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Trophically Unique Species Are Vulnerable to Cascading Extinction

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ABSTRACT: Understanding which species might become extinct and the consequences of such loss is critical. One consequence is a cascade of further, secondary extinctions. While a significant amount is known about the types of communities and species that suffer secondary extinctions, little is known about the consequences of secondary extinctions for biodiversity. Here we examine the effect of these secondary extinctions on trophic diversity, the range of trophic roles played by the species in a community. Our analyses of natural and model food webs show that secondary extinctions cause loss of trophic diversity greater than that expected from chance, a result that is robust to variation in food web structure, distribution of interactions strengths, functional response, and adaptive foraging. Greater than expected loss of trophic diversity occurs because more trophically unique species are more vulnerable to secondary extinction. This is not a straightforward consequence of these species having few links with others but is a complex function of how direct and indirect interactions affect species persistence. A positive correlation between a species' extinction probability and the importance of its loss defines high-risk species and should make their conservation a priority.

Keywords: biodiversity, redundancy, stability, food webs, species deletions.

In complex ecological communities, where species exhibit a diverse array of trophic and competitive strategies, species extinction can affect the remaining species, for example, by causing a cascade of secondary extinctions (Paine 1966; Pimm 1980; Borrvall et al. 2000; Sole and Montoya 2001; Dunne et al. 2002; Koh et al. 2004; Petchey et al. 2004; Ebenman and Jonsson 2005; Montoya et al. 2006). These secondary extinctions occur because a primary extinction creates an unfeasible (a consumer may have no prey) or dynamically unstable community. Secondary extinctions represent a process of relaxation that creates a feasible and persistent community. The removal of a sea star species (*Pisaster ochraceus*) from a rocky intertidal community allowed mussels to dominate and caused local extinction of many other species (Paine 1966). The loss of sea otters (*Enhydra lutris*) from the West Coast kelp forests in the United States also caused many local extinctions (Springer et al. 2003). In both examples, the loss of one species caused a large shift in community structure, including loss of many other species. These “secondary extinctions,” or “coextinctions,” that can result from a primary extinction could be a major source of biodiversity loss now and in the future (Koh et al. 2004; Montoya et al. 2006).

Theoretical studies have simulated secondary extinctions in both abstract models and models of observed communities (Pimm 1980; Borrvall et al. 2000; Sole and Montoya 2001; Dunne et al. 2002; Eklöf and Ebenman 2006; Ives and Carpenter 2007). Generally, these studies take a model community, remove a species (the primary extinctions), and observe secondary extinctions. Eventually, secondary extinctions result in a community that is persistent according to topological (Dunne et al. 2002) or permanence criteria (Law and Blackford 1992; Ebenman et al. 2004) or numerical integration (e.g., Jonsson et al. 2006). Such studies provide information about when secondary extinctions are particularly likely and for which species they are most likely. For example, if the species that suffers primary extinction is relatively highly connected to other species, there will likely be a relatively large number of secondary extinctions (Dunne et al. 2002;

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Quince et al. 2005; Eklöf and Ebenman 2006). The trophic position of the primary extinction is also important but tends to interact with connectance. In sparsely connected communities, extinction of a top predator is less likely to cause secondary extinctions than extinction of a basal species (Borrvall et al. 2000; Quince et al. 2005; Eklöf and Ebenman 2006). However, in more highly connected communities, extinction of a top predator can cause more secondary extinctions than extinction of a basal species. Other factors, such as structural properties of the community (e.g., geometry, omnivory, and interaction strength distributions) and properties of the species (e.g., their functional response, whether they can switch to new resources, and density dependence), also play a role in determining the likelihood and number of secondary extinctions (Pimm 1980; Borrvall et al. 2000; Sole and Montoya 2001; Dunne et al. 2002; Thebault et al. 2007).

Previous investigations also show which species are most likely to suffer secondary extinction. Intuitively, one might think that poorly connected species are at greatest risk, as they have to lose fewer links to be unfeasible (e.g., a consumer with no prey; MacArthur 1955). While this is true in relatively sparsely connected food webs, the opposite may be true in more complex ones. There, more-connected species can suffer greater risk of secondary extinction, possibly because they experience a greater number of indirect effects. Such a pattern has been observed in both model (Eklöf and Ebenman 2006) and microcosm communities (Fox and McGrady-Steed 2002).

Here we analyze the effect of the secondary extinctions themselves, with the implicit hypothesis that they are of nonrandom sets of species and will therefore have non-random effects on communities. Specifically, we ask whether the secondary extinctions have effects on trophic diversity that differ from those of random extinctions. Trophic diversity represents the range of different trophic roles played by the species in a community and should, in theory, be closely related to functional diversity (Petchey and Gaston 2002*b*; Naeem and Wright 2003). Here, trophic diversity is estimated using established methods for quantifying phylogenetic and functional diversity (Yodzis and Winemiller 1999; Purvis et al. 2000; Petchey and Gaston 2002*b*). Thus, two species represent higher trophic diversity if they have no trophic interactions in common, that is, if they have no common prey and no common predators. Species that share prey and/or predators represent lower trophic diversity. In sum, there are various ways in which species' trophic interactions can differ; trophic diversity is a summary of all of them.

The trophic similarities and differences among the species in a food web are the source of trophic diversity at the community level. We term the amount of these similarities or differences the "trophic uniqueness" of a species

and note that the concept resembles that of phylogenetic originality (Pavoine et al. 2005). Trophic uniqueness is related to how unique a species' niche is, in particular, how distant a species is from all other species in multi-dimensional niche space. Therefore, the trophic uniqueness of a species that has no prey or predators in common with any other species will be very high, and the more shared prey or predators, the less trophically unique are species. Trophic uniqueness is distinct from specialism/generalism. Whereas trophic uniqueness reflects the overlap among species in their resources and consumers, specialism/generalism is about the number (or range) of resources, independent of the species resource use pattern of other species. Consequently, trophic uniqueness can be independent of specialism/generalism and also trophic position: in the food web of the Benguela marine ecosystem (Yodzis 1998), the three most trophically unique species are seals (16 resources), other groundfish (12 resources), and macrozooplankton (three resources); the three least unique are tuna (12 resources), goby (two resources), and pilchard (two resources).

We analyzed both model and published binary food webs of natural communities. Model communities had 12 species distributed over three trophic levels: plants, herbivores, and predators. These model species interact via consumption, intraspecific competition, and interspecific competition, with generalized Lotka-Volterra dynamics. To better understand how robust our model results were, we analyzed models with different levels of connectance, trophic structures, levels of omnivory, functional responses, and interaction strength distributions and with consumers that can switch to new resources. We analyzed 17 binary food webs of well-documented ecological communities (Dunne et al. 2004; data for Lake Tahoe and Mirror Lake were unavailable). Hereafter, we term these "natural food webs."

Methods

Model Communities

There were 12 species distributed among three trophic levels. Three aspects of community structure were varied: shape, connectance, and omnivory. Shape was rectangular, with four species on each of three levels, or triangular, with six, four, and two species on the plant, herbivore, and predator levels, respectively (fig. 1). Connectance was 0.06, 0.1, or 0.20. Omnivory was present or not. For each combination of these three features, we assembled 1,000 permanent (Law and Blackford 1992; Ebenman et al. 2004) communities by selecting parameter values according to the following rules.

Feeding links were distributed at random, but each con-

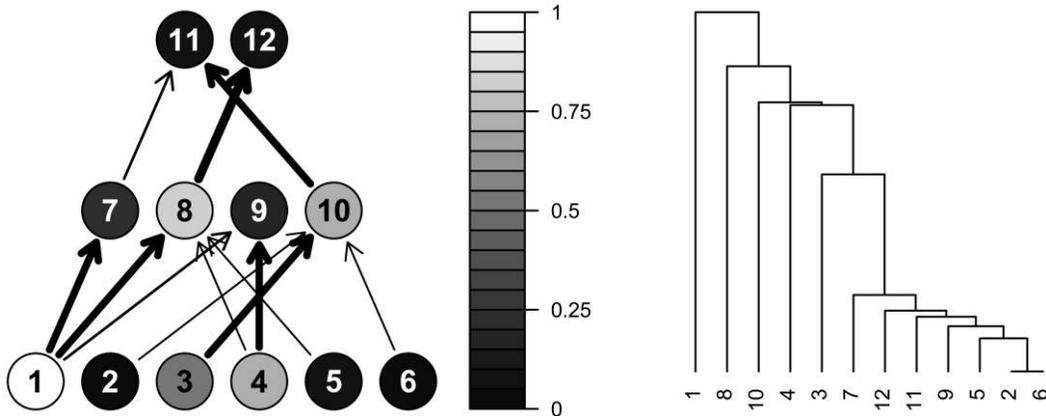


Figure 1: Trophic roles and the diversity of trophic roles result from the strength and arrangement of feeding links (arrows from prey to predator) between species. Direct intraspecific competition in all species and direct interspecific competition between all basal species are present but not shown in the figure. Species with arrangement, number, and strength of feeding interactions very different from any other in the community are relatively unique in their trophic role (lighter shades of gray) and contribute a proportionally large amount of trophic diversity to the entire community. In this example, species 1 is very unique because it has two strong links and a unique set of consumers. In contrast, species 2 and 6 have identical trophic roles; both are consumed by only species 10. We used Yodzis and Winemiller's (1999) method to construct a dendrogram of trophic roles (right) from the community matrix of interaction strengths. Trophic diversity is the total branch length of this dendrogram, a robust measure of diversity (Purvis et al. 2000; Petchey and Gaston 2002b). The trophic uniqueness of a species is the length of its terminal branch.

sumer was linked to at least one resource. There was direct competition among plants. Some webs contained omnivores. Species dynamics were described by generalized Lotka-Volterra equations: $dx_i/dt = x_i(b_i + \sum_{j=1}^S a_{ij}x_j)$, for $i = 1, \dots, S$, where x_i is the density of species i , b_i is its intrinsic growth (plants) or death (herbivores and predators) rate, and a_{ij} is the per capita effect of species j on the intrinsic growth/death rate of species i . The growth rates of primary producers were set to 1, and mortality rates for consumers were randomly drawn from the uniform distribution $[0, 0.001]$. These mortality rates were sorted so that predators had lower rates than their prey, because species at higher trophic levels are larger (Cohen et al. 2003) and large size often confers low mortality rate (Brown et al. 2004). When a consumer fed on multiple resources, the per capita effects on its resources a_{ij} included one strong feeding interaction (set to -0.4), and other links were weak (set to -0.1 divided by the number of prey species consumed minus 1). If a consumer fed on only one resource, the link was strong (-0.5). The resulting skewed distribution of interaction strengths matched that observed in real communities (Paine 1992; Wootton and Emmerson 2005). Effect of resources on consumers was $-a_{ij}$ times conversion efficiency. The conversion efficiency was set to 0.2 for nonomnivory links and 0.02 for omnivory links (a value less than 1 is to be expected when consumers are larger than their prey). We chose a smaller conversion efficiency for omnivorous links

because we assume that it takes more plant mass than animal mass to produce one predator offspring.

Intraspecific competition occurred in all species and was set to -1 for primary producers and -0.1 for consumers. Interspecific competition among plant species was modeled by setting the appropriate competition coefficients (randomly drawn from the uniform distribution $[-0.5, 0]$). Interspecific competition among consumer species was indirect through consumption of shared resources.

To check how robust results were to the assumptions of our model, we also simulated communities with type 2 (rather than linear) functional responses, with symmetric (rather than skewed) distribution of interaction strengths and with consumers that could switch resource species. For each of these, we assembled 500 "persistent" communities with connectance of 0.1 and omnivory. Persistent communities were those in which all species were present after 2,000 initial time steps. We did not simulate communities with different levels of connectance and without omnivory because of their large computational requirements.

Parameter values for type 2 functional responses were as follows: handling time of 0.01; attack rates randomly drawn from the uniform distribution $[-1, 0]$; and either equal or unequal preferences by consumers for their different prey species. Other parameters were the same as for the case of linear functional response. Diet switching happens if the primary extinction leaves a consumer without

any resource, in which case the consumer switches randomly to one of the remaining resources with half its original interaction strength. For more detailed information about these models, see Eklöf (2004) and Borrvall and Ebenman (2006).

Natural Food Webs

Binary food webs of 17 of the 19 communities in Dunne et al. (2004) were analyzed (data for Mirror Lake and Lake Tahoe were unavailable). These cover a wide range of ecosystem types, including terrestrial, fresh water, and marine. To aid comparison between analyses of the model and the natural food webs, which differ greatly in species richness, we initially removed one-twelfth of the species from each of the natural food webs and observed which species suffered secondary extinction according to topological criteria (consumers losing all their prey species). One-twelfth were removed because this corresponds to the one removal from the 12 species in the model communities. The primary extinctions were selected randomly, and secondary extinctions were recorded. We could not use the permanence criteria for natural food webs because of lack of information about strengths of interaction between species. This was carried out 50 times for each of the natural food webs.

Cascading Extinctions

Cascading extinctions occurred according to topological criteria, where a consumer suffers extinction if it has no resource species, and/or according to dynamic criteria, where a dynamically nonpermanent community loses species until it is permanent (Law and Blackford 1992; Ebenman et al. 2004). It is possible to distinguish between cases when only topological criteria are required to explain the observed secondary extinctions and cases when dynamic criteria are also required. Hereafter, the dynamic criteria may include secondary extinctions that occur through topological criteria as well as ones that occur dynamically.

Permanence analysis was not possible in the case of nonlinear functional response. Numerical integration over 25,000 time steps was then used to find the postextinction community. Here species became extinct if their densities fell below a certain threshold: 1% of the density of the initially rarest species at the relevant trophic level (Borrvall and Ebenman 2006). For example, a basal species was considered extinct if its density dropped below 1% of the density of the initially rarest basal species.

Measuring Trophic Diversity

We quantify trophic diversity in the model webs from the elements of the community matrix (with elements a_{ij}) de-

scribed in “Model Communities” (excluding competition), which describes the variety and strength of feeding strategies of the species (fig. A1 in the online edition of the *American Naturalist*). These feeding strategies reflect traits such as searching speed, radius of sensory field of predators, degree of prey crypsis, and specialism or generalism. Elements in the upper-right triangle of this matrix are nonzero if the species in row i is consumed by the species in column j , and elements in the lower-left triangle are nonzero if the species in row i consumes the species in column j . That is, the upper-right triangle documents the consumers of the species i in row i , while the lower-left triangle documents the resources of the species i in row i . To measure the trophic diversity using this information, we followed the general process of Yodzis and Winemiller (1999), which involves constructing a similarity matrix from the community matrix and using hierarchical clustering to construct the dendrogram of trophic relationships. We then used an established and robust measure of biodiversity, the branch length of the dendrogram, to measure the diversity represented by the species in a community (Purvis et al. 2000; Petchey and Gaston 2002*b*; fig. 1).

This paragraph and the next contain details of the quantitative methods used to select the measure of similarity and clustering algorithm required to transform the community matrix into a dendrogram of trophic relations. Yodzis and Winemiller (1999) tested a variety of measures of similarity and clustering algorithms and assessed their performance using the cophenetic correlation. This is the correlation between pairwise similarities and pairwise distances across the dendrogram (Sokal and Rohlf 1962); higher cophenetic correlations indicate less distortion of multivariate space. Yodzis and Winemiller (1999) used the Jaccard similarity index on the presence of trophic links and found that additively combining the predator and resource aspects of a species’ trophic role performed better than combining them multiplicatively. However, Jaccard similarity does not account for the shared absence of feeding links (Krebs 1999), which represents real data in food webs. The additive method can also make very different species appear very similar (e.g., species 5 and 12 in fig. 1; also see fig. A1). Furthermore, the multiplicative method that Yodzis and Winemiller tested can indicate that a pair of species are completely dissimilar, even though they may have some resources or predators in common. Because these properties seem somewhat undesirable, we assessed the performance of a variety of other measures of similarity, again using the cophenetic correlation to assess the most appropriate measure. In addition to the additive and multiplicative method for combining information about a species’ consumers and its resources, we used a third method, which we term “independence” (Williams and Martinez 2000; Cattin et al. 2004). This treats the con-

sumer and resources traits of a species as distinct, but not in a multiplicative manner; one can view it as being intermediate to the additive and multiplicative methods of Yodzis and Winemiller (1999).

The additive and independence methods outperformed the multiplicative method across different distance measures (e.g., Jaccard and Euclidean) and different data types (binary or continuous), as measured by the mean cophenetic correlation over all model webs. The performances of the additive and independence methods were very similar, and our general conclusions were insensitive to the method we used. We used Euclidean distances on continuous-interaction data because this produced the highest cophenetic correlation.

Accounting for Variation in the Loss of Trophic Diversity

There was considerable variation among food web types in the amount of trophic diversity lost. We examined whether differences among the simulated food webs and patterns of secondary extinctions could account for this variation, using regression trees. These are methods for assessing whether a response variable is associated with variation in a number of explanatory variables; they are robust to nonlinear relationships and can represent more complex interactions than multiple regression or ANOVA (De'ath and Fabricius 2000; Brose et al. 2005). The response variable was deviation from expected trophic diversity (observed trophic diversity remaining minus expected trophic diversity remaining), where expected trophic diversity remaining was the proportion of species remaining. Explanatory variables were connectance (0.06, 0.1, or 0.19), web shape (triangular or rectangular), omnivory (present or not), whether secondary extinctions were by topological or dynamic criteria, the identity of the initial extinction (basal, intermediate, or top species), the number of secondary extinctions, the identity of the secondary extinctions (seven possible combinations of basal, intermediate, and top species), the distribution of interaction strengths (skewed or even), the type of functional response (linear or type 2), and whether consumers could switch to new resources. The 1-SE rule defined the number of splits in the tree (De'ath and Fabricius 2000).

Which Species Became Extinct?

Regression tree analysis was also used to determine which properties of a species were associated with high secondary extinction probability. Secondary-extinction probability was the response variable, and explanatory variables were number of trophic links to and from the species, trophic position of a species, trophic uniqueness of the species, connectance, web shape, omnivory, distribution of inter-

action strengths, functional response type, consumer diet switching, and whether secondary extinctions were topological or dynamic. A species' trophic uniqueness was the branch length in the dendrogram unique to that species, and qualitative conclusions were qualitatively identical for two other measures of trophic uniqueness.

Results

Model Communities

Secondary extinctions left model communities with between 50% and 83% of their original species richness. The amount of trophic diversity remaining was lower than expected, given the proportion of species that suffered extinction (figs. 2, 3). For example, in model communities, a 25% reduction in the number of species caused a loss of 20%–72% of trophic diversity, with a mean of 39% (fig. 2*a*, 2*b*). Across all model communities and all extinctions, cascading extinctions resulted in a mean of ~10% less trophic diversity than expected. The qualitative pattern was consistent across model communities with triangular structure (fig. 2*a*, 2*b*), with rectangular structure (fig. 3*c*, 3*d*), with omnivory, without omnivory (fig. 2), and with connectance varying across the range found in natural food webs (fig. 2). The greater than expected loss of trophic diversity also occurred regardless of whether secondary extinctions were purely topological (fig. 2*a*, 2*c*; fig. 3*a*, 3*c*) or were due to both topological criteria and dynamic instabilities (fig. 2*b*, 2*d*; fig. 3*b*, 3*d*). Analyses of models with type 2 functional responses (fig. 3*a*, 3*b*) and consumers with ability to switch to new resources (fig. 3*c*, 3*d*) show the same pattern of greater than expected loss of trophic diversity.

When a null hypothesis was used that controlled for proportion of species lost and community feasibility, secondary extinctions still resulted in lower trophic diversity than if species loss was random but constrained by feasibility (fig. 4). This null hypothesis accounts for the structure of the dendrogram of trophic similarities among the species in a community. In some cases, the effect of dynamic secondary extinctions was to reduce trophic diversity by 50% below the level in communities that experience random extinctions that result in feasible communities.

Natural Food Webs

Greater than expected loss of trophic diversity also resulted when secondary extinctions occurred in a collection of natural food webs from a variety of communities (fig. 5). This resulted in food webs with between 58% and 92% of their original species richness. In 523 of the 560 comparisons, the effect of secondary extinctions was greater than proportional. The magnitude of the pattern was less

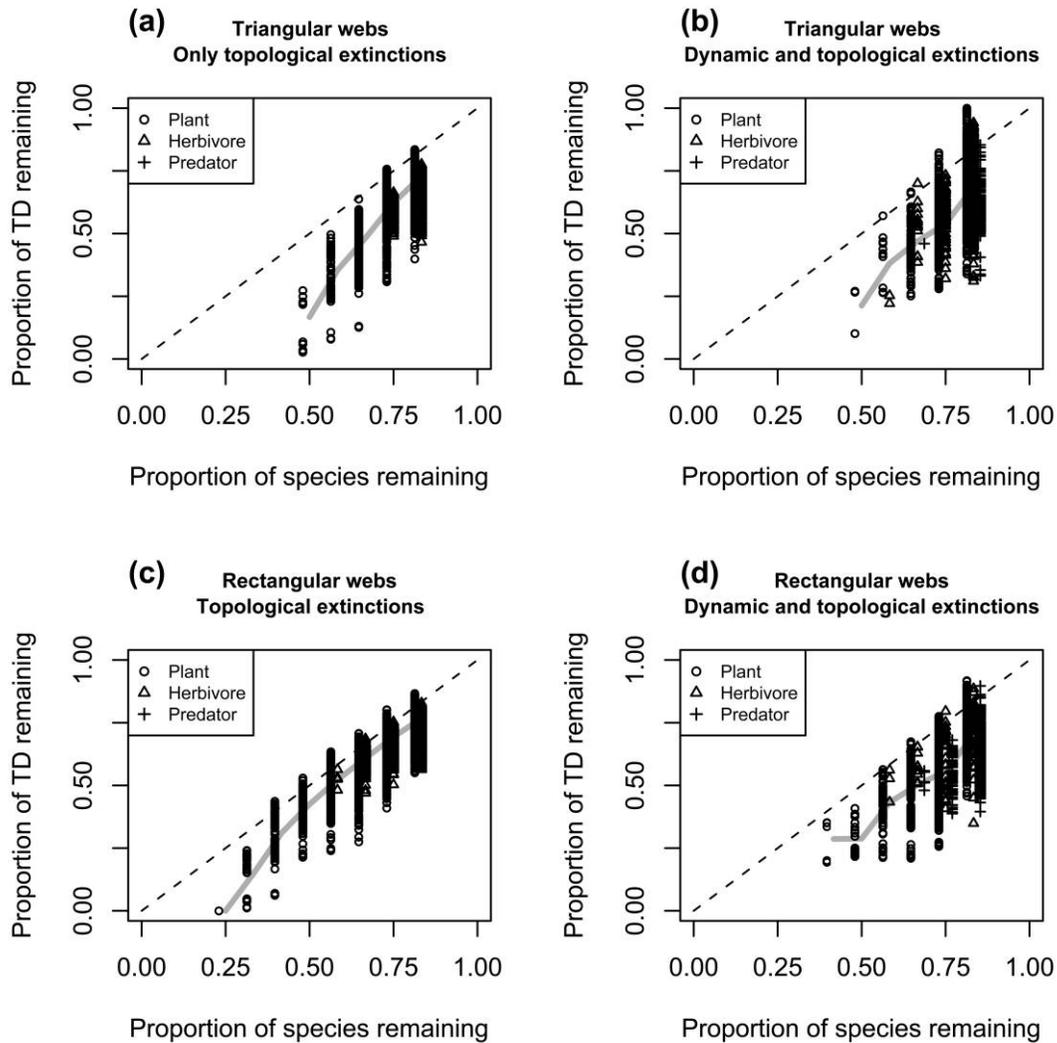


Figure 2: Cascades of secondary extinctions cause loss of trophic diversity in model communities. The proportional loss of trophic diversity (TD) is greater than the proportional loss of species in both triangular (*a, b*) and rectangular (*c, d*) communities and when extinctions are topological (*a, c*) or dynamic (*b, d*). In these model communities, 25 of 26 community types show lower-than-proportional levels of trophic diversity (binomial test, $\alpha = 0.05$). Symbols indicate from which trophic level the initial extinction occurred, and values are offset negatively and positively on the X-axis for clarity. The dashed line has intercept of 0 and slope of 1 for reference. Connectance (0.06, 0.10, or 0.19) and omnivory (present or absent) vary among the points within individual panels. Gray lines connect the means of the Y variable.

than for the model communities, however, with a loss of 25% of species leading to a loss of about 24%–37% of trophic diversity, with a mean of 30%.

Accounting for Variation in the Loss of Trophic Diversity

Although there was generally a greater than expected loss of trophic diversity, there was also a great deal of variation, even when the same number of secondary extinctions occurred. Differences in web structures and species interactions accounted for about 30% of this variation across all

webs (table 1), and the amount by which trophic diversity was reduced below the expected level was influenced by a variety of properties of the community and by the causes of secondary extinctions. For example, loss of trophic diversity was greater in highly connected webs than in sparsely connected communities, in triangular webs, and when more secondary extinctions had occurred (table 1).

Which Species Became Extinct?

Bottom species experienced lower extinction probability (0.005) than intermediate and top species (0.21; table 2).

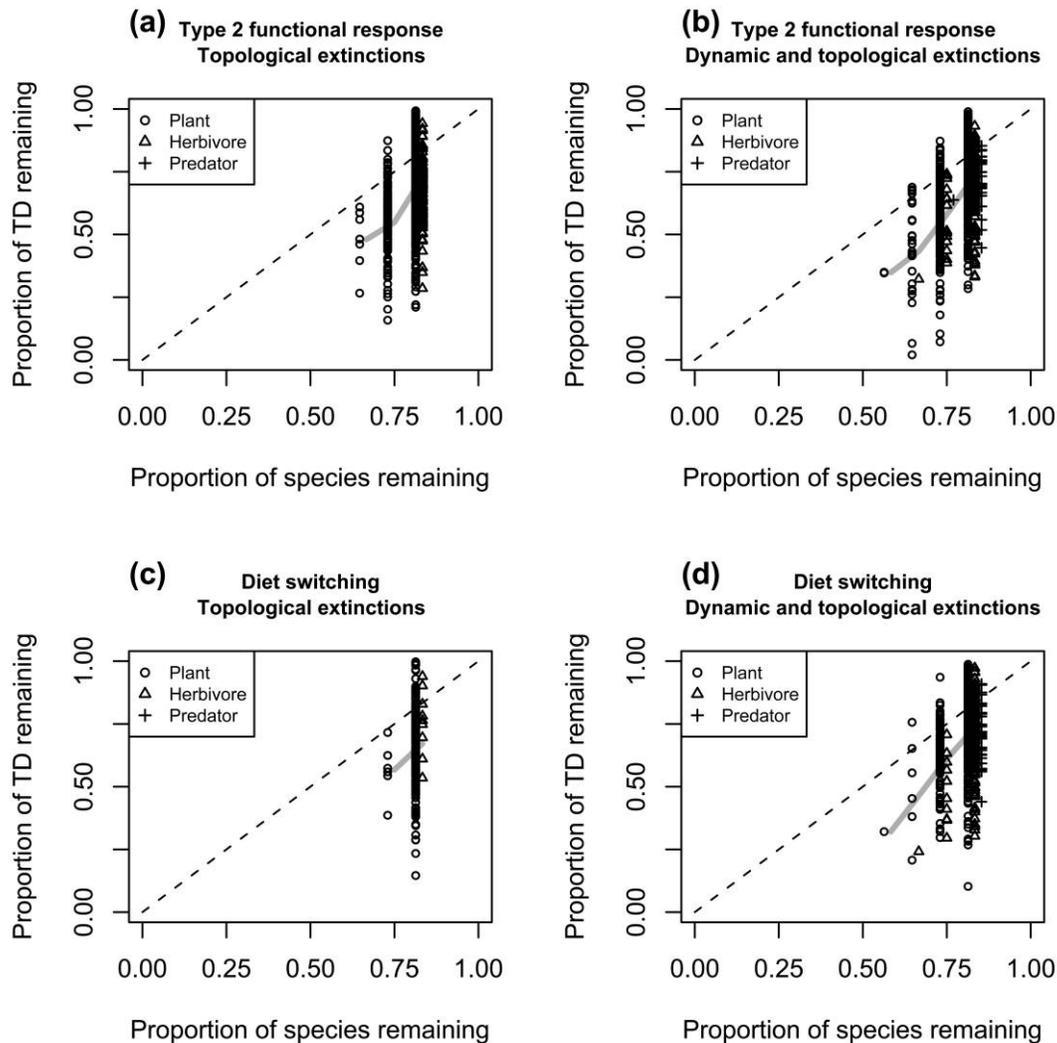


Figure 3: Cascades of secondary extinctions cause loss of trophic diversity in model communities. The proportional loss of trophic diversity (TD) is greater than the proportional loss of species in food webs where consumers have a type 2 functional response (*a*, *b*) or consumers can switch to new resources (*c*, *d*) and when extinctions are topological (*a*, *c*) or dynamic (*b*, *d*). All webs were triangular. Symbols indicate from which trophic level the initial extinction occurred, and values are offset negatively and positively on the X-axis for clarity. The dashed line has intercept of 0 and slope of 1 for reference. In all panels, connectance is 0.10 and omnivory is present. Gray lines connect the means of the Y variable.

Number of links was the next split in the regression tree, with species with fewer links suffering greater risk of extinction. In the remainder of the tree, two splits indicated that species that were more trophically unique were more likely to become extinct. There were also splits indicating that extinctions were more likely if both dynamic and topological extinction criteria were considered than when only topological extinctions occurred. One of the remaining splits indicated that species with more links were more likely to become extinct (table 2).

Inspection of the relationships between trophic unique-

ness and number of links in model (fig. A2 in the online edition of the *American Naturalist*) and natural (fig. A3 in the online edition of the *American Naturalist*) food webs reveals a variety of relationships. For different species (bottom, intermediate, or top) in model webs with different levels of connectance, there can be either no apparent relationship or a positive relationship between trophic uniqueness and number of links. In all cases there is much scatter, presumably because many factors other than number of links differ between species. Regression tree analyses of these data indicate that intermediate species tend to

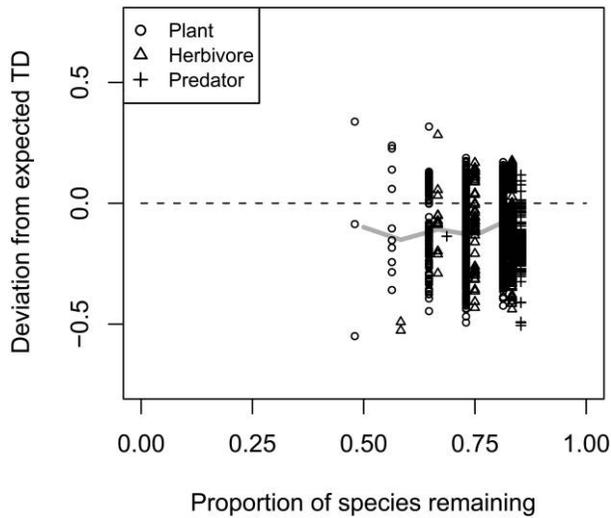


Figure 4: Deviation from expected trophic diversity, where the expected trophic diversity is the trophic diversity realized by the same number of species as results in a topologically feasible community. Deviation is (observed trophic diversity minus expected trophic diversity) divided by expected trophic diversity. The dashed line indicates no relative difference. Symbols indicate from which trophic level the initial extinction occurred, and values are offset negatively and positively on the X-axis for clarity. The gray line connects the means of the Y variable.

have greater trophic uniqueness than bottom or top ones and that, in general, species with more links are more trophically unique (table 3).

Discussion

Nonrandom loss of species reduces various components of biodiversity—including the amount of evolutionary history represented by an assemblage (Nee and May 1997; Purvis et al. 2000) and the functional diversity of an assemblage (Petchey and Gaston 2002a)—more than might be expected if extinctions occurred at random. Here we show that secondary extinctions cause large reductions in the total diversity of trophic roles played by species. This appears to happen because the extinctions are of a collection of species that represent a disproportionate amount of trophic diversity. Their relative uniqueness may also mean that loss of these species will have disproportionate effects on rates of ecosystem processes, although a more thorough understanding of the mechanisms that link trophic diversity and ecosystem processes will reveal whether this is true (Raffaelli et al. 2002; Worm and Duffy 2003; Thebault et al. 2007).

Similar results occur in model and natural food webs despite differences between the data, the types of secondary extinctions that occur, and the varied assumptions of the

models. Interspecific interactions in the model communities vary in strength, and competition occurs between basal species. In contrast, the natural food webs contain only trophic interactions, and these are binary (present or absent; i.e., no data are available on their strength). Because of this difference, the cascading extinctions in natural food webs accord with topological criteria only: consumers suffer extinction only if they have no resource species (a direct effect). In the model communities, however, secondary extinctions can be of any species and can result from dynamic instabilities caused by both direct and indirect interactions (Ebenman et al. 2004; Christianou and Ebenman 2005; Ebenman and Jonsson 2005; Quince et al. 2005).

What can explain the greater than expected loss of trophic diversity? One possible explanation for this result is that secondary extinctions occur for species that are poorly connected (i.e., specialists) and that these are also species that contribute disproportionately to trophic diversity. However, while poorly connected species were sometimes more likely to become extinct (table 2), more connected species (i.e., generalists) tended to be more trophically unique (table 3). Consequently, we cannot conclude that our results are caused by a correlation between extinction risk and trophic uniqueness that itself is caused by variation in number of links.

What, then, explains the relatively likely extinction of more trophically unique species? Our results show that

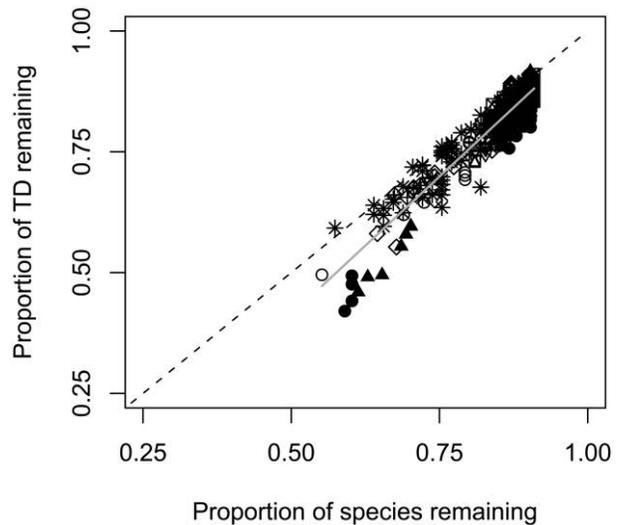


Figure 5: Cascades of secondary extinctions cause loss of trophic diversity (TD) in natural food webs. The dashed line has intercept of 0 and slope of 1 for reference. Symbols represent different natural food webs, although their identity is unimportant for the interpretation of results. The gray line is the linear regression through the data.

Table 1: Regression tree that explains variation in the deviation of the observed trophic diversity of a community from the expected trophic diversity

Split	Variable and value(s)	No. observations	Response value
1	Connectance = .20	8,259	-.16
2	Secondary extinctions ≥ 1.5	842	-.27
2	Secondary extinctions < 1.5	7,417	-.15
4	Top species removed	995	-.22
4	Intermediate or bottom species removed	6,422	-.14
1	Connectance = .06, .10	34,859	-.09
3	Shape = triangular	14,230	-.12
5	ID lost = {T}, {IT}, {BT}, {BI}, {BIT}	5,010	-.15
5	ID lost = {I}, {B}	9,220	-.10
7	Connectance = .06	3,346	-.07
7	Connectance = .10	5,874	-.12
9	Secondary extinctions ≥ 1.5	439	-.20
9	Secondary extinctions < 1.5	5,435	-.11
3	Shape = rectangular	20,629	-.07
6	Connectance = .10	10,974	-.09
6	Connectance = .06	9,655	-.05
8	Secondary extinctions ≥ 6.5	195	-.20
8	Secondary extinctions < 6.5	9,460	-.05

Note: Expected trophic diversity remaining was the proportion of species remaining. The first split is whether connectance was 0.20 (greater loss of trophic diversity) or 0.06 or 0.10 (smaller loss of trophic diversity). Overall, the regression tree explains about 30% of the variation in the response variable. Bold entries indicate terminal branches, all of which have negative response values that correspond to greater than expected loss of trophic diversity. ID lost is the identity of the species that suffered secondary extinction: B = bottom, I = intermediate, T = top; combinations indicate when more than one type became extinct.

Table 2: Regression tree that explains variation in secondary-extinction probability among species

Split	Variable and value(s)	No. observations	Response value
1	ID = {B}	9,850	.005
1	ID = {I}, {T}	13,952	.21
2	Links ≥ 2.5	11,220	.16
3	TU < .18	7,041	.07
4	ID = {T}	3,798	.02
4	ID = {I}	3,243	.12
3	TU $\geq .18$	4,179	.31
5	Extinction = topological	2,232	.23
5	Extinction = dynamic and topological	1,947	.41
6	Links < 4.5	683	.23
6	Links ≥ 4.5	1,264	.50
7	TU < .22	397	.32
7	TU $\geq .22$	867	.58
2	Links < 2.5	2,732	.40

Note: The first split is whether a species is bottom in the food web or not, the second split is the number of links to and from a species, and the third is the trophic uniqueness (TU) of a species, with higher values corresponding to higher extinction probability. Overall, the regression tree explains about 22% of the variation in the response variable. Bold entries indicate terminal branches. ID gives the trophic position of the species: B = bottom, I = intermediate, T = top.

Table 3: Regression tree that explains variation in trophic uniqueness among species

Split	Variable and value(s)	No. observations	Response value
1	ID = {B}, {T}	15,693	.10
2	Links < .5	1,382	.00
2	Links ≥ .5	14,311	.11
3	Links < 1.5	2,762	.08
3	Links ≥ 1.5	11,549	.12
4	ID = {T}	2,543	.11
4	ID = {B}	5,706	.14
5	Connectance = .20	1,756	.10
5	Connectance = .06, .10	3,950	.16
6	Links < 2.5	2,462	.13
6	Links ≥ 2.5	1,488	.20
1	ID = {I}	8,109	.19
7	Links < 3.5	2,832	.17
7	Links ≥ 3.5	5,277	.20
8	Connectance = .10, .20	4,692	.20
8	Connectance = .06	585	.27

Note: Overall, the regression tree explains about 36% of the variation in the response variable. Bold entries indicate terminal branches. ID gives the trophic position of the species: B = bottom, I = intermediate, T = top.

intermediate species (herbivores) tend to be more trophically unique than basal and top species (table 3). Intermediate species are also more likely to suffer secondary extinction (table 2). The mechanisms involved in the secondary extinctions of intermediate species are direct bottom-up effects (intermediate species become extinct when their resources are deleted) and indirect top-down effects (breakdown of predator-mediated coexistence when top species are deleted; Eklöf and Ebenman 2006). Moreover, indirect top-down effects are more common in highly connected communities than in those with low connectance (Eklöf and Ebenman 2006). These patterns suggest that our finding—the greater than expected loss of trophic diversity (especially in highly connected webs)—is caused by a higher extinction risk of intermediate species, which in turn are more trophically unique than species at other trophic levels.

Previous investigations suggest that, in addition to trophic position, the presence, position, and direction of feeding links can have important effects on the extinction risk of species (Bender et al. 1984; Yodzis 1988; Jonsson et al. 2006). Our results are also broadly consistent with this finding: extinction risk is influenced by details of the pattern of interaction with other species. We do not, however, have a complete mechanistic explanation of these patterns, and we leave them for further research.

Although the general pattern of greater than expected loss of trophic diversity was robust to changes in model structure and parameters, the amount of loss varied (table 1). For example, model food webs with high connectance

(0.20) experience greater loss of trophic diversity than those with lower (0.06, 0.10) connectance. The most likely explanation for this is that secondary extinctions caused by indirect effects are more common in highly connected networks and that these extinctions involve more trophically unique species (see above).

Our results suggest a correlation between the probability that a secondary extinction occurs and the magnitude of its effect: species that suffer higher probability of secondary extinction have greater effects on trophic diversity than species for which secondary extinction is less likely. The same pattern seems to apply to primary extinctions, where species with higher probability of extinction contribute disproportionately to community characteristics (Petchey and Gaston 2002a; Bunker et al. 2005; Gross and Cardinale 2005). This finding has significant conservation implications in terms of ecological risk assessment, where risk is defined as a combination of the probability that an event occurs and the severity of its consequences. First, redundant species (those whose loss has little effect) are unlikely to suffer extinction, limiting their contribution to system redundancy (Walker 1992). These are low-risk species. In contrast, high-risk species will probably become extinct and will have a large effect if they do. The correlation between probability of extinction and severity of effect results in relatively few intermediate-risk species. This correlation should, to some extent, give better return on conservation effort, because conserving a species with high probability of extinction also prevents large effects on ecosystems. Identifying these high-risk species in large and

complex ecological communities is a considerable challenge, but they may be indicated by their relatively unique pattern of interactions with other species.

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Literature Cited

- Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* 65: 1–13.
- Borrvall, C., and B. Ebenman. 2006. Early onset of secondary extinctions in food webs following the loss of top predators. *Ecology Letters* 9:435–442.
- Borrvall, C., B. Ebenman, and T. Jonsson. 2000. Biodiversity lessens the risk of cascading extinction in model food webs. *Ecology Letters* 3:131–136.
- Brose, U., E. L. Berlow, and N. D. Martinez. 2005. Scaling up keystone effects from simple to complex ecological networks. *Ecology Letters* 8:1317–1325.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
- Bunker, D. E., F. DeClerck, J. C. Bradford, R. K. Colwell, I. Perfecto, O. L. Phillips, M. Sankaran, and S. Naeem. 2005. Species loss and aboveground carbon storage in a tropical forest. *Science* 310:1029–1031.
- Cattin, M.-F., L.-F. Bersier, C. Banasek-Richter, R. Baltensperger, and J.-P. Gabriel. 2004. Phylogenetic constraints and adaptation explain food-web structure. *Nature* 427:835–839.
- Christianou, M., and B. Ebenman. 2005. Keystone species and vulnerable species in ecological communities: strong or weak interactors? *Journal of Theoretical Biology* 235:95–103.
- Cohen, J. E., T. Jonsson, and S. R. Carpenter. 2003. Ecological community description using the food web, species abundance, and body size. *Proceedings of the National Academy of Sciences of the USA* 100:1781–1786.
- De'ath, G., and K. E. Fabricius. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81:3178–3192.
- Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecology Letters* 5:558–567.
- . 2004. Network structure and robustness of marine food webs. *Marine Ecology Progress Series* 273:291–302.
- Ebenman, B., and T. Jonsson. 2005. Using community viability analysis to identify fragile systems and keystone species. *Trends in Ecology & Evolution* 20:568–575.
- Ebenman, B., R. Law, and C. Borrvall. 2004. Community viability analysis: the response of ecological communities to species loss. *Ecology* 85:2591–2600.
- Eklöf, A. 2004. Cascading extinctions in food webs: local and regional processes. *Linköping Studies in Science and Technology* no. 1135. Linköping University, Linköping.
- Eklöf, A., and B. Ebenman. 2006. Species loss and secondary extinctions in simple and complex model communities. *Journal of Animal Ecology* 75:239–246.
- Fox, J. W., and J. McGrady-Steed. 2002. Stability and complexity in microcosm communities. *Journal of Animal Ecology* 71:749–756.
- Gross, K., and B. J. Cardinale. 2005. The functional consequences of random vs. ordered species extinctions. *Ecology Letters* 8:409–418.
- Ives, A. R., and S. R. Carpenter. 2007. Stability and diversity in ecosystems. *Science* 317:58–62.
- Jonsson, T., P. Karlsson, and A. Jonsson. 2006. Food web structure affects the extinction risk of species in ecological communities. *Ecological Modelling* 199:93–106.
- Koh, L. P., R. R. Dunn, N. S. Sodhi, R. K. Colwell, H. C. Proctor, and V. S. Smith. 2004. Species coextinctions and the biodiversity crisis. *Science* 305:1632–1634.
- Krebs, C. J. 1999. *Ecological methods*. Benjamin/Cummings, Menlo Park, CA.
- Law, R., and J. C. Blackford. 1992. Self-assembling food webs: a global viewpoint of coexisting species in Lotka-Volterra communities. *Ecology* 73:567–578.
- MacArthur, R. 1955. Fluctuations of animal populations, and a measure of community stability. *Ecology* 36:533–536.
- Montoya, J. M., S. L. Pimm, and R. V. Sole. 2006. Ecological networks and their fragility. *Nature* 442:259–264.
- Naeem, S., and J. P. Wright. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters* 6:567–579.
- Nee, S., and R. M. May. 1997. Extinction and the loss of evolutionary history. *Science* 278:692–694.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- . 1992. Food-web analysis through field measurement of per capita interaction strength. *Nature* 355:73–75.
- Pavoine, S., S. Ollier, and A.-B. Dufour. 2005. Is the originality of a species measurable? *Ecology Letters* 8:579–586.
- Petchey, O. L., and K. J. Gaston. 2002a. Extinction and the loss of functional diversity. *Proceedings of the Royal Society B: Biological Sciences* 269:1721–1727.
- . 2002b. Functional diversity (FD), species richness, and community composition. *Ecology Letters* 5:402–411.
- Petchey, O. L., A. L. Downing, G. G. Mittelbach, L. Persson, C. F. Steiner, P. H. Warren, and G. Woodward. 2004. Species loss and the structure and functioning of multitrophic aquatic ecosystems. *Oikos* 104:467–478.
- Pimm, S. L. 1980. Food web design and the effect of species deletion. *Oikos* 35:139–149.
- Purvis, A., P.-M. Agapow, J. L. Gittleman, and G. M. Mace. 2000. Nonrandom extinction and the loss of evolutionary history. *Science* 288:328–330.
- Quince, C., P. G. Higgs, and A. J. McKane. 2005. Deleting species from food webs. *Oikos* 110:283–296.
- Raffaelli, D., W. H. van der Putten, L. Persson, D. A. Wardle, O. L. Petchey, J. Koricheva, M. G. A. van der Heijden, J. Mikola, and T. Kennedy. 2002. Multi-trophic processes and ecosystem func-

- tioning. Pages 147–154 in M. Loreau, S. Naeem, and P. Inchausti, eds. *Biodiversity and ecosystem functioning: syntheses and perspectives*. Oxford University Press, Oxford.
- Sokal, R. R., and F. J. Rohlf. 1962. The comparison of dendrograms by objective methods. *Taxon* 11:33–40.
- Sole, R. V., and J. M. Montoya. 2001. Complexity and fragility in ecological networks. *Proceedings of the Royal Society B: Biological Sciences* 268:2039–2045.
- Springer, A. M., J. A. Estes, G. B. van Vliet, T. M. Williams, D. F. Doak, E. M. Danner, K. A. Forney, and B. Pfister. 2003. Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences of the USA* 100:12223–12228.
- Thebault, E., V. Huber, and M. Loreau. 2007. Cascading extinctions and ecosystem functioning: contrasting effects of diversity depending on food web structure. *Oikos* 116:163–173.
- Walker, B. H. 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6:18–23.
- Williams, R. J., and N. D. Martinez. 2000. Simple rules yield complex food webs. *Nature* 409:180–183.
- Wootton, J. T., and M. Emmerson. 2005. Measurement of interaction strength in nature. *Annual Review of Ecology Evolution and Systematics* 36:419–444.
- Worm, B., and J. E. Duffy. 2003. Biodiversity, productivity and stability in real food webs. *Trends in Ecology & Evolution* 18:628–632.
- Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* 69:508–515.
- . 1998. Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. *Journal of Animal Ecology* 67:635–658.
- Yodzis, P., and K. O. Winemiller. 1999. In search of operational trophospecies in a tropical aquatic food web. *Oikos* 87:327–340.

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