (white bars, see table 1 for details). The Little Rock Lake web displays several bumps (two of them indicated), probably due to low-level taxonomic resolution (Montoya & Solé 2001). Bumps on the Ythan Estuary food web are not enough to discount fit to a power-law distribution (see table 1).

decrease in the fraction of species contained in the largest cluster. With random removal, the graph cannot be fragmented until extremely high species deletion has been introduced. This can be seen in the values of s, which remain at 0 (no species clusters different from S) or 1 (very few isolated species) (figure 3). What is more revealing is that extinction rates remain low even for high f, so secondary extinctions are almost non-existent. In fact, we can theoretically estimate the fraction of removed species, p_c, required for food-web fragmentation from random removal (Cohen *et al.* 2001):

$$p_c = 1 - \frac{1}{\kappa_0 - 1}, \qquad (3.1)$$

where κ_0 is estimated from:

$$\kappa_0 = \frac{\langle k^2 \rangle}{\langle k \rangle} = \frac{\sum_{k=1}^{k} P_k k^2}{\sum_{k=1}^{k} P_k k}, \qquad (3.2)$$

where K is the maximum connectivity. This value is shown in table 1 (non-directed case), where we can see

that food-web breaking only occurs at totally unrealistic values of f_c.

However, what happens when the most-connected species are successively removed is clearly different, both for the non-directed graph and for the prey-directed one. The webs are extremely vulnerable to this sort of removal. Their fragility can be seen from: first, the quick decay of S up to a critical fraction of removed species, f_c (see table 1); second, the high fragmentation of the food webs into disconnected species clusters, giving maximum local values of s at critical points, f_c; and, third, the large fraction of species that become extinct at low values of species deletion, which reveals how fast secondary extinctions occur (this is especially dramatic for our best-defined web (Silwood Park); figure 4*b*). A measure of this phenomenon is given by π_c, the fraction of removed species that leads to an extinction rate of one half. We can see that ecosystem collapse takes place close to π_c.

We can classify the trophic natures of the species for each community into three groups: top predators (no outward links), intermediate species (outward and inward links) and basal species (no inward links) (Pimm *et al.* 1991). For the non-directed graph, we find differences between the analysed food webs in terms of the group that contains more highly connected species, focusing the
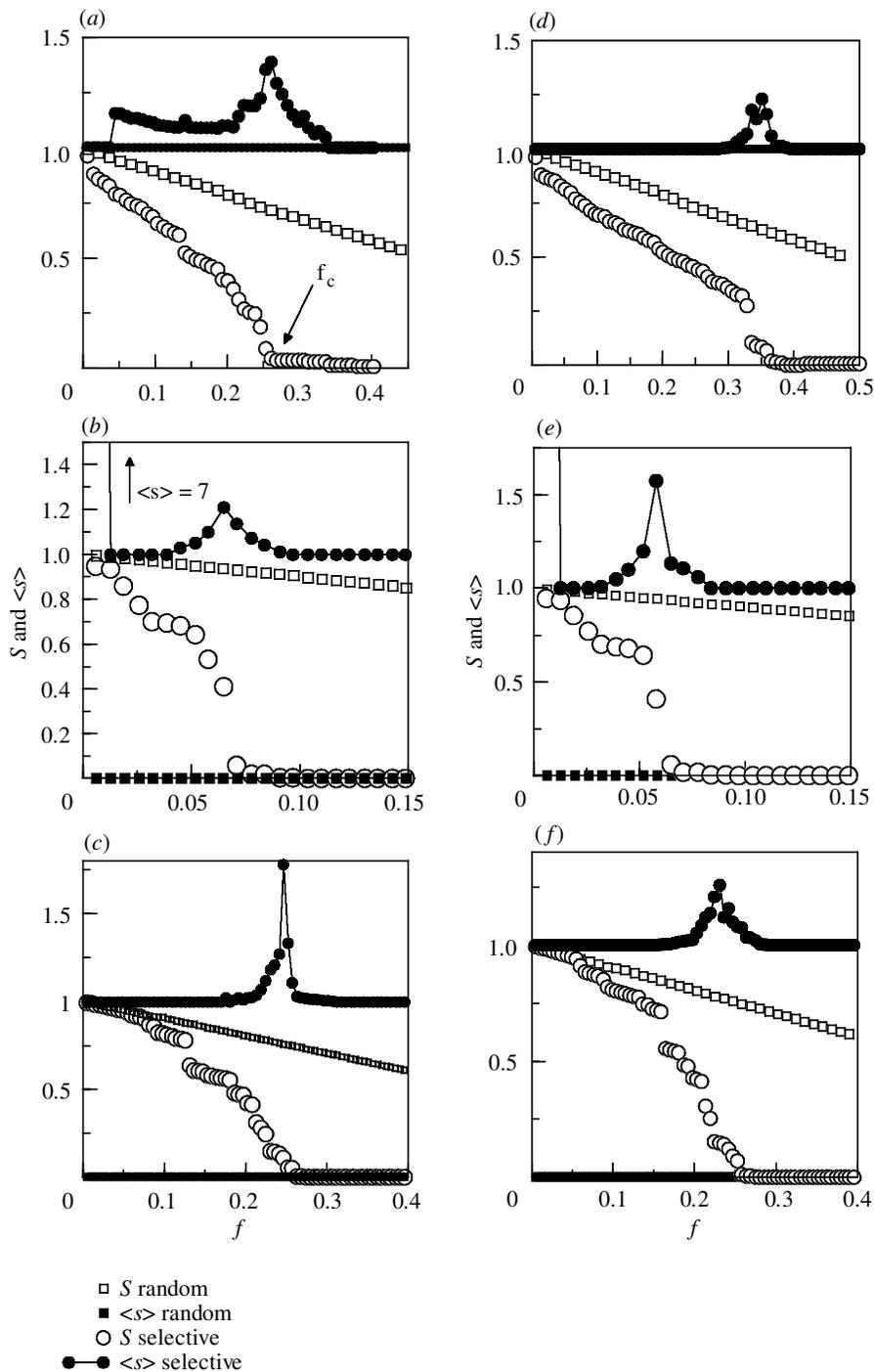
Figure 3. Responses of the Ythan Estuary (*a,d*), Silwood Park (*b,e*) and Little Rock Lake (*c,f*) food webs under random (squares) and selective (circles) species removal for non-directed (*a–c*) and prey-directed (*d–f*) graphs. *S* indicates the relative size of the largest species cluster (open symbols) and *s* indicates the average size of the rest of the species clusters (filled symbols) in relation to the fraction of removed species, *f*. Critical thresholds, f_c, are indicated (see table 1 for exact values).

set of species that are removed before reaching f_c. For the Ythan Estuary food web, these are mainly intermediate species (fishes and invertebrate organisms, 60%), with a few top predators (birds, 20%) and also parasites (15%) that cannot be easily included in any of the three groups. For the Silwood Park food web, most of these species are herbivores (66%), which can be considered as basal species because only one plant (*C. scoparius*) is present. Hemipteran omnivores are also important (26%), but, as with parasites in the Ythan Estuary web, they do not belong to any of the three trophic groups. Finally, for the

Little Rock Lake food web, no basal nodes are highly connected. Intermediate species of zooplankton and benthic invertebrates (70%) and top predators (such as fishes, 24%) are the most connected.

4. DISCUSSION

The trophic organization of species-rich communities is similar to other complex network topologies (Strogatz 2001). They are extremely heterogeneous and the topology is dominated by a few highly connected nodes,
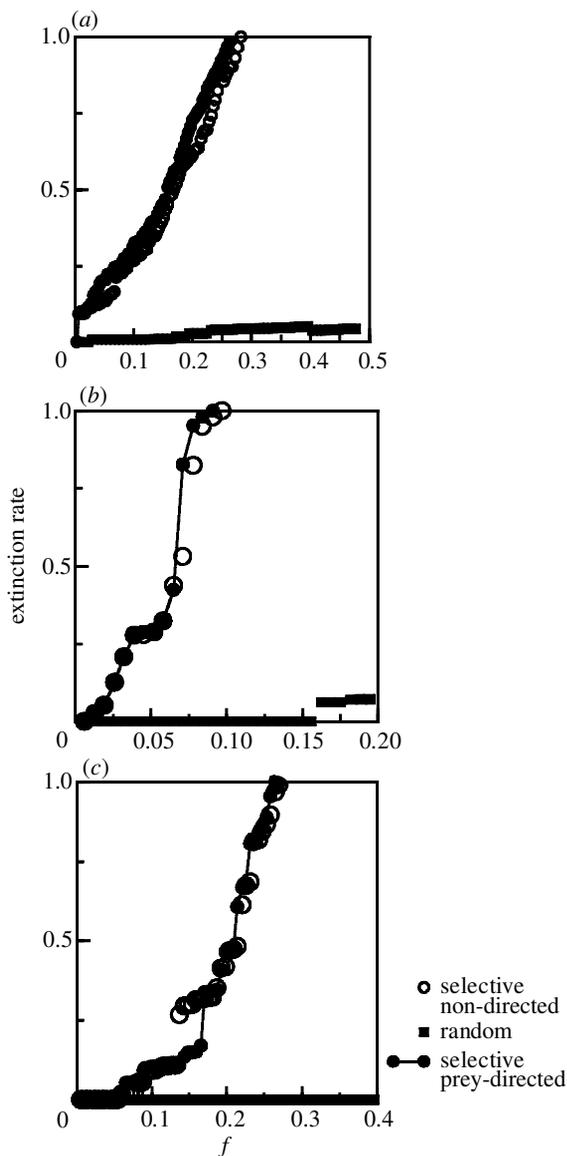
Figure 4. Extinction rates (fraction of secondary extinctions) in relation to the fraction of species removed, f, for the (*a*) Ythan Estuary, (*b*) Silwood Park and (*c*) Little Rock Lake food webs. Squares show responses under random species removal; circles correspond to selective attacks for the non-directed (open circles) and prey-directed (filled circles) graphs.

Table 1. Summary of the average properties of the ecological networks analysed using non-directed links.

(Due to the irregular shape of P_k, no good power-law fit for Little Rock Lake can be obtained. Power-law fits with least-squares regression on log-transformed data: Ythan Estuary, $r^2 = 0.83$, $p < 0.01$; Silwood Park, $r^2 = 0.79$, $p < 0.01$. $\langle k \rangle$: average connectivity; p_c: theoretical fraction of removed species required for food-web fragmentation; f_c: fraction of removed species required for food-web fragmentation; π_c: fraction of removed species leading to an extinction rate of one half.)

	Ythan Estuary	Silwood Park	Little Rock Lake
$\langle k \rangle$	8.71	4.78	26.15
γ	1.04	1.13	—
p_c	0.94	0.93	0.97
f_c	0.25	0.07	0.24
π_c	0.17	0.06	0.20

increase by orders of magnitude for the removal of highly connected species.

All the definitions of keystone species found in the ecological literature share one feature: these species have large effects on other species in the community. However, the effects involved in each definition are very different (Bond 1993). These effects have been studied mainly qualitatively through the removal or introduction of species (see Jórdan *et al.* 1999). Quantitative approximations have used simulated food webs (Pimm 1991; Jórdan *et al.* 1999). In this respect, our approximation to the fragility of species-rich food webs through topological changes may help to design new methods for *a priori* identification of keystone species. We can identify such species as highly connected because of the effects of their removal in terms of secondary extinctions and food-web fragmentation. The quick arrival at f_c and the high extinction rates linked to low values of f when these keystone species are removed stresses the importance of identifying and protecting highly connected species that maintain the stability of ecological communities.

Both non-directed and prey-directed graphs are highly sensitive to most-connected species removal, supporting the definition that we are proposing. However, the identity of the keystone species for each kind of graph is different, that is, the most-connected species are not always the same for non-directed as for prey-directed graphs. Which approximation is better for establishing the species that are more responsible for ecosystem stability? This depends on the effects that predation links (inward connections) have on the community. In prey-directed graphs, when a species is removed we only capture the direct effects of prey loss, assuming that predator removal has no effect on community stability. This is only true when donor control exclusively determines community dynamics. But, donor control is rare (e.g. Pimm 1980; Moran *et al.* 1996; Persson *et al.* 1996 and references therein; Schmitz 1997). Furthermore, it has been widely observed that most real communities are very sensitive to the removal of predators, and secondary extinctions are usually triggered via indirect effects (Pimm 1980, 1991; Owen-Smith 1987; Yodzis 1988; Schmitz 1997). Several studies address the importance of predator regulation (top-down control) on community

around which the rest of the network is organized. Two out of the three (non-directed) food webs examined here show a good fit to a SF distribution of connections, and the other web is clearly a long-tailed distribution. This complex organization has important implications for the stability of ecosystems in terms of their fragility and persistence. We have shown that SF food webs are very robust under random deletion of species. Secondary extinctions remain at low values because the probability of being removed decreases with k according to $P_k \approx k^{-\gamma}$, so it is unlikely that a highly connected species will be deleted. Such robustness becomes weakness under the selective removal of species with many connections, in non-directed graphs as much as in prey-directed graphs. We find especially significant the differences in extinction rates between random and selective attacks, which

dynamics (Bronmark *et al.* 1992; Persson *et al.* 1996; Schmitz 1998). Aquatic and terrestrial field experiments where predators are removed from the ecosystem have shown the important role that predation plays in maintaining community stability (Pimm 1980; Bond 1993). Non-directed graphs consider the effects of losing outward links as well as inward links when a species is removed. Thus, because of the scarcity of ecosystems controlled exclusively by prey, non-directed graphs may be considered to approximate better the global effects of species removal.

Through this approximation, it is the topology of the food web instead of the trophic position of the species that determines which species are keystone species. In this respect, not only top predators but also other organisms from different trophic levels must be considered as keystone species, in agreement with previous studies (Bond 1993; Davic 2000). By dividing species into the three classic trophic categories, we have seen that keystone species belong to different categories in each of the networks analysed. A common feature found in the two best taxonomically described food webs is that species that feed on more than one trophic level (omnivores and parasites; Polis & Strong 1996) are typical keystone species, enhancing the importance of omnivory for the stability of ecological communities (Fagan 1997; McCann & Hastings 1997).

Having a unique large food web with many species, instead of many small sub-webs with few species each, reduces the species risk of extinction because of the so-called insurance effect (Naeem & Li 1997; Levin 1999; McCann 2000). Increasing biodiversity increases the likelihood that an ecosystem will have, first, species that will respond differently under variable environmental conditions and perturbations, and second, functional redundancy, that is, species that are capable of functionally replacing extinct species. The higher levels of biodiversity present in a non-fragmented food web might support several ecosystem functions that a fragmented food web would not manage (Schulze & Mooney 1994; Levin 1999). Nutrient cycling, carbon and water fluxes, and many other functions might be altered if fragmentation occurs. High biodiversity also reduces the probability of secondary extinctions (Borvall *et al.* 2000).

Although the food webs analysed here are the best described in the ecological literature (N. D. Martinez, personal communication), they have two main caveats. First, higher taxonomic resolution is desired for the Little Rock Lake food web and for some nodes of the Ythan Estuary food web. However, almost none of the most-connected nodes are above species-level resolution, and thus a better taxonomic description of these nodes would have little effect on the distribution of connections. Moreover, some studies have shown that connectance is robust to both sampling effort and trophic aggregation (Martinez 1991, 1993; Martinez *et al.* 1999). Second, the weights of the links (interaction strengths) for these food webs are poorly known, with the exception of a few links from the Ythan Estuary food web (Raffaelli & Hall 1996). An analysis considering these interaction strengths would be very useful in confirming whether highly connected species are playing a stabilizing role in ecosystems.

In addition, further models involving species removal based on criteria other than the most-connected species would help to establish a more global view of the effects of human-driven disturbances. Current estimations of extinction rates are based on species–area relations, combined with estimates of habitat loss (May *et al.* 1995). The addition of secondary extinctions due to the removal of keystone species, together with other indirect effects, are likely to increase such projections (Solé & Bascompte 2001). Although food webs are described at a local scale, the estimated extinction rates obtained from our study might help to forecast extinction rates at regional and global scales.

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