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NETWORK TOPOLOGY AND BIODIVERSITY LOSS IN FOOD WEBS: ROBUSTNESS INCREASES WITH CONNECTANCE

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ABSTRACT :

Food-web structure and complexity can mediate effects of species loss such as cascading extinctions. We simulated species loss in 16 food webs from a variety of ecosystems. The food webs experienced much greater secondary extinctions when the most trophically connected species were removed compared to random species removals. These patterns appear related to skewed degree distributions in food webs, which generally display exponential or uniform distributions. Our analyses generalize prior research that found similar patterns of node loss in biological and non-biological networks with power-law distributions. Food web robustness (the level of primary removals required to induce 50% total species loss) to random and most-connected species loss does not relate to species richness or omnivory, but increases significantly with greater connectance (links/species²). We also found strong evidence for the existence of thresholds where food webs display greatly increased sensitivity to removal of most-connected species. Higher connectance delays the onset of this threshold. Least-connected species removal often has little effect, but in several food webs results in dramatic secondary extinctions. We relate these findings to the diversity-stability debate, effects of species richness on ecosystems, keystone species, and extinction rates.

KEYWORDS: biodiversity, connectance, food web, network, robustness, secondary extinctions, species function, species loss, species richness, topology

I. INTRODUCTION

Due to habitat destruction, alien species introduction, climate change, and pollution, most of the earth's ecosystems are experiencing slight to catastrophic losses of biodiversity. 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 a recent review see McCann 2000). Also, experimental and comparative research (e.g., Tilman and Downing 1994, Naeem et al. 1994, Hooper and Vitousek 1997) has yet to distinguish clearly the relative importance of changes in species richness versus loss or gain of particular species' functions in driving ecosystem functioning (Loreau et al. 2001).

Food webs, descriptions of who eats whom in ecosystems, provide complex yet potentially tractable depictions of biodiversity, species interactions, and ecosystem structure and function. Food webs, long central to ecological research (May 1986, Pimm et al. 1991, Levin 1992), have recently come under scrutiny as one type of "real-world" network, like a variety of biological and non-biological complex systems such as neural networks, metabolic networks, coauthorship networks, the world wide web, and power grids (for reviews see Strogatz 2001, Albert and Barabási 2002). One question is whether food webs have similar topology to other types of networks. Many networks display "small-world" topology, with small average shortest path length among nodes, similar to that observed for random networks, and much greater than random clustering of nodes (Watts and Strogatz 1998). However, most food webs do not display typical small world topology. While they do have "small" path lengths (Williams et al. 2001), they also have relatively low clustering due to their small size (Dunne et al. 2002). Also, most food webs do not display power-law, or "scale-free," degree distributions (the distribution of links per species), unlike many other real-world networks, and instead display exponential or uniform "single-scale" degree distributions (Dunne et al. 2002). Only a few food webs, generally with unusually low connectance (links/species²), display small-world and scale-free topologies (Montoya and Solé 2001, Dunne et al. 2002).

Power-law degree distributions are of particular interest in networks because such highly skewed distributions have been suggested as the primary reason that scale-free networks appear highly susceptible to "attack" (removal of the most highly connected nodes), while relatively robust to "errors" (loss of random nodes). In contrast, random networks with Poisson degree distributions display similar responses to loss of the most-connected or random nodes (Strogatz 2001). The 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 three food webs with skewed degree distributions, two of which appear scale-free, display a similar robustness to random species loss and fragility to removals of the most-connected species (Solé and Montoya 2001). However, because most food webs do not display scale-free degree distributions (Dunne et al. 2002), and few analyses of node loss have been conducted on networks that lack scale-free distributions, it is unclear how robust most food webs are likely to be to species loss.

Using a set of 16 relatively high-quality food webs from a variety of ecosystems, we assess the potential effect of different types and magnitudes of species loss in triggering cascading secondary extinctions. We explore the potential for thresholds in primary species

removals that result in dramatic increases in secondary extinctions. We examine what aspects of topology and complexity across all of the food webs appear to drive patterns of community response and robustness to species loss, something that has not been explored for any type of network before. Observed ecosystem responses to simulated species loss provide insights into how average effects of species loss compare to particularly strong and weak effects (i.e., species richness versus function), the predictability and identification of keystone species, and the estimation of extinction rates.

II. MATERIALS AND METHODS

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

We studied trophic species versions of the 16 food webs. The use of trophic species, functional groups of taxa that share the same set of predators and prey, is a widely accepted convention in structural food-web studies that reduces methodological biases related to uneven resolution of taxa within and among food webs (Williams and Martinez 2000). 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 ($\langle k \rangle$), 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 thought to be approximately constant at ~ 0.1 (i.e., a species tends to eat about 10% of species in a food

web) and orthogonal to S (Martinez 1992, Warren 1994), while L/S increases with S (Martinez 1992).

For each food web we simulated species loss by running systematic species removal sequences using four criteria: removal of (i) the most-connected species, (ii) random species (1000 random deletion sequences initiated for each web), (iii) the most-connected species excluding basal species (species with predators but no prey) and (iv) the least-connected species. For (i), (iii), and (iv), the most- or least-connected species in the web was determined at each step from the reconfigured webs, rather than ordered using the original web. Both incoming predator links and outgoing prey links were counted to determine total degree. A previous study of species removals that used both total degree and prey-directed degree (outgoing links only) found little difference between the two (Solé and Montoya 2001). Removal of the most-connected (i) and random (ii) species follows research on network tolerance of “attacks” and “errors” (Albert et al. 2000, Jeong et al. 2000, 2001, Solé and Montoya 2001). To our knowledge, criteria (iii) and (iv) have not been assessed for networks before.

We examined the impact of systematic species removals on one aspect of food web stability: the amount 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. In order to gain a better understanding of what aspects of network topology might drive the stability of food-web structure given progressive species loss of different types, for each web under all four species removal sequences we calculated 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 removal plus secondary extinctions). We refer to this measure as “robustness,” with maximum possible robustness of 0.50 and minimum possible robustness of $1/S$. Using linear regressions, we tested whether this measure of food-web robustness bears a significant relationship to three measures of food web complexity, species richness (S), connectance ($C = L/S^2$), and omnivory (O), and if so how such relationships compare among different removal sequences. We excluded links/species (L/S) from regression analysis because, as expected, it was highly correlated with S (using a Bonferroni correction for a 4-variable comparison, Pearson correlation of S with L/S , $R = 0.70$, $P = 0.014$).

III. 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 community food webs (Martinez 1992: 5 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.

When species are systematically removed from food webs in our simulations, potential secondary extinctions that result from the primary removals vary both among webs and depending on the type of removal sequence (Fig. 1). However, several general 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 ~20% of the most-connected species results in ~60-100% of the species undergoing secondary extinctions. The same amount of random removals results in ~20% secondary extinctions in the Grassland web and <10% in the other three webs. Similar results were reported for the taxonomic versions of the latter three webs, including the very extreme fragility of the Scotch Broom web to removal of the most-connected species (the “Silwood Park” web, Solé and 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 $\geq 10\%$). As a result, the basal nodes, the primary producers and carbon sources on which the entire web depends, tend to be highly connected and thus removed quickly in the most-connected species removal sequences, precipitating extensive secondary extinctions. This is especially apparent in the Scotch Broom web (Fig. 1b), a single-species based “source web.” Memmott et al. (2000) compiled the food web by starting with the shrub Scotch broom and tracing herbivore, predator, parasitoid, and pathogen trophic links upward from that plant species, ignoring pathways leading to other basal species present in the community. As a result, Scotch broom is both the only primary producer and the most-connected species in this food web. When Scotch broom is removed in the first round of the most-connected species deletion sequence, the entire food web disappears in a methodologically enforced sequence of cascading secondary extinctions (Fig. 1b). The same procedure leads to a similarly exaggerated loss of species in the Ythan Estuary webs, which primarily focus on vertebrates, their prey (Fig. 1d), and their parasites (Fig. 1c), but only include five basal taxa.

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

The other 12 food webs also display more secondary extinctions with most-connected versus random species removals. However, in webs with $C \geq 0.10$, this difference does not manifest strongly until ~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 as a result of continuing to remove the most-connected species, while secondary extinctions due to random species removals increase gradually. The four highest connectance webs ($C \geq 0.15$), Mirror Lake, Bridge Brook Lake, Coachella Valley, and Skipwith Pond, all display a high degree of robustness to removals of both most-connected and random species (Fig. 1m-p). It is generally not until removal of ~40% of the most-connected species that secondary extinctions increase beyond the response to random species removals. The highest connectance web, Skipwith Pond ($C = 0.32$, Fig. 1p), composed of highly omnivorous invertebrates, does not display any secondary extinctions with most-connected species deletions until its single basal node, detritus, is removed during the 10th step of the deletion sequence, at which point the web collapses. It also displays almost no secondary extinctions with random removals until >50% of species are removed.

If we focus on removal of the most-connected species, webs with connectance ≥ 0.07 display thresholds at which secondary extinction levels increase dramatically. This threshold is apparent at ~ 0.2 to 0.3 primary species removals for webs with $0.06 < C < 0.14$ (Fig. 1f-l), and at ~ 0.4 to 0.5 primary species removals for webs with $C \geq 0.15$ (Figs. 1m-p). The only webs that don't display such thresholds have $C < 0.07$ (Fig. 1a-e), with the four lowest connectance webs collapsing completely with less than 0.25 primary species removals. Once a threshold is reached, the sensitivity of a web to most-connected species removals increases by a factor of ~ 4 to 8 , and removal of an additional 0.1 to 0.3 species results in total collapse of the web. While lacking such thresholds, webs undergoing random species removals also display increased sensitivity, with secondary extinctions following generally upturned trajectories in webs with $C > 0.03$.

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 unless there are very few basal species, as discussed previously. Thus, for about half the food webs, protecting basal species does little to alter secondary extinction levels due to removal of most-connected species. However, the other webs display lower levels of secondary extinction when basal species are protected, although the secondary extinctions are still greater than when random species are removed (Fig. 1).

For most food webs, removing the least-connected species results in minimal secondary extinctions that 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 versus 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 removal of least-connected species primarily occur as a result of 1) the removal of basal species, which tend to have lower degree but form the foundation of food webs and/or 2) removal 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 deletion sequence, there are three species with only one incoming predator link apiece that are targeted first. One is the grass *Ammophila arenaria*, whose removal results in no secondary extinctions, since its single herbivore also feeds on another grass species. A second possible species for deletion is the grass *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 of the grass *Phalaris arundinaceae* 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 sub-webs of specialized or closely interdependent herbivore and parasitoid species.

Across all 16 food webs, the robustness of webs under the four deletion sequences 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). Interactive, backward-stepping multiple regression analyses with the three complexity variables did not reveal any additional significance of S or O for any of the classes of robustness (data not shown).

More specifically, the data suggest that robustness and connectance are logarithmically related according to curves that saturate at ~ 0.3 connectance, the upper bound for empirically observed food web connectance values (Fig. 2). Linear fits to connectance explain 0.46 to 0.67 of the variability in robustness while logarithmic fits explain 0.64 to 0.91 of the variability in robustness (Table 2, Fig. 2). The robustness curves for the deletion 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 $\sim 10\%$ additional primary species removals required to achieve the same level of total species loss. Increased robustness to random versus most-connected species removals is most pronounced in low connectance webs. In these webs, $\sim 30\%$ more random than most-connected species must be removed to attain 50% species loss, with the difference decreasing with higher C (Fig. 2).

IV. DISCUSSION

The robustness of real-world networks to “errors,” the loss of random nodes, and fragility to “attacks,” the loss of the most-connected nodes, has been attributed primarily to scale-free degree distributions (i.e., where most nodes have few connections and a few nodes have a very large number of connections) in small-world networks (Albert et al. 2000, Jeong et al. 2000, 2001, Solé and Montoya 2001). Our study shows that these responses are not unique to those types of networks, since food webs, which mostly display single-scale exponential or uniform degree distributions and often lack typical small-world topology (Dunne et al. 2002), display similar types of responses to simulated species removals. The robustness and fragility of networks to errors and attacks thus appears related more fundamentally to the non-random, skewed degree distributions of real-world networks, whether scale-free, broad-scale, or single-scale (Amaral et al. 2000). However, our study does demonstrate that the difference in response to removal of random versus most-connected species is generally greatest in the few food webs with more highly skewed scale-free and broad-scale distributions. This finding makes topological and ecological sense. The greater the degree of a species relative to other species in the web, the more likely that its loss will have a significant impact on ecosystem structure and function. For a highly connected species, its potential direct and indirect 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. 2001).

Because our study is the first to look at the impacts of node loss in a wide array of networks of varying size and topology (prior studies focus on one to four networks), 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 theoretical and experimental research, and of increasing conservation importance given extensive biodiversity loss due to human activities (Loreau et al. 2001). Robustness, defined as the potential for food webs to experience secondary extinctions with varying levels of primary species loss, does not vary systematically with species richness or omnivory in our study. 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.” In addition, there is strong evidence that greater 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 to removal of most-connected species from the outset, middle connectance webs have a threshold of ~0.2 to 0.3 removals before onset of such sensitivity, and high connectance webs have a threshold of at least 0.4 primary removals.

These results differ from findings of Lotka-Volterra studies that have focused explicitly on risk of secondary extinction in simple dynamical model food webs. Borrvall et al. (2000) found that the risk of secondary extinctions due to loss of a single random species decreases with increasing number of species per functional group (i.e., trophic species) in food webs with three functional groups (autotrophs, primary consumers, and secondary consumers) and two to six species per functional group, with connectance approximately constant. They found greatest risk of secondary extinctions with removal of an autotroph and least risk with removal of a top predator. Secondary extinctions increased with skewed interaction strengths and lower omnivory. Their model and results differ somewhat from early Lotka-Volterra food web studies suggesting that webs with higher S and C are more likely to experience secondary extinctions following loss of a species than simpler webs (Pimm 1979, 1980) and that omnivory tends to destabilize food webs (Pimm and Lawton 1978). Similarly, Lundberg et al. (2000), using two to ten species model communities with an unrealistically high constant connectance of 0.5 (Williams and Martinez 2000), found that the random removal of a single species resulted in one or more secondary extinctions 32% of the time, and that secondary extinctions increased sharply with increasing species richness.

While our study suggests that topological robustness increases with connectance, the Lotka-Volterra studies generally suggest that dynamical robustness decreases with overall species richness and connectance, but increases with species functional redundancy. Before this comparison between topological and dynamical outcomes is taken too seriously, it is important to note aspects of observed ecosystems inadequately captured by Lotka-Volterra food web studies. These studies generally fail to incorporate 1) large numbers of species, 2) potential loss of multiple species, 3) non-random, complex, yet predictable topology of trophic structure (Williams and Martinez 2000), 4) realistic predator-prey dynamics (Williams and Martinez 2001), and 5) skewed interaction strengths (e.g., Paine 1992, Wootton 1997). In order to better compare topology- versus dynamics-driven robustness and other measures of stability, modeling should be improved by incorporating more naturalistic ecosystem structure and dynamics. A recent study using a “Lotka-Volterra cascade model” is a step in this

direction since it combines Lotka-Volterra dynamics with non-random cascade model food-web structure (Chen and Cohen 2001). They found that three measures of stability, global stability, local stability, and permanence, all decrease monotonically with increasing food web complexity, whether measured as species richness or connectance. However, their model ecosystems still have few species compared to natural ecosystems ($S = 10$), and the cascade model has been demonstrated to poorly predict natural food web structure (Williams and Martinez 2000).

Our results support aspects of MacArthur's (1955) hypotheses on community stability and the interrelations of food web structure and dynamics. MacArthur suggested that community stability (the likelihood that population fluctuations in one species will effect other species) will increase as the number of links in a food web increases, since an increasing number of paths through a species will dampen the impacts of a population fluctuations in that species. Thus, within a web, increasing connectance should increase stability. Along similar lines, Law and Blackford (1992) and Law and Morton (1993) used Lotka-Volterra community assembly models to suggest that communities with high omnivory and connectance have more permanent paths, can reassemble themselves more readily, and thus may be less vulnerable to disturbance than simple communities. These types of hypotheses are often contrasted with the findings of May (1973), who found that increasing species diversity in random food webs could decrease the local stability of species populations because greater numbers of interactions in speciose communities increase the likelihood of positive feedback loops that tend to drive populations to infinity or extinction. However, May's formulation of this stability criterion as a trade-off between interaction strength, connectance, and species richness is an analytical elaboration on another speculation from MacArthur (1955). MacArthur suggested that across food webs, a trade-off between efficiency (small diet breadth) and stability would result in similar stabilities for food webs with many species with restricted diets (low C , high S) and those with few species with wide diets (high C , low S). From a topological perspective, we found no such trade-off between connectance and species richness.

While our measure of ecosystem robustness does not appear related to species richness, our analyses offer an interesting perspective on a modern variation of the diversity-stability debate: the relationship between biodiversity and ecosystem function, and particularly whether species richness *per se* has a systematic relationship with ecosystem function. This issue has largely been explored through experimental and comparative research, with additional supporting theoretical work concerning potential mechanisms driving observed patterns, including species complementarity, sampling effects, and insurance effects (for review see Loreau et al. 2001). The mean effect of removing random species may be seen as the effect of reducing species richness *per se* free of reference to functional distinctions. This effect is typically a generally consistent moderate rate of secondary extinctions resulting from primary removals within webs with $C < 0.04$. Within webs with $C > 0.03$, the rate tends to increase from low during initial removals to moderate during later removals. The Skipwith Pond food web is a notable exception as described previously. Comparing different types of removals quantifies how reducing species richness *per se* differs from removing species with particular functional traits, in this case related to their trophic role in an ecosystem. The "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. Across food webs, the 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.

While removal of species with few trophic links often results in very few secondary extinctions, there are several examples where targeting such species has large effects. As a result, the robustness of food webs to loss of low-degree species 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 somewhat unpredictable effects on ecosystem structure and function. While this represents a structural perspective, it is conceptually similar to findings from a population dynamics perspective that some so-called “weak interactors” can actually have strong effects on abundances of species in a community, depending on the scale at which data are collected and analyzed (Martinez and Dunne 1998, Berlow 1999). Such effects can be masked by a focus on “strong interactors,” species that display statistically significant average effects dependent on relatively low variance in the data (Berlow 1999).

It has been suggested that highly connected species within a food web may be thought of as keystone species (Solé and Montoya 2001), in the sense that keystone species are those that have a 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. While web topology does not encapsulate information about species abundance, low-degree species with large effects on community structure may act as the structural equivalent of keystone species, whereas high-degree species may be more equivalent 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.

The numerical simulation and network topology methods of this and related food-web studies (Montoya and Solé *in press*, Solé and Montoya 2001, Williams et al. 2001, Dunne et al. 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 modeling, experimental, and comparative approaches traditionally used to explore questions in stability-diversity and species richness-ecosystem function research. In addition, the clearly demonstrated potential for secondary extinctions in ecosystems, as a result of loss of species and their trophic roles, suggests that current extinction rate estimates, generally based on species-area relationships and estimated habitat loss, underestimate potential biodiversity loss (Holt et al. 2000, Solé and Montoya 2001). Feeding relationships and other direct and indirect effects need to be taken into account when considering the effects of species loss (Terborgh et al. 2001).

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

Food Web	Taxa	Res.	<i>S</i>	$C (L/S^2)$	L/S	<i>O</i>	Citation
Grassland	75	100	61	0.026	1.59	0.21	Martinez et al. 1999
Scotch Broom	154	99	85	0.031	2.62	0.28	Memmott et al. 2000
Ythan Estuary 1	134	86	124	0.038	4.67	0.62	Huxham et al. 1996
Ythan Estuary 2	92	86	83	0.057	4.76	0.53	Hall and Raffaelli 19991
El Verde Rainforest	156	49	155	0.063	9.74	0.56	Waide & Reagan 1996
Canton Creek	108	94	102	0.067	6.83	0.08	Townsend et al. 1998
Stony Stream	112	89	109	0.070	7.61	0.11	Townsend et al. 1998
Chesapeake Bay	33	55	31	0.071	2.19	0.52	Baird and Ulanowicz 1989
St. Marks Seagrass	48	71	48	0.096	4.60	0.71	Christian & Luczkovich 1999
St. Martin Island	44	34	42	0.116	4.88	0.60	Goldwasser & Roughgarden 1993
Little Rock Lake	182	93	92	0.118	10.84	0.38	Martinez 1991
Lake Tahoe	800	99	172	0.131	22.59	0.58	Martinez unpublished data
Mirror Lake	586	96	172	0.146	25.13	0.59	Martinez unpublished data
Bridge Brook Lake	75	95	25	0.171	4.28	0.40	Havens 1992
Coachella Valley	30	3	29	0.312	9.03	0.76	Polis 1991
Skipwith Pond	35	91	25	0.315	7.88	0.60	Warren 1989

Table 1 footnotes: “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). “Res.” refers to resolution, the percentage of taxa identified to the genus or species level. *S* = trophic species, *L* = trophic links, *C* = connectance, and *O* = omnivory. In several webs, “Taxa” may differ from what is reported by the original investigators because we exclude disconnected taxa, i.e., species or small sub-webs that lack links to the main web (e.g., exclusion of the small disconnected fern-based 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).

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

Table 2 footnotes: 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 $P \leq 0.0125$ ($0.05/4$) was used to determine significance. Significant regressions are shown in bold. SYSTAT 7.0 was used for statistical analyses.

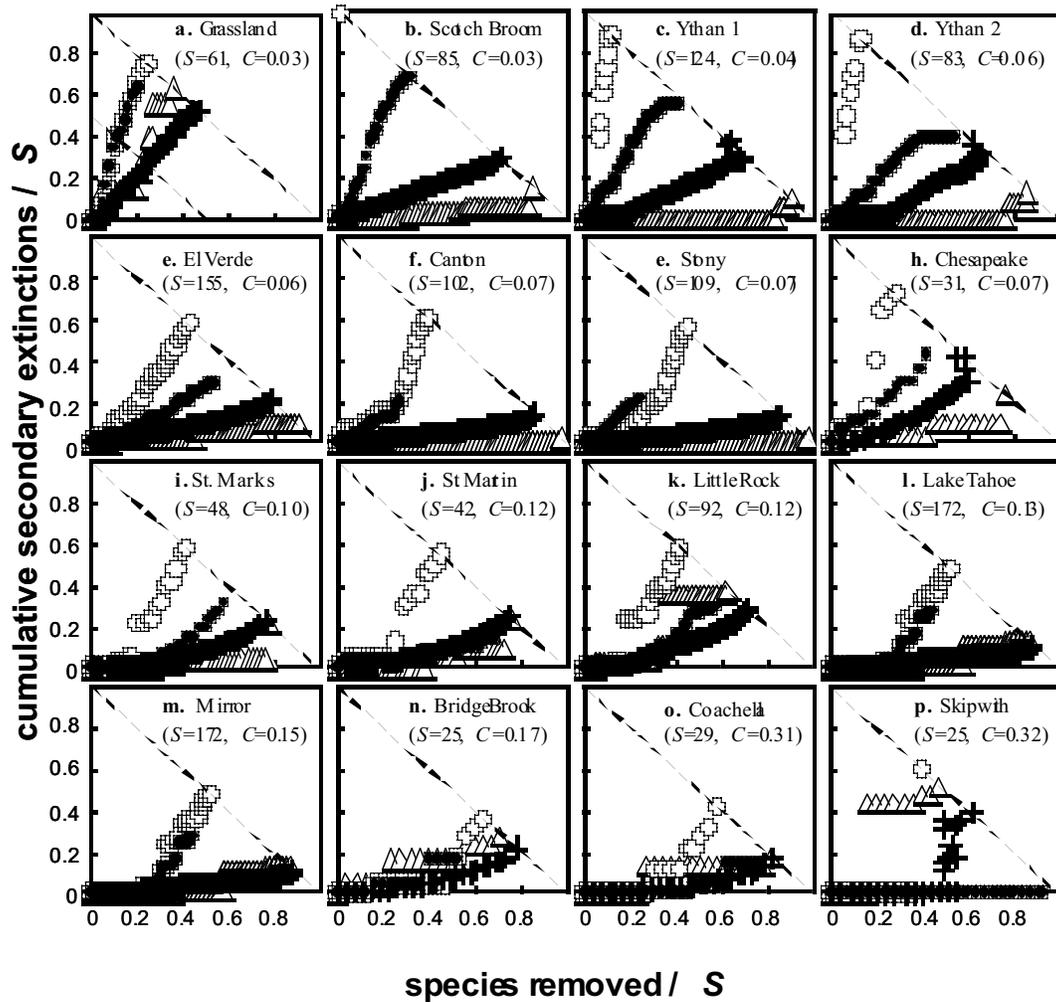


Figure 1. Secondary extinctions resulting from primary species loss in 16 food webs ordered by increasing connectance (C). 95% error bars for the random deletions fall within the size of the symbols and are not shown. For the most-connected, least-connected, and random deletion sequences, the data series end at the diagonal dashed line, where primary removals plus secondary extinctions equal S and the web disappears. For the most-connected species deletions with basal species preserved, the data points end when only basal species remain. The shorter diagonal dashed line in Fig. 1a shows the points at which 50% of species are lost through combined removals and secondary extinctions (“robustness” of Figure 2).

Species Deletions
 ○ most-connected
 ● most-connected, no basal deletions
 + random
 △ least-connected

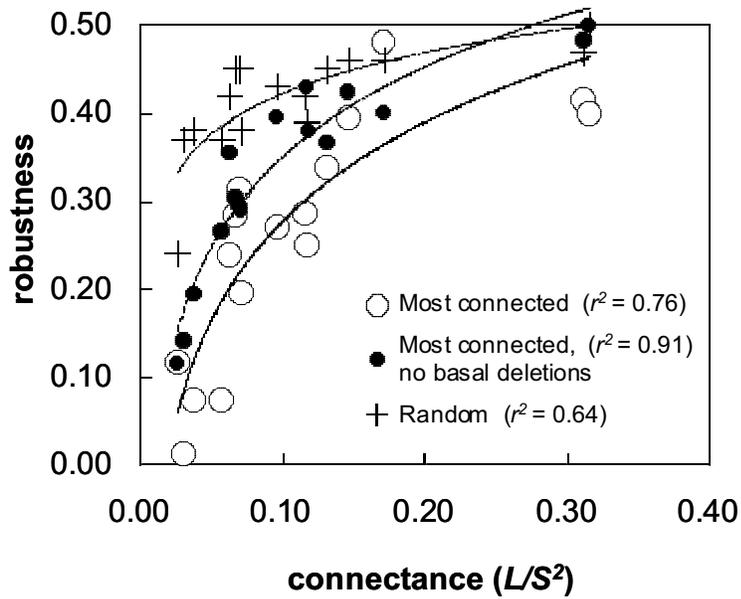


Figure 2. The proportion of primary species removals required to induce a total loss (primary removals plus secondary extinctions) of 50% of the species in each of 16 food webs (“robustness,” see the shorter dashed line of Fig. 1a for visual representation) as a function of the connectance of each web. 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: $y = 0.162\text{Ln}(x) + 0.651$ for most-connected species deletions, $y = 0.148\text{Ln}(x) + 0.691$ for most-connected species deletions with basal species preserved, and $y = 0.067\text{Ln}(x) + 0.571$ for random species deletions.