



# Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure

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The consequences of species loss on cascading extinctions in food webs have been the focus of several recent theoretical studies, with differing results. Changes in ecosystem properties consecutive to cascading extinctions have received far less attention even though such dramatic events might strongly alter ecosystem functioning. Here we use various food web models to investigate the effects of species loss and diversity on both secondary extinctions and their associated changes in ecosystem properties. Our analysis shows that diversity has contrasting effects depending on the presence of self-limiting terms at consumer levels and, to a lower extent, on connectance and interspecific competition. Ecosystems that lose a high proportion of species through cascading extinctions exhibit the most important changes in ecosystem properties. Linking studies on cascading extinctions in food webs with studies that investigate the effects of biodiversity on ecosystem functioning appears crucial for a better understanding of the consequences of species extinctions.

The current erosion of biodiversity has led an increasing number of scientists to investigate the consequences of changes in diversity on community properties and ecosystem functioning. An important part of this research is concerned with the long-term consequences of species loss on ecosystem processes. The effects of diversity on both the magnitude of various ecosystem processes and the temporal variability of these processes are now generally admitted (see syntheses in Loreau et al. 2001, 2002, Kinzig et al. 2002, Hooper et al. 2005). These results have revived the long-standing debate on the relationship between the complexity and stability of ecological systems. Recent theoretical studies propose to resolve this debate by suggesting that population-level stability decreases while community-level stability increases as diversity increases (Tilman 1996, Thébault and Loreau 2005). However, these studies measure stability mainly by the temporal variability of species biomass while other measures of stability have also been used in pioneering studies (Pimm 1984). The notion of species deletion stability was introduced more than two decades ago by Pimm

(1980). This notion is particularly interesting in a context of rapid declines in biodiversity (Sala et al. 2000) as it measures the risk of cascading extinction events after the loss of one species in a food web. The extinction of one species can lead to secondary extinctions, and hence cause dramatic changes in species diversity and composition (Paine 1966, Estes and Palmisano 1974, Power et al. 1996).

Species deletion stability can also be linked easily to removal experiments that address the consequences of species loss for ecosystem functioning. There is a need for studies that directly investigate impacts of local extinctions as most studies on the relationship between biodiversity and ecosystem processes have used assembled communities (Diaz et al. 2003). With few exceptions, theoretical work on the direct impact of species loss has focused on the study of secondary extinctions but has not considered associated changes in ecosystem properties (but see King and Pimm 1983, Petchey et al. 2004). However, the number and trophic level of species lost can affect ecosystem properties (Petchey et al. 2004). Species loss has been shown to

modify food web structure due to secondary extinctions (Ebenman et al. 2004), which may lead to strong changes in ecosystem processes by altering trophic cascades (Duffy 2002). The compensation potential of a community can also decrease as the number of extinctions increases (Ives and Cardinale 2004). If the loss of a species causes further extinctions, then the capacity of the ecosystem to remain functionally equivalent can be greatly reduced. It seems therefore important to extend the study of species deletion stability to the consequences of species loss on ecosystem functioning.

The relationship between diversity and species deletion stability is still debated. Studies of the impact of diversity on the risk of secondary extinctions have led to opposite results: while Pimm (1980) found a negative impact of complexity (including diversity and connectance) on species deletion stability, Borrvall et al. (2000) emphasised a positive impact of biodiversity on resistance against further species extinctions. It appears essential to understand the reasons for such contrasting effects of diversity and to assess the consequences of these patterns on ecosystem properties. While the effects of food web connectance, interaction strength of trophic interactions, omnivory and food web shape have received particular attention (Pimm 1980, Borrvall et al. 2000, Dunne et al. 2002, Petchey et al. 2004, Ebenman et al. 2004, Christianou and Ebenman 2005), the impact of intraspecific and interspecific competition on species deletion stability has been far less investigated in food webs. Yet the presence of intraspecific competition (or self-limitation) has been shown to strongly affect stability (Saunders 1978), and hence the relationship between stability and other food web properties (Sternler et al. 1997).

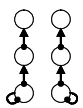
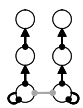
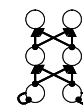
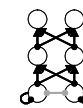
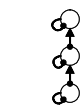
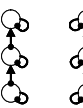
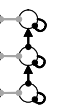
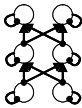
In this study we determine which properties of food web models most strongly affect the impact of diversity on the consequences of species loss. We investigate several aspects: the presence of intraspecific competition at consumer trophic levels, the presence of direct interspecific competition at all trophic levels, and the impact of food web connectance. We assess the

consequences of species loss in terms of secondary extinctions that occur after the loss of one species from the model food web. We also investigate the consequences of species loss on the biomass of the species that remain in the food web. By combining these two types of effects, this study proposes to link the traditional debate on the relationship between diversity and stability to the current study of the relationship between biodiversity and ecosystem functioning.

## Methods

To investigate the impact of species richness on the consequences of the loss of one species, we consider food web models with four diversity levels: there are either 6, 9, 12 or 15 species in the community. The model food webs comprise three trophic levels: autotrophs (“plants”), primary consumers (“herbivores”), and secondary consumers (“carnivores”). The initial food web is rectangular, i.e. the number of species is identical at each trophic level. Food web structure differs in the level of connectance (low or high), the presence of intraspecific competition at consumer trophic levels, and the presence of interspecific competition at the trophic levels where self-limitation occurs (Table 1). Eight different food web structures are thus simulated. 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. Connectance is thus defined in the same way as in recent studies on the consequence of species loss on cascading extinctions (Ebenman et al. 2004). In our model, low connectance is equal to  $1/9$ , and high connectance is equal to  $2/9$ . In the former case, all consumers are specialist in the six species web and at higher diversity levels, consumers consume on average half of the species at the next trophic level below it. In the latter case, each consumer species preys on all species at the next trophic level below it. Note that we also performed simulations for an intermediate connectance level (connectance =  $1/6$ ) in the absence of interspecific

Table 1. Rank coefficient correlations between the proportion of species lost compared to the initial community and the absolute value of the ratio of total biomass before the removal relative to the biomass after the removal minus 1. Organigrams depict different model configurations: low connectance in A, B, E, F vs high connectance in C, D, G, H; absence of intraspecific competition at consumer level in A–D versus presence of intraspecific competition at consumer level in E–F; absence of interspecific competition in A, C, E, G vs presence of interspecific competition in B, D, F, H.

	A	B	C	D	E	F	G	H
Models								
Plant extinction	0.606	0.651	0.796	0.786	0.597	0.685	0.539	0.538
Herbivore extinction	0.491	0.497	0.663	0.621	0.169	0.345	0.193	0.292
Carnivore extinction	0.425	0.384	0.753	0.723	-0.063	0.075	-0.078	0.063

competition. The results from these simulations were qualitatively the same as for the low connectance case and are not presented here for the sake of clarity in the figures.

Community dynamics are described by the generalized Lotka-Volterra equations:

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

where  $x_i$  is the biomass of species  $i$  in a set of  $n$  species,  $b_i$  is the intrinsic rate of increase of species  $i$ , and  $\alpha_{ij}$  is the per capita effect of species  $j$  on the per capita rate of increase of species  $i$ . For all our food webs, basal species are self-limited and the intraspecific competition term  $\alpha_{ii}$  is taken at random from a uniform distribution in the range  $-1$  to  $0$ . The effect of consumer  $j$  on resource  $i$ ,  $\alpha_{ij}$ , is also drawn from the random distribution  $[-1, 0]$ . The reverse effect of the prey species on the consumer is  $\alpha_{ji} = -e\alpha_{ij}$ , where  $e$  is the conversion efficiency (the fraction of consumer prey that is converted into predator biomass) and is here set to  $0.1$ . For basal species,  $b_i = 1$  while for consumer species,  $b_i$  is chosen randomly from a uniform distribution in the range  $-0.01$  to  $0$ . The self-limitation term for consumers is either zero (in the case of no intraspecific competition at consumer levels) or drawn from the random distribution  $[-1, 0]$  (in the presence of intraspecific competition at all trophic levels). Interspecific competition between species from the same trophic level is either zero or drawn from the random distribution  $[-0.1, 0]$ .

We randomly generated 500 permanent food webs for each of the eight food web cases with four diversity levels each. The consequences of species loss are assessed using three response variables: (1) the probability that the system remains permanent after the removal of one species (hereafter termed ‘resistance’), (2) the mean number of secondary extinctions at each trophic level after the loss of one species, and (3) the relative effect of a species deletion on total biomass at each trophic level, expressed as the ratio of biomass before removal relative to the biomass after removal. For simplicity, biomasses are calculated as equilibrium values as was done in a previous study (Petchey et al. 2004). Biomass ratios smaller than  $1$  correspond to a decrease in biomass while biomass ratios greater than  $1$  correspond to an increase in biomass after species deletion. Biomass ratios are used here because they are directly analogous to the measures of response sizes used in experiments (Shurin et al. 2002, Hillebrand and Cardinale 2004).

We chose to use permanence rather than local asymptotic stability as a criterion for stability because permanence is a global property of a model community and it allows for asymptotically stable communities as well as unstable systems in which populations fluctuate

cyclically or chaotically (Law and Morton 1996). A community of  $k$  species is permanent if the boundary of the  $k$ -species phase space is a repeller to orbits that start in the interior of the phase space (Hofbauer and Sigmund 1988). We use permanence as in recent studies on the consequence of species loss on cascading extinctions to make our study more comparable with previous studies. From each permanent replicate community, one species is randomly deleted at each trophic level, one at a time. Following the deletion, either the reduced community is permanent and the remaining species continue to coexist, or it is not permanent and secondary extinctions occur. In the latter case, the post-extinction community is found by examining all the subsets of the reduced community for a subset that is (1) permanent, and (2) uninvadable by species absent from the subset and present in the reduced community. There could in principle be more than one subset with these properties but such cases are very rare and other studies found they had no impact on the results. We considered these cases as negligible in the present study for simplicity. Once a permanent attracting subsystem was found, the response variables were calculated.

To explore the linkage between the number of secondary extinctions and the changes in biomass at each trophic level after species deletion, we calculated the correlation coefficients between these two types of response variables. In this case we considered the amplitude of changes in biomass, measured as the absolute value of the difference between the biomass ratio and  $1$ . The number of secondary extinctions was expressed as the proportion of species lost from the initial community. We also calculated the correlation coefficient between changes in biomass and the absolute number of species going extinct, but we chose to present here only the results using the proportion of species lost because correlation coefficients were generally higher in this case. Since the frequency distribution of these variables was far from normal, we used nonparametric (Spearman) correlations coefficients. All statistical analysis were performed using SPSS. Statistical significance should not be over-interpreted since it is partly a function of the number of replicates chosen.

## Results

### Resistance and number of secondary extinctions

Both the resistance to cascading extinctions and the mean number of secondary extinctions after deletion of one species are strongly affected by the diversity of the initial community (Fig. 1). Furthermore, the relationships between diversity and resistance and between diversity and the mean number of secondary extinctions depend on the models considered, and particularly on the

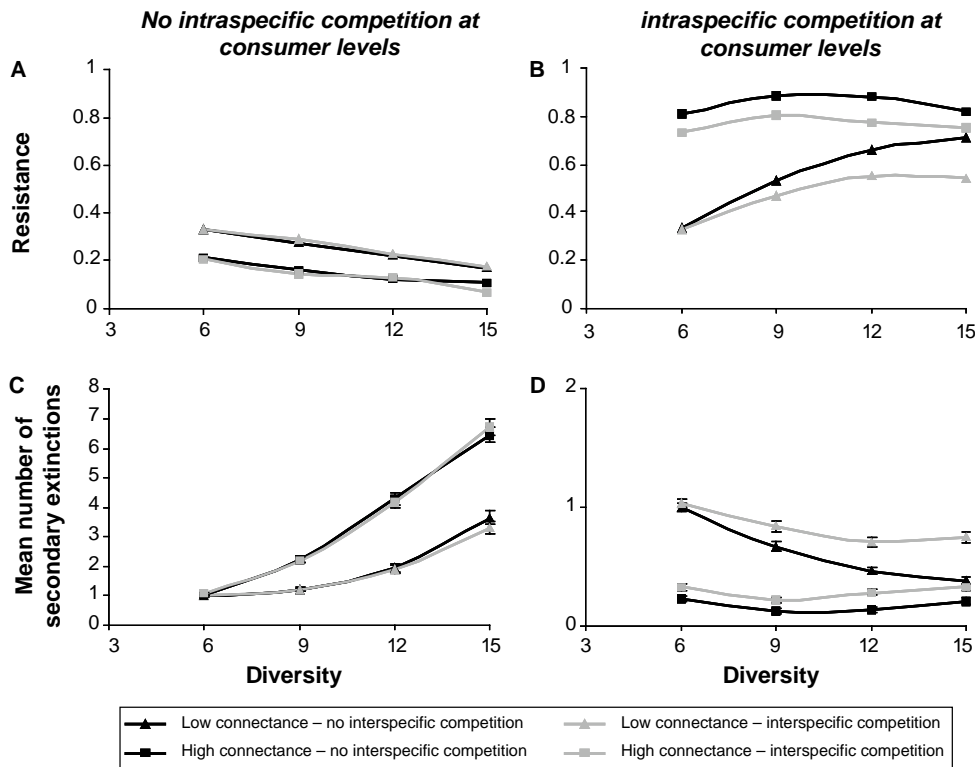


Fig. 1. Resistance and mean number of secondary extinctions ( $\pm$ SEM) against species diversity depending on food web models (500 simulations each). Connectance is either low ( $= 1/9$ , triangles) or high ( $= 2/9$ , squares). Black lines correspond to the cases where interspecific competition is zero while for grey lines interspecific competition is present. (A) and (C): there is no intraspecific competition at consumer levels. (B) and (D): there is intraspecific competition at all trophic levels.

presence of intraspecific competition at consumer levels (compare left and right panels in Fig. 1). When there is no intraspecific competition at consumer levels, resistance decreases as diversity increases while the mean number of secondary extinctions increases. In contrast, when there is self-limitation at all trophic levels, resistance is higher and can increase with diversity while the mean number of secondary extinctions is lower and can decrease as diversity increases. Interspecific competition and connectance also have different effects depending on the presence of intraspecific competition at consumer levels. When there is no intraspecific competition at consumer levels, a lower connectance leads to a higher resistance and to a lower number of secondary extinctions. Connectance has the opposite effect in the presence of intraspecific competition at all trophic levels: resistance is lower, and the number of secondary extinctions is higher, when connectance is lower. While interspecific competition has no effect on resistance and the number of secondary extinctions when there is no self-limitation in consumers, the presence of interspecific competition leads to a lower resistance and to a larger number of secondary extinctions if self-limitation occurs at all trophic levels. In the latter case, interspecific competition also dampens the positive

effects of diversity on resistance and on the mean number of secondary extinctions.

The consequences of species loss on the number of secondary extinctions also depend on the trophic level from which the species is deleted (Fig. 2), and trophic levels are differently affected by species loss (Fig. 3). When there is intraspecific competition at consumer levels, the mean total number of secondary extinctions is lower after carnivore loss than after herbivore or plant loss and the number of secondary extinctions is generally lower after herbivore loss than after plant loss (right panel, Fig. 2). When there is no intraspecific competition at consumer levels, the mean number of secondary extinctions after plant, herbivore and carnivore deletion is generally similar (left panel, Fig. 2). Consumer trophic levels are generally more affected by secondary extinctions than are producers in all food web configurations (Fig. 3). For all food web models, after plant deletion secondary extinctions occur mainly at herbivore and carnivore levels, while after the deletion of a herbivore more carnivores than plants and herbivores become extinct. When a carnivore species is deleted, the mean number of secondary extinctions is highest at the herbivore level (Fig. 3).

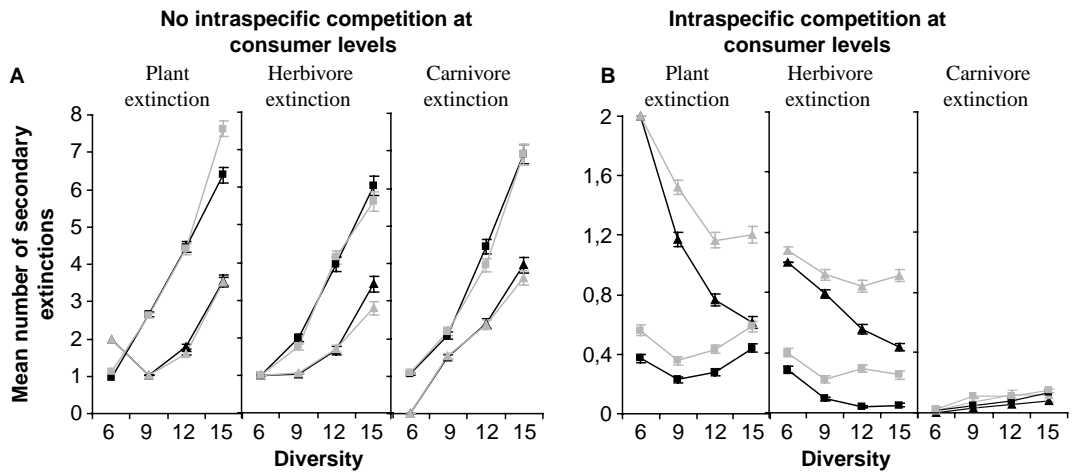


Fig. 2. Mean number of secondary extinctions ( $\pm$ SEM) against species diversity depending on the trophic level from which the species is deleted. (A) there is no intraspecific competition at consumer levels. (B) there is intraspecific competition at all trophic levels. Line code as in Fig. 1.

In the absence of intraspecific competition at the consumer levels, the mean number of secondary extinctions always increases with diversity at high diversity levels whatever the trophic level considered and the trophic level of the species deleted (Fig. 2, 3). In this case the trend is the same as for the total number of secondary extinctions after species loss (Fig. 1). In contrast, when there is intraspecific competition at all trophic levels, the relationship between diversity and the number of secondary extinctions depends on the trophic level from which the species is deleted (Fig. 2). The total number of secondary extinctions decreases as diversity increases after plant or herbivore deletion when connectance is low and after plant deletion when connectance is high (Fig. 2, right panel). In contrast, after carnivore deletion, the total number of secondary extinctions increases with diversity even though it remains far lower than after plant or herbivore deletion. The total number of secondary extinctions after plant deletion when connectance is high first decreases and then increases as diversity increases, leading to non-monotonic changes in the number of secondary extinctions with diversity. Interspecific competition has the same impact on the number of secondary extinctions at all trophic levels (Fig. 1, 2). If there is intraspecific competition at all trophic levels, the shape of the relationship between diversity and the number of secondary extinctions depends on the trophic level considered (Fig. 3). After plant deletion, while the number of secondary extinctions of carnivores generally decreases as diversity increases, the number of secondary extinctions of herbivores can either decrease (in the case of low connectance, Fig. 3B) or increase (in the case of high connectance, Fig. 3D). Interspecific competition also has an impact on the relative numbers of secondary

extinctions at the different trophic levels: after plant deletion the number of secondary extinctions is higher at the herbivore level than at the carnivore level when there is no interspecific competition; the opposite is true in presence of interspecific competition (Fig. 3B).

### Changes in biomass at the various trophic levels

The consequences of species loss on changes in total biomass differ among trophic levels and depend on the trophic level from which the species is deleted (Fig. 4). Total biomass at each trophic level always decreases after plant deletion. After herbivore deletion, total plant biomass can increase while both total herbivore biomass and total carnivore biomass always decrease. After carnivore deletion, total herbivore biomass can increase while total plant biomass always decreases. In parallel, total carnivore biomass generally decreases after carnivore deletion, except at low diversity when there is no intraspecific competition at consumer levels and connectance is high (Fig. 4C).

The amplitude of the changes in biomass depends on the food web models considered (Fig. 4). When there is no intraspecific competition at consumer levels, an extreme increase in total biomass of herbivores can occur after carnivore deletion in comparison with the corresponding cases where intraspecific competition is present at all trophic levels (compare left and right panels in Fig. 4). Similarly, high increases in total plant biomass can occur after herbivore deletion when connectance is low, self-limitation is present at all trophic levels and there is no interspecific competition (Fig. 4B). Despite the latter case, absolute changes in total biomass at the various trophic levels are generally

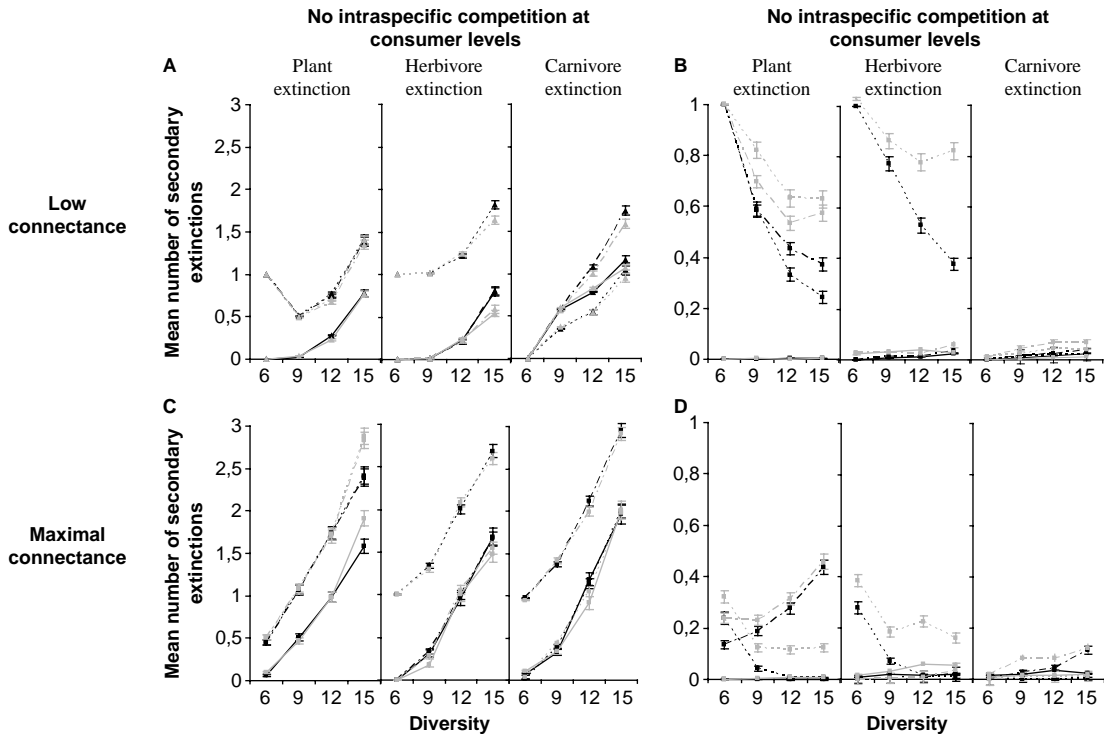


Fig. 3. Mean number of secondary extinctions of plants, herbivores and carnivores ( $\pm$  SEM) against species diversity depending on the trophic level from which the species is deleted and on the food web model. Solid lines correspond to secondary extinctions of plants, semi-dotted lines to secondary extinctions of herbivores and dotted lines to secondary extinctions of carnivores. (A) Connectance is low and there is no intraspecific competition at consumer levels. (B) Connectance is low and there is intraspecific competition at all trophic levels. (C) Connectance is high and there is no intraspecific competition at consumer levels. (D) Connectance is high and there is intraspecific competition at all trophic levels. Line code as in Fig. 1.

lower when there is intraspecific competition at consumer levels, particularly when diversity is high.

Connectance has contrasting effects on changes in biomass depending on model assumptions. When there is intraspecific competition at all trophic levels, a higher connectance leads to smaller changes in total biomass at each trophic level (compare Fig. 4B and 4D). When there is no intraspecific competition at consumer levels, the effect of connectance is more complex. After carnivore deletion, a higher connectance leads to smaller changes in total herbivore biomass; at the same time it also leads to larger changes in total carnivore biomass. Furthermore, at high diversity levels, the decrease in total biomass is higher at high connectance than at low connectance in all cases (compare Fig. 4A and 4C).

Interspecific competition also affects changes in total biomass at the various trophic levels. While it has few effects when there is no self-limitation at consumer levels, in the opposite case changes in biomass are always at least equal, or even lower, when interspecific competition is present than when it is absent (Fig. 4B, 4D).

Lastly, the shape of the relationship between diversity and changes in total biomass depends on the food web model considered. When there is intraspecific competition at all trophic levels, changes in total biomass at each trophic level due to species deletion tend to decrease as diversity increases (the ratio between biomass after deletion and initial biomass tends to 1). In contrast, when there is no self-limitation at consumer levels, the biomass ratio is generally lower than 1 at high diversity and it decreases as diversity increases, except after carnivore deletion at low connectance. Generally, if there is no intraspecific competition at consumer levels, changes in total biomass at each trophic level tend to increase with species richness.

### Correlations between changes in biomass at each trophic level and the number of extinctions

All correlations were significantly different from zero ( $p < 0.01$ , Spearman correlation). Changes in biomass at each trophic level generally show a positive correlation with the proportion of species going extinct in the system in all food webs and in the three cases of species

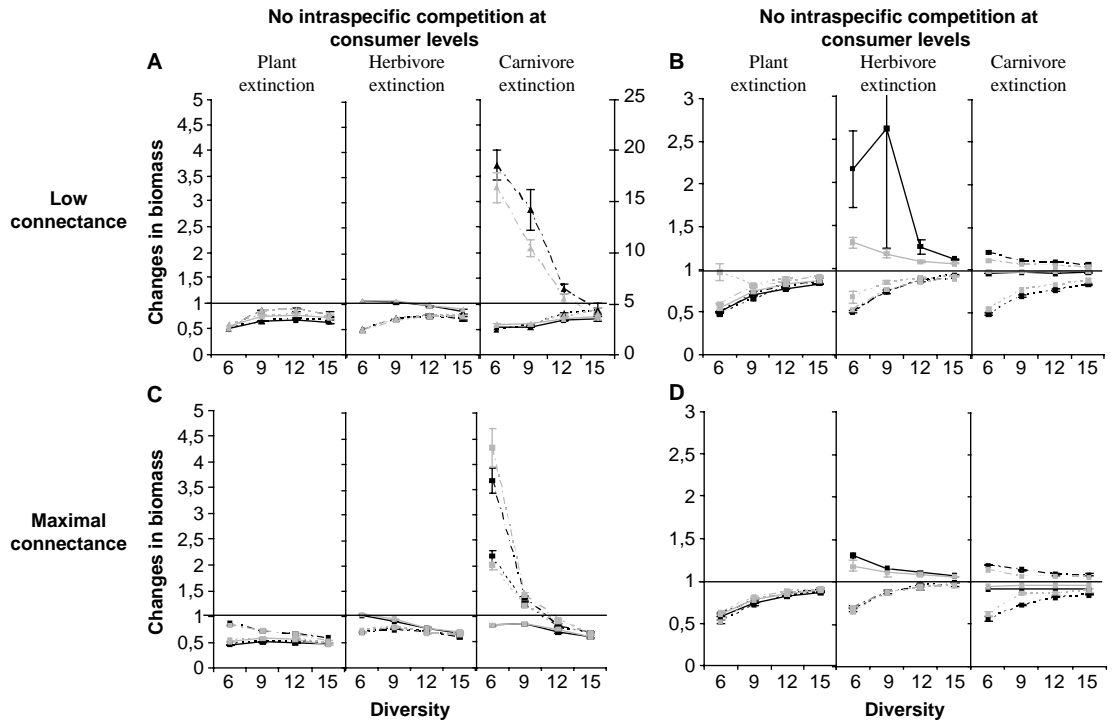


Fig. 4. Changes in total biomass at plant, herbivore and carnivore levels ( $\pm$ SEM) against species diversity depending on the trophic level from which the species is deleted and on the food web model. Changes in biomass is expressed as the ratio of total biomass before the removal relative to the total biomass after the removal. Values below the horizontal line (changes in biomass = 1) correspond to a decrease in biomass at the trophic level concerned while values above correspond to an increase. (A) Connectance is low and there is no intraspecific competition at consumer levels. (B) Connectance is low and there is intraspecific competition at all trophic levels. (C) Connectance is high and there is no intraspecific competition at consumer levels. (D) Connectance is high and there is intraspecific competition at all trophic levels. Other line code as in Fig. 1.

deletion (Table 1). The communities that suffer from a high proportion of species loss are often those which show large changes in total biomass at each trophic level.

The correlation coefficients are high when connectance is high and intraspecific competition is zero at consumer levels (models C and D, Table 1, test of comparison of two correlation coefficients,  $p < 0.001$ ). In contrast, in the cases of carnivore deletion with self-limiting terms at all trophic levels (models E-H, Table 1), the coefficients of correlation are very low. It should be noted, however, that these two cases correspond, respectively, to the case where there is either the maximum number of secondary extinctions (case with a high correlation coefficient) or the minimum number of secondary extinctions (case with a small positive correlation).

## Discussion

This analysis emphasizes several key features of food-web structure and species interactions that affect the

impact of diversity on both cascading extinctions and changes in total biomass after the extinction of a species. In particular, our results provide insights on (1) the debate on the relationship between diversity and stability as measured by resistance to species loss; and (2) the link between studies on cascading extinctions and general studies on the relationship between diversity and ecosystem functioning.

### Risk of secondary extinctions and effect of diversity on cascading extinctions depend on model structure

Our results extend previous analyses of trophic cascades and the distribution of extinctions within food webs since we analysed here the impact of two factors – intraspecific competition and interspecific competition – that have not been considered explicitly in previous studies. Interspecific and especially intraspecific competition can have strong effects on the mechanisms that underlie secondary extinctions. Although uncommon when there is intraspecific competition at consumer

levels, top-down mediated secondary extinctions are important when there is no intraspecific competition at consumer levels. Competition might also affect bottom-up cascading extinctions: many consumers in competition for the same resources may lead to a higher risk of secondary extinctions for weaker competitors after deletion of a resource. This could partly explain the increase in the number of secondary extinctions in the presence of interspecific competition or the negative impact of diversity and connectance after plant or herbivore deletion in some food web configurations in our study. In contrast, the positive effect of connectance and diversity in other cases can be explained by the fact that consumers feeding on many resource species have a lower risk of being extinct than more specialized consumers (Borrvall et al. 2000).

Our results bring new insights into the debate on the relationship between diversity and stability. The contrasting results on the relationship between diversity and stability have been mostly explained by differences in the measure of stability (Pimm 1980, Loreau et al. 2002). Several studies have also demonstrated that stability and its relation to connectance depend on assumptions on interaction strength, functional response or food web structure (DeAngelis 1975, Kondoh 2003, Emmerson and Yearsley 2004). While it has been shown that the impact of diversity on resistance can also depend on food web structure (Borrvall et al. 2000), the contrasting results on the diversity – resistance relationship found by Borrvall et al. (2000) and Pimm (1980) have not been explained yet. We found here that the impact of diversity on the risk of cascading extinctions depends strongly on the presence of self-limiting terms at the consumer levels. In the absence of intraspecific competition for consumers, the risk of cascading extinctions increases with diversity whereas it generally decreases in the opposite case. The presence of intraspecific competition at consumer levels in Borrvall et al. (2000) explains why opposite trends to those revealed by Pimm (1980) were found in this study. In a recent study where intraspecific competition was included implicitly through a ratio-dependent functional response, resistance was however found to have a weak negative correlation with species diversity (Quince et al. 2005). However, in this analysis, the effect of diversity was separated from the effect of redundancy i.e. the fraction of species occupying identical ecological roles. Here, we did not consider separately the effect of redundancy which may explain the difference with Quince et al.'s results. In our study, redundancy and diversity might be positively correlated and therefore, the positive impact of diversity on resistance might also be partly explained by an increase in the fraction of species occupying identical ecological roles. Some results, however, are valid

regardless of whether consumers are self-limited or not: in both cases, we found a decrease in the proportion of permanent systems as diversity increases (unpubl.). The impact of self-limiting terms at consumer levels has been already shown for other measures of stability. In a study on the relationship between the length of food chains and stability (Sternler et al. 1997), the number of self-limiting terms, not the number of trophic levels, seemed to have the greatest influence over the return time to equilibrium. Both types of models, with intraspecific competition only at producer levels (Pimm 1980, Petchey et al. 2004) or with intraspecific competition at all trophic levels (Borrvall et al. 2000, Ebenman et al. 2004, Christianou and Ebenman 2005), can be found frequently in the literature. It is essential that comparison between such studies take into account the potential impact of self-limiting terms on stability in food webs. Opposite effects of diversity on stability do not result here from using different measures of community stability as found previously (Pimm 1984), the contrasting impacts of diversity depend on the structure of the food webs.

The importance of intra- and interspecific competition has been a topic of much debate in ecology. Both competition and predation appear to have substantial effects in field experiments (Sih et al. 1985, Gurevitch et al. 2000) and density dependence is frequently found in natural populations (Silva Matos et al. 1999, Webb and Peart 1999). Direct competition is susceptible to occur in nature in many ways such as through territoriality and mutual interference. Intra- and interspecific competition should rarely occur separately because the mechanisms that explain competition between individuals of the same species equally apply to individuals of different species, at least when they are closely related. Reality probably lies between the different cases considered in this study; the occurrence of cascading extinctions will then depend on the strength and distribution of competition between species. Several reviews of trophic cascades show that top-down trophic cascades are less common and less strong in communities with a high diversity (Schmitz et al. 2000, Hillebrand and Cardinale 2004). These decreases in the strength of trophic cascades with diversity are more in accordance with a model considering high intraspecific competition and relatively low interspecific competition. However, examples of community “collapses” following the loss of predators also exist in the literature (Paine 1966, Estes and Palmisano 1974, Terborgh et al. 2001), and these would correspond more to cases with relatively low intraspecific competition. The relative strength of top-down effects compared with competition probably depends on the ecosystem considered; for instance, top-down effects of predators are generally stronger in

aquatic systems than in terrestrial systems (Shurin et al. 2002), which might lead to a higher risk of secondary extinctions in aquatic systems. There is a need to incorporate the study of the relative strength and distribution of competition to understand the consequences of species loss in food webs.

### **Linking studies of cascading extinctions with studies on the effects of diversity on ecosystem properties**

The results from this study point out that species extinctions in multitrophic systems can either increase or decrease the total biomass within a trophic level as already found in previous theoretical and experimental studies (Thébault and Loreau 2003, Petchey et al. 2004, Duffy et al. 2005, Gamfeldt et al. 2005). In a food web with three trophic levels, the deletion of a consumer species generally leads to an increase in the total biomass of the trophic level below due to a decreased top-down control on the prey. In parallel, total biomass at the other two trophic levels often decreases after the species loss. Our results, however, show that the presence of secondary extinctions can modify these patterns. In the absence of self-limiting terms at consumer levels, total biomass generally decreases at all trophic levels at high diversity, which is probably explained by the high number of secondary extinctions at all trophic levels.

This study lays a bridge between studies of cascading extinctions and studies that focus more on ecosystem properties. The positive correlation between the proportion of species lost and biomass changes show that studying the number of secondary extinctions can also provide information on how the loss of species affects ecosystem processes. Our work suggests that ecosystems that have lost a high proportion of their species will show the most important changes in ecosystem properties as measured here by total biomass at each trophic level. This correlation might be explained by the fact that when a high proportion of species is lost, the few remaining species in the community are insufficient to compensate for this relatively important loss. It is also consistent with some general experimental findings on the relationship between diversity and ecosystem functioning. The relationship between diversity and various ecosystem processes often becomes weaker at high diversity (Hector et al. 1999, Tilman et al. 2001). Thus, the impact of species loss in these studies is lower on average when diversity is high than when diversity is low, which is similar to our present results in the case of self-limited consumers.

In addition to secondary extinctions, other factors also affect changes in biomass at the various trophic

levels. Interspecific competition can lead to a higher number of secondary extinctions but to lower changes in biomass at each trophic level. These contrasting effects of interspecific competition have already been found in another food web model comprising one consumer and an arbitrary number of plant species (King and Pimm 1983, Pimm 1984). The dampening effect of interspecific competition on changes in biomass is probably explained by greater compensatory changes in the remaining species after the loss of a species. When competition is present, a species' extinction's may lead to a competitive release for the other species of the same trophic level, which then causes an increase in their biomass. Consumer generalism is susceptible to have the same impact when consumers share the same prey: when there is intraspecific competition at all trophic levels, the magnitude of changes in biomass decreases when connectance increases. A dampening effect of consumer generalism on changes in biomass is consistent with recent findings on the relationship between diversity and ecosystem functioning in multitrophic systems. A positive diversity–production relationship was absent in an experiment where all herbivores consumed the same prey (Fox 2004) while positive effects of consumers arose when herbivores differed in their food intake (Gamfeldt et al. 2005).

### **Outlook on model improvement and future studies**

This study provides several new insights into the consequence of species loss on ecosystem functioning depending on food web structure and species diversity. Various assumptions on food web properties and the strength of intra- and interspecific competition have strong impacts on the results. Several other aspects would deserve to be tested. First, we assumed here that interaction strength between species was not modified after the deletion of a species. A recent theoretical study showed that the stability of a community increased with connectance if consumers were allowed to adaptively switch their prey preferences in response to variations in prey availability (Kondoh 2003). We can suspect that such an adaptative behaviour may lead to greater compensation after species loss. Secondly, extinctions in our model were random within trophic levels. However, extinction risk is known to differ among species (Pimm et al. 1988), and depends on such features as population size (Tracy and George 1992), trophic position (Petchey et al. 1999) and sensitivity to environmental stress (Thomas et al. 2004). Ordered species extinctions can have different functional consequences than random extinctions (Gross and Cardinale 2005) and might strongly affect cascading

extinctions. Lastly, food web shape and the degree of omnivory have been shown to affect the consequences of species loss (Petchey et al. 2004) as well as the relationship between diversity and cascading extinctions (Borrvall et al. 2000) in simple three-trophic-level models similar to the one studied here. Furthermore, it would certainly be interesting to introduce other forms of species interactions, such as mutualism, that are important in real food webs but often neglected in models. Linking the study of cascading extinctions in more complex and realistic food webs (Dunne et al. 2002) to the study of ecosystem functioning is an exciting avenue for future research.

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