Deleting species from model food webs

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In natural biological communities the disappearance of one species can have knock-on effects causing extinction of further species from the food web. To investigate these effects we used an evolutionary model to assemble many independent simulated food webs, and studied their dynamical behaviour when one species was deleted. On average, only 2.1% of the remaining species went extinct as a result of the deletion. However, the probability of extinction of predators and indirect predators (more than one link up the chain) of the deleted species was several times larger than for an average species. The model allows predators to adapt their choice of prey in response to changing frequencies of the prey. It was found that the larger the proportion of the deleted species in the predator's diet, the greater its probability of extinction. The probability of extinction of prey of the deleted species was also significantly higher than for an average species. This is due to increased competition between prey species after removal of their predator. The effect was largest for prey species that formed an intermediate fraction of the diet of the deleted species. The number of further extinctions increased significantly with the number of links in the food web to the deleted species prior to deletion, and was also correlated with the bottom-up and top-down keystone species indices. We also considered which properties of the web as a whole influenced its robustness to species deletion. This revealed a significant correlation between ecosystem redundancy and deletion stability, but no clear relationship with complexity.

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The world's ecosystems are increasingly being subjected to stresses that result in large-scale changes in species population densities. These stresses often directly or indirectly arise from human activities and include pollution, over-exploitation, species invasions and habitat destruction (Carlton and Geller 1993, Milner-Gulland and Bennett 2003). Understanding how ecosystems respond to such perturbations is therefore highly important.

We will use an evolutionary model of community assembly to generate food webs with which to study species deletion. Species deletion is a large-scale perturbation of particular relevance, as it is a commonly used empirical tool to measure interaction strengths within real communities, and can be considered a reasonable approximation to other large perturbations (Paine 1980, Pimm 1980).

The theory of small perturbations in dynamical models of ecosystems is well developed. It began with May's seminal work showing that the probability of an ecosystem with random interactions being locally stable decreases with both the number of species, the frequency of interactions and the strength of those interactions (May 1972, 1973). This result was an important contribution to the complexity–stability debate and contradicted earlier ideas that complexity should naturally lead to stability (Odum 1953, MacArthur 1955, Elton 1958). A crucial conceptual element in May's work is that only

a local knowledge of the dynamics, encapsulated in the "community matrix", is necessary to determine the stability of the population equilibrium to small perturbations. This is also true of perturbations that actually alter the position of the equilibrium, provided that they are small enough (Yodzis 1989). The results of small perturbations can be determined using only "local models", where the species growth rates are approximated by linear functions of the population densities (Yodzis 2001).

In contrast the study of large-scale perturbations requires a "global model" – one defined over the whole of phase space. The use of such a model will inevitably involve a modeling choice, but it is important that it incorporates phenomena such as nonlinear functional responses and adaptive foraging, which will be likely to operate over these large changes in population density (Abrams 1996).

A global model with these features has already been developed as part of a larger model of community coevolution by some of us (Drossel et al. 2001). This model assembles ecosystem communities through the repeated addition of new species that are modified versions of those already present. It is therefore conceptually similar to community assembly models (Drake 1990, Law and Morton 1996, Morton and Law 1997, Lockwood et al. 1997), the difference being that new species are generated in situ rather than being taken from a species pool. In the model, species are constantly being subjected to large perturbations in population densities as new species are added and existing species go extinct. Crucially, species are allowed to alter their foraging strategies in response to these changes. Thus, the population dynamics of the model are particularly well suited to the study of species deletion and will be used in this study. Since previous studies of deletion have used the Lotka–Volterra equations or the equivalent discrete time Ricker dynamics, this will give a unique perspective on the problem (Pimm 1979, 1980, Borrvall et al. 2000, Lundberg et al. 2000, Fowler and Lindström 2002).

We will not only use the model's population dynamics, we will also use the evolutionary assembly model to generate the food webs from which species will be deleted. It might be preferable to use real food web structures, but then interaction strengths that possess a stable equilibrium for that structure would have to be determined, which is likely to be difficult for a large food web. The only studies of deletion that have used large empirical food webs circumvent this problem by adopting a network approach, without using explicit population dynamics (Solé and Montoya 2001, Dunne et al. 2002). Their procedure reveals interesting features of the network topology, but by using the simple rule that species go extinct when none of their prey remain, they ignore the complex realities of the dynamics. Our model

allows us to generate a data set of food webs with reasonably realistic topologies and interaction strengths (Drossel et al. 2001), suitable for investigating the complex dynamics of deletion in multi-species communities.

The outline of the rest of the paper is as follows. We begin with a brief review of the model, followed by the details of the generation of the food web data set and the deletion experiments themselves. The next sections concern the results of these experiments. We also investigate how the trophic relationship between a pair of species influences the outcome of deleting one of them. We then go on to consider which species properties correlate with large changes in community composition following that species removal, and we consider the stability of the communities as a whole to deletion and the extent to which this is determined by their food web structure. We end with a discussion of the major results of the paper.

The model

We will now give an overview of the model we will use to evolve the food webs. A more detailed description is given in Appendix 1, or alternatively in Caldarelli et al. (1998), Drossel et al. (2001) and Quince et al. (2002).

The dynamics of the model has two time scales. On time scales of the order of the lifetimes of individuals, the number of species is fixed and the dynamics is determined by a set of coupled ordinary differential equations for the species population densities. This population dynamics uses a multi-species variant of the ratio-dependent functional response (Arditi and Michalski 1996). The functional responses are parameterised by interaction scores that give the degree to which a species is adapted to exploit a particular prey. The interaction scores are themselves a function of an abstract set of 'features' possessed by individual species.

Adaptive foraging is incorporated into the population dynamics through the definition of an effort matrix f, whose elements f_{ij}, give the fraction of the population of species i that exploits species j. The values of these efforts are constantly updated such that there is always an ideal free distribution of predators across prey (Fretwell and Lucas 1970). This distribution will depend on the population densities and interactions scores in the community, therefore allowing the efforts to adjust with the changing composition of the food web.

Ratio-dependent functional responses model sharing of prey between predators. In our multi-species setting we assume sharing between all individuals of all species that exploit the same prey. This implies interference competition between species utilising the same resource. The strength of this competition is reduced if species differ in the features they possess. The magnitude of this reduction is parameterised by the competition constant (c).

Autotrophy is modelled by including an extra 'environment' species with features that are fixed throughout a run. Other species may exploit the environment but its population density remains constant and proportional to the model parameter R, which therefore controls the rate of input of external resources into the food webs. Two further model parameters arise from the population dynamics. They are the saturation constant in the ratio-dependent functional response, denoted by b, which determines the overall effectiveness of predation in the food webs, and the 'ecological efficiency' λ, which is the ratio of the numerical to the functional response.

The system is allowed to change according to the population dynamics for what may be relatively long intervals until equilibrium is reached, that is, until the populations of the different species present remain unchanged. If, during the population dynamics, the density of a species falls below a value N^{min}, usually taken to be 1, it is assumed to have become extinct and is removed from the system.

Once an equilibrium of the population densities is reached, a speciation event is initiated: a new species is generated by changing one of the features of a randomly chosen species. This new species is then added to the system with a population density N^{child}, also taken to be 1 in these simulations. The system is then again allowed to develop under the deterministic equations of the population dynamics. The small population of the new species may give rise to a viable population, or it may die out, but eventually when a new equilibrium is reached, a new speciation event will take place. By repeating this procedure tens of thousands of times an entire food web can be evolved, using a combination of conventional population dynamics and stochastic speciation events. On these very long evolutionary time scales the discrete time steps where speciation occurs are the main aspect of the dynamics.

A thorough understanding of this assembly process is not required to understand the study that follows. It is sufficient to note that it allows us to generate a data set of food webs from which we can remove species. The model also provides the population dynamics used to determine the results of the species deletions, but we have deliberately made our analysis independent of the dynamics. The food web properties used are all derived from the energy flows between species in the community. These change during the population dynamics as a consequence of the changing species population densities and diet compositions represented by the efforts, but once the food web reaches dynamical equilibrium after a speciation event, they become constant and could be measured for a real web. The details of the population dynamics and the representation of species have been placed in Appendix 1.

Deletion experiments

The set of model food webs used in this study was obtained by performing four hundred independent simulations of the model, each simulation lasting for 120 000 speciations. These simulations were independent, in the sense that different pseudo-random number sequences were used in their generation. Thus the simulations differed in their random feature matrices, environment features and speciation events. The same parameters were used in all the simulations; these being $R = 1 \times 10^5$, $b = 5 \times 10^{-2}$, $c = 0.5$, $\lambda = 0.1$ and $N^{min} = N^{child} = 1.0$.

The above choice of parameters generates reasonably realistic food webs of a tractable size (Drossel et al. 2001). Larger food webs can be assembled by increasing R which is effectively proportional to the primary productivity of the food web. Reducing c increases the links per species through a reduction in the strength of inter-specific competition. The food web structure is less sensitive to the other parameters, although b must be smaller than some critical value for a large web to evolve (Quince et al., 2005).

The 400 final food webs from these simulations, which after 120 000 speciations will have structures drawn from a stationary distribution, constituted the ecosystem data set.

A typical food web is shown in Fig. 1. Each species in this diagram is represented as a circle, the sizes of which are the same for all species. This differs from the convention adopted in Quince et al. (2002), where the radii of the circles were proportional to the logarithm of
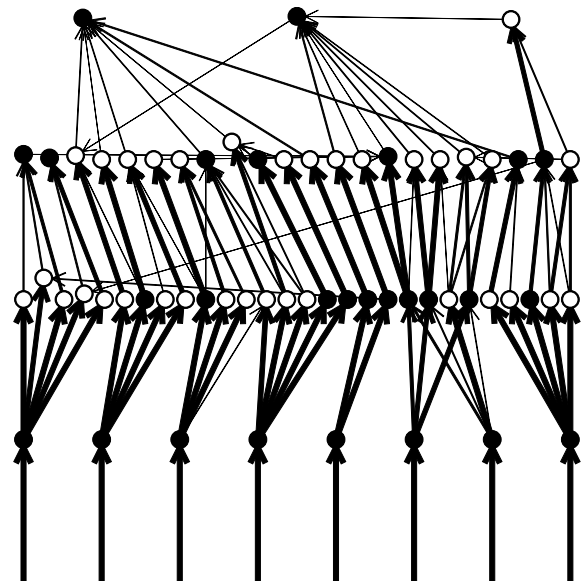

Fig. 1. A typical model food web with 61 species. The 27 species whose deletion causes further extinctions have been coloured in black.

the population densities. The arrows represent predator–prey interactions, with the arrow pointing from the prey to the predator. The intensity of the arrow is proportional to the fraction of the predator's diet that consists of that particular prey. The vertical arrows originating from the base of the diagram, rather than from another species, indicate that the species is feeding off the environment. The species are positioned vertically according to trophic height, defined as the average path length from the species to environment, the average being weighted by predator diet fractions.

The 400 food webs in the model data set span a range of structures. We shall quantify this variation with five food web statistics:

1) The total number of species in the food web denoted by S.
2) The links per species denoted by L/S. This quantity is simply the number of predator–prey interactions divided by the number of species, where we will use the convention of counting a link if it constitutes greater than 1% of a predator's diet.
3) The fraction of omnivorous species in the food web denoted by O. We define omnivorous species as those which feed at more than one trophic level and define the trophic level of a species to be the shortest path from that species to the environment. The justification for this choice is the observation (Yodzis 1984) that the shortest path between a species and the environment tends to be the most important energetically.
4) The degree of cycling denoted by C. The method we adopt for measuring the amount of cycling of energy in the food webs is based on both the ideas presented in Ulanowicz (1983) and on source code kindly provided by the author. Essentially a backtracking algorithm was first used to identify each cycle in a food web. Having done this, the amount of energy flowing in a cycle was identified with the strength of the weakest link of the cycle, exactly as in Ulanowicz (1983). To define C we measure the proportion of a predator's prey obtained through cyclic flow averaged over the species in the web.
5) The ecosystem redundancy denoted by ρ. The redundancy of an ecosystem is the proportion of species which can be considered superfluous to the functioning of the ecosystem as a whole (Walker 1992). We define a species to be redundant in our food webs if at least one other species possesses the same pattern of trophic links i.e. the same predators and prey. As for the calculation of L/S, only links forming greater than 1% of the predator's diet are used in this calculation. Then the redundancy, ρ, is the fraction of redundant species in the food web.

In Table 1 the means and standard deviations of the five statistics are shown for the four hundred food webs in the data set.

This data set was then used to investigate the effect of species deletion. A single species was removed from a web and the population dynamics iterated until a stable equilibrium was reached. If, during this process, the population of a species fell below N^{min}, then it was removed ("went extinct") in accordance with the criterion applied when evolving the communities. For each web every species was deleted independently, that is, the webs were returned to their original state between deletions. In total, over all the food webs, 25 531 species were deleted. In Fig. 2 we show the frequency distribution of number of further extinctions for these deletions. This distribution does not decay exactly exponentially with further extinction number, but it does have a characteristic size of just a few species. The number of further extinctions seems bounded, the largest number is seventeen, and on no occasion is the whole web of typically sixty species close to collapse. The effect of deleting a species is localised in the webs.

Trophic relationships and species deletion

In this section we investigate how the trophic relationship between a pair of species influences the impact that deleting one of the pair will have on the other. For each of the single species deletion experiments described in the previous section, we counted the number of other species in the web that were predators, prey, competitors and indirect predators of the deleted species. A competitor is any species that shares a prey with the deleted species. We define an "indirect predator" as any species which derives part of its resources from the deleted species but is not a direct predator. Thus it will be linked to the deleted species by a path of trophic interactions directed from prey to predator with length of at least two. In calculating the categories all links which formed less than one percent of the predator's diet were ignored.

For each category and each species deletion we calculated the number of species with the corresponding trophic relationship to the deleted species that went extinct, and the total number of such species. These quantities were then summed over every extinction in every web and divided to give an estimate of the

Table 1. Means and sd of five food web statistics for the 400 model food webs in the data set.

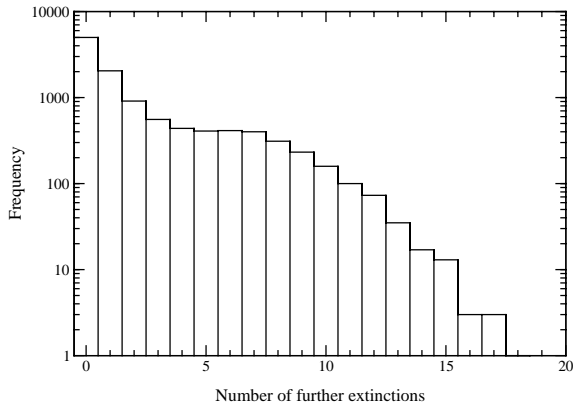| Statistic	Symbol	Mean	sd
Number of species	S	63.8275	7.5152
Links per species	L/S	1.6881	0.1258
Fraction of omnivores	O	0.1606	0.0474
Degree of cycling	C	0.0049	0.0022
Redundancy	ρ	0.1884	0.0706

Fig. 2. Frequency distribution of the number of further extinctions for the 25 531 species deletions.

extinction probability. These results are shown in Table 2. The first row shows the results for all species, in order to aid comparison with the other results. Examining the next row we see that a predator of a deleted species is more than seventeen times as likely to go extinct following the deletion of its prey than an average species in the web. This is intuitively sensible.

More interestingly it is also found that the prey of a deleted species is three times as likely to go extinct as an average species in the web when its predator is removed. Since the direct effect of a predator on its prey is positive then indirect effects, involving the change in population density of a third species, must be responsible for these prey extinctions (Abrams et al. 1996). An examination of individual extinction events reveals that a number of different mechanisms are operating but the simplest, known as predator-mediated coexistence or keystone predation, dominates. This is a mechanism whereby a predator allows inferior competitors to coexist with a superior competitor by predation of the competitively dominant species. Thus the deletion of the predator can lead to extinctions amongst its prey. This has been observed in real communities (Paine 1974, Lubchenco 1978, Navarrete and Menge 1996) and in theoretical studies of simple dynamical systems (Fujii 1977, Shigesada and Kawasaki 1988).

Table 2. The effect of trophic relationship on the probability and relative probability of extinction following deletion of a species from a food web. The relative probability of extinction is defined relative to the probability of extinction for the trophic relationship "All species". In all cases trophic relationship was judged by χ^2 tests to have a significant effect on extinction probability.

Trophic relationships	Probability of extinction	Relative probability of extinction
All species	0.021	1.000
Predators	0.360	17.066
Prey	0.068	3.241
Competitors	0.004	0.178
Indirect predators	0.244	11.547

It is difficult to unequivocally identify the causes of species extinctions from the population densities before and after the removal of the deleted species. Circumstantial evidence for the importance of predator-mediated coexistence is however provided by the observation that in 37% of prey extinctions following predator removal, a competitor species exploited by the same deleted predator more than doubled in size.

The plausibility of the above mechanism is also supported by the fact that competitors of the deleted species are more than five times less likely to go extinct than an average species, suggesting that competition plays an important part in structuring these communities. The effect on indirect predators is also significant: they are eleven times as likely to go extinct following the removal of their indirect prey compared to the average. It is interesting to note that the effect on an indirect predator is less than that on a direct predator. We will return to this later.

Predator−prey interaction strengths and extinction probabilities

The results in Table 2 show that removing the prey, or indirect prey, of a species has a negative effect on the predator. Clearly the importance of a prey species to its predator will vary between predator–prey pairs. A measure of the positive effect that a prey species has on the predator will be the effort f_{ij}, corresponding to the in the predator's prey fraction diet (Ulanowicz and Puccia 1990).

We can derive a similar quantity for the positive effect that an indirect prey species has on its indirect predator. Consider the square of the f matrix $:f_{ij}^2 = \Sigma_{k=0}^{S} f_{ik} f_{kj}$, where the sum is over all species in the web and $k = 0$ corresponds to the environment. Since f_{kj} is the fraction of species k's diet that comes from species j, then $f_{ik} f_{kj}$ is the fraction of species i's diet that comes from species j via species k. If we now sum k over all species in the web, we obtain the fraction of species i's diet that comes from species j through all paths of length 2. Therefore if we define the matrix:

$$F = \sum_{n=1}^{\infty} f^n \tag{1}$$

then its elements F_{ij} give the fraction of species i's diet that comes from species j via all possible paths. Since all resources originally derive from the environment, $F_{i0} = 1$ for any species i. For the direct matrix f, normalisation ensures that $\Sigma_{j=0}^{S} f_{ij} = 1$, whereas for the indirect matrix $\Sigma_{j=0}^{S} F_{ij} \geq 1$. Nevertheless each individual element $F_{ij} \leq 1$ because F_{ij} is defined as the fraction of the diet of i that passes through j in some way.

If the infinite series of matrices converges, it can be calculated using $F = (1 - f)^{-1} f$. All 400 f matrices in this

study were such that the sum was finite, however we have not been able to prove the convergence of the sum for a general web.

We are interested in separating the effects of indirect and direct predation. This can be achieved by defining a further matrix I such that

$$I_{ij} = \begin{cases} F_{ij}, & \text{if } f_{ij} = 0 \\ 0, & \text{if } f_{ij} > 0 \end{cases} \qquad (2)$$

Thus if $I_{ij} > 0$, then species i will be an indirect predator of species j according to the definition given above.

We can now examine how the probability that a predator or indirect predator goes extinct, following removal of its prey, varies with the proportion of the prey in the predator's diet. An initial analysis using histograms suggested a polynomial form for the probability. Thus polynomials of increasing order were fitted to the data by maximum-likelihood until the extra coefficient failed to significantly (tested with χ^2) improve the fit. The results are shown in Fig. 3.

The interpretation of Fig. 3 is quite straightforward. Both curves are monotonic, as the fraction of the predators, or indirect predators, diet that is obtained from the deleted species increases, so does the probability of predator extinction. However the probability of extinction does not become large until the prey constitutes a significant fraction of the predators diet. For direct predators it does not reach 10% until $f_{ij} \sim 0.65$ and for indirect predators this occurs when $I_{ij} \sim 0.50$. This probably arises from incorporating adaptive foraging into the population dynamics: predators can survive events that remove a large portion of their prey. In both cases the extinction probability rapidly approaches, but does not quite reach 100%, as f_{ij} (I_{ij}) approaches 1, the limiting values being 97.8% (99.1%).

The two curves in Fig. 3 have a similar form, but at any given f_{ij} or I_{ij} value the probability of extinction is greater for indirect predators. This seems to contradict Table 2, which shows a greater probability of deletion for direct predators than indirect predators. However this can be explained by the distribution of the nonzero elements of the I and f matrices. If there are more small values of I_{ij} than f_{ij}, then defining a predator (indirect predator) as having $f_{ij} > 0.01$ ($I_{ij} > 0.01$) will lead to a lower probability of deletion for indirect predators than direct predators, even though for a given value of f_{ij} (I_{ij}) the effect of removing the prey on the indirect predator is more significant.

In Fig. 4 the probability distributions of f_{ij} and I_{ij} for all $f_{ij} > 0.01$ and $I_{ij} > 0.01$ are shown. Both these distributions have a U-shaped appearance that is characteristic of the model generated food webs. This means that most species have a dominant prey from which the majority of their resources are derived and a number of minor prey that together constitute only a small fraction of their diet. There are more of these minor prey for
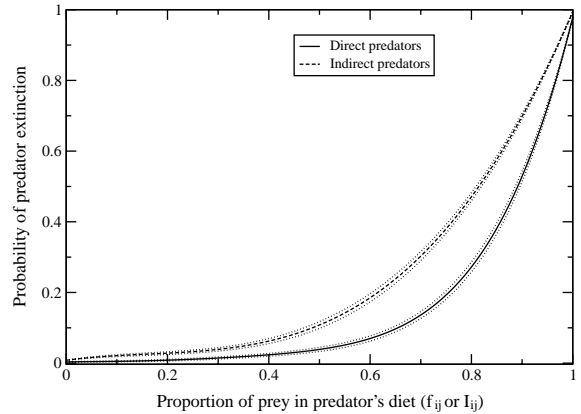
Fig. 3. The probability of predator (indirect predator) extinction upon prey removal as a function of the proportion of that prey (indirect prey) in the predator's diet. The probability was estimated by maximum likelihood fitting of a fifth order polynomial to the data for direct predators (coefficients 0.0036 ± 0.001, 0.019 ± 0.06, 0.66 ± 1.0, -0.15 ± 0.6, 1.4 ± 2, -3.4 ± 3, 3.1 ± 1) and a third order polynomial for indirect predators (coefficients 0.0082 ± 0.0004, 0.19 ± 0.04, -0.76 ± 0.2, 1.55 ± 0.06). The dotted lines show the 95% confidence intervals.

indirect predators as indicated by the weighting of $P(I_{ij})$ at small values compared to $P(f_{ij})$, which explains the apparent contradiction.

This does not of course explain why an indirect predator is more likely to go extinct when a prey constituting a given fraction of its diet is removed. This may arise from the assumption implicit in Eq. 1 that the net importance of multiple paths to the predator can be obtained by simply summing their individual weights. We showed in Table 2 that a prey species has an increased probability of extinction following removal of its predator. We might also expect that this effect will depend on the prey fraction in the predator's diet. This is investigated in Fig. 5, where the probability of prey extinction following predator removal has been
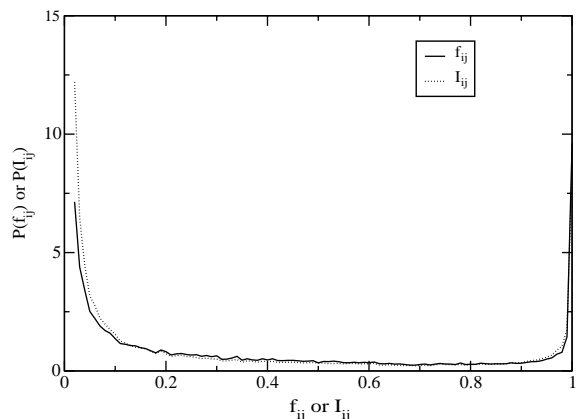
Fig. 4. The probability distribution of f_{ij} and I_{ij} for all $f_{ij} > 0.01$ and $I_{ij} > 0.01$. These results are a compilation over the 400 food webs described.
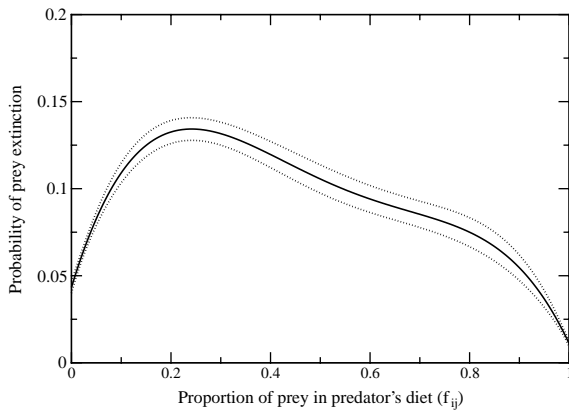
Fig. 5. The probability of prey extinction upon predator removal as a function of the proportion of that prey in the predator's diet. The probability was estimated by maximum likelihood fitting of a fourth order polynomial to the data (coefficients 0.04 ± 0.004, 0.94 ± 0.06, -3.2 ± 0.6, 4.1 ± 1, -1.8 ± 0.5). The dotted lines show the 95% confidence intervals.

estimated by fitting a fourth order polynomial of f_{ij} to the data. Prey extinction probability peaks at an intermediate value around $f_{ij} = 0.25$, where slightly less than 15% of prey are going extinct.

Note that if f_{ij} is close to 1, the predator is specialized to exploit the prey and none of the latter's competitors will gain from the predators removal. Similarly, as f_{ij} tends to zero, the likelihood that the predator is exploiting the prey's competitors will decrease and its probability of causing the extinction of the prey will be no greater than average. If predator-mediated coexistence is the dominant mechanism causing prey extinction we would predict that removal of the predator would have the greatest impact on a prey that was an intermediate fraction of the predator's diet, as we see in Fig. 5.

Trophic levels

In Table 2 we categorised species according to their trophic relationship to the deleted species. Another way to categorise species in a food web is by trophic level. As mentioned above we use the minimum path length definition of trophic level (Yodzis 1984). Having assigned a trophic level to each species in our ecosystems, we were able to calculate the percentage of deletions that caused further extinctions in each trophic level as a function of the level of the deleted species. These results are shown in Table 3. They are a collation of results from the deletions of all species in the four hundred model communities.

The analysis of this data is aided by statistics on how the number of species S, the average prey number k_{prey} and average predator number k_{pred} vary between trophic levels. The number of species S in each trophic level was

Table 3. The percentage of deletions which caused further extinctions on each trophic level, as a function of the level of the deleted species.

Level of deleted species	Level of further extinctions				
	All	1	2	3	4
All	43.5	1.1	26.4	32.3	3.1
1	94.4	1.2	93.1	83.1	14.7
2	38.2	1.3	9.2	35.0	1.3
3	33.6	0.9	26.3	12.6	1.8
4	52.8	0.6	32.7	41.0	1.0

calculated by averaging over the four hundred webs in this study, the other statistics were averaged over the total number of species in each trophic level. These statistics, together with standard deviations in brackets, are shown in Table 4.

The results in Table 3 can be explained in terms of the same bottom-up and top-down effects observed in the previous two sections. There is a high chance (93%) that deleting a level 1 species will lead to extinctions on level 2 because each level 1 species has an average of just over four predators and these are specialised, usually with only one prey. It is also likely that extinctions on level 3 (83%) and to a lesser extent on level 4 (14%) will follow as these losses propagate up the web. The strength of this bottom-up effect decreases with the trophic level of the deleted species – 35% of deletions from level 2 caused extinctions on level 3 and only 2% of level 3 deletions affected level 4 – as the average number of predators on the level above decreases and those predators become less specialised.

Conversely the strength of the top-down effect increases with the trophic level of the deleted species. Only 1% of deletions from level 2 caused extinctions on the bottom trophic level whereas 26% of level 3 deletions impacted level 2 and removing 41% of level 4 species resulted in extinctions amongst level 3. This is also due to the changes in predator specialisation with trophic level. As the level increases so does the average number of prey k_{prey}. Each prey will then only comprise part of the predator's diet, and so the region of intermediate f_{ij} values in Fig. 5 with high prey extinction probability applies. The question of why the model food webs show these characteristic changes in mean predator and prey number with trophic level is discussed in Quince et al. (2005).

Table 4. The dependence of average number of species S, number of prey k_{prey}, and number of predators k_{pred}, on trophic level. The figures in brackets are standard deviations.

Level	S	k_{prey}	k_{pred}
1	7.76 (1.06)	0 (0)	4.26 (1.34)
2	30.19 (4.41)	1.13 (0.37)	1.68 (0.74)
3	24.63 (4.27)	2.71 (1.62)	1.25 (0.49)
4	1.26 (0.84)	5.84 (3.31)	1.09 (0.29)

Keystone species

Thus far the focus of this study has been on pairs of species and how the trophic relationship between them influences the effect that deleting one species will have on the other. It was found that the effects of deletion can propagate both up and down food webs. We now consider the related question of what factors determine the impact that deleting a species will have on the whole web. Specifically, we ask whether there are any consistent differences between species whose removal causes little change in the food web, and those which play a major role in structuring the community. The latter are sometimes referred to as "keystone species", although this term can be restricted to those species whose importance is large relative to their population size (Power et al. 1996). Here we will simply be interested in identifying factors that statistically influence the number of further extinctions that follow the removal of a species.

The trophic level of the deleted species has an effect on the expected number of further extinctions. This is shown in the first column of Table 3, where the probability of further extinctions in the web as a whole is seen to be largest for species on trophic level 1. This probably reflects the greater importance of effects propagating up, rather than down, the food web. An alternative way to categorise species according to trophic role, which is better at separating these two processes, is into the following three classes: 'top' (species with no predators), 'intermediate' (species with both predators and prey) and 'basal' (species with no prey). When this is done, it is found that 95% of basal species removals caused further extinctions as opposed to 37% of intermediate and 35% of top species deletions. Comparing

the figures for basal and top species reveals that top-down processes are indeed statistically less important than bottom-up in these communities.

The above categories are quite broad. One property which we can use to more finely discriminate between species is the number of other species they interact with through predator–prey links. We might expect this to correlate with the impact of deleting the species on the food web. That this is indeed the case is shown in Fig. 6, where the median number of further extinctions is plotted as a function of the node degree k, in network terminology. In the case of food webs, the latter corresponds to the number of predators plus the number of a prey of a species. The results are shown for basal, intermediate and top species separately. For all three classes the median number of further extinctions increases with k, so the most connected species are the ones whose removal has the greatest effect on the food web structure. The results for top species provide further support, albeit circumstantial, that the top-down effect in our webs is predator-mediated coexistence, since we would expect the importance of this effect to increase with the number of prey of the predator. They can be contrasted with an earlier study that failed to find such a relationship (Pimm 1980).

These results have relevance for the studies of real food web robustness to deletion mentioned in the Introduction. These obviated the need for an explicit dynamics by considering multiple removals, and judging a further extinction to have occurred when all the prey of a species are absent (Solé and Montoya 2001, Dunne et al. 2002). These studies found that removing the most connected species resulted in more secondary extinctions
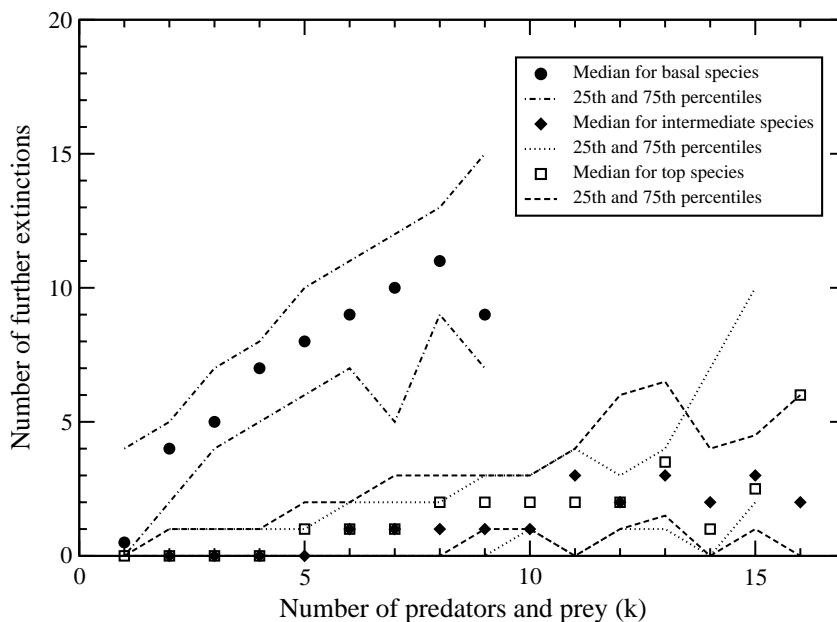

Fig. 6. The number of further extinctions following the deletion of a species as a function of its total number of predators and prey – also known as the node degree k. The results are subdivided according to whether the deleted species is basal, intermediate or top. The symbols give the medians of the distributions and the various dotted lines the 25th and 75th percentiles.

for the same number of species removed. Our results suggest that if population dynamics were included in these studies, the food web structures would be even more sensitive to the removal of highly connected species.

The correlation between k and further extinction number appears surprisingly good from Fig. 6, especially given that it quantifies the number of direct interactions of a species, and does not give information on the strength of indirect effects, which we have already shown to be important (Jordán and Scheuring 2002). It is difficult to devise measures of species importance that do incorporate indirect effects. Potential candidates are the bottom-up and top-down keystone indices of Jordán et al. (1999). These were originally devised for binary food webs, but it is easy to extend them to the model food webs which include diet compositions considered here. In fact the bottom-up keystone index for a species i is simply

$$K_b^i = \sum_{j=1}^{s} F_{ji} \qquad (3)$$

Here the matrix F is defined by Eq. 1 and, as discussed in the previous section, its elements give the fraction of species i's diet that comes from species j via all possible paths. This makes the meaning of K_b^i clear: it is the total number of species that depend on i directly or indirectly for resources. A complementary quantity K_t^i measures the strength of top-down effects. For nonbinary food webs this is the row sum of the matrix formed by summing all powers of p greater than or equal to one. Here p is a matrix whose elements, p_{ij}, give the fraction of the total resources lost by j that are consumed by i.

There is a good correlation between K_b^i and further extinction number for basal species, as can be seen from a plot of median K_b^i values for each number of further extinctions (Fig. 7). There is some significant deviation at low K_b values which probably derives from the assumption implicit in the definition of K_b^i that the probability of predator (indirect predator) extinction is proportional to the F_{ij} values. In fact we know from Fig. 3 that the probability is smaller than this, particularly for small F_{ij} values, which may explain the over-estimation of the probable further extinction number for species with small K_b values. The correlation between K_t^i and the number of extinctions following removal of a top species is less good than for K_b, although a definite trend exists (Fig. 8).

We can quantify these correlations and compare the effectiveness of these indices to simply using the number of direct interactions up or down (k_{pred}, k_{prey}), by performing linear regressions of the number of further extinctions as a function of these variables. These results are shown in Table 5. Examining the R^2 values which measure the explanatory power of the independent variables, reveals that for basal species, K_b is a much better predictor of the number of further extinctions than k_{prey}, the index is measuring the resultant cascade of extinctions up the web. On the other hand K_t is no better than k_{pred} at predicting extinctions following removal of a top species: it is not quantifying the more subtle indirect effects that propagate down a web. The results for intermediate and all species confirm these conclusions, but also allow us to quantify from the regression coefficients (1.0581 and 0.7177 for K_b and K_t from all the species) the relative strengths of bottom-up and top-down effects in these communities.
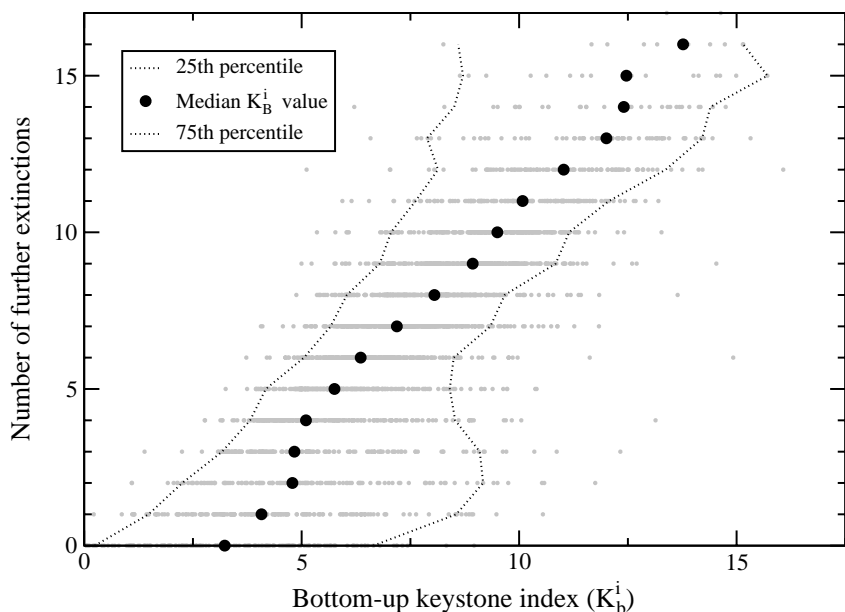

Fig. 7. The number of further extinctions following the deletion of a basal species i plotted against its bottom-up keystone index (K_b^i). The faint grey dots give individual data points present in order to give a sense of the distribution. The black dots give medians and the dotted lines the 25th and 75th percentiles of the distribution of K_b^i values for each number of further extinctions.
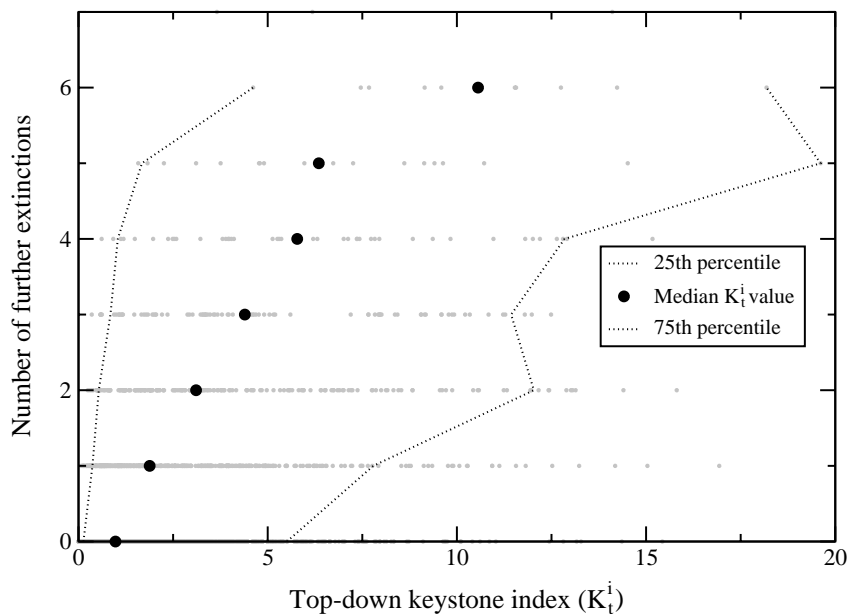
Fig. 8. The number of further extinctions following the deletion of a top species i plotted against its top-down keystone index (K_t^i). The faint grey dots show individual data points. The black dots are the medians, and the dotted lines the 25th and 75th percentiles, calculated for the distribution of K_t^i values for each number of further extinctions.

Stability of food webs to deletion

In the previous two sections we focused on the effect that deleting one species has on the others in the model food webs. Here we will consider the stability of the communities as a whole. In particular we will ask whether that stability is determined by the topological structure of the ecosystem. We begin by defining deletion stability (S_d) as the fraction of species that have the property that, when they alone are deleted, further extinctions do not take place. This definition is similar to that given by Pimm (1979), and has the advantage that it should not have any built-in dependence on species number. For the food web in Fig. 1 we have $S_d = 34/61$ or 0.557, a fairly typical value for this data set.

We will use the four hundred model food webs detailed above as our data set and describe their topological structure with the five food web statistics also defined there. These five statistics quantify four food web properties that it has been suggested may impact

ecosystem stability: complexity in terms of number of species and linkage density (S, L/S), the amount of omnivory in the web (O), the importance of cycles (C) and the redundancy (ρ). We remind the reader that the means and standard deviations of these statistics for the data set are given in Table 1.

If we possessed a range of food webs that vary for each property independently, whilst the other properties remain fixed, then this analysis would be quite simple. Indeed this was the approach adopted in previous studies using small pre-defined food web structures (Pimm 1979, 1980, Borrvall et al. 2000). However by generating the food webs by evolving a number of communities at a particular set of parameter values, we are faced with a less straightforward situation. The food webs vary for all properties simultaneously, and some of the properties are significantly correlated with one another. In fact, the situation is much like analysing real food web structures. The advantage is that our range of structures are much more complex and realistic, the

Table 5. Linear regressions of further extinction number as a function of either number of predators k_{pred}, and number of prey k_{prey}, or the keystone indices K_b and K_t. The deleted species are subdivided into the categories basal, intermediate and top. All the regressions were significant with $p < 1 \times 10^{-8}$ for the null hypothesis of no correlation. The calculations were performed using the software package S-Plus 6.0 (Mathsoft Inc. 2000).

Deleted species category	Independent variables	Coefficients b_j	se	R^2
Basal species	k_{pred}	1.1156	0.0426	0.1810
	K_b	1.1090	0.0140	0.6709
Intermediate species	k_{pred}, k_{prey}	0.3262, 0.1428	0.0121, 0.0060	0.0507
	K_b, K_t	1.1951, 0.7222	0.0145, 0.0167	0.2540
Top species	k_{prey}	0.2350	0.0084	0.2402
	K_t	0.1953	0.0071	0.2343
All species	k_{pred}, k_{prey}	1.3674, 0.1262	0.0102, 0.0083	0.4466
	K_b, K_t	1.0581, 0.7177	0.0044, 0.0148	0.7802

disadvantage is that we are forced to adopt a statistical approach.

We will commence our analysis by examining the correlation matrix for all the variables, both the dependent variable S_d, and food web properties. This is shown in Table 6. The deletion stability is significantly correlated with the fraction of omnivores (negatively) and the redundancy (positively). However because of the many significant correlations between the variables themselves, we cannot conclude that a smaller proportion of omnivores or greater redundancy will be associated with higher deletion stability, all other properties being unchanged.

One way to shed some light on this problem is to use multivariate regression. Performing a simple linear regression such as those in Table 5 would not be appropriate in this case since the deletion stability is restricted to lie between 0 and 1. It is better to use a logistic regression, where the probability that a species removal fails to cause further extinctions, p_i, in each food web i, is taken to depend on the independent variables, not through a linear, but rather through a 'logistic relationship':

$$\pi_i = \frac{1}{1 + \exp(-\mathbf{x}.\mathbf{b})} \rightarrow \ln\left(\frac{\pi_i}{1 - \pi_i}\right) = \mathbf{x}.\mathbf{b}. \qquad (4)$$

Here $b = (b_0, \ldots, b_p)$ is the vector of coefficients of the linear regression and x a $(p+1)$ vector of independent variables $x_i = (x_{i0}, \ldots, x_{ip})^T$ with $x_{i0} = 1$ for all i, to conveniently include an intercept (McCullagh and Nelder 1989). The coefficients are then determined so as to maximise the probability of the observed number of species removals that failed to cause further extinctions, under the assumption that these will be binomially distributed.

The results of such an analysis for our dataset are shown in Table 7. Examining the individual regression coefficients reveals that all but the degree of cycling are judged to have significant effect on the stability of the food webs to species deletion. Of these, the influence of the variables is ordered (decreasing) as follows: ρ, L/S, O and S. The first two of these have a positive effect and

the last two have a negative effect. Considering the fit as a whole, a significant fraction of the variance remains unexplained (residual deviance $\chi^2 = 1012.744$, df $= 394$, $p < 1 \times 10^{-8}$). In fact only 7.8% of the deviance of the null model is accounted for by the fit-but the fit is still significant ($\chi^2 = 85.196$, df $= 5$, $p < 1 \times 10^{-8}$).

We conclude that for this data set a fairly robust positive relationship exists between the proportion of redundant species in the web and the stability of the web to deletion. This result makes sense. We defined a redundant species as one that is functionally equivalent, in the sense of possessing the same predators and prey, to at least one other species. Thus the removal of a redundant species is unlikely to cause further species to go extinct, since its functional equivalents should be able to increase their population sizes and compensate for the loss. This supports the hypothesis that increased redundancy in ecosystems will result in increased functional reliability (Walker 1992, Naeem 1998).

There is a slight negative relationship between the community size and stability but also a more significant positive relationship between links per species and the robustness of the food webs to deletion. Therefore there is no clear evidence that complexity is destabilising. This can be compared to early work on deletion stability in small food webs modelled with Lotka–Volterra dynamics, where it was found that increasing either the number of species or connectance, L/S^2, rapidly decreased stability (Pimm 1980). A similar pattern of decreased stability with community size was also found in studies of assembled competition communities with Ricker dynamics (Lundberg et al. 2000, Fowler and Lindström 2002). The difference between these results and ours can probably be attributed to the more realistic structures and global dynamics used here, in particular incorporating adaptive foraging into the population dynamics.

This result can also be compared to a recent work examining the effect of deleting species from simple

Table 6. The correlation matrix for the variables: deletion stability (S_d), number of species (S), links per species (L/S), fraction of omnivores (O), degree of cycling (C) and redundancy (ρ). The values given are the linear correlation coefficients r between the pairs of variables calculated over the 400 food webs. The correlations judged to be significant, those with a probability p of no correlation smaller than the Bonferroni corrected value of 0.05/15, are highlighted with an asterisk.

	S_d	S	L/S	O	C	ρ
S_d	–	−0.054	0.063	−0.162*	−0.111	0.197*
S	–	–	0.354*	0.073	−0.129	0.034
L/S	–	–	–	0.197*	−0.196*	−0.264*
O	–	–	–	–	0.359*	−0.282*
C	–	–	–	–	–	−0.085

Table 7. The multivariate logistic regression of the number of species removals that failed to cause further extinctions as a function of number of species (S), links per species (L/S), fraction of omnivores (O), degree of cycling (C) and redundancy (ρ). The regression was performed for the 400 food webs described, it had a null deviance of 1097.94 on 399 degrees of freedom, and a residual deviance of 1012.744 on 394 degrees of freedom. The variables which had a significant effect on the deletion stability ($p < 0.05$) have been highlighted with an asterisk. The calculation was performed using the software package S-Plus 6.0. (Mathsoft Inc. 2000).

Variable	b_j	se	t	ρ
Intercept	−0.3818	0.2904	−1.8230	0.0683
S*	−0.0061	0.0018	−3.3288	0.0009
L/S*	0.5966	0.1165	5.1189	$\sim 10^{-7}$
O*	−1.1104	0.3705	−3.6115	0.0003
C	−4.0117	6.4374	−0.6232	0.5332
ρ*	1.1904	0.1950	6.1056	$\sim 10^{-8}$

three level food webs, constructed such that all species on a trophic level were functionally equivalent (Borrvall et al. 2000). These authors found that stability to deletion increased with the number of species on each trophic level. Their set-up corresponds to keeping ρ constant and equal to one, whilst increasing the total number of species, S, a variable for which a slight negative effect was observed here. This study also used Lotka–Volterra dynamics and this may explain the discrepancy. In particular, they observed that removing a predator had no effect on its prey, in contrast to the results detailed above.

We also found that the increased omnivory in the foods webs reduced stability. This may simply be a statistical aberration caused by the fact there is a significant negative correlation between the redundancy and the degree of omnivory. This is an interesting phenomenon in itself. It follows from the tendency of omnivory to increase the number of functionally distinct species on the same trophic level. Assuming that increased omnivory does decrease stability to deletion in these ecosystems, this differs from the findings of those who use Lotka–Volterra models (Pimm 1979, Borrvall et al. 2000).

We end this section by noting that none of these relationships were very strong, and in fact all the structural properties taken together explained very little of the variation between the webs. It may be that the measure of deletion stability we used is intrinsically noisy-it does seem sensitive to the presence of one or two vulnerable species – or it may be that our statistics are not capturing the properties that are important in determining robustness to deletion.

(Solé and Montoya 2001, Dunne et al. 2002) or use Lotka–Volterra equations (Pimm 1979, 1980, Borrvall et al. 2000, Lundberg et al. 2000, Fowler and Lindström 2002).

In addition to a realistic dynamics, effective studies of species removal require a realistic set of structures. By using a set of large webs composed of species spanning a range of trophic roles, we were able to show that removing the most connected species resulted in the most further extinctions and that recently developed 'keystone indices' were effective at predicting the importance of basal species. The range of food web structures studied allowed us to show the important role that redundant species play in increasing food web robustness to deletion, and find that there was no clear correlation between increased complexity and decreased stability to deletion. This adds another component to the stability–complexity debate.

This paper represents the first attempt to join complex food web structures with realistic population dynamics to study species loss from communities. It would be interesting to see if the results would change if real, rather than evolved, food web structures were used with such a dynamics or if the particular choice of dynamics were changed. In any case, we believe that we have shown that it is crucial for models to display a degree of realism, if reliable deductions concerning the consequences of species deletions are to be made.

Conclusion

In this paper we have shown that deletion experiments, which are very difficult and time consuming to carry out in real communities, can be easily implemented on model webs, which have been shown to have many of the characteristics of real webs (Drossel et al. 2001). We found a number of interesting results on species removal from communities which differed from some previous studies. The food webs as a whole were shown to be quite robust to deletions, and individual species were able to survive the loss of prey constituting a major fraction of their diet. Deletions were shown to cause further extinctions amongst species both above and below the deleted species in the food web. These phenomena arose out of the complex population dynamics used in the model which incorporates adaptive foraging. They illustrate the importance of using a realistic global dynamics when considering community responses to large scale perturbations such as deletion. This contrasts with studies that either lack an explicit dynamics

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Appendix 1. Description of the model

In this appendix we describe the model we used to produce the food webs discussed and analysed in the main text. For further details, the following earlier papers on the model may be consulted: Caldarelli et al. (1998), Drossel et al. (2001) and Quince et al. (2002).

Species in the model are characterised by features. These are specified by integers: $\alpha = 1, \ldots, K$. Any subset of L of these features constitutes a species. It is assumed that the effectiveness of predator–prey relationships among species is due to the effectiveness of individual features against each other. The $K \times K$ matrix $m_{\alpha\beta}$ gives the score of feature α against feature β, and these scores are used to define the score of one species, i, against another, j, denoted by S_{ij}:

$$S_{ij} = \max\left\{0, \sum_{\alpha \in i} \sum_{\beta \in j} m_{\alpha\beta}\right\} \qquad (A-1)$$

The matrix $m_{\alpha\beta}$ is antisymmetric. Its independent elements are random Gaussian variables with zero mean and unit variance chosen at the beginning of a simulation run and not changed during that particular run. This allows the score of one species against another to be calculated from (A-1): if $S_{ij} > 0$ then species i is adapted for predation against species j, if $S_{ij} = 0$ then it is not. We will also need to define the overlap q_{ij}, between two species i and j, as the fraction of features of species i that are also possessed by species j. The external environment is represented by a species indexed 0. This is assigned a random set of L features at the beginning of a run, and is not changed throughout the course of the run.

Having described the structure of a species in the model, and used this to define the score (A-1) and overlap, we will now use these quantities in the construction of the population dynamics that governs the changes in population densities between speciation

events. The rate of change of $N_i(t)$, the population density of species i at time t, is given by

$$\frac{dN_i}{dt} = -N_i + \lambda \sum_j N_i g_{ij} - \sum_j N_j g_{ji} \qquad (A\text{-}2)$$

The function g_{ij} is the functional response: the rate at which one individual of species i consumes individuals of species j. The choice of g_{ij} essentially defines the nature of the population dynamics. We will give the explicit form chosen below, but it is here that the dependence on the score and the overlap functions will enter. It will also depend on the other population densities in the food web and so will change with time.

The terms on the right-hand side of (A-2) are simply interpreted. The last factor represents the loss in resources for species i due to predation by all of the other species. On the other hand, the factor $\Sigma_j N_i g_{ij}$ represents the gain to species i from predation on the set of species j, including the environment, species 0. The environment is assigned a fixed population, $N_0 = R/\lambda$, thus R is a parameter of the model that controls the rate of input of external resources. If it is assumed that a fraction λ of the resources gained through predation are used to create new members of species i, the second term on the right-hand side of (A-2) is obtained. Finally, the first term simply represents the rate of death of individuals in the absence of interaction with other species.

In order to briefly motivate the form of the functional response we will use, let us first discuss the case of a single predator i feeding on a single prey j. In this case

$$g_{ij}(t) = \frac{S_{ij} N_j(t)}{b N_j(t) + S_{ij} N_i(t)} \qquad (A\text{-}3)$$

where b is a constant. We can gain more understanding of the structure of g_{ij} by noting that when the predators are far more numerous than the prey ($N_i \gg N_j$), $N_j \sim g_{ij} N_i$: the feeding rate of the predators is limited only by the number of prey. In the other limit, when the prey is very abundant compared with the predators ($N_j \gg N_i$), $g_{ij} \sim S_{ij}/b$: each predator feeds at a constant maximum rate. This latter result also gives an interpretation to the constant b. Having introduced the basic form (A-3), we can now state the general form for the functional response used in the model:

$$g_{ij}(t) = \frac{S_{ij} f_{ij}(t) N_j(t)}{b N_j(t) + \sum_k \alpha_{ki} S_{kj} f_{kj}(t) N_k(t)} \qquad (A\text{-}4)$$

There are two new aspects present in (A-4) and absent in (A-3):

1) Interference competition between predators of prey j is modelled by the factors α_{ki}. We take $\alpha_{ii} = 1$ and $\alpha_{ki} < 1$, $i \neq k$ to reflect the fact that competition between members of the same species is typically stronger than competition between different species. In fact, we expect that the more species are alike, the greater will be the competition between them, and therefore take

$$\alpha_{ij} = c + (1-c)q_{ij} \qquad (A\text{-}5)$$

where c is a constant lying between zero and one, which is the residual degree of competition that exists even if two competing predators have no features in common.

2) Adaptive foraging is modelled using the factors f_{ij}. The effort f_{ij} can be viewed as the fraction of time an individual of species i spends predating on species j or the fraction of the population of species i dedicated to consuming only j. These efforts must satisfy $\Sigma_j f_{ij} = 1$ for all i. To determine the f_{ij} it seems reasonable to assume that the gain which an individual of species i makes in consuming individuals of species j (that is, g_{ij}), divided by the amount of effort i puts into this task (that is, f_{ij}), should be the same for all prey species j. Using this condition, together with the normalisation of the f_{ij}, leads to

$$f_{ij}(t) = \frac{g_{ij}(t)}{\sum_k g_{ik}(t)} \qquad (A\text{-}6)$$

This choice of efforts can be shown to be an evolutionary stable strategy (Drossel et al. 2001), or in the terminology of foraging theory, an ideal free distribution of predators across prey (Fretwell and Lucas 1970).

The calculation of the efforts, through (A-6), effectively introduces a new behavioural time scale into the problem. We assume that the efforts change on a much shorter time scale than the population densities $N_i(t)$, and therefore that they may be found by iterating (A-4) and (A-6) assuming constant population densities. When this process has been completed, we may then move on to updating the population densities. Thus we do not treat the efforts as dynamical variables, instead we assume that they are a function of the population densities, even if we have no explicit form for this function.