REPORT

Network structure and biodiversity loss in food webs: robustness increases with connectance

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Abstract

Food-web structure mediates dramatic effects of biodiversity loss including secondary and 'cascading' extinctions. We studied these effects by simulating primary species loss in 16 food webs from terrestrial and aquatic ecosystems and measuring robustness in terms of the secondary extinctions that followed. As observed in other networks, food webs are more robust to random removal of species than to selective removal of species with the most trophic links to other species. More surprisingly, robustness increases with food-web connectance but appears independent of species richness and omnivory. In particular, food webs experience 'rivet-like' thresholds past which they display extreme sensitivity to removal of highly connected species. Higher connectance delays the onset of this threshold. Removing species with few trophic connections generally has little effect though there are several striking exceptions. These findings emphasize how the *number* of species removed affects ecosystems differently depending on the trophic *functions* of species removed.

Keywords

Biodiversity, connectance, ecosystem function, food web, network structure, robustness, secondary extinctions, species loss, species richness, topology.

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INTRODUCTION

Most of the earth's ecosystems are experiencing slight to catastrophic losses of biodiversity, caused by habitat destruction, alien species introduction, climate change, and pollution (Wilcove *et al*. 1998). The effects of these losses are likely to depend on the complexity of the ecosystem impacted, as well as the number and function of species lost. However, theoretical work related to the diversity–stability debate (e.g. MacArthur 1955; May 1973) has not resolved the role of various aspects of ecosystem complexity in stabilizing ecosystems (for recent review see McCann 2000). Also, experimental and comparative research (e.g. Naeem *et al*. 1994; Tilman & Downing 1994; Hooper & Vitousek 1997) has yet to distinguish clearly the relative importance of changes in species richness vs. loss or gain of particular species functions in driving ecosystem functioning (Martinez 1996; Loreau *et al*. 2001).

Food webs, descriptions of who eats whom in ecosystems, provide complex yet tractable depictions of biodiversity, species interactions, and ecosystem structure and function. Food webs have long been central to ecological research (May 1986; Levin 1992) and have recently come under scrutiny as one of several types of complex networks subject to node loss, such as neural, metabolic, and co-authorship networks, the World Wide Web, and power grids (Strogatz 2001; Albert & Barabási 2002). Many of these networks are 'small worlds' in which perturbation effects are distributed rapidly through large, complex, highly clustered systems because of surprisingly short path lengths between nodes (Watts & Strogatz 1998). This is partly true of food webs, which typically have short paths between species (Williams *et al*. 2002), but unlike other networks have unusually low clustering, relatively small size, and high link densities (Dunne *et al*. 2002). Another unusual aspect of food web structure is that their distributions of links among species or 'degree distributions' are not like the highly skewed 'scale-free' distributions typically found in other complex networks. In scale-free networks, the degree distribution follows a power law, where a very few nodes have many connections and most nodes have few connections. Instead, food webs generally display less skewed exponential or uniform degree distributions (Dunne *et al*. 2002). Still, a few food webs with unusually low connectance

(links/species^2) display small-world and scale-free structure (Montoya & Solé 2002; Dunne *et al.* 2002).

Networks with highly skewed link distributions characterized by power laws appear very sensitive to losing the rare highly connected nodes, while relatively robust to randomly losing the more highly abundant less connected nodes. In contrast, random networks with Poisson degree distributions, which are relatively unskewed since nodes have similar numbers of connections, display similar responses to loss of highly connected and random nodes (Strogatz 2001). The extreme susceptibility of power-law networks to removal of the most connected nodes has been found in Internet, WWW, metabolic, and protein networks (Albert *et al.* 2000; Jeong *et al.* 2000, 2001). Similar analyses suggest that food webs with highly skewed degree distributions display comparable patterns of response to loss of random and most connected species (Solé & Montoya 2001). However, the recent recognition that most food webs lack small-world and scale-free network structure questions the generality of such findings (Dunne *et al.* 2002).

Using a set of 16 relatively high quality food webs from a variety of terrestrial and aquatic ecosystems, we assess the potential effect of different types and magnitudes of species loss in triggering cascading secondary extinctions. We explore the potential for 'rivet-like' thresholds (Ehrlich & Ehrlich 1981) in primary species removals that result in dramatically increased secondary extinctions. Perhaps most significantly, our use of 16 food webs allows us to examine what general aspects of food web structure may drive patterns of community robustness to species loss, something that may be applicable to other types of networks. Previous node-loss studies were unable to do this type of cross-system analysis because they looked at very few networks. Food-web responses to simulated species loss may complement more traditional dynamics- and function-based approaches by providing novel insights from a structural perspective into the stability–diversity debate, the relationship of biodiversity and ecosystem function, and the identification of keystone species.

MATERIALS AND METHODS

We analysed a set of 16 food webs, two of which are variants of the same web. The food webs represent a wide range of species numbers, linkage densities, taxa, habitat types, and methodologies (Table 1). The webs studied, in order of increasing connectance, are (1) Grassland: co-occurring grass species and their associated endophytic

Table 1 Structural properties of food webs, listed in order of increasing connectance

Food web	Taxa[1]	Res[2]	S	$C\ (L/S^2)$[3]	L/S	O[4]	Distribution[5]
Grassland	75	100	61	0.026	1.59	0.21	Power law
Scotch Broom	154	99	85	0.031	2.62	0.28	Partial power law
Ythan Estuary 1	134	86	124	0.038	4.67	0.62	Exponential
Ythan Estuary 2	92	86	83	0.057	4.76	0.53	Exponential
El Verde Rainforest	156	49	155	0.063	9.74	0.56	Exponential
Canton Creek	108	94	102	0.067	6.83	0.08	Exponential
Stony Stream	112	89	109	0.070	7.61	0.11	Uniform
Chesapeake Bay	33	55	31	0.071	2.19	0.52	Exponential
St. Marks Seagrass	48	71	48	0.096	4.60	0.71	Uniform
St. Martin Island	44	34	42	0.116	4.88	0.60	Exponential
Little Rock Lake	182	93	92	0.118	10.84	0.38	Exponential
Lake Tahoe	800	99	172	0.131	22.59	0.58	Uniform
Mirror Lake	586	96	172	0.146	25.13	0.59	Exponential
Bridge Brook Lake	75	95	25	0.171	4.28	0.40	Uniform
Coachella Valley	30	3	29	0.312	9.03	0.76	Uniform
Skipwith Pond	35	91	25	0.315	7.88	0.60	Uniform

[1]'Taxa' refers to the number of compartments in the original food web, which can range from ontogenetic stages (e.g. largemouth bass juveniles) to non-phylogenetic categories (e.g. detritus, seeds) to highly aggregated taxa (e.g. microbes). In several webs, 'Taxa' may differ from what is reported by the original investigators because we exclude disconnected taxa, i.e. species or small subwebs that lack links to the main web (e.g. exclusion of small disconnected webs in the Grassland food web), or because of taxa consistency issues (e.g. lumping bacteria into the organic carbon compartments of the Chesapeake Bay food web).

[2]'Res' refers to resolution, the percentage of taxa identified to the genus or species level.

[3]C, connectance; L, trophic links; S, trophic species.

[4]O, omnivory, the fraction of species that feed at multiple trophic levels.

[5]'Distribution' refers to the shape of the degree distribution, or distribution of trophic (both predator and prey) links among species. Summarized from Dunne *et al.* (2002).

insects in Great Britain (Martinez *et al.* 1999); (2) Scotch Broom: primarily insects associated with the Scotch broom shrub *Cytisus scoparius* in Silwood Park, England (Memmott *et al.* 2000); (3) Ythan Estuary 1: mostly birds, fishes, invertebrates, and metazoan parasites in a Scottish Estuary (Huxham *et al.* 1996); (4) Ythan Estuary 2: a reduced version of Ythan Estuary 1 with no parasites (Hall & Raffaelli 1991); (5) El Verde Rainforest: primarily insects, spiders, birds, reptiles, and amphibians in a Puerto Rican rainforest (Waide & Reagan 1996); (6) Canton Creek: mostly invertebrates and algae in a tributary, surrounded by pasture, of the Taieri River in the South Island of New Zealand (Townsend *et al.* 1998); (7) Stony Stream: similar to Canton Creek but in native tussock habitat (Townsend *et al.* 1998); (8) Chesapeake Bay: primarily the pelagic portion of an eastern U.S. estuary, with an emphasis on larger fishes (Baird & Ulanowicz 1989); (9) St. Marks Seagrass: mostly macroinvertebrates, fishes, and birds associated with an estuarine seagrass community in Florida (Christian & Luczkovich 1999); (10) St. Martin Island: primarily bird predators and arthropod prey of *Anolis* lizards on the Caribbean island of St. Martin (Goldwasser & Roughgarden 1993); (11) Little Rock Lake: pelagic and benthic species, particularly fishes, zooplankton, macroinvertebrates, and algae of a small Wisconsin lake (Martinez 1991); (12) Lake Tahoe: detailed benthic and pelagic species in a large California lake, including hundreds of planktonic autotrophs (Martinez unpublished data); (13) Mirror Lake: detailed benthic and pelagic species in a small New Hampshire lake (Martinez unpublished data); (14) Bridge Brook Lake: pelagic species from the largest of a set of 50 New York Adirondack lake food webs (Havens 1992); (15) Coachella Valley: a wide range of highly aggregated taxa in a southern California desert (Polis 1991); and (16) Skipwith Pond: invertebrates in an English pond (Warren 1989). In the case of the New Zealand stream food webs, we report results for 2 of 10 published webs, selecting the most speciose webs from each of two land-use types sampled.

All food-web data are limited, since some species, links, functional groups, and even taxonomic kingdoms are usually left out, and the included taxa are often unevenly resolved. However, studies of resolution, aggregation, and sampling effort of taxa and trophic links in food webs have provided detailed understanding of many effects of these methodological aspects of food-web structure (e.g. Martinez 1991, 1993, 1994; Martinez *et al.* 1999), and we feel that such empirical limitations are unlikely to change our general conclusions. We reduced the influence of such limitations by restricting our analyses to the best-characterized food webs available, many of which have been very useful in contemporary analyses and modelling of food-web structure (e.g. Williams & Martinez 2000). We studied trophic species versions of the 16 food webs, since the use of trophic species (hereafter referred to as species), functional groups of taxa that share the same set of predators and prey (Briand & Cohen 1984), is a widely accepted, although sometimes criticized, convention in structural food-web studies that reduces methodological biases related to uneven resolution of taxa within and among food webs (Williams & Martinez 2000). Current understanding of food-web structure may change as more complete food webs are assembled, or as detailed food webs from under-represented systems (e.g. soil microbial communities) are documented.

We report four statistics of food web complexity: (1) species richness (S), the number of trophic species in the food web; (2) connectance (C), the fraction of all possible trophic links including cannibalism that are realized (L/S^2); (3) links per species (L/S), which when doubled gives the average node degree ($< k >$), the mean number of incoming and outgoing links per species; and (4) omnivory (O), the fraction of species that feed at multiple trophic levels. C is *c.* 0.1 in most food webs (i.e. species tend to eat an average of 10% of all species in the web) and independent of S, whereas L/S increases with S (Martinez 1992; Warren 1994).

For each food web we simulated species loss by sequentially removing species using one of four criteria: removal of (1) the most connected species; (2) randomly chosen species (1000 random deletion sequences initiated for each web); (3) the most connected species excluding basal species (species with predators but no prey); and (4) the least connected species. Rather than determining the most or least connected species at each removal step based on the original web, it was determined based on the web remaining after all previous primary removals and secondary extinctions. Both predator and prey links were counted to determine total trophic connections ('degree') for each species. A previous study of species removals that looked at both total degree and prey-directed degree found little difference between the two (Solé & Montoya 2001). Removal of the most connected (1) and random (2) species follows research on network tolerance of 'attacks' and 'errors' (Albert *et al.* 2000; Jeong *et al.* 2000, 2001; Solé & Montoya 2001). To our knowledge, criteria (3) and (4) have not been assessed for networks before.

We examined the impact of species loss on one aspect of food web stability: the number of potential secondary extinctions. A secondary extinction occurs when a non-basal species loses all of its prey items, and also when a cannibalistic species loses all of its prey items except itself. Given this algorithm, basal species may experience primary removals, but not secondary extinctions. 'Robustness' of food webs to species loss was quantified as the fraction of species that had to be removed in order to result in a total loss of $\geq 50\%$ of the species (i.e. primary species removals plus secondary extinctions). Maximum possible robustness

is 0.50 and minimum is $1/S$. We used linear regressions to examine the relationship between robustness and three measures of food web complexity; species richness (S), connectance ($C = L/S^2$), and omnivory (O). We excluded links/species (L/S) from regression analysis because, as expected (Martinez 1992), it was highly correlated with S (using a Bonferroni correction for a four-variable comparison, Pearson correlation of S with L/S, $R = 0.70$, $P = 0.014$).

RESULTS

The 16 food webs range in size from 25 to 172 trophic species (S), connectance (C) from 0.026 to 0.315, links per species (L/S) from 1.59 to 25.13, and omnivory (O) from 0.08 to 0.76 (Table 1). The average connectance over all 16 webs is 0.11 (SD = 0.09), similar to mean connectance values reported for other reliable sets of food webs (Martinez 1992: five webs, mean $C = 0.11$, SD = 0.03; Havens 1992: 50 webs, mean $C = 0.10$, SD = 0.04). Connectance, species richness, and omnivory are not significantly correlated with each other. The two lowest connectance webs, Grassland and Scotch Broom, are also the webs with the most skewed degree distributions, displaying power-law relationships over all (Grassland) or part (Scotch Broom) of their range (Table 1, Dunne *et al*. 2002). The other 14 webs display less skewed exponential or uniform distributions (Table 1).

When species were systematically removed from food webs in our simulations, potential secondary extinctions varied both among webs and among types of removal sequences (Fig. 1). However, several clear trends emerge. For example, more secondary extinctions occur due to removing highly connected species compared to random removals. This is particularly true for the four very low connectance webs ($C < 0.06$), Grassland, Scotch Broom, and Ythan Estuary 1 & 2 (Fig. 1a–d), where removal of *c.* 20% of the most connected species results in *c.* 60–100% of the species undergoing secondary extinctions. The same amount of random removals results in *c.* 20% secondary extinctions in the Grassland web and < 10% in the other three webs. Similar results were reported for taxonomic versions (original taxa used rather than trophic species) of the last three webs including the extreme fragility of the Scotch Broom web to removal of the most connected species (the 'Silwood Park' web, Solé & Montoya 2001).

However, the Scotch Broom and Ythan Estuary webs are unusual among the 16 data sets in having very low connectance and very few ($\leq 6\%$) basal taxa represented (12 of 13 other webs have basal taxa $\geq 10\%$). Removing basal taxa from these webs generally precipitates extensive secondary extinctions, since any food web is ultimately supported by the presence of primary producers and carbon sources. Under a random extinction scenario, the probability of early removal of one of very few basal species, with resulting cascading extinctions, is quite low. This probability is greater when highly connected species are targeted, because if there are relatively few basal species, they tend to have more consumers than in webs with more comprehensive basal species lists.

Scotch broom is both the only basal species and one of the two highest connected species in the Scotch Broom web. This web was compiled as a 'source web', with herbivore, predator, parasitoid, and pathogen trophic links traced upward from one shrub species (Memmott *et al*. 2000). When Scotch broom is removed in the first or second step of the most connected species removal sequence, the entire food web disappears in a methodologically enforced sequence of cascading secondary extinctions (Fig. 1b). The results are similarly exaggerated in the Ythan Estuary webs although the few basal taxa are not removed as early as in the Scotch Broom web. For example, the basal taxon 'particulate organic matter' is removed in the eighth step of deleting the most connected species in Ythan Estuary 1 (Fig. 1c) and the fifth step for Ythan Estuary 2 (Fig. 1d). This leads to 32 and 37 secondary extinctions, respectively, or 37% and 30% of the species in the initial food webs.

Although the Grassland web is a source web, it has a more comprehensive set of basal taxa (eight grass species) than the Scotch Broom or Ythan Estuary webs. The Grassland web still displays dramatic secondary extinctions with removal of the most connected species, but levels are not as extreme as in the other three low connectance webs (Fig. 1a). When basal species in the Scotch Broom and Ythan Estuary webs are protected from removal, their patterns of secondary extinctions due to most connected species removals appear more similar to those of the Grassland web (Fig. 1a–d).

The other 12 food webs also display more secondary extinctions due to removal of the most connected species compared to random species. However, this difference does not manifest strongly in webs with $C \geq 0.10$ until *c.* 20% or more species are removed (Fig. 1i–p). After an initial period of minimal secondary extinctions, the food webs undergo a sharp increase in secondary extinctions due to removing the most connected species, whereas secondary extinctions resulting from randomly removing species increase gradually. The four highest connectance webs ($C \geq 0.15$) all display similar low levels of secondary extinctions to loss of both most connected and random species (Fig. 1m–p) until *c.* 40% primary removals, at which point secondary extinctions increase more for most connected species removals. The highest connectance web, Skipwith Pond ($C = 0.32$, Fig. 1p), composed of highly omnivorous invertebrates,
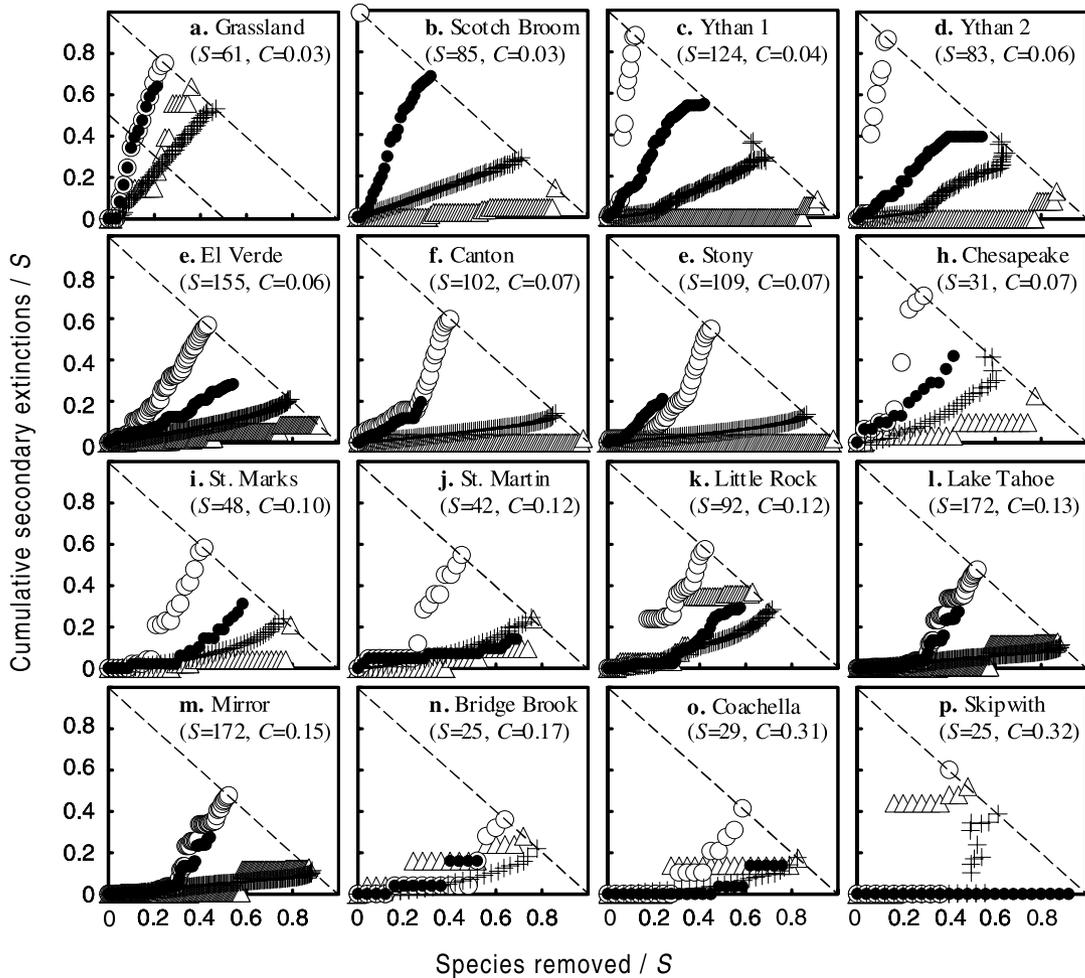
Figure 1 Secondary extinctions resulting from primary species loss in 16 food webs ordered by increasing connectance (C). 95% error bars for the random removals fall within the size of the symbols and are not shown. For the most connected, least connected, and random removal sequences, the data series end at the diagonal dashed line, where primary removals plus secondary extinctions equal S and the web disappears. For the most connected species removals with basal species preserved, the data points end when only basal species remain. The shorter diagonal dashed line in Fig. 1(a) shows the points at which 50% of species are lost through combined removals and secondary extinctions ('robustness' of Fig. 2).

does not display any secondary extinctions with most connected species removals until its single basal node, detritus, is removed during the 10th step, at which point the web collapses. It also displays almost no secondary extinctions with random removals until > 50% of species are removed.

Food webs with connectance ≥ 0.07 display thresholds past which secondary extinction levels increase dramatically due to removing the most connected species. This threshold is apparent at *c.* 20–30% primary species removals for webs

with 0.06 < C < 0.14 (Fig. 1f–l), and at *c.* 40–50% primary species removals for webs with C ≥ 0.15 (Fig. 1m–p). The only webs that do not display such thresholds have C < 0.07 (Fig. 1a–e), with the four lowest connectance webs collapsing completely with less than 25% primary species removals. Once a threshold is reached, the sensitivity of a web to removing the most connected species increases by a factor of *c.* 4–8, and removal of 10–30% more species results in total web collapse. Although lacking such thresholds, webs undergoing random species removals also

display increased sensitivity with greater removal level, as shown by the generally upturned trajectories in webs with $C > 0.03$ (Fig. 1).

In all webs, basal species lack prey, which reduces their overall potential number of links to other species. This decreases the likelihood that basal species will be removed early in most connected removal sequences. Thus, for about half the food webs, protecting basal species does little to alter secondary extinction levels due to removal of most connected species. The other webs display lower levels of secondary extinctions when basal species are protected. Still, their secondary extinctions are greater than when random species are removed (Fig. 1).

Removing the least connected species usually results in minimal secondary extinctions, which are lower than or similar to extinctions seen with random species removals. However, the Grassland, Little Rock Lake, Bridge Brook Lake, Coachella Valley, and Skipwith Pond food webs display greater secondary extinctions with removal of least connected vs. random species. In Bridge Brook Lake and Skipwith Pond, the secondary extinctions associated with removal of least connected species generally exceed those observed with removal of most connected species (Fig. 1). High secondary extinctions due to loss of least connected species primarily occur as a result of (1) loss of basal species, which tend to have lower degree but form the foundation of food webs and/or (2) loss of species that may have only one specialist predator and thus low degree, but that predator is in turn preyed upon by several specialist predators, resulting in a multi trophic-level cascade of secondary extinctions.

Both phenomena are well illustrated in the Grassland web (Martinez *et al.* 1999). At the start of the least connected species removal sequence, there are three species, all grasses, with only one 'predator' link apiece that are targeted first. One is *Ammophila arenaria*, whose removal results in no secondary extinctions, since its single herbivore also feeds on another grass species. A second species is *Dactylis glomerata*, whose removal results in the secondary extinction of the specialist herbivore wasp *Tetramesa longula*. That loss leads to the secondary extinction of a specialist parasitoid wasp (*Homoporus fluviventris*) of *T. longula,* which leads to the secondary extinction of a wasp at yet a higher trophic level (*Chlorcytus* sp.) that parasitizes both *T. longula* and *H. fluviventris*. The third possible removal, *Phalaris arundinacea*, results in the extinction of the specialist herbivore wasp *Tetramesa longicomis*, which leads to cascading extinctions of five additional parasitoid species at higher trophic levels, including one species that loses a prey link when the second grass species is removed. Thus, in a food web with eight grass species and 53 species at higher trophic levels, the removal of just two grass species with minimum degree leads to nine secondary extinctions via cascading effects that ripple through subwebs of specialized or closely interdependent herbivore and parasitoid species.

Across all 16 food webs, the robustness of webs under the four removal criteria did not vary significantly with S or O (Table 2). In addition, the robustness of webs to removal of the least connected species did not vary significantly with C. However, robustness increased significantly with increasing connectance when the most connected (with or without basal species protected) or random species were targeted (Table 2). Multiple regression analyses with the three complexity variables did not reveal any additional significance of S or O (data not shown).

More specifically, the data suggest that robustness and connectance are logarithmically related according to curves that saturate at *c.* 0.3 connectance, the upper bound for empirically observed food web connectance values (Fig. 2). Linear fits to connectance explain 0.46–0.67 of the variability in robustness while logarithmic fits explain 0.64–0.91 of it (Table 2, Fig. 2). The robustness curves for the removal sequences of the most connected species with and without basal species protected have a similar slope. However, protecting basal species confers additional robustness to food webs at any particular connectance level, with *c.* 10% additional primary species removals required to achieve the same level of total species loss. Increased

Table 2 Robustness of food webs under four different species deletion sequences as a function of three measures of food web complexity

Deletion sequence	Species richness (S)			Connectance (C)			Omnivory (O)		
	Slope	P	r^2	Slope	P	r^2	Slope	P	r^2
Least connected	0.001	0.038	0.27	−0.617	0.033	0.29	−0.014	0.915	0.00
Most connected	0.000	0.645	0.02	**1.160**	**0.001**	**0.57**	0.143	0.419	0.05
Most, no basal deletions	0.000	0.513	0.03	**1.005**	**0.000**	**0.67**	0.301	0.028	0.30
Random	0.000	0.892	0.00	**0.468**	**0.004**	**0.46**	0.091	0.246	0.09

Simple linear regressions of a measure of robustness of 16 food webs to species loss (the fraction of species that have to be removed in order to induce $\geq$ 50% total species loss) as a function of S, C, and O. A Bonferroni-corrected value of $P = 0.0125$ (0.05/4) was used to determine significance. Significant regressions are shown in bold. SYSTAT 7.0 was used for statistical analyses.
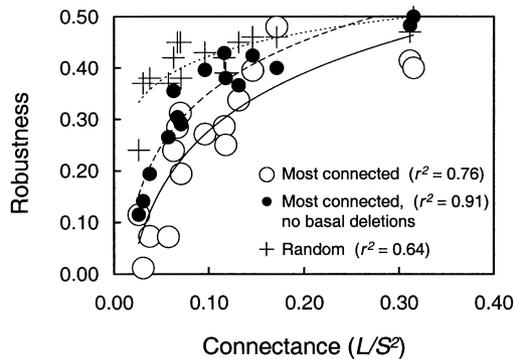
Figure 2 The proportion of primary species removals required to induce a total loss (primary removals plus secondary extinctions) of ≥ 50% of the species in each of 16 food webs ('robustness', see the shorter dashed line of Fig. 1a for visual representation) as a function of the connectance of each web. Logarithmic fits to the three data sets are shown, with a solid line for the most connected deletion order, a long dashed line for the most connected with basal species preserved deletion order, and a short dashed line for random deletion order. The maximum possible y-value is 0.50. The equations for the fits are: $y = 0.162\mathrm{Ln}(x) + 0.651$ for most connected species removals, $y = 0.148\mathrm{Ln}(x) + 0.691$ for most connected species removals with basal species preserved, and $y = 0.067\mathrm{Ln}(x) + 0.571$ for random species removals.

robustness to random vs. most connected species removals is most pronounced in low connectance webs. In these webs, *c.* 30% more random than most connected species must be removed to attain 50% species loss, with the difference decreasing with higher C (Fig. 2).

DISCUSSION

The robustness of real-world networks to the random loss of nodes ('errors') and fragility to the selective loss of the most connected nodes ('attacks') has been attributed to extremely skewed power-law distributions of links found in many small-world networks (Albert *et al.* 2000; Jeong *et al.* 2000, 2001) including a few food webs (Solé & Montoya 2001). Our study shows that these responses are not unique to small-world, scale-free networks. Most food webs, which generally have less-skewed exponential or uniform degree distributions and often lack typical small-world topology (Dunne *et al.* 2002), display similar patterns of response to node loss. More secondary extinctions result from simulated removal of highly connected species than random species for all 16 food webs examined. The difference in network response to errors and attacks thus appears related more generally to skewed degree distributions, rather than being restricted to power-law distributed networks. However, the few food webs with power-law distributions, such as the very low connectance Grassland and Scotch Broom food

webs, are the most vulnerable to attacks. This finding makes topological and ecological sense. The more trophic links that a species has to other species in a food web, the more potential it may have to affect community structure. For a highly connected species, its potential direct and indirect trophic effects on species one and two links away will encompass the vast majority if not all of the species in the web, since on average 80% of species in food webs are within two trophic links of each other (Williams *et al.* 2002).

Because our study is the first to look at the impacts of node loss in a wide array of networks of varying size and structure, we can assess if various topological measures of network complexity drive the relative robustness of networks to node loss. Aspects of this question are of central concern in ecology, where the role of species richness in the stability and functioning of ecosystems is a controversial and challenging focus of basic and applied research in light of extensive biodiversity loss due to human activities (Loreau *et al.* 2001). Robustness, defined in our study as the proportion of primary species removals that lead to ≥ 50% total species loss, does not vary systematically with species richness or omnivory. Instead, food-web structure displays increasing robustness to loss of either random or highly connected species with another measure of ecosystem complexity, connectance, a measure of 'interaction richness.' Increasing connectance delays the point at which food webs display high sensitivity to removals of the most highly connected species. Low connectance webs display extreme sensitivity from the outset. Intermediate connectance webs have a threshold of *c.* 20–30% removals before onset of extreme sensitivity, while high connectance webs have a threshold of at least 40% primary removals. Thus, across food webs, the structurally stabilizing role of increased connectance is apparent as the magnitude of secondary extinctions due to all types of species removals generally decreases, the onset of higher rates of secondary extinctions becomes increasingly delayed, and the difference between strong, average, and weak effects tends to decrease (Fig. 1).

These results from a structural and empirical perspective differ somewhat from findings of Lotka–Volterra dynamical studies that have focused on risk of secondary extinctions in simple model food webs. For example, Borrvall *et al.* (2000) studied secondary extinctions that result from removal of a single species in food webs with three functional groups and two to six species per functional group, with connectance approximately constant. They found that the risk of secondary extinctions decreases with increasing number of species per functional group, and that the greatest and least risk of secondary extinctions resulted from removal of an autotroph and top predator, respectively. Their results differ from other Lotka–Volterra studies that suggested that greater species richness increases the likelihood of secon-

dary extinctions (Pimm 1979, 1980; Lundberg *et al.* 2000). These studies either did not examine the role of connectance or found that higher connectance increased secondary extinctions, contrary to our result that robustness increased with connectance. Our structural finding supports MacArthur's (1955) hypothesis that community stability will increase as the number of links in a food web increases, due to an increasing number of paths through a species dampening the impacts of its population fluctuations. Borrvall *et al.* (2000) also reported that omnivory reduced secondary extinctions, contrary to the destabilizing influence found by Pimm & Lawton (1978), and different from our finding of no relationship between structural robustness and omnivory.

The differences between structural- and dynamics-based results may relate to the well-known limitations of both approaches. Lotka–Volterra dynamical studies are difficult to parameterize with empirical data, and the models generally fail to adequately portray many aspects of observed ecosystems, including large numbers of species and non-random, complex, yet predictable topology of trophic structure (Williams & Martinez 2000). Structural studies embrace both modelling and empirical data analysis of large numbers of taxa, but strip away population dynamics and quantification of links in terms of energy flow or interaction strength. Both approaches focus on very few types of ecological interactions such as predator–prey relationships and competition. Ideally, these two approaches will be drawn together in future studies to understand the relationship between structural and dynamical robustness and stability in complex ecosystems. A recent study using a 'Lotka–Volterra cascade model' which combines dynamics with nonrandom cascade model food-web structure is a step in this direction (Chen & Cohen 2001). They found that three stability measures decrease monotonically with increasing food web complexity, whether measured as species richness or connectance, similar to other dynamics-based results starting with May (1973). However, their model ecosystems still have few species compared to natural ecosystems ($S = 10$), and the cascade model has been demonstrated to poorly predict empirical food web structure (Williams & Martinez 2000).

Although our use of unweighted trophic links may mask important dynamics, such as the role of skewed interaction strengths (e.g. many weak and few strong links – Paine 1992; McCann *et al.* 1998), the potential robustness that structure may confer on an ecosystem is important to identify. Still, our simple algorithm for generating secondary extinctions is limited, and may overestimate secondary extinctions since species can survive by switching to less preferred prey, which is one of many possible types of compensatory dynamics in ecosystems (e.g. Brown *et al.* 2001). Our approach accounts for this effect only to the degree that less preferred trophic links are included in the original food web and thus delay the onset of a secondary extinction. However, our algorithm may also underestimate the potential for cascading extinctions, since species losses can result in strong non-trophic and indirect effects. Thus, the loss of 'ecosystem engineer' taxa like corals or beaver that provide habitat can have profound consequences for dependent taxa (Jones *et al.* 1997).

Our analyses offer a novel perspective on the relationship between biodiversity and ecosystem function and particularly how the functional relevance of species richness *per se* differs from functions of particular species. This issue has largely been explored through experimental and comparative research on the relationship of ecosystem functions such as productivity, nutrient retention, and respiration to species or functional group richness, with additional supporting theoretical work concerning potential mechanisms driving observed patterns (Loreau *et al.* 2001). Although our study lacks a conventional measure of ecosystem function, potential secondary extinctions indicate an ecosystem's functional ability to provide species with trophic resources. The mean effect of removing random species from food webs may be seen as the effect of reducing species richness *per se* free of reference to trophic functional distinctions. The removal of most and least connected species, on the other hand, targets species with particular trophic functions – in this case, taxa with very many or very few trophic interactions.

For most webs, the average effect of randomly removing species is a generally low rate of secondary extinctions that increases slightly with increasing primary losses. This 'species richness' effect is always above zero (no secondary extinctions at any level of species loss), and is generally bracketed by stronger effects of targeting the most connected species and weaker effects of targeting the least connected species. With removal of the most connected species, particularly in food webs with connectance ≥ 0.07, thresholds emerge past which the potential for cascading extinctions increases dramatically, suggesting a 'rivet' type of response of food web structure to this type of species loss (Ehrlich & Ehrlich 1981). This increased sensitivity is much less pronounced when randomly removing species and when selectively removing the least connected species in most webs.

While removal of species with few trophic links often results in few or no secondary extinctions, there are several examples where targeting such species has large effects. As a result, the robustness of food webs to loss of species with few trophic links does not vary predictably with standard measures of web complexity. These findings underscore the notion that apparently unimportant species, in this case species with very few trophic links to other species, can have unusually large and unpredictable effects

on ecosystem structure and function. Although this represents a structural perspective, it is conceptually similar to findings from a population dynamics perspective that some so-called 'weak interactors' may have strong effects on abundances of species in a community, depending on the scale at which data are collected and analysed (Berlow 1999).

It has been suggested that highly connected species within food webs may be keystone species (Solé & Montoya 2001), or species that have an unexpectedly large effect on other species in a community. However, a careful taxonomy of species' roles in ecosystems narrows the definition of keystones to species that have large impacts on communities or ecosystems out of proportion to their abundance (Power *et al.* 1996). Species that have both large abundances and large impacts are considered dominants instead of keystones. While web structure lacks information about species abundances, species with few trophic connections that have large effects on community structure may act as the structural equivalent of keystone species, whereas species with many trophic linkages may be more conceptually similar to dominant species. In both cases, topological analyses provide another method for assessing the potential importance of species in ecosystems, one that may provide insights overlooked in other kinds of studies.

Our results suggest that highly connected communities will tend to be more robust to species losses, and that random species losses will tend to have fewer effects on food webs than losses of species with many trophic connections. Are actual extinctions random? With particular regard to anthropogenically caused species and population extirpations (or massive reductions), it appears that such effects are not random. For example, humans, following our own feeding proclivities, have historically tended to impact higher trophic levels through the overfishing and hunting of shellfish and large coastal marine vertebrates, with associated cascading trophic and non-trophic effects (Jackson *et al.* 2001). Even if human activities do not preferentially extirpate highly connected species, it is still likely that real-world extinctions are triggering trophic-related secondary extinctions at greater levels than expected from random species losses. In addition, the clearly demonstrated potential for secondary extinctions due to losing species and their trophic roles suggests that current extinction rate estimates, generally based on species-area relationships and estimated habitat loss, underestimate biodiversity loss (Holt *et al.* 1999; Solé & Montoya 2001). Feeding relationships and other direct and indirect effects need to be taken into account when considering the effects of species loss (Jackson *et al.* 2001; Terborgh *et al.* 2001).

The numerical simulation and network topology methods of this and related food-web studies (Solé & Montoya 2001; Williams *et al.* 2002; Dunne *et al.* 2002; Montoya & Solé 2002) provide little-used approaches by which to explore the relationship of species richness and other measures of complexity to ecosystem properties. These methods complement more conventional dynamical modelling, experimental and comparative approaches traditionally used to explore questions in diversity–stability and species richness–ecosystem function research.

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