

# Species loss and secondary extinctions in simple and complex model communities

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## Summary

1. The loss of a species from an ecological community can trigger a cascade of secondary extinctions. Here we investigate how the complexity (connectance) of model communities affects their response to species loss. Using dynamic analysis based on a global criterion of persistence (permanence) and topological analysis we investigate the extent of secondary extinctions following the loss of different kinds of species.
2. We show that complex communities are, on average, more resistant to species loss than simple communities: the number of secondary extinctions decreases with increasing connectance. However, complex communities are more vulnerable to loss of top predators than simple communities.
3. The loss of highly connected species (species with many links to other species) and species at low trophic levels triggers, on average, the largest number of secondary extinctions. The effect of the connectivity of a species is strongest in webs with low connectance.
4. Most secondary extinctions are due to direct bottom-up effects: consumers go extinct when their resources are lost. Secondary extinctions due to trophic cascades and disruption of predator-mediated coexistence also occur. Secondary extinctions due to disruption of predator-mediated coexistence are more common in complex communities than in simple communities, while bottom-up and top-down extinction cascades are more common in simple communities.
5. Topological analysis of the response of communities to species loss always predicts a lower number of secondary extinctions than dynamic analysis, especially in food webs with high connectance.

*Key-words:* cascading extinction, connectance, food web, keystone species, resistance.

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## Introduction

It is predicted that human-induced changes in the global environment will cause unprecedented rates of population and species extinction in the near future (Hughes, Daily & Ehrlich 1997; Brooks, Sodhi & Ng 2003; Myers & Worm 2003; Thomas *et al.* 2004). How will ecological communities respond to these forecasted rates of species loss? Empirical as well as theoretical work show that the loss of a single species can trigger a cascade of secondary extinctions, and hence lead to dramatic changes in the trophic structure of an ecological community (Paine 1966; Estes & Palmisano 1974; Borrvall, Ebenman & Jonsson 2000; Solé & Montoya

2001; Dunne, Williams & Martinez 2002a; Ebenman, Law & Borrvall 2004; Koh *et al.* 2004; reviewed by Ebenman & Jonsson 2005). Such changes in community structure caused by species loss and subsequent secondary extinctions may alter the resistance of a community to future perturbations (Ives & Cardinale 2004). Thus, in light of the present and forecasted rates of species loss, it is important to assess the risk and likely extent of secondary extinctions.

The risk and extent of secondary extinctions following the loss of a species is likely to depend on the structure of the affected community as well as on the characteristics of the lost species. An important task for the science of ecology is to find methods to identify fragile community structures and species whose loss is likely to cause a large number of secondary extinctions – keystone species. One structural characteristic of a community that might affect its response to species loss

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is its complexity, and more specifically its connectance (the proportion of possible interaction links that are realized). The question of the relationship between complexity and fragility of ecological communities has a long history in ecology (MacArthur 1955; May 1972; Pimm 1984; Hall & Raffaelli 1993; Warren 1994; Haydon 2000; McCann 2000; Chen & Cohen 2001; Rozdilsky & Stone 2001; Dunne *et al.* 2002a; Fussmann & Heber 2002; Jansen & Kokkoris 2003; Kondoh 2003). That is also the case for the question of keystone species (Paine 1969; Mills, Soulé & Doak 1993; Menge *et al.* 1994; Power *et al.* 1996; Jordán & Scheuring 2002).

Two approaches have been used to investigate theoretically the response of ecological communities to species loss: dynamic analysis of model communities (Pimm 1979, 1980; Borrvall *et al.* 2000; Ebenman *et al.* 2004; Christianou & Ebenman 2005) and topological (static) analysis of natural communities (Solé & Montoya 2001; Dunne *et al.* 2002a; Melian & Bascompte 2002; Allesina & Bodini 2004; Dunne, Williams & Martinez 2004; Melian & Bascompte 2004). Topological analyses suggest that communities with high connectance are more robust to species loss than communities with low connectance (Dunne *et al.* 2002a) and that loss of highly connected species have more far-reaching consequences than the loss of species with few links, although there are important exceptions (Sole & Montoya 2001; Dunne *et al.* 2002a).

The topological approach has both strengths and weaknesses. One potential problem with topological analysis is that it does not take into account the dynamics of ecological communities (see Borer *et al.* 2002). Secondary extinctions revealed by topological analysis are consumer species that become disconnected from primary producers. Thus, secondary extinctions caused by the loss of top predators cannot be revealed using topological analysis; neither can secondary extinction of basal species be revealed. The reason for this is that important mechanisms such as indirect effects of top predators on primary producers (top-down trophic cascades), apparent competition and predator-mediated coexistence are not accounted for. Moreover, the strength of interactions between species is not considered in topological analysis. It is becoming increasingly clear that the distribution of interaction strengths in an ecological community affects its response to perturbations (for recent work see Kokkoris *et al.* 2002; Neutel, Heesterbeek & deRuiter 2002; Berlow *et al.* 2004; Emmerson & Raffaelli 2004; Christianou & Ebenman 2005). Thus, topological analysis may paint a misleading picture of the response of a community to species loss.

In this work we take a dynamic approach to investigate the response of ecological communities to species loss. More specifically, using a global criterion of persistence (permanence) we explore: (1) how the connectance of a community affect its response to species loss; (2) how the connectivity (number of links) and trophic

position of a species affect the consequences of its loss; (3) which species are most vulnerable to go secondarily extinct; and (4) the structure of the resulting post-extinction community.

## Methods

### MODEL COMMUNITIES

We consider model communities with four different configurations: rectangular webs (equal number of species at each trophic level) with and without omnivory and triangular webs (number of species decreases with increasing trophic level) with and without omnivory. The number of species is the same in all configurations (12 species); in the rectangular webs there are four basal species (primary producers), four primary consumers and four secondary consumers/omnivores. In the triangular webs there are six basal species, four primary consumers and two secondary consumers/omnivores. In each web configuration we vary connectance ( $C$ );  $C = 0.063$ ,  $C = 0.097$  and  $C = 0.194$  (corresponding to 9, 14 and 28 predator-prey links, respectively) which are within the range of observed values in natural food webs (Dunne, Williams & Martinez 2002b; Montoya & Solé 2003). Connectance  $C$  is equal to  $L/S^2$  where  $S$  is the number of species and  $L$  is the number of consumer-resource links in the community. Predator-prey links are distributed randomly with the constraint that each consumer must have at least one prey (that is, a web must be feasible). In addition to the predator-prey links there are direct interspecific competition links connecting each basal species with all other basal species. These competition links are not included in the connectance values given above. In the web configurations with omnivory 10.7–14.3% of the links are omnivorous (one link of nine, two links of 14 and three links of 28 for webs with connectance values of 0.063, 0.097 and 0.194, respectively) corresponding to a fraction between 0.08 and 0.17 of the species in the webs being omnivores. This is within the range observed for natural food webs, although on the low end (Dunne *et al.* 2002a, 2004).

For a given connectance and web configuration there is variation among replicates with respect to the distribution of feeding links among species (degree distribution). For each replicate we calculate the skewness of the degree distribution, which gives the degree of deviation of the distribution from symmetry (skewness being equal to 0 for any perfectly symmetric distribution). Degree distributions in natural food webs are systematically related to connectance: webs with high connectance display uniform distributions (i.e. low skewness), webs with intermediate connectance display exponential distributions and webs with low connectance display power-law distributions (Dunne *et al.* 2002b; Montoya & Solé 2003). That is, skewness of degree distribution increases with connectance. This is also the case for our model webs.

## DYNAMICS AND PARAMETERS

Community dynamics are described by generalized Lotka–Volterra equations:

$$\frac{dx_i}{dt} = x_i \left( b_i + \sum_{j=1}^S \alpha_{ij} x_j \right) \text{ for } i = 1, \dots, S.$$

Here  $S$  is the number of species in the community,  $x_i$  is the density of species  $i$ ,  $b_i$  is the intrinsic per capita growth rate of species  $i$ , and  $\alpha_{ij}$  is the per capita effect of species  $j$  on the per capita growth rate of species  $i$ .  $\alpha_{ij} < 0$  when species  $j$  consumes species  $i$  and  $\alpha_{ij} > 0$  when species  $j$  is a prey of species  $i$ . Basal species grow in the absence of consumers ( $b_i > 0$ ) and consumers die in the absence of prey ( $b_i < 0$ ). The growth rate for the basal species is set to 1. The mortality rates for the consumers are randomly drawn from the uniform distribution  $(-0.001, 0)$  and are then sorted in such way that the secondary consumers are assigned lower rates than their prey. That is because species at higher trophic levels are expected to be larger (Cohen, Jonsson & Carpenter 2003) and a large body size often confers low mortality rate (Calder 1984).

Empirical estimates of interaction strengths in ecological communities show skewed distributions with mostly weak and only a few strong interaction links. We therefore assume each consumer to have a strong effect on one of its prey species (assigned randomly) and weak effects on the others. If a consumer  $j$  has only one prey species  $i$ , that link is assumed to be strong and is given the value  $\alpha_{ij} = -0.5$ . If a consumer has more than one prey species, one of the links (assigned randomly) is assumed to be strong and is given the value  $-0.4$  and the other links are assumed to be weak and are given the value  $-0.1$  divided by the number of prey species consumed  $-1$ . Thus, the mean per capita effect of a predator on its prey decreases with the number of prey species it consumes. The effect of prey species on consumers is given by  $\alpha_{ji} = -e^* \alpha_{ij}$ , where  $e$  is the efficiency with which prey is converted into predators. The conversion efficiency  $e$  is set to 0.2 for non-omnivorous feeding links and 0.02 for omnivorous links (a value smaller than 1 is to be expected when consumers are larger than their prey). The strength of intraspecific competition is given by  $\alpha_{ii}$ ; for basal species,  $\alpha_{ii} = -1$  and  $\alpha_{ii} = -0.1$  for primary and secondary consumers. There is direct interspecific competition between all basal species and the strength of this interaction is randomly drawn from the uniform distribution  $(-0.5, 0)$ . Consumers compete indirectly by sharing prey species.

## ANALYSES

We use permanence as a criterion for the long-term coexistence (persistence) of interacting species. A community of  $S$  species is permanent if the boundary of the  $S$ -species phase space is a repeller to orbits that start in the interior of the phase space (Hofbauer & Sigmund

1988: 97, 160; Law 1999). In contrast to the criteria of local and global asymptotic stability, permanence is a criterion of persistence that makes no assumptions about the dynamic behaviour of the system; equilibrium behaviour as well as more complex dynamic behaviour is allowed. Thus, complex dynamics that might be consistent with community persistence, such as periodic and chaotic attractors, are not excluded. To check for permanence we used Jansen's (1987) sufficient condition for permanence.

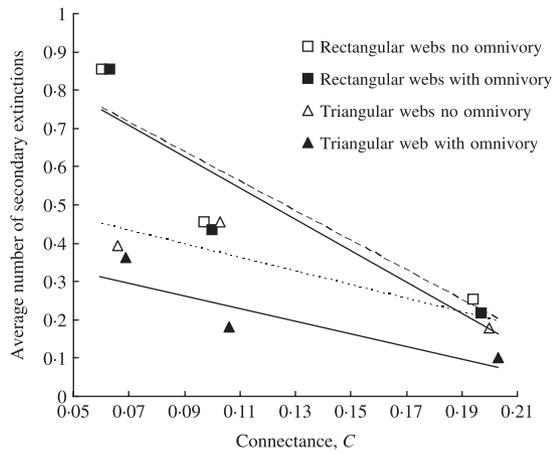
To investigate the response of communities to species loss we generate 1000 permanent replicate communities for each value of connectance in each food web configuration. From each of these permanent replicate communities we delete one species at a time and this is repeated for each species in the community. If the reduced community with  $S-1$  species is permanent this means that the remaining species continue to coexist. If it is not, this means that one or more secondary extinctions will take place. To find the post-extinction community in the second case, we check all the subsets of the  $S-1$  community for a subset that is (1) permanent and (2) uninvadable by species absent from the subset and present in the  $S-1$  community. Occasionally, none or more than one of the subsets had these properties; in such cases we numerically integrated the system (see Ebenman *et al.* 2004 for detailed information about the use of the permanence criterion). To quantify the extent of secondary extinctions we calculate the average number of secondary extinctions (including replicates where no secondary extinctions occurred).

In addition to the dynamic analysis we also perform a topological analysis of the response of the model food webs to species deletion. In this analysis no dynamics is involved: the criterion of secondary extinction being that a species has no prey left to feed on (i.e. the number of secondary extinctions is the number of consumers disconnected from primary producers). This allows us to investigate to what extent the predictions of the two methods of analysis deviate from each other and hence to establish the importance or not of considering dynamics.

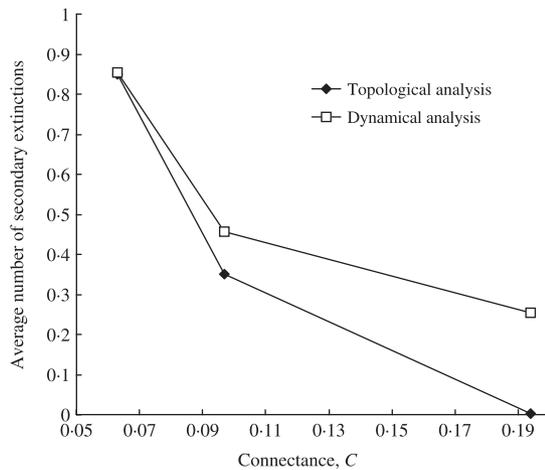
## Results

## FOOD WEB STRUCTURE

Using dynamic analysis we find an overall trend of increasing resistance to species loss, that is, a decreasing number of secondary extinctions, with increasing connectance (Fig. 1). This clear trend is present in all food web configurations. Triangular webs are, on average, more resistant to species loss than rectangular ones (Fig. 1). Also the effect of connectance on resistance to species loss is weaker in triangular webs than in rectangular ones. Omnivory enhances resistance to species loss especially in triangular webs (Fig. 1). Topological analysis of the response of communities to species loss reveals the same overall trend: number of secondary



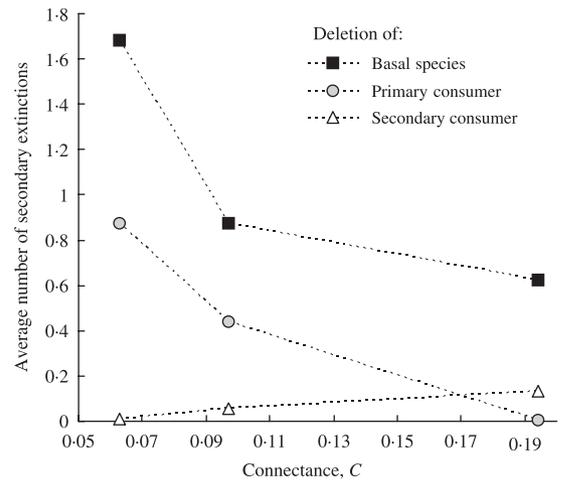
**Fig. 1.** Average number of secondary extinctions as a function of web connectance for different web configurations. The lines are regression lines. Coefficients of determination,  $R^2$ , are equal to 0.749 (rectangular webs with omnivory), 0.706 (rectangular webs without omnivory), 0.484 (triangular webs with omnivory) and 0.441 (triangular webs without omnivory). Each point is based on calculations from 1000 replicate communities. From each replicate community each species in the food web is deleted, one at a time. Each data point is therefore an average calculated from 12 000 deletion events. Symbols are somewhat displaced from the true connectance values (0.063, 0.097 and 0.194) for ease of reading.



**Fig. 2.** Average number of secondary extinctions as a function of connectance in rectangular food webs without omnivory. Results from dynamic analysis (open squares) and topological analysis (filled diamonds).

extinctions decreases with increasing connectance. However, topological analysis always predicts a lower number of secondary extinctions than dynamic analysis, especially for food webs with high connectance (Fig. 2).

Separating the deletions with respect to the trophic level of the deleted species we find that the average number of secondary extinctions decreases with increasing connectance when a basal species or a primary consumer is deleted. However, when a secondary consumer is deleted the average number of secondary extinctions increases with increasing connectance (Fig. 3).



**Fig. 3.** Average number of secondary extinctions as a function of web connectance and trophic level of deleted species. Results for rectangular web without omnivory. Each data point is an average calculated from 4000 deletion events.

#### CHARACTERISTICS OF THE DELETED SPECIES

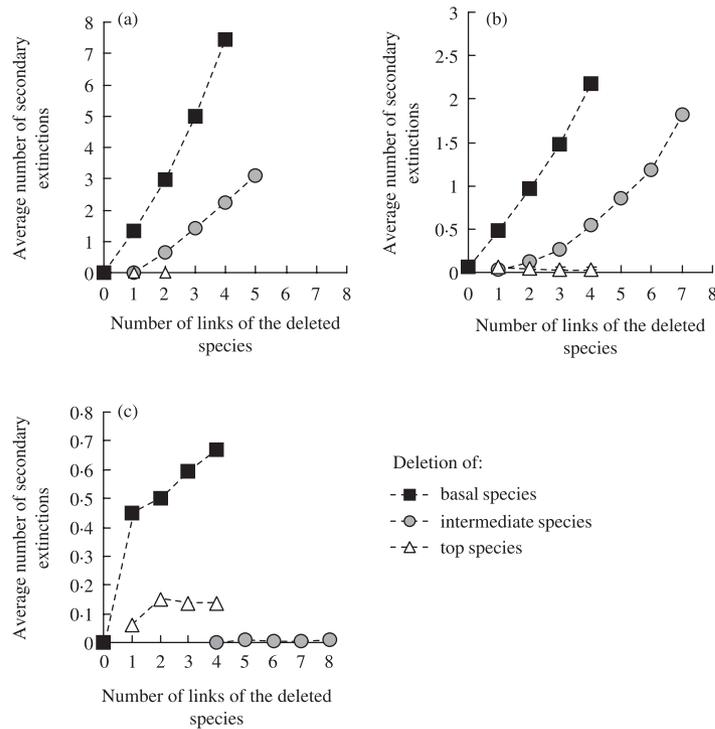
For a given connectance, the number of secondary extinctions is highest when a basal species is lost and lowest when a secondary consumer is lost, except in the webs with the highest connectance where loss of secondary consumers cause more secondary extinctions than loss of intermediate species (Fig. 3). That is the case for all food web configurations. This result points to the potential keystone role of top predators in complex ecological communities. It also shows that the keystone status of a species depends on the structure (connectance) of the web where it is embedded.

Considering the effects of the connectivity of the deleted species we find that deletion of highly connected basal species and primary consumers leads to more secondary extinctions than deletion of species with few links to other species (Fig. 4a,b). In webs with the highest connectance this trend is only weakly present for basal species (Fig. 4c).

#### STRUCTURE OF POST-EXTINCTION COMMUNITY

Secondary extinctions cause changes in community structure: the connectance of the post-extinction community (the community that is left after the secondary extinctions have taken place) differs from the connectance of the original community. In communities with low connectance secondary extinctions result in an increased connectance, while in the most highly connected communities it result in a decreased connectance.

The species going secondarily extinct are predominantly consumers. It is rare that a basal species goes secondarily extinct following the loss of another species. This is the case for all food web configurations. When a basal species is deleted it is the primary consumers that are, on average, most vulnerable to secondary extinction



**Fig. 4.** Average number of secondary extinctions as a function of the connectivity of the deleted species. Results for rectangular webs without omnivory. (a) Web connectance,  $C = 0.063$ , (b)  $C = 0.097$  and (c)  $C = 0.194$ . Note that the scale of the y-axis differs among panels.

**Table 1.** Average number of secondary extinctions affecting basal species, primary consumers and secondary consumers, respectively, in rectangular webs without omnivory (each value is an average calculated from 4000 deletion events)

Deleted species type, by web connectance ( $C$ )	Average number of secondary extinctions		
	Basal species	Primary consumer	Secondary consumer
<b>Basal</b>			
0.063	0	0.883	0.799
0.097	0	0.592	0.281
0.194	0	0.617	0.007
<b>Primary consumer</b>			
0.063	0.001	0.002	0.871
0.097	0.001	0.003	0.438
0.194	0.001	0.001	0.004
<b>Secondary consumer</b>			
0.063	0	0.004	0.006
0.097	0	0.045	0.013
0.194	0	0.136	0

(Table 1). However, in webs with low connectance secondary consumers are almost as vulnerable to secondary extinction as primary consumers following the loss of basal species (Table 1). Thus, the risk of bottom-up extinction cascades increases with decreasing connectance. When a primary consumer is deleted secondary consumers are the ones that are most vulnerable to secondary extinction. In webs with the

highest connectance almost no secondary extinctions occur at all when a primary consumer is deleted. Deletion of secondary consumers seldom leads to secondary extinctions. However, in webs with high connectance loss of secondary consumers sometimes trigger secondary extinctions of primary consumers (Table 1). Thus, the risk of disrupting predator-mediated coexistence through deletion of top predators increases with increasing connectance.

The connectivity of a species affects its vulnerability to secondary extinction. In webs with low and intermediate connectance lowly connected species are disproportionately vulnerable to secondary extinction. On the other hand, in webs with high connectance highly connected species are disproportionately vulnerable to go secondarily extinct following the deletion of a species. Thus, the vulnerability of a species depends on the structure (connectance) of the web where it is embedded. This is the case for all web configurations. This context dependent pattern of vulnerability explains the altered connectance observed in the post-extinction communities (see above).

## Discussion

Earlier studies, based on topological analysis of natural food webs (Dunne *et al.* 2002a, 2004) and local stability analysis of model food webs (Pimm 1979, 1980), show that the connectance of an ecological community affects its response to species loss. These studies also

suggest that the connectivity of a species influences the consequences of its loss (see also Solé & Montoya 2001; Allesina & Bodini 2004). Here we expand on these studies using the recently developed methods of permanence analysis (a global stability analysis) and community viability analysis (Ebenman *et al.* 2004). This allows us to investigate the effects of direct as well as indirect interactions between species on the response of a community to species loss (which is not possible using topological analysis).

#### FOOD WEB CONNECTANCE

We find that highly connected food webs are, on average, more resistant to species loss than webs with low connectance. The fact that this holds both for rectangular and triangular webs and for webs with and without omnivorous species indicates that the result is quite robust. The most probable explanation of this pattern is that in highly connected webs most consumers have several prey species, so the loss of one of them will not be that catastrophic (see also MacArthur 1955). Consistent with this is the fact that consumers feeding on many resources show less temporal variation in their densities than do those feeding on few resource species (see Petchey 2000).

There might be additional reasons behind the pattern we have found. As the number of links (and hence connectance) in our model webs increases so does the proportion of these links that are weak because we assume each consumer to have a strong effect on one of its prey species and weak effects on the others. Thus, mean per capita interaction strength decreases with increasing connectance. Theoretical studies suggest that decreased mean and variance of interaction strengths in a community increase local stability (May 1972; Kokkoris *et al.* 2002; Jansen & Kokkoris 2003; see also McCann, Hastings & Huxel 1998). Hence, depending on how connectance affects the mean and variance of interaction strengths, increased connectance can either increase or decrease local stability (see also Rozdilsky & Stone 2001). These results are based on the response of communities to small pulse perturbations while we apply large press perturbations (deletion of species) on our model communities. It is not clear if results based on local stability analysis also holds for perturbations such as species loss.

Recent work by Dunne *et al.* (2002a, 2004), based on topological analysis of natural food webs, suggests that webs with high connectance are more robust to species loss than webs with low connectance. They defined robustness as the number of species that had to be deleted in order to cause a 50% reduction in species number. This finding is in line with the results from our dynamic analysis that the number of secondary extinction decreases with increasing connectance. However, comparing the results from dynamic and topological analyses of our model webs we find that topological analysis predict fewer secondary extinctions following

the loss of species, especially in highly connected webs, than analysis taking dynamics into account. This is to be expected (see Introduction).

We find that the risk of secondary extinction to take place as well as the average number of secondary extinctions decrease with increasing connectance following the deletion of a basal species or primary consumer species, while they increase with connectance following the loss of secondary consumer species (see also Pimm 1979). The relationship is more pronounced for basal and primary consumer species deletions than for secondary consumer deletions (Fig. 3). Thus, averaged over all species deletions, highly connected webs are more resistant to species loss than lowly connected webs. Pimm (1979), on the other hand, found that the relationship between connectance and the risk of secondary extinction to take place was most pronounced in the case of top species deletions. Thus, he reached the opposite conclusion: webs with high connectance are, on average, less resistant to species loss than webs with low connectance. The pioneering studies of Pimm were based on local stability analysis while our study is based on the global stability criterion of permanence. Another difference between our studies is that we assume the presence of direct interspecific competition between basal species and the presence of intraspecific density dependence in consumer species, as well as in basal species. This might explain the different conclusions reached. Presence of intraspecific density dependence in consumer species can be expected to decrease the risk of top-down cascades and disruption of predator-mediated coexistence following the loss of a top species (see Borrvall *et al.* 2000; Ebenman *et al.* 2004).

The loss of a species may lead to changes in the interactions between the remaining species. For instance, species may switch to less preferred prey species if their main prey goes extinct. Such adaptive behaviour is not taking into account in our models. Thus, we may overestimate the risk and number of secondary extinctions following the loss of a species in webs with low connectance. A recent theoretical study (Kondoh 2003) suggests that the long-term persistence of ecological communities is enhanced if consumers are allowed to adaptively switch their prey preferences. We have conducted preliminary analyses where we include some degree of adaptability of the consumers. Allowing for some degree of adaptability we still find an increased resistance to species loss with increasing connectance. This is an interesting question that deserves further investigation.

#### CONNECTIVITY OF DELETED SPECIES

We find that, on average, the loss of highly connected basal and primary consumer species cause more secondary extinctions than loss of species with few links to other species. This is in line with results from studies using topological analysis (Solé & Montoya 2001;

Dunne *et al.* 2002a). Our results also suggest that the number of consumers with which a species interact is more important than the number of resources with which it interacts. Thus, the connectivity of a secondary consumer has a small effect on the number of secondary extinctions its loss will cause. The effect of the connectivity of a species is strongest in webs with low connectance, except for secondary consumers. The most likely explanation for this is that almost all consumers have more than one prey in webs with high connectance, so even the loss of highly connected basal and primary consumer species will not cause consumers to lose all their prey species.

The response of a community to species loss might depend not only on the connectivity of the deleted species but also on the linkage pattern of its neighbours (Pimm 1980; Dunne *et al.* 2002a; Jordan & Scheuring 2002). For instance, it has been suggested that the so-called degree correlation (or assortativity) might be important for the response of communities to perturbations (Melian & Bascompte 2002, 2004). A negative degree correlation means that lowly connected species have neighbours that are likely to be highly connected and vice versa.

#### POST-EXTINCTION COMMUNITY

The trophic levels and connectivities of the species that go secondarily extinct will determine the structure of the post-extinction community and hence the resistance of the post-extinction community to future disturbances. We find that secondary consumer species are, on average, the species most vulnerable to secondary extinction in communities with the lowest connectance. In communities with the highest connectance almost all secondarily extinct species are intermediate species. Secondary extinction of basal species is rare and only occurs in triangular communities. Here the mechanisms involved are top-down cascades (following loss of top species), disruption of predator-mediated coexistence (following loss of intermediate species) and probably disruption of indirect mutualism among basal species (following loss of basal species). Several reviews have dealt with the question of indirect interactions such as trophic cascades and predator-mediated coexistence in ecological communities (e.g. Abrams *et al.* 1996; Chase 2000; Shurin *et al.* 2002; Borer *et al.* 2005). Overall, our results suggest that bottom-up and top-down extinction cascades should be more likely to occur in communities with low connectance than in those with high connectance, while secondary extinctions due to disruption of predator-mediated coexistence should be more likely to occur in highly than in lowly connected communities.

There are some interesting patterns with respect to the connectivity of the species going secondarily extinct. In lowly connected communities, species with very few links are the ones most prone to go secondarily extinct whereas in highly connected communities

species with many links (that is intermediate species) are most vulnerable. Thus, secondary extinctions causes highly connected communities to become less connected and lowly connected communities to become more connected, affecting their resistance to future species losses in opposite directions. On the other hand, as a result of the initial species loss and subsequent secondary extinctions the post-extinction communities will, of course, have fewer species than the original communities, making them more vulnerable to further future species losses (Borrvall *et al.* 2000; Ebenman *et al.* 2004). In balance secondary extinctions are far from random. This can have important consequences for the resistance of the communities to further future perturbations (see also Ives & Cardinale 2004) and for the functional diversity in the post-extinction communities (Petchey & Gaston 2002; Solan *et al.* 2004).

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