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## Effects of extinction on food web structures on an evolutionary time scale

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## ABSTRACT

Extinction affected food web structure in paleoecosystems. Recent theoretical studies that examined the effects of extinction intensity on food web structure on ecological time scales have considered extinction to involve episodic events, with pre-extinction food webs becoming established without dynamics. However, in terms of the paleontological time scale, food web structures are generated from feedback with repeated extinctions, because extinction frequency is affected by food web structure, and food web structure itself is a product of previous extinctions. We constructed a simulation model of changes in tri-trophic-level food webs to examine how continual extinction events affect food webs on an evolutionary time scale. We showed that under high extinction intensity (1) species diversity, especially that of consumer species, decreased; (2) the total population density at each trophic level decreased, while the densities of individual species increased; and (3) the trophic link density of the food web increased. In contrast to previous models, our results were based on an assumption of long-term food web development and are able to explain overall trends posited by empirical investigations based on fossil records.

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## 1. Introduction

Food webs are networks that describe who eats whom, and their characteristics change on a paleontological time scale (Vermeij, 1977; Bambach, 1993). Variation in extinction intensity (Raup and Sepkoski, 1984; Hallam and Wignall, 1997; Keller, 2005) is probably responsible, in part, for changes in food web properties. Based on the fossil record, Roopnarine et al. (2007) reconstructed food web structures around the Permian–Triassic boundary and found that food webs during the early Triassic had unusually high trophic link density. The end-Permian mass extinction that occurred immediately before this period most likely altered the structures of food webs.

In this study, we simulated the effects of extinctions on food webs on an evolutionary time scale. Food web structure influences ecosystem properties, such as extinction risk (Borrvall et al., 2000; Dunne et al., 2002; Thébault et al., 2007) and resistance to invasive species (Case, 1990; Dzialowski et al., 2007). Thus, it is important to investigate the factors that determine food web structure. Conversely, Ebenman et al. (2004) and Eklöf and Ebenman (2006) demonstrated theoretically how extinction induces changes in species diversity and food web connectance. However, in exposing given food webs to extinction, Ebenman

et al. (2004) and Eklöf and Ebenman (2006) removed only one species and examined the occurrence of secondary cascading extinctions. No study has examined the effects of extinctions on food webs on a paleontological time scale. Extinction has occurred many times over long time scales. When extinctions occur, the number of species decreases and any trophic links connected to the now-extinct species are lost, altering food web structure. In addition, new species can join a food web by speciation or immigration. Altered food webs react in turn to new extinction events (Ives and Cardinale, 2004; Eklöf and Ebenman, 2006; Thébault et al., 2007). Thus, some feedback between extinction and food web development should exist, but no study has examined how this feedback affects food web characteristics. By contrast, our model contains this feedback effect by considering long time scales.

Some simulation studies have used complex procedures to emulate predator–prey interactions (Yoshida, 2006) or optimal foraging (Drossel et al., 2001) to develop realistic food webs. It has also been suggested that body size and allometric relationships govern food web structure and dynamics (Yodzis and Innes, 1992; Woodward et al., 2005), and some algorithms incorporate these relationships (Loeuille and Loreau, 2005). However, we did not assume the action of such mechanisms in our model. As our focus was to examine the reaction of a food web to extinction, we avoided adding excess complexity that could obscure the relationship between extinctions and changes in food web characteristics. Instead, we used a simple tri-trophic-level model

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that could express bottom-up and top-down effects in ecosystems in a simple manner. Tri-trophic models have been utilised to simulate extinctions in food webs on shorter time scales (Borrvall et al., 2000; Solé et al., 2002; Eklöf and Ebenman, 2006; Thébault et al., 2007); therefore, our model can be compared to these results with relative ease.

We considered two types of extinctions. The first arises from ecological interactions (intense competition, predation, or starvation). Extinctions caused by invasive species are also included, as immigrants become new competitors or predators and sometimes cause the extinction of indigenous species (Mack et al., 2000). Likewise, eutrophication can bring about this type of extinction by changing the outcome of interspecific competition (Suding et al., 2005) or increasing productivity, leading to transitions in interaction strength (Clark et al., 2007). The second type of extinctions involves stochastic extinction, which occurs independently of energy input and predator–prey relationships. This second category represents extinctions caused by habitat destruction, environmental changes that remove species with specific traits, or infectious diseases, such as pathogenic fungi specific to amphibians (Lips et al., 2006). Instead of varying ecological parameters through time, as was done by Borrvall and Ebenman (2008), we incorporated stochastic extinctions by removing species randomly; the random selection of a species emulates a catastrophic extinction. During past mass extinctions, both types of extinction have occurred. Extinctions caused by ecological interactions have occurred when primary productivity has dropped (Alvarez et al., 1980; Rhodes and Thayer, 1991), and stochastic extinctions have resulted when habitats have been destroyed or temperature or oxygen levels have shifted drastically (Hallam and Wignall, 1997; Aberhan and Baumiller, 2003). This type of stochastic extinction is often incorporated into mathematical models to examine extinction dynamics (Amaral and Meyer, 1999; Solé et al., 2002), extinction patterns (Quince et al., 2005), or food web resistance against subsequent secondary extinctions (Borrvall et al., 2000; Dunne et al., 2002; Eklöf and Ebenman, 2006; Roopnarine, 2006; Roopnarine et al., 2007; Thébault et al., 2007; Petchey et al., 2008). However, these theoretical studies have not examined the effects on food web structure. In this study, we examined these effects by controlling the intensity of stochastic extinctions.

## 2. Model

We considered tri-trophic food webs composed of primary producers, herbivores, and predators. Here, some predators feed on both primary producers and herbivores, which behave as omnivores. In this model, the number of constituent species increases by immigration or speciation and decreases by extinction, producing changes in food web structure. The initial condition involves a vacant habitat. A primary producer invades and the ecosystem develops by immigration or speciation and degrades by extinction. The structure of the model is described below. Detailed procedures and parameter values are available in the Appendix A.

### 2.1. Dynamics

We adopted Lotka–Volterra equations to represent the population dynamics of each species. The dynamics of all species (primary producers, herbivores, and predators) are described by

$$\frac{dx_i}{dt} = x_i(b_i + \sum_{j=1}^S \alpha_{ij}x_j), \quad (1)$$

which was numerically calculated by the fourth-order Runge–Kutta method. Here,  $S$  is the total number of species in the community, and  $x_i$  is the density of species  $i$ . The term  $b_i$  represents the intrinsic growth rate ( $b_i > 0$ ) if species  $i$  is a primary producer, or the basal mortality rate ( $b_i > 0$ ) if species  $i$  is an herbivore or predator; this recognises that consumers cannot survive without food. The summation in parentheses represents the effects of species interactions. If species  $i$  and species  $j$  are competitors, both species suffer negative effects in the presence of the opponent species ( $\alpha_{ij} < 0$ ,  $\alpha_{ji} < 0$ ). We assumed direct interspecific competition only for primary producers and that competition is asymmetrical ( $\alpha_{ij} \neq \alpha_{ji}$ ). With regard to herbivores and predators, interspecific competition occurs through feeding. If species  $i$  exploits species  $j$ , the presence of species  $i$  reduces the rate of increase of species  $j$  ( $\alpha_{ji} < 0$ ), whereas species  $i$  can increase further ( $\alpha_{ij} = -e \times \alpha_{ji} > 0$ ) by exploitation. The value  $e$  is the efficiency with which resources are converted into consumer growth. Consumer species determine each exploitation rate ( $\alpha_{ij}$ ) by dividing their foraging efforts among resource species so that the total foraging effort will be constant for all species irrespective of the number of their resources. Detailed explanations regarding the determination of interspecific interaction strength are found in the Appendix A.1. Intraspecific competition ( $\alpha_{ii}$ ) is assumed for all species; Thébault et al. (2007) showed that the presence of self-limitation at consumer levels has a major effect on the resistance of food webs to cascading extinction. We included intraspecific competition among consumers, as they are likely to compete directly for sites.

We considered that when the population density of a certain species becomes smaller than a threshold value  $\varepsilon$ , that species goes extinct and the population density  $x$  becomes 0. This assumption corresponds to the Allee effect in natural ecosystems. To avoid excessive complexity, we prevented any evolution in intrinsic growth rate by not differentiating intrinsic growth rates among different plant species; we assumed that  $b_i$  was constant for all primary producers. The parameter values used in the model are available in the Appendix A.3.

### 2.2. Immigration and speciation

We assumed that immigration or speciation occurs much more slowly than population dynamics. We incorporated one new species at every 10,000 time steps in the numerical calculation of Eq. (1). A previous theoretical study by Yoshida (2007) considered two extreme cases where entirely new species emerged through immigration or speciation. Our model assumed the medium condition: a new species is an immigrant with probability  $m$  and a descendant species with probability  $1 - m$ . If the new species is an immigrant, its trophic position is assigned randomly. That is, the probability that the new species is a primary producer, herbivore, or predator is  $1/3$  in all cases. (We tested another case where immigrant species have a similar trophic level ratio to the food webs under consideration, but the fundamental results did not change.) The position and strength of trophic links (or the strength of interspecific competition if the focal species is a primary producer) for the new species are also determined randomly. The population density  $x$  of the immigrant species is set to a small value equal to  $\varepsilon$  (the extinction threshold value). If the new species is the product of speciation (i.e., a descendant of an indigenous species), we considered that it inherits the trophic position and has similar trophic links to those of the ancestor. That is, we create new species by slightly differentiating the position and strength of the trophic links (or the strength of interspecific competition) of the ancestor species. The ancestor species is randomly chosen from the entire food web. We

considered that new species have population densities equal to  $\varepsilon$ . Detailed explanations regarding trophic links and parameter values are found in the Appendices A.2 and A.3, respectively.

### 2.3. Extinction

As stated previously, our model included two types of extinctions. When resources become too limited, competition becomes too severe, or predation becomes too intense, the population growth rate  $dx/dt$  becomes negative, approaching a very small value. As a consequence, if  $x$  falls below  $\varepsilon$ , the species goes extinct, as described under “Dynamics.” Stochastic extinctions occur apart from this process. At every 10,000th time step within the model, species are chosen at random to become extinct. Each species has a fixed probability  $\mu$  of becoming extinct at any stochastic extinction event. We assumed that this probability was equal for all species irrespective of their population densities. Perhaps, some large catastrophic extinctions were not random but depending on feeding type (Rhodes and Thayer, 1991; Aberhan and Baumiller, 2003), or body size (Sahney and Benton, 2008). However, we consider that including such selectivity will not differentiate the results drastically. Actually, the selectivity among trophic levels did not cause qualitative change in our preliminary calculation. Rather, we chose random extinction in all cases to extract the effects of extinction intensities. Although we parameterised  $\mu$  so that stochastic extinctions were not frequent compared with extinctions caused by ecological interactions, stochastic extinctions greatly affected food web structure as secondary extinctions may occur following the random removal of a species. If one resource species is removed from a food web, a consumer species loses this resource and may go extinct. In addition, after the extinction of a resource species, a generalist consumer species allocates more effort to other resources, which may result in secondary extinctions of other resource species. If consumer species are eliminated, competition among resource species intensifies, which can cause an extinction of resource species. We examined the effects of the intensity of stochastic extinction on food web structure by varying the value of  $\mu$ . When constructing the program, we placed the stochastic extinctions routine immediately after the species introduction event, but reversing the order of these events did not change the fundamental outcome; therefore we considered the timing of these events to be inconsequential.

### 2.4. Food web measurement

After a specified number of immigrations and speciations (here, 5000 new species introduction events), we assessed the following food web indices at the final state. To track the diversity of the food web, we recorded the number of species in each category: primary producers, herbivores, and predators. We also recorded total population density at each trophic level and average population density per individual species. The relative number of species at each trophic level describes the shape of the food web. We used connectance as an index for trophic link density. Connectance is usually measured as  $l/S^2$ , indicating the proportion of realised links over the total number of potential trophic links, where  $l$  is the total number of predator–prey links in the food web and  $S$  is the number of species (Gardner and Ashby, 1970). However, this model included neither consumer–resource relationships within a trophic level nor bi-directional energy flows. Consequently, we removed these links from the denominator and defined connectance as  $l/(S_1S_2 + S_2S_3 + S_3S_1)$ , where  $S_1$ ,  $S_2$ , and  $S_3$  are the numbers of primary producers, herbivores, and predator species, respectively. We checked these indices under

various stochastic extinction intensities ( $\mu=0.002, 0.004, 0.006, 0.008, 0.01, 0.012, \text{ or } 0.014$ ). Because food webs were highly variable in time and among trials, we generated 25 food webs for each parameter set to clarify trends. The effects of extinction intensity on food web indices were tested using linear regression analysis. To determine the robustness of the results, the analyses were conducted using several environmental parameter sets ( $b_i$  and  $m$ ). Indices involving fractional expressions sometimes yield invalid data when the denominator becomes 0; therefore we excluded such data from our analysis.

## 3. Results

Fig. 1 shows an example of species number dynamics. Initially, primary producers invade a vacant habitat and increase in diversity, followed by the establishment of and increase in the diversity of herbivores and then predators. Species numbers fluctuate over time, sometimes increasing and sometimes declining. Drastic extinctions that remove almost all species simultaneously have often been reported in food web models (Amaral and Meyer, 1999; Solé et al., 2002), but we did not observe such events in our model. Throughout the simulations, direct stochastic extinctions were rare compared to ecological extinctions (at most, the proportion of stochastic extinction was approximately 0.35), indicating the importance of secondary extinctions in this system.

Figs. 2–6 show the indices of food web structure under different extinction intensities after the occurrence of 5000 species introduction events. The intrinsic growth rate of primary producers,  $b_i$ , was set at 1.0, and the immigration frequency,  $m$ , was set at 0.5. As Fig. 2 shows, when extinction intensities were high, the species diversities of primary producers, herbivores, and predators became low. Regression analyses (Table 1) indicated that increased extinction rates significantly decreased species diversities. Multiple effects from direct and secondary extinctions worked there. In terms of the ratio of the number of species among trophic levels (Fig. 3, Table 1), primary producers increased in proportion to  $\mu$ , whereas herbivores decreased slightly and predators declined markedly, indicating that the shape of the food web changed from trapezoidal to triangular as the probability of secondary extinctions following direct eliminations was greater for higher trophic-level species. The relatively weak tendency in herbivore species (Fig. 3, Table 1) was likely to be produced by the conflicting effects; they benefit from increased resources and decreased predators on one hand, they

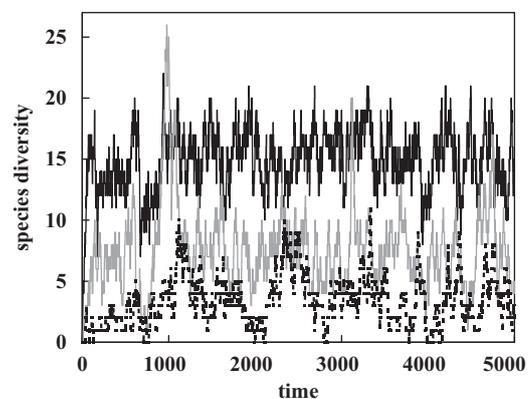
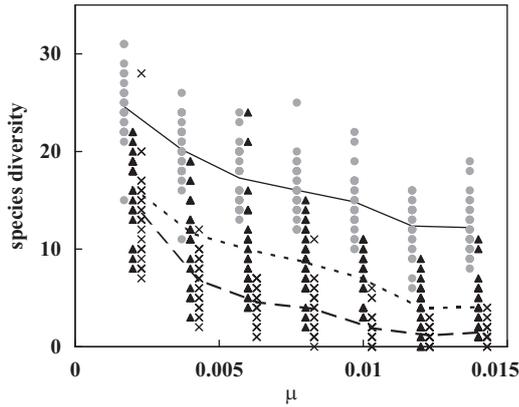
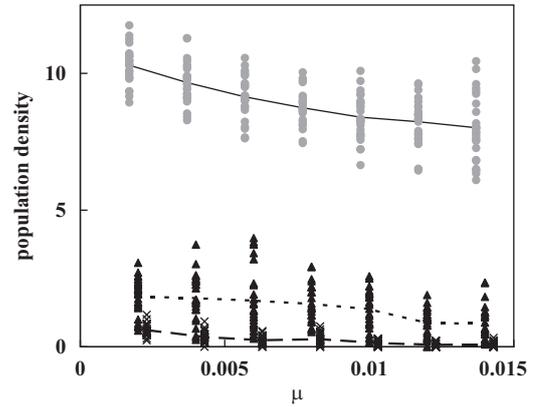


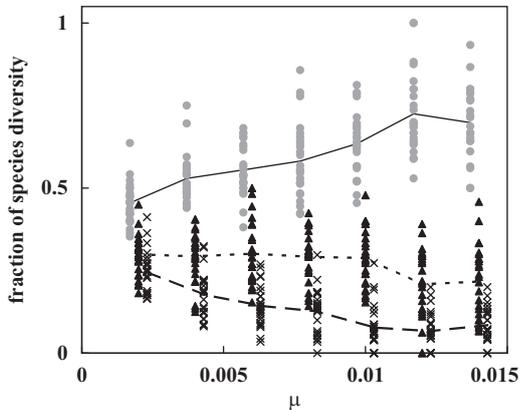
Fig. 1. An example of species diversity dynamics for primary producers (black line), herbivores (grey line), and predators (dotted line). Time ( $x$ -axis) is scaled by the number of species introduction events. In this calculation,  $\mu=0.008$ . Other parameter values are described in the Appendix A.



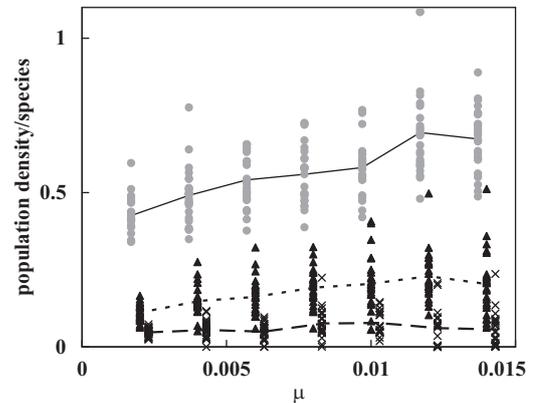
**Fig. 2.** Effects of extinction intensity on species diversity for primary producers (grey circles and solid line), herbivores (black triangles and dotted line), and predators (crosses and dashed line). The lines connect the mean values of 25 sample points. Symbols are slightly displaced along the  $x$ -axis to increase clarity. Note that each point represents the species diversity of a single food web; the number of symbols appears to be lower than the reported sample size because symbols overlap. The parameter values are described in the Appendix A.



**Fig. 4.** Effects of extinction intensity on the total population density of each trophic level: primary producers (grey circles and solid line), herbivores (black triangles and dotted line), and predators (crosses and dashed line). The lines connect the average values of 25 sample points. Symbols are slightly displaced along the  $x$ -axis to increase clarity. Note that each point represents the population density of a single food web; the number of symbols appears to be lower than the reported sample size because symbols overlap. The parameter values are described in the Appendix A.



**Fig. 3.** Effects of extinction intensity on the species number fraction for each trophic level: primary producers (grey circles and solid line), herbivores (black triangles and dotted line), and predators (crosses and dashed line). The lines connect the average values of 25 sample points. Symbols are slightly displaced along the  $x$ -axis to increase clarity. Note that each point represents the species number fraction of a single food web; the number of symbols appears to be lower than the reported sample size because symbols overlap. The parameter values are described in the Appendix A.



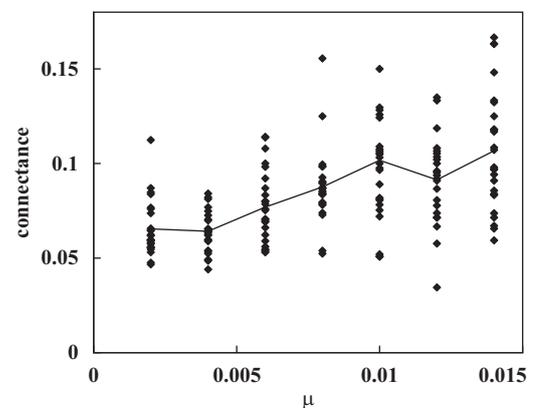
**Fig. 5.** Effects of extinction intensity on the population density of individual species: primary producers (grey circles and solid line), herbivores (black triangles and dotted line), and predators (crosses and dashed line). The lines connect the average values of 25 sample points. Symbols are slightly displaced along the  $x$ -axis to increase clarity. Note that each point represents the population density of a single food web; the number of symbols appears to be lower than the reported sample size because symbols overlap. The parameter values are described in the Appendix A.

suffered increased risk of direct and secondary extinction risks on the other hand.

The total population density at each trophic level was negatively correlated with extinction intensity (Fig. 4, Table 1). This was caused solely by the reduction of species diversity at high  $\mu$  values. The population densities of individual primary producer and herbivore species actually increased (Fig. 5, Table 1) because competing species were reduced, whereas predators showed no significant change (Table 1). When the stochastic extinction rate was intense, food webs were composed of a smaller number of abundant species.

Connectance increased with the intensity of stochastic extinction (Fig. 6, Table 1). Generalist consumers can consume alternate species when a resource is removed, whereas specialists face an extinction crisis. Therefore, generalists have a higher tolerance in the face of extinction pressure, and frequent stochastic extinctions impart high connectance values on the food webs.

Figs. 3, 5, and 6 show that the variances of some indices (the fraction of species belonging to each trophic level, population density per species, and connectance) became high at large  $\mu$



**Fig. 6.** Effects of extinction intensity on the connectance of the food web. The lines connect the average values of 25 sample points. Note that each point represents the connectance of a single food web; the number of symbols appears to be lower than the reported sample size because symbols overlap. Connectance and the parameter values are described in the Appendix A.

**Table 1**

The results of regression analyses which test the influences of extinction intensities ( $\mu$ ) on food web indices.

	Regression line	$r^2$	$F$	$p$
Species diversity (primary producers)	$-988\mu + 24.7$	0.607	267	$6.31 \times 10^{-37}$
Species diversity (herbivores)	$-989\mu + 16.7$	0.531	196	$3.17 \times 10^{-30}$
Species diversity (predators)	$-897\mu + 12.0$	0.570	230	$1.49 \times 10^{-33}$
Fraction of primary producer species	$21.4\mu + 0.426$	0.444	138	$7.91 \times 10^{-24}$
Fraction of herbivore species	$-7.67\mu + 0.333$	0.105	20.3	$1.24 \times 10^{-5}$
Fraction of predator species	$-13.8\mu + 0.242$	0.410	120	$1.49 \times 10^{-21}$
Total population density (primary producers)	$-187\mu + 10.4$	0.440	136	$1.62 \times 10^{-23}$
Total population density (herbivores)	$-91.1\mu + 2.15$	0.185	39.3	$2.81 \times 10^{-9}$
Total population density (predators)	$-40.5\mu + 0.579$	0.465	150	$2.82 \times 10^{-25}$
Density/species (primary producers)	$21.3\mu + 0.396$	0.428	129	$9.59 \times 10^{-23}$
Density/species (herbivores)	$8.59\mu + 0.110$	0.187	39.3	$2.85 \times 10^{-9}$
Density/species (predators)	$1.31\mu + 0.0496$	0.016	2.54	$1.13 \times 10^{-1}$
connectance	$3.65\mu + 0.0558$	0.264	61.2	$5.14 \times 10^{-13}$

The column 'Regression line', ' $r^2$ ', ' $F$ ', and ' $p$ ' indicate the estimated regression lines,  $r^2$ ,  $F$  and  $p$  values, respectively. Parameter values are described in the text and the Appendix A.

**Table 2**

Correlation coefficients and significance ( $p$  values) of correlation between extinction intensity and food web indices when the intrinsic growth rate,  $b_i$ , is varied.

Intrinsic growth rate of primary producers	$b_i = 0.5$		$b_i = 1.0$		$b_i = 1.5$	
	$r$	$p$	$r$	$p$	$r$	$p$
Species diversity (primary producers)	-0.815	$8.29 \times 10^{-43}$	-0.779	$6.31 \times 10^{-37}$	-0.797	$1.08 \times 10^{-39}$
Species diversity (herbivores)	-0.770	$1.57 \times 10^{-35}$	-0.728	$3.17 \times 10^{-30}$	-0.631	$8.02 \times 10^{-21}$
Species diversity (predators)	-0.773	$5.08 \times 10^{-36}$	-0.755	$1.49 \times 10^{-33}$	-0.765	$7.89 \times 10^{-35}$
Fraction of primary producer species	0.680	$4.07 \times 10^{-25}$	0.666	$7.91 \times 10^{-24}$	0.583	$2.70 \times 10^{-17}$
Fraction of herbivore species	-0.443	$8.62 \times 10^{-10}$	-0.324	$1.24 \times 10^{-5}$	-0.145	$5.58 \times 10^{-2}$
Fraction of predator species	-0.600	$3.58 \times 10^{-33}$	-0.640	$1.49 \times 10^{-21}$	-0.635	$3.58 \times 10^{-21}$
Total population density (primary producers)	-0.635	$4.15 \times 10^{-21}$	-0.663	$1.62 \times 10^{-23}$	-0.641	$1.19 \times 10^{-21}$
Total population density (herbivores)	-0.574	$1.05 \times 10^{-16}$	-0.430	$2.81 \times 10^{-9}$	-0.257	$5.98 \times 10^{-4}$
Total population density (predators)	-0.683	$2.16 \times 10^{-25}$	-0.682	$2.82 \times 10^{-25}$	-0.724	$9.57 \times 10^{-30}$
Density/species (primary producers)	0.752	$3.58 \times 10^{-33}$	0.654	$9.59 \times 10^{-23}$	0.664	$1.29 \times 10^{-23}$
Density/species (herbivores)	0.451	$4.40 \times 10^{-10}$	0.432	$2.85 \times 10^{-9}$	0.422	$6.87 \times 10^{-9}$
Density/species (predators)	0.084	$2.91 \times 10^{-1}$	0.126	$1.13 \times 10^{-1}$	0.077	$3.39 \times 10^{-1}$
Connectance	0.387	$1.18 \times 10^{-7}$	0.513	$5.14 \times 10^{-13}$	0.442	$8.73 \times 10^{-10}$

Other parameter values are described in the Appendix A.

values. When  $\mu$  was high, the number of species decreased, lowering the denominator values of the indices ( $S$ ,  $S_1$ ,  $S_2$ ,  $S_3$ , or  $S_1S_2 + S_2S_3 + S_3S_1$ ), thereby amplifying any differences in the numerators. This high variance probably contributes to the relatively low  $r^2$  value of connectance in part (Table 1). The  $r^2$  values of "population densities per trophic levels" also became lower for higher trophic levels (Table 1), which can again be attributed to the higher variances owing to the lower denominator values ( $S_1$ ,  $S_2$ ,  $S_3$ , Fig. 2).

Other environmental factors (e.g., productivity or immigration frequency) also affected food web structure, and some theoretical studies have focused on these factors (Caldarelli et al., 1998; Drossel et al., 2001; Yoshida, 2007). We examined whether the intrinsic growth rate of primary producers,  $b_i$ , or the immigration frequency,  $m$ , affected the relationship between extinction intensity and food web structure. Tables 2 and 3 show the changes in correlation coefficients and  $p$  values of food web indices when the values of those environmental parameters are varied, indicating that the values of  $b_i$  and  $m$  had little effect on overall trends. That is, the indices that showed significance in Table 1 remained significant when the values of  $b_i$  or  $m$  were varied. The exceptions were the fraction of herbivore species index and the

population density per predator species. The fraction of herbivore species reduced the correlation coefficients when  $b_i = 1.5$  or  $m = 0.75$ , thereby weakened significance. On the other hand, the population density per predator species strengthened significance when  $m = 0.75$ , although its correlation coefficient still remain to low value, 0.237. Table 3 indicates that small  $m$  values tended to yield weak correlations, because species diversity dynamics showed huge fluctuations when immigration was rare, yielding variable calculation results. In contrast, increments (or decrements) of  $b_i$  values did not consistently change correlation strength.

#### 4. Discussion

We used a simulation model to examine the effects of continual extinction events on the generation of food web structure. We found that intense stochastic extinctions tend to produce (1) a decrease in the number of species at all trophic levels (Fig. 2), (2) a change to a more triangular food web shape (Fig. 3), (3) a decrease in total population densities at all trophic levels (Fig. 4), (4) an increase in the population densities of

**Table 3**  
Correlation coefficients and significance ( $p$  values) of correlation between extinction intensity and food web indices when the immigration fraction,  $m$ , is varied.

Relative immigration frequency	$m = 0.25$		$m = 0.5$		$m = 0.75$	
	$r$	$p$	$r$	$p$	$r$	$p$
Species diversity (primary producers)	-0.723	$1.31 \times 10^{-29}$	-0.779	$6.31 \times 10^{-37}$	-0.815	$8.93 \times 10^{-43}$
Species diversity (herbivores)	-0.560	$8.16 \times 10^{-16}$	-0.728	$3.17 \times 10^{-30}$	-0.766	$4.63 \times 10^{-35}$
Species diversity (predators)	-0.699	$5.39 \times 10^{-27}$	-0.755	$1.49 \times 10^{-33}$	-0.819	$1.32 \times 10^{-43}$
Fraction of primary producer species	0.530	$4.57 \times 10^{-14}$	0.666	$7.91 \times 10^{-24}$	0.670	$3.66 \times 10^{-24}$
Fraction of herbivore species	-0.263	$4.42 \times 10^{-4}$	-0.324	$1.24 \times 10^{-5}$	-0.178	$1.85 \times 10^{-2}$
Fraction of predator species	-0.678	$6.95 \times 10^{-25}$	-0.640	$1.49 \times 10^{-21}$	-0.720	$3.03 \times 10^{-29}$
Total population density (primary producers)	-0.441	$9.80 \times 10^{-10}$	-0.663	$1.62 \times 10^{-23}$	-0.763	$1.33 \times 10^{-34}$
Total population density (herbivores)	-0.403	$3.23 \times 10^{-8}$	-0.430	$2.81 \times 10^{-9}$	-0.339	$4.40 \times 10^{-6}$
Total population density (predators)	-0.634	$4.33 \times 10^{-21}$	-0.682	$2.82 \times 10^{-25}$	-0.769	$1.98 \times 10^{-35}$
Density/species (primary producers)	0.526	$8.13 \times 10^{-14}$	0.654	$9.59 \times 10^{-23}$	0.736	$4.57 \times 10^{-31}$
Density/species (herbivores)	0.255	$1.04 \times 10^{-3}$	0.432	$2.85 \times 10^{-9}$	0.557	$1.14 \times 10^{-15}$
Density/species (predators)	-0.034	$7.17 \times 10^{-1}$	0.126	$1.13 \times 10^{-1}$	0.237	$2.00 \times 10^{-3}$
Connectance	0.346	$6.35 \times 10^{-6}$	0.513	$5.14 \times 10^{-13}$	0.560	$7.81 \times 10^{-16}$

Other parameter values are described in the Appendix A.

individual primary producer and herbivore species (Fig. 5), and (5) an increase in trophic link densities within food webs (Fig. 6). These trends were maintained when the intrinsic growth rates of primary producers or the immigration frequency were varied (Tables 2 and 3).

Previous theoretical studies that explored the effects of secondary extinctions on food web structure (Ebenman et al., 2004; Petchey et al., 2004, 2008; Eklöf and Ebenman, 2006) established fixed food webs before perturbations, whereas we generated variable food webs that included immigration, speciation, and extinction. A theoretical study conducted by Lewis and Law (2007) showed that such processes alter the properties and structures of food webs. Therefore, our study examined the effects of long time-scale phenomena on food webs that are more realistic than those used in other studies.

As our model generated various food webs for different environments, our results are not restricted to specific food webs, unlike those of previous studies. Our results confirm some previous findings (e.g., the appearance of triangular webs under high extinction pressure), but some of the implications of our model differ from those of previous models. Eklöf and Ebenman (2006) found that in short-term events, secondary extinctions increase connectance when the initial web has low connectance, whereas connectance decreases if the initial food web includes many predator–prey linkages. In contrast, we found that in evolutionary food webs in which extinction is an environmental factor, extinction consistently produces high connectance (Fig. 6). When considering evolutionary time scales, food web structures fluctuate, and conflicting and contradicting effects will occur. There is a possibility that the food webs in our model tend to have low connectance where extinction increase connectance. Petchey et al. (2004) showed that the effect of a species deletion on increases or decreases in total biomass depends on the shape of the food web and the trophic level of the deleted species. In contrast, we found that on an evolutionary time scale, a general trend of extinction causes population density to decrease at each trophic level. According to Petchey et al. (2004), the case where extinction increase total biomass is few and its increment is relatively little, so this effect is probably masked by the opposing effect in our model where food web shape and which species are deleted are not fixed.

In this work, we used a simple model which does not incorporate body sizes and obtained the basic results of food

web structures change against extinctions. However, body size is known to be an important factor which affects food web structures and dynamics (Yodzis and Innes, 1992; Woodward et al., 2005). The comparison between our study and future studies which consider body size will reveal the role of body size in food web development. Incorporating body sizes will also enable us to examine the extinction selectivity relating to body size.

Our results agree with trends found in empirical work based on fossil records. Roopnarine et al. (2007) estimated food web structures from fossil data both immediately before and after the end-Permian mass extinction. They showed that direct extinction sequences reduced the number of guilds and increased the density of trophic links connecting guilds. Our findings that low species diversity and high connectance (Figs. 2 and 4) were generated under high extinction pressure are in agreement with the fossil results. Duffy (2003) showed that consumers are more prone than plants to going extinct in natural ecosystems. This trend was reproduced in the model of ecological time scale (Eklöf and Ebenman, 2006), and our results (Fig. 3) validate their findings also on an evolutionary time scale.

Food web structure has a large impact on ecosystem resistance against cascading extinctions. Eklöf and Ebenman (2006) noted that food webs containing few consumers are more extinction resistant than rectangular food webs. Highly connected food webs are also resistant to further extinctions (Dunne et al., 2002; Eklöf and Ebenman, 2006; Thébault et al., 2007; but see Roopnarine et al., 2007). We demonstrated that under intense extinction rates, highly connected triangular food webs evolved. These results suggest that food webs evolve resistance against further extinctions when the extinction rate is high. However, our results also suggest an opposing possibility. We found that intense extinctions decreased species diversity, and previous theoretical studies have shown a positive relationship between resistance and diversity (Borrvall et al., 2000; Thébault et al., 2007). Further studies are necessary to understand the exact effects of extinctions on the evolution of food web resistance against extinction.

Other ecosystem properties, such as resistance to invasive species (Case, 1990; Dzialowski et al., 2007) and the diversity–biomass relationship (Thébault and Loreau, 2003), also depend on food web structure. Although we did not examine the concrete changes in functioning of food webs, our model provides a basis for future studies.

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## Appendix A. Model details

### A.1. Foraging coefficient

We assumed that each consumer had a potential foraging efficiency on each resource, with  $\gamma_{ij}$  denoting the efficiency of species  $i$  on species  $j$ . The realised foraging coefficient is then determined by

$$\alpha_{ij} = \frac{\gamma_{ji}}{\sum_{k \in \text{resource}} \gamma_{jk}}, \quad (\text{A.1})$$

which ensures a constant foraging effort by all consumer species,

$$\sum_{j \in \text{resources}} \alpha_{ji} = \text{const.} = 1. \quad (\text{A.2})$$

The Eqs. (A.1) and (A.2) represent a trade-off where specialist species can spend greater effort on a specific prey species compared to generalist consumers. This calculation can prevent consumer species from evolving foraging abilities infinitely. The foraging effort of a species is calculated when the species appears in the ecosystem. In addition, the value of  $\alpha_{ij}$  is recalculated by Eq. (A.2) when the number of resource species increases or decreases. If a new species is added to the menu, the foraging effort on other resources is reduced, whereas when a species goes extinct, consumer species utilise surviving resources more strongly than previously.

### A.2. Interspecific interactions of new species

If a new species is an immigrant, trophic links between it and other species are determined randomly. Each link that joins the new species to an existing species in the next higher (or lower) trophic level is realised randomly with a probability  $p_1$ , and omnivorous links (predator–primary producer relationships) connect to the new species with a probability  $p_2$ . That is, a new species has an equal chance of feeding on (or being fed on by) any species in the trophic level below (above). After establishing the new trophic links, we determined the foraging efficiency for each new predator–prey relationship. Immigrants find new resources (or consumers) and then develop a potential foraging efficiency, starting at 0 and increasing. We assigned the efficiency of new immigrant consumer species  $k$  for indigenous resource species  $j$ ,  $\gamma_{kj}$  (or efficiency of indigenous consumer species  $i$  on new immigrant resource species  $k$ ,  $\gamma_{ik}$ ) by  $|E|$ , where  $E$  is defined as a random value drawn from the standard normal distribution. When the immigrant is a primary producer, the competition coefficient between immigrant species  $k$  and indigenous species  $i$ ,  $\alpha_{ik}$ , and  $\alpha_{ki}$  is given separately by  $-0.1 \times |E|$ .

When a new species emerges through speciation, the foraging efficiency of a new consumer species  $k$  on resource species  $j$ ,  $\gamma_{kj}$  (or the efficiency of consumer species  $i$  on the new resource

species  $k$ ,  $\gamma_{ik}$ ) is given by adding mutations,  $\gamma_{ki} = \gamma_{k'i} + 0.5 \times E$  and  $\gamma_{ik} = \gamma_{i'k} + 0.5 \times E$ , where  $k'$  represents the ancestor species, with the restriction that the  $\gamma$  value is reset to 0 if  $\gamma$  falls below 0 after the mutation, which means the link in question disappears. If the new species  $k$  is a primary producer, interspecific competition is given by  $\alpha_{ki} = \alpha_{k'i} + 0.05 \times E$  and  $\alpha_{ik} = \alpha_{i'k} + 0.05 \times E$ . The value of  $\alpha$  is reset to 0 if it has a positive value, as we assumed no mutualism among primary producers. The population density of the new species  $x_k$  is set to  $\varepsilon$ .

### A.3. Parameter values

As standard values, we assigned  $b_i = 1.0$  for primary producers,  $b_i = -0.01$  for herbivores, and  $b_i = -0.005$  for predators. We made a simple assumption of equal intrinsic growth rates for all primary producers. To reflect empirical reality, we followed Eklöf and Ebenman (2006) in adopting a higher mortality rate for herbivores than for predators. For intraspecific competition, we set  $\alpha_{ii} = -0.5$  for primary producers and  $\alpha_{ii} = -0.1$  for herbivores and predators. We used the value  $e = 0.2$ , except for omnivorous links between primary producers and predators, where  $e = 0.02$ . These are the same values used by Eklöf and Ebenman (2006). The extinction threshold  $\varepsilon$  was set to 0.0001. We assumed the immigration–speciation ratio to be 1 to 1, i.e.,  $m = 0.5$ . The values of  $p_1$  and  $p_2$  were 0.05 and 0.0025, respectively.

These values, which influence species diversity, population density, and connectance, were chosen to establish food webs of a tractable size (not too large to compute, not too small to maintain food webs). To fine-tune the parameters, we tested various combinations of values; however, the fundamental results presented here were consistent. We assumed a constant extinction threshold ( $\varepsilon$ ) for all trophic levels, but varying this assumption did not alter the model results. In Tables 1 and 2, we present the results when  $b_i$  for primary producers and  $m$  are changed.

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