

RESPONSE OF COMPLEX FOOD WEBS TO REALISTIC EXTINCTION SEQUENCES

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Abstract. Although an ecosystem's response to biodiversity loss depends on the order in which species are lost, the extinction sequences generally used to explore such responses in food webs have been ecologically unrealistic. We investigate how several extinction orders affect the minimum number of secondary extinctions expected within pelagic food webs from 34 temperate freshwater lakes. An ecologically plausible extinction order is derived from the geographically nested pattern of species composition among the lakes and is corroborated by species' pH tolerances. Simulations suggest that lake communities are remarkably robust to this realistic extinction order and highly sensitive to the reverse sequence of species loss. This sensitivity is not well explained by the known sensitivity of networks to the loss of highly connected species but appears to be better explained by our observation that trophic specialists preferentially consume widely distributed species at low risk of extinction. Our results highlight an important aspect of community organization that may help to maintain biodiversity amidst changing environments.

Key words: acidification; Adirondack lakes; biodiversity; complex networks; extinction order; food web; lake communities; nestedness; pelagic; random extinctions; robustness; species loss.

INTRODUCTION

Sweeping losses of biodiversity are occurring worldwide, and a crucial challenge facing ecology is to understand how this sixth mass extinction will affect the functioning of ecosystems (Pimm et al. 1995, Loreau et al. 2002, Millennium Ecosystem Assessment 2005). Investigating the responses of ecosystems to local extinctions is a key step in addressing this challenge. Local extinction events do not occur randomly with respect to species' identity, but depend on factors such as body size, population size, sensitivity to environmental stress, range, trophic level, and degree of specialization (Rafaelli 2004). Such extinctions are often part of a sequence of losses in response to one or more stresses. Recent work has shown that ordered extinctions impact ecosystems differently than do random losses, the differences depending on the correlation between species' risks of extinction and their functional traits (Petchey et al. 1999, Dunne et al. 2002, Melián and Bascompte 2002, Ives and Cardinale 2004, Memmott et al. 2004, Solan et al. 2004, Zavaleta and Hulvey 2004, Bunker et al. 2005, Gross and Cardinale 2005, Larsen et al. 2005, Fortuna and Bascompte 2006). The impacts of sequential extinctions have been explored for ecosystem functions such as the maintenance of biodiversity in

resource–consumer and mutualistic networks (Solé and Montoya 2001, Dunne et al. 2002, Ives and Cardinale 2004, Memmott et al. 2004, Gross and Cardinale 2005, Fortuna and Bascompte 2006), the resistance to invasive species (Zavaleta and Hulvey 2004), the release of mineralized nutrients (Solan et al. 2004), and the storage and sequestration of carbon (Bunker et al. 2005). Still, the consequences of ecologically realistic extinction sequences in food webs spanning multiple trophic levels in nature have yet to be explored, even though an understanding of these outcomes is urgently needed (Rafaelli 2004).

Few studies of sequential extinctions in food webs have employed extinction sequences based on more than one species trait. Dunne et al. (2002) studied the robustness of empirical food webs to the simulated extinction of species ordered according to their connectedness within the food webs. Species were removed from most- to least-connected, least- to most-connected, and in random order. Memmott et al. (2004) used similar link-based methods to examine species loss in two large, empirical, plant-pollination networks. In both studies, the preferential removal of the most-connected species was most destructive (Solé and Montoya 2001), as seen in other types of networks (Albert et al. 2000, Jeong et al. 2001). Loss of species in this order, however, is ecologically unlikely. For the networks examined in Memmott et al. (2004), the order of species loss from least- to most-linked was put forth as a probable extinction sequence, because specialist pollinators tend

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to be rare and prone to extinction. Yet, level of linkage remains only one criterion for risk. In another approach, researchers have used dynamic modeling to explore the impacts of species losses ordered by theoretical extinction risk (Ives and Cardinale 2004, Gross and Cardinale 2005). Although these and other studies have provided valuable insights into the functional consequences of species loss and the role of compensation by survivors, they have not addressed both the realistic assignment of primary extinction risk and the exploration of secondary extinction consequences within multitrophic level ecosystems in nature.

Although several means of assessing species' extinction risks in a realistic manner based on traits or responses to environmental change have been studied (Díaz et al. 2003, Solan et al. 2004, Bunker et al. 2005), we found an approach based on geographical prevalence to be most applicable to our study of lake food webs. In a grassland investigation of biodiversity loss and resistance to an invasive species, Zavaleta and Hulvey (2004) derived a plausible order of species loss based on the variation in plant species composition among sites using the technique of nested-subset analysis. Here, we focus on sites that shared a common species pool over a time scale of thousands of years. Our nested-subset analysis determines the order in which species disappear when moving from species-rich sites to relatively species-poor sites. Communities are geographically nested when species at low-diversity sites are nested subsets of species in successively richer sites. Such nonrandom patterns of species composition have been widely observed in ecological communities covering a broad range of taxa, geographic regions, and spatial scales (Patterson and Atmar 1986, Cutler 1994, Wright et al. 1998). Well known for terrestrial communities, strong patterns of geographical nestedness have also been observed for marine, aquatic, and wetland assemblages (Schneider and Frost 1996, Wright et al. 1998, Baber et al. 2004).

The main mechanism underlying geographical nestedness appears to be selective extinction, whereby species systematically disappear from sites that are insufficient to sustain them, whether due to a lack of area or for reasons unrelated to area (Patterson and Atmar 1986, Cutler 1994, Wright et al. 1998). Differential extinction is believed to be particularly dominant among assemblages where colonization has been "turned off" through isolation. Thus, the analysis of nested patterns has been used to infer empirical extinction orders (Patterson and Atmar 1986, McDonald and Brown 1992, Wright et al. 1998), which may account for risk factors such as population size, range, and resilience to environmental stresses. Hadley and Maurer (2001) corroborated the ecological realism of such a sequence for montane mammals by showing that their nested geographical distribution is correlated to their persistence over evolutionary time. They argued that species with ecological tolerances, life cycles, and dispersal abilities that allow them to be most widely present throughout

the sites of a region appear to be least vulnerable to the stochastic environmental variation that drives local extinction over long time scales. In addition, several studies have investigated the role of disturbance in generating geographical nestedness, with results suggesting that species' differential tolerances to disturbance can engender nested patterns (Worthen et al. 1998, Fernandez-Juricic 2002, Baber et al. 2004). Thus the integrative information contained in nested patterns has been used as an empirical means of evaluating species' responses to perturbations such as climate change, habitat fragmentation, habitat degradation, agriculture, and human presence (McDonald and Brown 1994, Hansson 1998, Worthen et al. 1998, Baber et al. 2004, Michalski and Peres 2005, Wethered and Lawes 2005).

Here, we study the impacts of simulated species loss using a data set of 50 Adirondack lake food webs (Havens 1992), each consisting of up to 75 species and four trophic levels. Nested-subset analysis appears to be a suitable technique for inferring a plausible extinction sequence for these lakes because they are located in a common geographical region, were formed by glaciation, and have historically shared in a common species pool. We explore how the extinction order derived from nestedness and other orders affect the functioning of the complex predator-prey networks. In addition, we examine the relationship between extinction order and the trophic generality of consumers that undergo secondary extinction. Our findings suggest that communities may be organized in a manner that increases species' probability of persisting within their habitats.

METHODS

We analyzed 50 food webs describing the pelagic communities of small lakes and ponds in the Adirondack Mountains of New York State, USA (Havens 1992). Using species lists for each lake, Havens derived the webs from a cumulative web that he constructed for all of the species (Sutherland 1989) and diet information from several sources. Consumer diet preference was assumed to be constant among all lakes; that is, if A is deemed to eat B from diet information, A eats B in all lakes where both are present (Havens 1992). The food webs contain a total of 210 taxa, with all but five resolved to the genus or species level. The five nonspecific taxa include nanoflagellates, benthic detritus, and three ontogenetic life stages: fish eggs, fish fry, and copepod nauplii. Each web contains 13–75 species, with a maximum trophic level ranging from 2.00 to 4.07, estimated using the short-weighted trophic-level algorithm of Williams and Martinez (2004). Directed connectance, C , of the food webs ($C = L/S^2$, where L is the number of links and S the number of species in a food web; Martinez 1992) ranges from 0.058 to 0.15. We classified the taxa into six basic trophic categories: (1) benthic detritus, (2) phytoplankton, (3) herbivorous

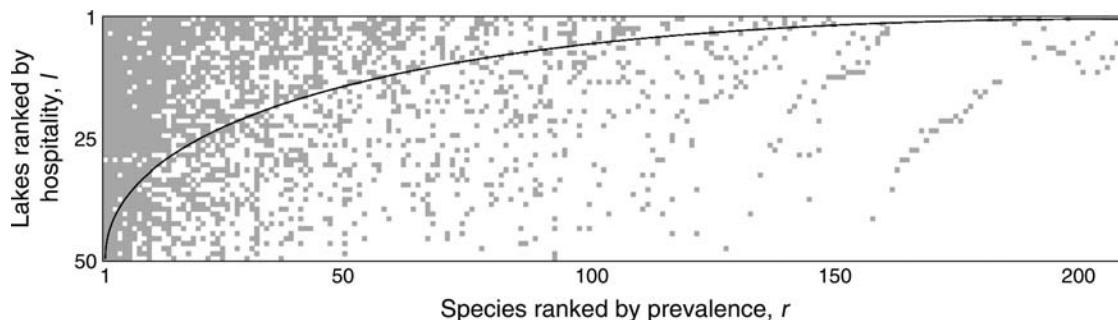


FIG. 1. Species \times site occurrence matrix for 210 taxa in 50 Adirondack lakes after reorganization to maximize nestedness, N ($N = 0.80$, $P \ll 0.001$). A filled box represents the occurrence of a species in a lake. Data points are “mapped” by rank on the axes: species by prevalence (r , scale 1–210) and lakes by hospitality (l , scale 1–50). The curve represents the isocline of perfect nestedness as calculated by the Nestedness Temperature Calculator (NTC). The rankings of species by their prevalence across all lakes (r) and lakes by their hospitality to species (l) are illustrated.

rotifers, (4) herbivorous crustaceans, (5) carnivorous zooplankton, and (6) fish.

Following Zavaleta and Hulvey (2004), we used nested-subset analysis to determine a local extinction order among the species. We analyzed the species \times site occurrence matrix for the 210 taxa over all 50 lakes using the Nestedness Temperature Calculator (NTC; Atmar and Patterson 1995). First, the NTC reorganizes a matrix to maximize its nestedness. The cells are rearranged to optimize both the ranking of species according to their distribution among the sites (from most- to least-prevalent, starting at the left of the matrix and moving right) and the ranking of sites by their species richness (from richest to poorest, beginning at the top of the matrix proceeding down). To calculate the index of matrix nestedness, T , the NTC determines an “isocline of perfect nestedness” for the matrix, with all occurrences beyond and absences before the isocline counted as deviations from perfect order. Distances to the isocline are then squared and summed for all deviations; T equals the ratio of this sum to its maximum value determined for the matrix, multiplied by 100. ($T=0$ for a perfectly nested species \times site matrix, where each site is composed of a proper subset of the species found at the next more diverse site, and $T > 0$ for an imperfectly nested matrix (Atmar and Patterson 1993)). We evaluated the level of nestedness $N = (100 - T)/100$ (Bascompte et al. 2003) with values ranging from 0 to 1, where 1 indicates maximal nestedness. We assessed the statistical significance of nestedness by Monte Carlo simulation of random matrices generated according to two null models (500 matrices each). The first model employed by the NTC constrains the number of sites and the size of the species pool, and sets the probability of cell occupancy for all cells as the number of presences in the original matrix divided by the total number of cells; the second, more stringent, model that we used additionally constrains the probability of cell occupancy to the average of the probabilities of the site (row) and species (column) occupancies (Fischer and Lindenmayer 2002, Bascompte et al. 2003).

The NTC provides two rankings. The first is a geographical most- to least-prevalent ranking of all 210 species over all lakes ($r = 1, 2, 3, \dots, 210$) from species found at the greatest number of sites to those found at the fewest, typically most speciose sites (illustrated in Fig. 1). This order was converted to normalized lake-specific rankings r_l according to each species' relative prevalence rank within the lake divided by S . Thus the most- and least-prevalent species have normalized ranks of $1/S$ and 1, respectively. The second is a ranking of the lakes ($l = 1, 2, 3, \dots, 50$) from most- to least-hospitable (Fig. 1). Linear regressions were used to investigate the relationships between species rank r_l and lake presence, and lake rank l and various lake properties such as species richness S , surface area A , and lake pH (data from Sutherland 1989, Havens 1992, Adirondack Lakes Survey Corporation 2005).

We assumed that a species' geographical prevalence rank r is a likely index of extinction proneness so that, in a plausible extinction scenario, the least prevalent, or lowest ranked species in the community is the first to disappear, with extinctions proceeding in order of reverse r . We checked this assumption for the lakes that we studied by determining whether least prevalent species predicted as high risk do indeed possess relatively narrow environmental tolerances. The Adirondack lakes have experienced large variations in pH and the effects of acidic deposition on these communities have been intensively studied (Driscoll et al. 1991, Havens 1993b, Jenkins et al. 2005:177–189). For the lakes and species that we analyzed, Havens (1993b) found species richness (y) and lake pH positively and strongly related ($R^2 = 0.59$, $P \ll 0.001$) (we independently calculated the same regression and list the P value we derived using data from Adirondack Lakes Survey Corporation [2005]). For fish, diversity falls sharply with decreasing pH (Baker and Christensen 1991, Driscoll et al. 1991, Jenkins et al. 2005:177–189). Using data on the pH ranges of Adirondack lakes where particular fish species were found (Driscoll et al. [1991]; data collected over 1984–1987), linear regression gives a positive relation-

ship between the lower bounds of species' pH ranges and our prevalence ranks (y), when considering fish for which our prevalence ranking is based on more than one lake presence (18 species, $y = 57x - 202$, $R^2 = 0.61$, $P < 0.001$). A caveat is warranted here because prevalent species are likely to be observed in lakes spanning broader pH ranges and thus at lower pH than species found in few lakes. Indeed, our prevalence ranking of species correlates strongly with the number of lakes used to determine the pH ranges cited in Driscoll et al. (1991) ($R^2 = 0.87$, $P \ll 0.001$). However, when we examine the critical pH ranges of fish (assembled from 88 papers from the 1970s and 1980s in Baker and Christensen [1991]), below which the species experience stress and difficulties in growth and reproduction, linear regression also reveals a positive relationship between average critical pH and prevalence rank (y), again only considering fish found in more than one of the lake webs that we studied (14 species, $y = 88x - 383$, $R^2 = 0.58$, $P = 0.001$). In this case, our prevalence ranking and the number of measurements used to derive the critical pH ranges of species are not significantly related ($P > 0.05$). Thus despite limited data, the acidic tolerance of fish species corroborates our hypothesis regarding prevalence rank as a proxy for robustness.

Similarly for rotifers, *Keratella taurocephala*, a species known to be dominant in acidic waters, is widely prevalent in our study (prevalence rank $r = 2$), whereas species observed to decline with decreasing pH are less prevalent (e.g., *Conochilus unicornis*, $r = 44$; *Keratella cochlearis*, $r = 60$) (Arnott et al. 2001). Among crustacean zooplankton, it is again the acid-tolerant species that exhibit top prevalence ranks (e.g., *Leptodiantomus minutus*, $r = 3$; *Bosmina longirostris*, $r = 4$; *Mesocyclops edax*, $r = 10$; *Diaphanosoma birgei*, $r = 15$), with sensitive species ranked lower (e.g., *Epischura lacustris*, $r = 61$; *Daphnia pulex*, $r = 67$; *Daphnia galeata mendotae*, $r = 131$; *Alona quadrangularis*, $r = 145$) (Havens 1991, Marmorek and Korman 1993, Arnott et al. 2001). Thus, a central assumption regarding the environmental tolerance underlying the ecological realism of our nestedness-derived sequence appears to be empirically supported with respect to pH.

We simulated species losses in the food webs by conducting five extinction sequences: (1) removal of species based on the nested pattern from least- to most-prevalent (normalized lake-specific rank $r_i = 1, \dots, 1/S$); (2) removal of species in the reverse order from most- to least-prevalent ($r_i = 1/S, \dots, 1$); (3) removal from least- to most-linked; (4) removal from most- to least-linked; and (5) random removal. We consider the first order to be ecologically plausible, whereas its reverse in the second sequence explores a kind of less plausible "attack tolerance" of the network (Albert et al. 2000) to strategic removal of the most widely distributed species, as might occur in the spread of a pathogenic disease or the consumption of common species by humans (Bunker et al. 2005). The third and fourth sequences were

conducted in order to compare our results from the nested-subset analysis-derived orders to the link-based ones from Dunne et al. (2002) and Memmott et al. (2004). A species' level of linkage was calculated in terms of its normalized connectedness c within the food webs where it is found; for a particular species i in a given food web, c_i equals the number of i 's trophic links normalized by dividing that number by the species richness of the web, S . (Note that species' normalized connectedness is calculated differently than lake connectance (Martinez 1992, Dunne et al. 2002)). Species were ranked by c in two ways, first considering all trophic links and second considering links only to consumer species. This latter ranking is particularly pertinent to our analyses of secondary extinctions, as we will explain. Random removal sequences were repeated 500 times for each lake in order to generate null results against which we compared the results from other removal sequences. The five nonspecific taxa (nanoflagellates, benthic detritus, fish eggs, fish fry, and copepod nauplii) were excluded from all extinction sequences and subsequent analyses due to their aggregated nature. Because these lakes were sampled only once and species richness vs. sampling effort was not investigated (Havens 1993b), nanoflagellates, a group of autotrophic taxa ubiquitous in lakes (Tadonleke et al. 2004), were recorded in only 16 of the 50 lake webs. Because we excluded nanoflagellates from the deletion sequences, these 16 lakes are almost completely robust to secondary extinctions as a direct or indirect pathway by which nanoflagellates could supply energy to nearly every consumer species is retained (results not shown). To avoid biasing our results with this effect, we analyzed extinction patterns for only the 34 lakes without nanoflagellates. For these lakes, we assumed that even if nanoflagellates had been present, their presence alone could not ensure their predators' survival.

Following Dunne et al. (2002), we analyzed the effects of these extinction sequences by quantifying the secondary extinctions caused by the ordered primary deletions. A consumer species was deemed to undergo secondary extinction in a particular lake when it had lost all of the resource species upon which it fed. Havens (1992) extracted the lake webs from a cumulative "metaweb" synthesized from many sources, so predator populations may not necessarily feed on all potential prey identified by this approach. Because the data generally identify the prey that predators are morphologically capable of eating, this approach may overestimate prey items utilized at a particular time and place, thus accounting to some degree for potential prey switching (Havens 1993b, Dunne 2006). Thus, secondary extinctions counted in this way are controlled by resources and suggest a near-minimum level of extinctions that may reasonably occur in response to primary deletions.

Our model is not dynamic and does not consider compensation, and therefore cannot account for addi-

tional consumer-controlled extinctions that may occur (Brett and Goldman 1997). Although each removal order includes all 210 taxa, each lake does not include every taxon. Following Dunne et al. (2002), our results are normalized for these differences so that we analyze the removal occurring in each lake in terms of the fraction of S species removed. We also compared the responses of the food webs when subjected to the various extinction sequences by applying the robustness metric R from Dunne et al. (2002). Dunne et al. defined R as the minimum fraction of primary deletions that cause $\geq 50\%$ of all species in a web to go extinct through both primary removals and secondary extinctions. Maximum R in this case is 0.50. Here we provide more detail by implementing 25% and 75% thresholds as well. Thus, for $n = 25, 50,$ and 75 , maximum values of R_n equal to 0.25, 0.50, and 0.75 are observed when no secondary extinctions result from the sequential removal of the first n percentage of the species in a lake. Linear regressions were used to investigate the relationships between R_n for all extinction orders and lake S and C . Additionally, two-tailed Student's heteroscedastic t tests were used to find out whether the mean R_n values of lakes are related to the presence of certain species.

To explore our results further, we investigated whether the normalized prevalence rank of a species within a lake is related to its "short-weighted" trophic level (Williams and Martinez 2004), its trophic category, its connectedness to its consumers within the lakes where it is found, or the normalized trophic generality of its consumers. For a particular resource species, the normalized trophic generality of its consumers is calculated as the average number of species eaten by all of its consumers within a lake divided by S , producing values for each lake where the ranked species occurs. We also examined the trophic generality of the predators that undergo secondary extinction in response to the ordered primary deletions, focusing on specialists because they would seem much more sensitive to primary extinctions than generalists (MacArthur 1955). We considered specialist consumers as those with normalized trophic generality $g/S \leq 0.2$, and did not consider species without consumers in a lake.

RESULTS

The species \times site occurrence matrix for the 50 Adirondack lakes was strongly nested (Fig. 1; nestedness, $N = 0.80$, $P \ll 0.0001$ for both null models) showing that species losses are highly ordered from species-rich to species-poor lakes. As expected, species rank r and level of prevalence among the lakes were highly correlated, as were lake rank l and S (both $P \ll 0.001$). There were 12 ties for species prevalence rank $r = 1$ and no ties among l . The order (y) in which the 12 tied species were listed by the NTC was well-correlated with the species' level of occurrence among the lakes ($y = -1.09x + 51$; $R^2 = 0.87$; $P \ll 0.001$), so we retained this order. The top species prevalence rank ($r = 1$) was given

to copepod nauplii, found in 49 of the 50 lakes, followed by the herbivorous rotifer *Keratella taurocephala* ($r = 2$), also present in 49 lakes. The species with the lowest rank ($r = 210$) was *Amphoblites rupestris*, or rock bass, found in only one lake. For these lakes, linear regression revealed significant relationships between species richness (y) and lake area, A , in hectares ($y = 0.87x - 14$; $R^2 = 0.21$; $P = 0.0008$; linear regression of $\log S$ (y) vs. $\log A$ gives $R^2 = 0.079$; $P = 0.048$) as in (Havens 1993b, Brose et al. 2004), as well as between lake pH (y) and lake surface area ($y = 0.0093x + 5.3$; $R^2 = 0.11$; $P = 0.019$). Lake rank l (y) was significantly related to lake surface area A ($y = -0.71x + 38$; $R^2 = 0.14$; $P = 0.008$) and lake pH (x) ($y = -0.043x + 6.6$; $R^2 = 0.62$; $P \ll 0.001$).

The impacts of removing species from the lake food webs differed markedly depending on the removal sequence. In Fig. 2, both axes are normalized by lake species richness so that for all lakes, the x - and y -axes indicate the proportion of S species primarily removed and secondarily lost, respectively. The food webs were highly robust to deletion of species according to the nestedness-derived, ecologically plausible removal of least- to most-prevalent species. Secondary extinctions occurred in all lakes considered only after $> 50\%$ of the species were removed (Fig. 2a), yielding a maximum mean R_{50} of 0.500 (SE = 0.000). In contrast, lakes responded with relatively early and dramatic secondary extinctions when subjected to the reverse order of most- to least-prevalent (Fig. 2b) with a significantly weaker mean R_{50} of 0.339 (SE = 0.015). Removal of species from least- to most-linked, considering links to consumers only (Fig. 2c), gave similar results to the nestedness-based least- to most-prevalent order, with a maximally robust mean R_{50} of 0.500 (0.000). Removal of most- to least-linked species, again in view of links to consumers only (Fig. 2d), resulted in the most sensitive mean R_{50} observed: 0.261 (0.015). Secondary extinctions due to random deletions averaged over 500 iterations were observed to increase gradually over the sequences (Fig. 2e), yielding the fairly robust mean R_{50} of 0.450 (0.005). Lastly, regarding mean R_n values for link-based removals ordered by species' links to both consumers and resources, for the 50% and 75% thresholds, the values for the most- to least- and least- to most-linked orders fall between the corresponding values considering links to consumers only.

Linear regressions showed no significant relationships between the lakes' robustness R_n and their species richness S and connectance C values (all $P > 0.05$). In general, the R_{50} values were not significantly related to either S or C (all $P > 0.05$, except for R_{50} and S in the most- to least-prevalent order, $P = 0.0449$). (If we included the lakes with nanoflagellates, however, lake robustness would be correlated with the presence of nanoflagellates, as predicted. The 16 lakes with nanoflagellates exhibit nearly maximal robustness to random primary extinctions, with a mean R_{50} of 0.497 (0.003).

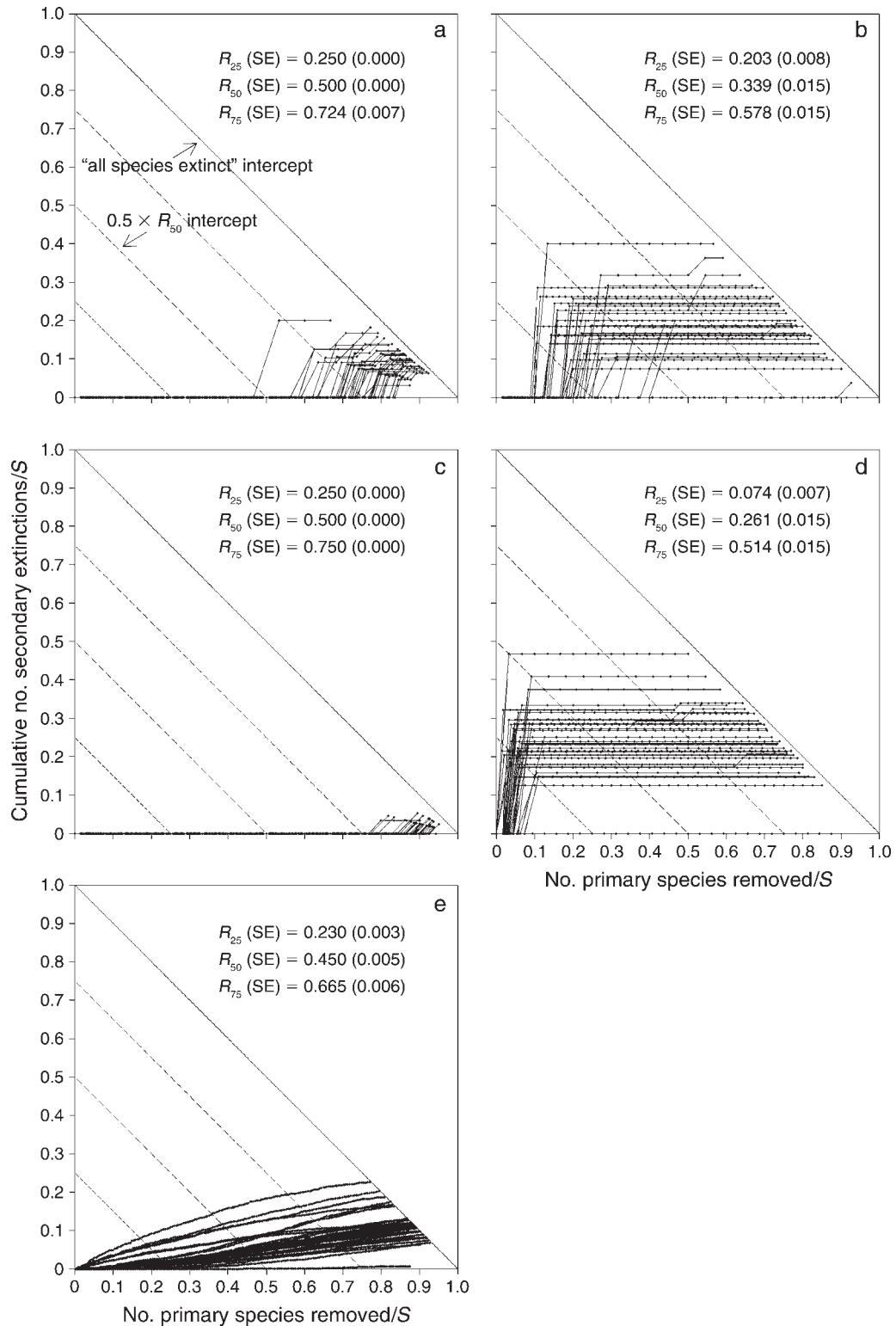


FIG. 2. Cumulative secondary extinctions due to primary species losses for 34 lake food webs using five extinction orders: (a) the order derived from nested-subset analysis, in which species are removed from least- to most-prevalent (normalized lake-specific rank $r_j = 1, \dots, 1/S$), where S is the number of species in a food web; (b) the reverse order, most- to least-prevalent ($r_j = 1/S, \dots, 1$); (c) least-linked to most-linked, considering links to consumers only; (d) most-linked to least-linked, considering links to consumers only; and (e) random removal averaged over 500 sequences for each lake. The solid lines in each plot indicate where the lake food webs disappear entirely, i.e., where primary plus secondary extinctions equal the total species richness of a lake. The dashed lines

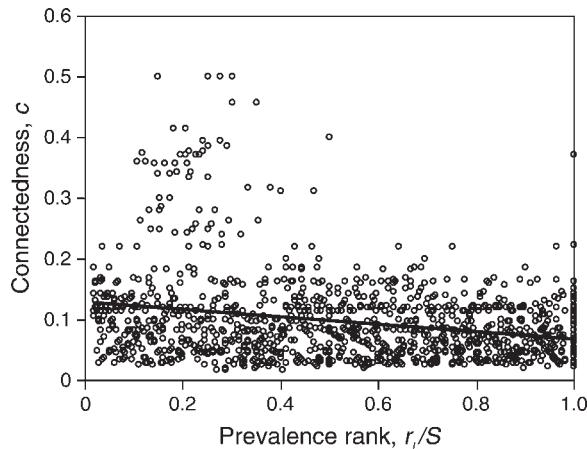


FIG. 3. Species' normalized lake-specific prevalence rank (r_i/S) vs. connectedness c to consumers for all species in 34 lakes. Here, S excludes the five aggregated taxa, and links to species' consumers are considered only. The equation for the linear fit is: $y = -0.060x + 0.13$ ($R^2 = 0.057$, $P \ll 0.001$).

In order to explain the substantial variation in lake food-web robustness to species loss order, we explored various correlates of the species' normalized lake-specific prevalence ranks. Considering all lakes with species ranked from most- to least-prevalent, we found only a weak relationship between a species' normalized rank (y) and its trophic level within the lake ($y = -0.14 + 1.69x$; $R^2 = 0.0031$; $P = 0.020$), and no significant relationship between normalized rank (y) and trophic category (two-tailed Student's heteroscedastic t tests, $P > 0.05$). In addition, we found weak, yet significant, relationships between a species' normalized rank (y) and its connectedness c within the lake, when considering links to the species' consumers only (Fig. 3; $y = -0.060x + 0.13$; $R^2 = 0.057$; $P \ll 0.0001$), as well as links to consumers and resources ($y = -0.087x + 0.24$; $R^2 = 0.024$; $P \ll 0.0001$). A species' normalized rank was not significantly related to the average trophic generality of its consumers ($P > 0.05$).

Specialist consumers are most vulnerable to secondary extinctions in our study; therefore, to elucidate the patterns in Fig. 2, we investigated the trophic generality of consumers that undergo secondary extinction (Fig. 4). For the nestedness-based, least- to most-prevalent order of primary deletions, we found that specialist consumers are secondarily extirpated on average (mean, with SE in parentheses) only when 74.3% (1.26%) of the S primary deletions have already taken place. In contrast the reverse order of primary deletions elicits specialist secondary extinctions on average when just 26.5%

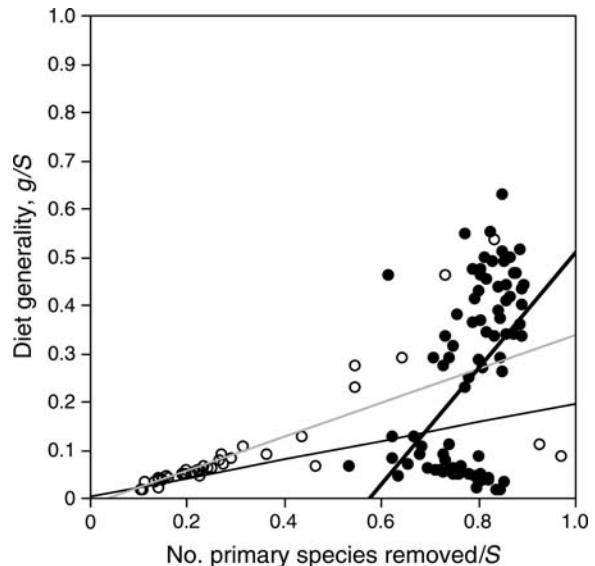


FIG. 4. Diet generality (g/S) of consumers that experience secondary extinction due to primary species losses for 34 lake food webs in the following sequences: from least- to most-prevalent (solid circles and thick black line; regression $y = 1.20x - 0.69$, $R^2 = 0.24$, $P \ll 0.001$, $SE_{sl} = 0.24$, where subscript "sl" is "slope"), most- to least-prevalent (open circles and thin black line; regression $y = 0.35x - 0.01$, $R^2 = 0.50$, $P \ll 0.001$, $SE_{sl} = 0.056$), and in random order (gray line with data points not shown; regression $y = 0.19x + 0.004$, $R^2 = 0.22$, $P \ll 0.001$, $SE_{sl} = 0.0046$). Both axes are normalized by S .

(3.41%) of the S primary deletions have occurred. For random removals, an average of 49.1% (0.323%) of primary deletions are required before the specialists are secondarily extirpated: significantly different results than those from either prevalence-based orders. From these results, the diets of specialist consumers appear to be protected in the least- to most-prevalent order and targeted in the reverse order. In contrast, specialist consumers seem to preferentially eat widespread, widely distributed species.

DISCUSSION

At present, the fresh waters of the world are undergoing accelerating rates of degradation, which impacts biodiversity in myriad ways (Wetzel 2001). Here, we have explored the simulated responses of complex lake food webs within a geographical region to various extinction scenarios, most notably one that reflects the preferential loss of species with limited geographical distribution. Derived from nested-subset analysis of lake community composition, this extinction order may reflect the cumulative shaping of the

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show where 25%, 50%, and 75% of all species are lost through combined primary removals and secondary extinctions. For example, for a particular lake, R_{50} equals the value at which the lake's extinction trajectory crosses the 50% dashed line. Values of the mean robustness statistic R_n are shown with $n = 25\%$, 50%, and 75%. For removals considering all links (plots not shown), R_{25} , R_{50} , and R_{75} mean values (with SE), respectively, for least- to most-connected removals are 0.250 (0.000), 0.485 (0.006), and 0.677 (0.009); and for most- to least-connected removals are 0.250 (0.000), 0.495 (0.002), and 0.617 (0.008).

community over time by several types of disturbance. Indeed the nested ranking of species cannot be explained simply by species' trophic levels or their trophic categories, nor is the nested ranking of lakes explained well by species-area effects. Rather, as we have shown, this extinction order is correlated with at least one important type of environmental sensitivity relevant to the Adirondack lakes: pH tolerance. Lake acidity and species richness are well correlated for these lakes, with clear evidence that acidification of the Adirondack lakes has diminished the biodiversity of nearly all biological groups (including zooplankton, phytoplankton, rotifers, and pelagic fish), thus abbreviating the food chains (Havens 1991, 1993*b*, Jenkins et al. 2005:177–189). Below species' critical pH levels, species experience physiological and reproductive stress, in addition to stress from increased toxic metal and decreased nutrient concentrations (Baker and Christensen 1991, Driscoll et al. 1991, Havens 1993*a*, Jenkins et al. 2005:177–189). Much of the acidification has been attributed to chronic acid deposition from human activities between 1930 and 1960, although natural, episodic acidification from snowmelt is known to cause species mortality in these lakes as well (Jenkins et al. 2005:177–189).

In addition to acidification, the extinction order from nestedness probably also reflects species' responses to other forms of natural and anthropogenic environmental variation until the time of census. It has been estimated that there is no area in the northeastern United States where 50% of the lakes have not experienced ecological stress (Whittier et al. 2002). For the Adirondack lakes, the main anthropogenic stresses other than direct acidification include introduction of nonnative species, increased mercury contamination of fish, shoreline alteration, increased ultraviolet exposure, and, to a lesser extent, eutrophication (Baker et al. 1993, Schindler et al. 1996, Whittier et al. 2002). Of course, natural processes have also pruned the lake community over longer time scales. From the time the lakes were created through several cycles of glaciation and sediment deposition, with the last glaciation ending between 14 000 and 12 000 years ago (Driscoll et al. 1991), natural variation in the connectivity of the lakes, climate, and dissolved oxygen concentration, among other factors (Driscoll et al. 1991, Wetzel 2001), have gradually shaped the species composition of the lakes. The extinction sequence from nestedness may encapsulate some fingerprint of the local extinctions that occurred during the history of the lakes' development. The nested ranking of diatom species in the lakes could corroborate this if it were correlated with the diatoms' extinction probabilities as expressed through sediment cores.

Although we recognize that nested patterns can arise due to sampling errors (Fischer and Lindenmayer 2002), we interpret the high level of geographical nestedness of species among the lakes compared to the two null models that we used to mean that species losses from

compositional changes due to the processes we have described have been highly ordered. Making use of this plausible extinction order, our simulations predict remarkably robust responses among the lake food webs to biodiversity loss, suggesting that similar extinctions have already helped to shape the communities. Our results do not imply, however, that the community will be similarly tolerant to extinctions due to stressors either more intense or otherwise different than those experienced by the community before the time of census (e.g., new types of anthropogenic pollution, or faster rates of climate change or habitat degradation from shoreline development). We should also note that some have questioned whether results from pelagic webs are applicable to other types of food webs (Havens 1997), but parallel claims, for example that marine food webs are similarly unique, have not been supported in recent work by the use of more comprehensive food-web data sets and empirically successful models (Dunne et al. 2004). Also, Bridge Brook Lake, the largest among Havens' Adirondack lake webs (see Plate 1), does not appear to be structurally unique with respect to two statistics of food-web complexity (connectance and omnivory) when compared to the other 15 relatively comprehensive terrestrial and aquatic webs analyzed by Dunne et al. (2002). Furthermore, this pelagic web is represented fairly well by the niche model, a model that successfully describes food webs from a wide variety of habitats (Williams and Martinez 2000).

How is it that this nestedness-based extinction sequence causes so few secondary losses in the lake food webs? Because each lake's secondary extinction trajectories in Fig. 2 are normalized by the lakes' species richness, there should be no spuriously statistical reason why deleting of the first half of the species from lakes in the least- to most-prevalent order should produce different results than the same proportion of lake deletions in any of the other orders explored; between the various orders it is the identity of the species deleted that creates the differences. Also, we reiterate that species' normalized prevalence rankings were only weakly related to their trophic levels within the lakes, so the least- to most-prevalent order does not result in fewer secondary extinctions by deleting the higher trophic levels first. As the nestedness-based order elicits similar extinction responses to those of the least- to most-linked order considering consumer links only (both give maximally robust mean R_{25} and R_{50} values), we might expect that the purported robustness of ecological networks to the loss of minimally linked nodes (Dunne et al. 2002, Memmott et al. 2004) is at work. Again, however, we found no strong correlation between the geographical nestedness-based and link-based rankings, but instead only a weak relationship between a species' normalized (lake-specific) prevalence rank and its connectedness within the lake food web (Fig. 3). Species' normalized rankings were not correlated with the trophic generality of their consumers.

The robustness of the webs to loss of the least-prevalent species, and conversely, the sensitivity to loss of the most-prevalent species, may be better explained by further observations on the diet generality of consumers (Fig. 4). We focused on specialist consumers because they appear to be particularly vulnerable to extinction, whether primary or secondary (MacArthur 1955, Dunne et al. 2002). When species are removed in random order, approximately half of the species in the food webs, on average, must be lost through primary deletions before the specialist consumers undergo secondary extinction. The situation for the nestedness-derived prevalence orders is significantly different; the specialist consumers are lost, on average, when three-quarters of the species have been deleted for the least- to most-prevalent sequence, and only one-quarter of the species for the reverse sequence. It appears that the most- to least-prevalent order preferentially targets the diets of specialist consumers in a statistically unlikely manner. This suggests that specialist consumers preferentially feed upon widely prevalent species, whereas generalists tend to eat species that are less prevalent. On the other hand, by considering species' links to all consumers, the most- to least-linked sequence targets specialists' and generalists' resources and produces even lower robustness values. A comparison of the most- to least-link-based removals ordered by consumer links vs. all links shows that the latter lead to higher robustness values, as expected, because the all-links order removes both generalist resources and generalist consumers first, reducing the occurrence of secondary consumer extinctions.

Therefore, although previous work has suggested that ecological networks are extremely sensitive to the loss of highly connected species (Solé and Montoya 2001, Dunne et al. 2002, Memmott et al. 2004), we also suggest high sensitivity to the loss of widely prevalent or distributed species, which although unlikely, might occur due to disease. In contrast to results in Dunne et al. (2002), which included simulations on the largest lake food web analyzed here (Bridge Brook Lake), secondary extinctions in our simulations due to loss of either highly linked or widely distributed species did not occur gradually, but showed a more step-like behavior (Fig. 2). In addition, we did not find a correlation between lakes' robustness values and their connectances C , either for the most- to least-linked order (all links), as was found by Dunne et al. (2002), or for any of the other extinction orders. These differences may be attributed to our use of taxonomic-species food webs as opposed to the use of trophic-species webs by Dunne et al. (2002). Trophic-species webs are aggregated versions of taxonomic ones, in which taxa that share identical links to predators and prey are grouped into a single node. Although no trophically identical species remain after the removal of a trophic species, removing taxonomic species often allows trophically identical species to persist, thus reducing the possibility of secondary

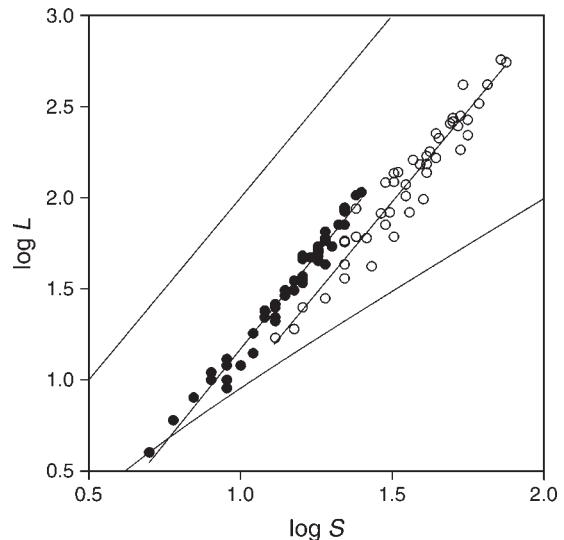


FIG. 5. Number of links L vs. species richness S for the 50 taxonomic (open circles) and trophic (solid circles) lake food webs analyzed by Havens (1992) and Martinez (1993). Note that the trophic-species webs are much smaller, accounting for the significant discrepancies between our results and those of Dunne et al. (2002). Among the taxonomic-species webs, log-log regression estimates $L = 0.093 S^{2.01}$ ($\log L = 2.01 \log S - 1.03$, $SE_{sl} = 0.078$, $SE_{con} = 0.12$, $R^2 = 0.93$), where subscripts "sl" and "con" represent "slope" and "constant." Among the trophic-species webs, log-log regression gives $L = 0.13 S^{2.07}$ ($\log L = 2.07 \log S - 0.90$, $SE_{sl} = 0.049$, $SE_{con} = 0.057$, $R^2 = 0.97$). Among taxonomic-species webs, 6.7% of the variation of the regression is left unexplained. Aggregation into trophic species reduces this unexplained variation by a factor of ~ 2.5 , leaving only 2.6% of the variation of $\log L$ unexplained by $\log S$.

extinctions. Also, $C (L/S^2)$ in taxonomic food webs exhibits more variation with S than in trophic species webs, as shown in Fig. 5 (Martinez 1993, Martinez et al. 1999). These factors contribute to more step-like or clustered secondary extinctions in taxonomic webs compared to trophic webs and confound the relationship between R and C in taxonomic webs. We note that we were unable to use trophic webs in this paper because the aggregation of taxonomic species across lakes would result in the loss of the geographical information upon which the nested ranking is based.

Although we found the lake food webs to be more robust to the realistic nestedness-derived order than to random extinctions, in work by Zavaleta and Hulvey (2004) nestedness-ordered species losses caused a disproportionate decline in the resistance of grassland communities to invasion by starthistle compared to random losses. Of course, robustness to invasion by a particular species is fundamentally different from robustness to primary extinction. Differences in our results may also have arisen because Zavaleta and Hulvey studied a single trophic level using an experimental manipulation. Recently, empirical and theoretical modeling studies have shown that differences in the functional consequences of ordered and random extinctions are deter-

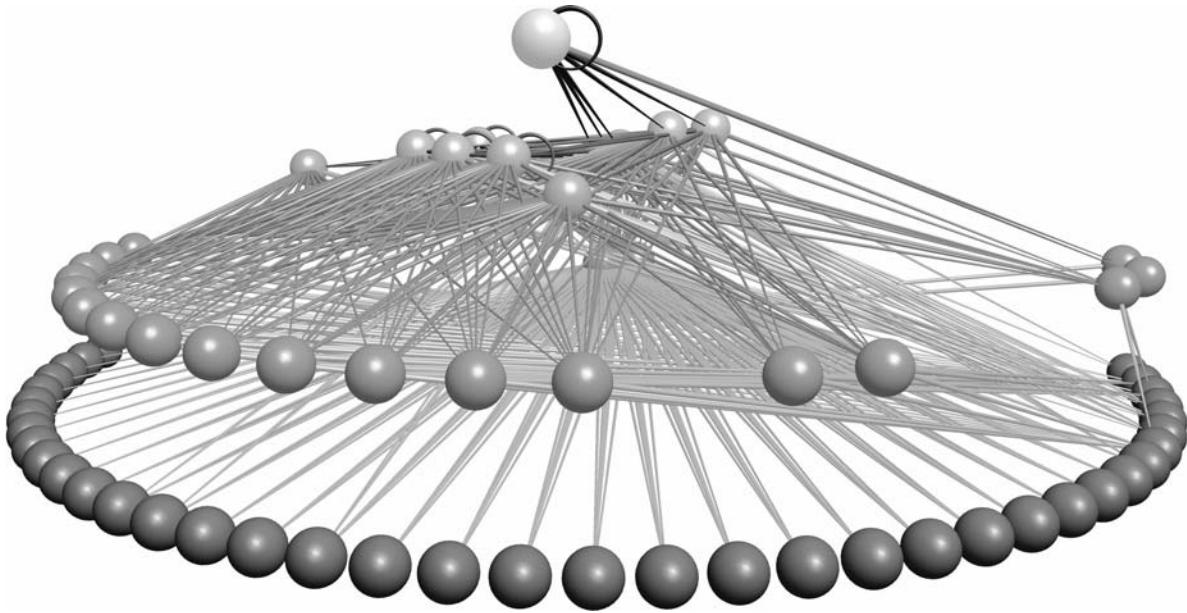


PLATE 1. Food web of Bridge Brook Lake, New York, USA, the most speciose of the Adirondack lake food webs analyzed in this study. Spheres represent species, and tapered links represent feeding relations among species. Basal species such as phytoplankton are at the base of the food web, with herbivores such as zooplankton species above the phytoplankton and higher trophic level species including omnivores, carnivores, and cannibals such as fishes further above the herbivores. The illustration was produced by FoodWeb3D written by Rich Williams and provided courtesy of the Pacific Ecoinformatics and Computational Ecology (PEaCE) Lab.

mined in large part by the covariance between species' risks of extinction and their functional traits (Petchey et al. 1999, Ives and Cardinale 2004, Solan et al. 2004, Bunker et al. 2005, Gross and Cardinale 2005, Kremen 2005). In our work, species with low prevalence rank and high risk of extinction are weak preservers of food-web biodiversity because few if any species depend exclusively on them, whereas the low-rank species of Zavaleta and Hulvey (2004) include a large share of the late-season, perennial, and nitrogen-fixing plants that promote starthistle resistance. It is important to note that neither our study nor that of Zavaleta and Hulvey considered the role of compensation by surviving species, which has been shown to reshuffle species' extinction risks in dynamic community models (Ives and Cardinale 2004, Gross and Cardinale 2005).

Our results linking the nested ranking of species to their interactions within food webs may have implications for community organization (Bascompte and Jordano 2006). Bascompte et al. (2003) gained important insights into the structure of mutualistic and competitive networks by investigating the nested-subset pattern of the plant–animal and resource–consumer interactions. They found that for individual mutualistic networks, these interactions were neither randomly organized nor compartmentalized, but highly nested; specialist species tend to interact mainly with nested subsets of species that interact with the more generalist species. The implications are significant: first, that interactions between the most connected, or generalist, consumers and resources

form the central core of the food webs; and second, that specialist species interact mainly with generalists (Bascompte et al. 2003). By investigating the geographical prevalence of resources and the trophic generality of their consumers, we have shown that the diets of specialist consumers in these lakes are composed of more widely prevalent resources than those of generalists, when considering only the variety of resource species eaten, not the quantity. This appears to be the first instance in which a relationship between the geographical nested pattern in species composition among sites and the trophic interactions within the site food webs has been identified. We speculate that this situation arises from specialist consumers outcompeting generalists for resources whose wide geographical distribution imply higher dependability over time. This potentially more effective resource competition on the part of specialists may force generalists, who lose a smaller fraction of their diet from the loss of a particular resource species, to consume geographically rarer and less dependable resources. Such a strategy could help to ensure the persistence of specialists and maintain the biodiversity of the community. This finding should be explored further through the use of dynamic food-web models (e.g., Brose et al. 2005, Fortuna and Bascompte 2006) to analyze the consequences of dynamic balances of shared resource consumption and other more subtle aspects of ecological networks such as consumer preference switching not addressed by the relatively simple structural approach employed here. In addition, by requiring secondary

extinctions to be resource-controlled, our study considers a near-minimum level of secondary extinctions that may occur from the ordered primary extinctions, and thus it cannot explore the additional effects of top-down or consumer control. Future work should explore the effects of top-down forces on the secondary extinction outcomes, as top-down control of zooplankton has been shown to be particularly important in freshwater pelagic food webs (Brett and Goldman 1997).

In conclusion, this paper advances the study of the effects of realistic extinctions in complex food webs. We have demonstrated that a simple approach for determining an empirical extinction order, nested-subset analysis, can be applied to communities spanning several trophic levels and does not require determination of complex feeding interactions, in contrast to similar studies conducted previously. Although this ranking of species' extinction risks is derived solely from presence-absence data within a landscape, we have shown that it reflects species' tolerances to a significant form of environmental stress for the webs that we considered. Although we have employed several simplifications in order to simulate extinctions in food webs, our prediction of a highly robust response for the community to the realistic extinction scenario in comparison to random removals may shed light on the way communities are structured to preserve biodiversity. Communities may have developed such that nested patterns in the geographical distribution of species combined with food-web interactions between species buffer the effects of these expected losses and magnify the impacts of the reverse sequence. These results do not imply that the community will be similarly robust to more rapid, anthropogenic drivers of biodiversity loss to which the lakes were not exposed before the census. Nevertheless, by generalizing the approach taken here, it may be possible to infer extinction scenarios for particular stressors by analyzing nested patterns of species composition across sites of varying disturbance (Martinez et al. 2006).

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