The form of direct interspecific competition modifies secondary extinction patterns in multi-trophic food webs

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Forcibly removing species from ecosystems has important consequences for the remaining assemblage, leading to changes in community structure, ecosystem functioning and secondary (cascading) extinctions. One key question that has arisen from single- and multi-trophic ecosystem models is whether the secondary extinctions that occur within competitive communities (guilds) are also important in multi-trophic ecosystems? The loss of consumer–resource links obviously causes secondary extinction of specialist consumers (topological extinctions), but the importance of secondary extinctions in multi-trophic food webs driven by direct competitive exclusion remains unknown. Here I disentangle the effects of extinctions driven by basal competitive exclusion from those caused by trophic interactions in a multi-trophic ecosystem (basal producers, intermediate and top consumers). I compared food webs where basal species either show diffuse (all species compete with each other identically: no within guild extinctions following primary extinction) or asymmetric competition (unequal interspecific competition: within guild extinctions are possible). Basal competitive exclusion drives extra extinctions across all trophic levels, with the effect amplified in larger ecosystems, though varying connectance has little impact on results. Secondary extinction patterns based on the relative abundance of the species lost in the primary extinction differ qualitatively between diffuse and asymmetric competition. Removing asymmetric basal species with low (high) abundance triggers fewer (more) secondary extinctions throughout the whole food web than removing diffuse basal species. Rare asymmetric competitors experience less pressure from consumers compared to rare diffuse competitors. Simulations revealed that diffuse basal species are never involved in extinction cascades, regardless of the trophic level of a primary extinction, while asymmetric competitors were. This work highlights important qualitative differences in extinction patterns that arise when different assumptions are made about the form of direct competition in multi-trophic food webs.

Extinction cascades have become a classical theme in ecosystems ecology following almost half a century of research. Secondary (cascading) extinctions have been observed in both empirical and theoretical studies after the primary removal of a species from the ecosystem (Paine 1966,Estes and Palmisano 1974, Pimm 1979, 1980, Fox and McGrady-Steed 2002, Kondoh 2003,Petchey et al. 2004,Ebenman and Jonsson 2005,Montoya et al. 2006) and affect both species diversity and ecosystem functioning (Thébault et al. 2007, Zavaleta et al. 2009). If the remaining members of an ecosystem persist following primary deletion, it can be termed ‘species deletion stable’ (Pimm 1979) or ‘permanent’ (Law and Morton 1993, 1996); otherwise, secondary extinctions will occur as the ecosystem fragments to a state with fewer species.


An important issue arising from these approaches concerns the alternative possible routes to secondary extinctions (Christianou and Ebenman 2005, Ebenman and Jonsson 2005, Thébault et al. 2007, Fowler et al. 2010). If a specialist consumer loses its only resource in a primary extinction event, this topological breakdown will lead directly to secondary extinction of the specialist consumer. Resource (basal or intermediate) species may also be lost through indirect exclusion via apparent or exploitative competition (consumer or resource mediated coexistence). Here I aim to investigate the
importance of one extinction route that is apparent in single trophic-level systems, but has not yet been explicitly studied in multi-trophic food webs: secondary extinctions via direct competitive exclusion (Fowler 2010). Thébault et al. (2007) recently studied direct within guild competition across all trophic levels, showing quantitative effects of direct, asymmetric competition among consumers, but did not compare different forms of competition, considering only the presence/absence of within guild competition. Here, I consider the impact of (a)symmetric competition among producer/basal species on secondary food web extinction cascades.

I study this issue using two otherwise identical food web models, with either asymmetric or symmetric (diffuse) basal competition, where only asymmetric competition leads to direct competitive exclusion among basal species. In food web models of different size or connectivity, basal competitive exclusion via asymmetric competition is shown to alter extinction cascade patterns across the whole food web, following primary deletion of species from any trophic level. Different forms of basal competition are associated with qualitatively different secondary extinction patterns when primary extinctions are based on species’ relative abundances. This work illustrates that important differences arise in secondary extinction patterns in food web models, depending on species traits and the particular assumptions made about direct interspecific competition.

Methods

Food web assembly

Multi-trophic consumer–resource dynamics were modelled using a multi-species logistic growth model with linear (Lotka–Volterra) type interactions between species, as

$$\frac{dx_i}{dt} = x_i \left( b_i + \sum_{j=1}^{m_T} \alpha_{ij} x_j \right)$$

(1)

where $x_i$ is the density of species $i$ in an $m_T$ species ecosystem, $b_i$ gives the intrinsic rate of increase (or mortality) and $\alpha_{ij}$ gives the per capita effect of species $j$ on the per capita growth rate of species $i$. The food webs were assumed to be triangular, with $m_p$ top consumers (carnivores), $m_{ij}$ intermediate consumers (herbivores, $m_{ij} = m_p + 1$) and $m_N$ basal (producer, $m_N = m_{ij} + 1$) species.

Basal species had positive intrinsic growth rates ($b_i > 0$), set here as $b_i = 1 (i = [m_p + m_{ij} + 1]...m_T)$, while consumer species were assumed to have negative intrinsic growth rates ($b_i < 0, i = 1...[m_p + m_{ij}]$). Consumer species’ mortality rates ($b_i$) were drawn randomly from a continuous uniform distribution with limits $b_i - U[-0.01, 0]$. These values were then sorted such that top consumers had the lowest intrinsic rates of decline ($b_i$ values closest to zero), while intermediate consumers had relatively faster rates of decline (more negative $b_i$ values). This approach has previously been used (Borrvall and Ebenman 2006, Thébault et al. 2007, Petchey et al. 2008, Kanerdy et al. 2012) to model food webs where species at higher trophic levels are larger (Cohen et al. 2003), while assuming larger species have lower mortality rates (Brown et al. 2004).

Food webs were composed of $m_T = 6, 9, 12, ...24$ species. Connectance among consumer species and their resources was $C = L / m_T^2$ where $L$ is the realised number of consumer-resource links. When the number of species in the food web was varied, connectance was set as $C = 0.2$. Connectance was varied between 0.1 and 0.3 (the range reported for natural food webs; Dunne et al. 2002), illustrated here with an 18 species food web. Consumer species experienced relatively weak intraspecific feedback ($\alpha_{ij} = -0.1$), basal species had stronger intraspecific feedback ($\alpha_{ij} = -1$).

Links were assigned randomly between consumer-resource pairs, based on $C$, with certain constraints, i.e. all consumers required a link to at least one resource species in the adjacent (lower) trophic level. Top predators could behave as omnivores, feeding strongly on at least one intermediate consumer species and weakly on at least one basal resource, with the effect of consumer species $i$ on resource species $j$ given as $\alpha_{ij} = -0.4$. Generalist consumers had weak links to one or more intermediate or basal species ($\alpha_{ij} = -0.1 / [n - 1]$, where $n$ is the total number of resource species for generalist predator $i$). Alternatively, specialist predators fed only on a single resource species in the intermediate trophic level ($\alpha_{ij} = -0.5$). The effect of the resource species ($j$) on a consumer ($i$) includes a conversion efficiency, $e$, given as $\alpha_{ij} = -e \alpha_{ij}$. Here, $e = 0.2$ for resources on the adjacent trophic level and $e = 0.02$ for omnivorous links.

Interspecific competition between basal species was either assumed to be equal across all species pairs ($\alpha_{ij} = \alpha_k = \alpha$, $i \neq j$), which has been referred to as ‘diffuse’ competition (Hughes and Roughgarden 2000), or asymmetric ($\alpha_{ij} \neq \alpha_k$, $i \neq j$). These two scenarios allow exploration of the effects of secondary extinctions driven by competitive exclusion in the basal trophic level, in the context of a trophic food web. Primary deletion of species in a diffuse competitive community (here $\alpha = 0.5$ between basal species) does not directly lead to secondary extinction cascades via direct basal competitive exclusion, while primary deletion of species in an asymmetric competitive community ($\alpha_{ij} \sim U[-1, 0], i \neq j$) can directly induce secondary extinction cascades via basal competitive exclusion.

Food webs were initially selected for further analysis by ensuring that they were feasible (all $x_i^* > 0$) and locally (asymptotically) stable. The $m_T$ by 1 column vector of species’ equilibrium densities is found as $x^* = A^{-1} \cdot b$, where $A$ is the $m_T$ by $m_T$ matrix of $\alpha_{ij}$ values, and $b$ is the $m_T$ by 1 column vector of intrinsic growth (mortality) rates, $b_i$. Local stability occurs when all real parts of the eigenvalues from the Jacobian matrix ($J$) evaluated around the equilibrium are less than zero ($\text{Re}[\lambda_j] < 0$), where the elements of the Jacobian are $J_{ij} = x_i^* \alpha_{ij}$.

Food web topology for both diffuse and asymmetric competition was based on diffuse web architecture. For each persistent diffuse web that was assembled, the same topological consumer–resource structure was then used to assemble an asymmetric web. Here, all $\alpha_{ij}$ values corresponding to basal species were sampled simultaneously and repeatedly from the corresponding random distribution until a feasible, locally stable food web was found. This approach ensured results were not driven by differences in the underlying topology of diffuse and asymmetric food webs. Persistent food webs were replicated 10 000 times.
for each level of species richness ($m_f$), connectance ($C$) and form of competition.

**Secondary extinctions**

For each persistent food web that was assembled, equilibrium densities were used to rank each species according to relative abundance, within a trophic level. Each species was removed independently (primary deletion) and the feasibility and local stability of the remaining ($m_f - 1$) species food web was assessed. If the remaining food web was feasible and locally stable, it was assumed to be ‘species deletion stable’ (Pimm 1979), i.e. persistent with no further species loss. If not, secondary extinctions were assumed to occur. The probability of secondary extinctions in these models was therefore determined initially by post-primary extinction food webs being classified as either unfeasible, or locally unstable if feasible. These numerically based results were tested and corresponded to simulated food webs, with at least one species showing exponential decline in density in unfeasible or locally unstable communities. Therefore ‘species deletion stable’ food webs here were also the only permanent assemblages (Law and Morton 1993, 1996). Consumer–resource interactions with type II functional responses were tested using simulations, following the assembly approach outlined in Borrvall and Ebenman (2006), but did not generate qualitatively different results (results not shown).

The probability of secondary extinction cascades following a primary extinction in food webs with asymmetric [P(Ext$_{A,D}$)] or diffuse basal competition [P(Ext$_{D}$)] was calculated from numerically derived results based on (Eq. 1). Each replicate food web that was species deletion stable following the primary extinction was scored 0 (no secondary extinctions occurred), while each food web that was not species deletion stable was scored 1 (at least one secondary extinction occurred). $P$(Ext$_{A,D}$) was calculated as the mean of this score across all replicate food webs for a given parameter set and form of competition. The impact of basal competitive exclusion on secondary extinction cascades is simply defined as $P$(Ext$_A$) – $P$(Ext$_D$). In other words, the difference in the probability of extinction cascades that occurs as a result of the presence of competitive asymmetries amongst basal species is assumed to be driven, directly or indirectly, by competitive exclusion within that guild, compared to the baseline of secondary extinctions in food webs with diffuse basal competition, where direct basal competitive exclusion does not occur.

The trophic level of species that were lost in extinction cascades was determined by simulating food web dynamics. Post-primary extinction food webs that were unfeasible or locally unstable were simulated over 5000 time units with a 2nd and 3rd order Runge–Kutta solver using MatLab R2008b. Any species in a simulated food web that declined in density over all of the final 50 integrated time-steps (corresponding to at least 100 time-units) was considered to be on an unavoidable extinction trajectory, therefore scored as being extinct. These declining species were removed from the food web and feasibility and local stability were reassessed. If reduced food webs were unfeasible or locally unstable, simulations were repeated. Further simulation was never required in practice: i.e. all food webs were persistent following the removal of species on unavoidable extinction trajectories. The frequency of extinction for species in each trophic level (predators, herbivores and basal/producer) was recorded, and is presented as the mean frequency of extinction within each trophic level following a primary extinction, when secondary cascades occurred.

The number of consumer links to each basal resource species was also recorded, and used to calculate the ratio of: the number of consumer links to 1) the least abundant, or 2) most highly connected basal species: to the average number of consumer links across the basal trophic level. This assessed how important trophic and within guild interactions were for determining basal species’ relative abundances.

**Results**

**Probability of secondary extinctions across the food web**

Asymmetric competition among basal (producer) species following a primary deletion increased secondary extinction risk across the whole food web (Fig. 1). Increasing food web size ($m_f$) increased the probability of secondary extinctions across the food web under both diffuse and asymmetric competition, with the difference between them (reflecting the impact of basal competitive exclusion) increasing with the number of species in the food web (Fig. 1A).

Increasing connectance stabilised food webs slightly following primary species loss, with a decreasing probability of secondary extinctions under both diffuse and asymmetric competition (Fig. 1B, inset). Again, there was always a higher probability of extinction cascades under asymmetric competition, but this changed very little with connectance (Fig. 1B).

These general patterns hold when considering the trophic level of the species involved in the primary deletion (Fig. 2). The probability of secondary extinctions increased with increasing food web size, following removal of species from any trophic levels (Fig. 2A). The effects of basal competitive exclusion also increased with food web size, following deletion from any trophic level; the largest increases followed primary removal of basal species (Fig. 2C).

Secondary extinctions across the food web declined with increasing connectivity following primary deletion of intermediate consumers, but varying connectivity had little effect following primary deletion of top consumers or basal species (Fig. 2B). Increasing connectivity was associated with a slight reduction in the effect of competitive exclusion on secondary extinctions following removal of top consumers or basal species, balanced by the slight increase in effect following the removal of intermediate consumers (Fig. 2D). These results reflect the interaction of top–down and bottom–up regulation on intermediate consumers.

**Removing species with different abundances**

Primary deletion of species according to their relative abundance (within a trophic level) revealed contrasting patterns of secondary extinctions across the food web, under diffuse and asymmetric basal competition. This difference was
Food web topology and species’ relative abundances

Differences in food web extinction probabilities reflect the different mechanisms that drive relative abundance ranks under diffuse and basal competition. For a given food web size, variation in diffuse basal species relative abundances was determined only by differences in trophic (consumer-resource) patterns, while variation in asymmetric basal abundances was driven by both trophic and within-guild interactions (Fig. 4). While the least abundant basal species in food webs with either form of competition had more consumers than average (i.e. a ratio of C–R links > 1), the least abundant asymmetric competitors had fewer consumers than the least abundant diffuse competitors (Fig. 4).

This occurred even though food webs were constrained to have the same trophic structure for pairs of diffuse and asymmetric basal competition: the least abundant asymmetric basal species did not necessarily share the same consumers as the least abundant diffuse basal species.

The least abundant basal species also had fewer links to consumers than the basal species experiencing most consumer pressure (the species with most consumer–resource links; upper lines/circles in Fig. 4). This indicates that the least abundant basal species have low densities due to specialist (strong) consumer interactions. The most highly connected species tended to have higher densities due to the presence of multiple weak links from generalist consumers.

Which trophic levels are and aren’t involved in secondary extinctions?

Further differences between diffuse and asymmetric basal competition arose in the frequency that species from different trophic levels were lost in secondary extinctions (Fig. 5). There were differences in the frequency of secondary extinctions within a trophic level according to: the trophic level and relative abundance of the species lost in the primary extinction, and the food web size. The most striking differences occurred for basal/producer species: diffuse basal species were never involved in extinction cascades, while asymmetric basal species were (Fig. 5 G–I). This result confirms the idea that extra extinctions in asymmetric competition food webs were driven by competitive exclusion, which subsequently drives other extinction routes across the food web. For example, herbivores were rarely involved in extinction cascades when other herbivores were lost in the primary extinction from diffuse basal competition webs: mean frequency of herbivore extinctions following herbivore removal was always < 0.022 (Fig. 5 D–F, black circles). Thus, the form of direct basal competition had important impacts on the species lost in secondary extinctions that in turn cascaded through the food web.

Discussion

Secondary extinction cascades driven by competitive exclusion amongst basal (producer) species with asymmetric competition have important consequences across all trophic levels in multi-trophic ecosystem models. The effect of competitive exclusion, demonstrated here by the complete
absence (presence) of basal species loss with diffuse (asymmetric) competition (Fig. 5), increases with food web size, but is relatively unaffected by connectance. These results hold regardless of the trophic level of the species involved in the primary extinction, but patterns of secondary extinctions driven by competitive exclusion were highly sensitive to the relative abundance of the deleted species within a trophic level (Fig. 3, 5). Results from food webs with asymmetric basal competition corroborate previous insight based on single trophic-level, competitive community models: primary removal of the most abundant basal species is associated with the highest risk of extinction cascades (Fowler 2005, 2010). However, comparison with food webs based on diffuse basal competition reveals a previously unappreciated, relatively stabilising effect of the least abundant basal species with asymmetric competition (Fig. 4), which can be understood by considering the different mechanisms that drive relative abundances under diffuse and asymmetric basal competition (Fig. 4).

Previous work has identified various routes to secondary extinctions in model ecosystems (Christianou and Ebenman 2005, Ebenman and Jonsson 2005, Thébault et al. 2007, Fowler 2010). Direct competitive exclusion in the context of a multi-trophic food web has received little attention previously (but see Thébault et al. 2007, discussed below). The results here show that secondary extinction cascades can occur through at least three other important routes: 1) removal of a basal species can lead directly to the loss of other basal species through competitive exclusion amongst the remaining basal species; 2) removal of an intermediate or top consumer releases a basal species from predation pressure, which then allows it to outcompete and exclude (an)other basal species; 3) removal of a top consumer reduces pressure on an intermediate consumer, which in turn increases pressure on basal species, which can in turn trigger direct competitive exclusion. Routes 2) and 3) both involve trophic cascades and more complex, indirect routes; however, the secondary extinctions highlighted here arise through previously unconsidered processes.

Relative abundance has previously been proposed as a useful metric for characterising species lost in primary deletions, in terms of driving secondary extinction cascades in simple, competitive communities (Fowler 2005, 2010). Christianou and Ebenman (2005) used the number of strong consumer-resource links to (or from) the species lost in the primary deletion to predict food web responses to primary deletion, in a nine species, rectangular, but otherwise similar food web model. They showed a trend for increasing secondary extinction risk with an increasing number of strong links from a resource species, where an increasing number of links was also positively (negatively) correlated to consumer (resource) abundance. Here I showed that the response of the food web to removal of rare species in any trophic level is strongly dependent on the form of basal competition. However, while the least abundant basal species have more consumer
'trophic uniqueness' of the species lost in the primary extinction (Petchey et al. 2008), a measure that requires accurate estimates of species interaction strengths for calculation, which can be very difficult to gain from the typically short, noisy data available from field populations (Berlow et al. 2004, but see Berlow et al. 2009, O’Gorman et al. 2010). Estrada (2007) and Jordán (2009) also review different network measures that can be used to identify keystone species in food webs. A full comparison of the predictive ability of these different methods would provide an interesting avenue for future study.

Christianou and Ebenman (2005) noted very few secondary extinctions amongst basal species following primary deletion in their food web models. The difference between their results and those presented here can be understood through the specific choice of parameter values for interspecific basal competition ($a_{ij}$). By selecting $a_{ij} \sim U[-0.5, 0]$, Christianou and Ebenman (2005, their Table 1) generate basal species that behave more like diffuse competitors, with a lower variance (and mean) amongst competitors than examined here ($\sigma^2(U[-0.5,0]) = 1/48; \sigma^2(U[-1,0]) = 1/12$). Thébault et al. (2007) examined the same range of within guild competition strengths as examined here ($\alpha_j \sim U[-1, 0]$), including direct competition between consumer species, but compared this with the absence of direct consumer competition, rather than diffuse competition. Reducing the variance of basal competition strength (e.g. $\alpha_j \sim U[-0.75$,

While relative abundance was used here to characterise species lost in primary extinctions, another possibility for predicting secondary extinction risk is by characterising links than average, they are not the most highly connected of basal species.

Figure 3. The probability of secondary extinctions is strongly affected by the relative abundance of the species involved in the primary extinction, in food webs with diffuse (black squares) or asymmetric competition (grey circles). Connectance = 0.2, food web size is 6 (A, D; $m_p=1, m_H=2, m_N=3$), 15 (B, E; $m_p=4, m_H=5, m_N=6$) or 24 species (C, F; $m_p=7, m_H=8, m_N=9$), continuous lines connect species within the same trophic level. The impact of basal competitive exclusion on secondary extinctions (D–F) reveals a relatively stabilising effect of the least abundant basal species with asymmetric basal competition: $P(\text{Ext}_A) – P(\text{Ext}_D) < 0$.

Figure 4. The ratio of consumer–resource links to the least abundant (squares) or most highly connected basal species (circles) compared to the average number of consumer–resource links in the basal trophic level, in food webs with diffuse (black) or asymmetric basal competition (grey).
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investigated the impact of stochastic environmental variation on community extinction patterns (Enberg et al. 2006, Ruokolainen et al. 2007, Borrvall and Ebenman 2008, Ruokolainen and Fowler 2008, Kaneryd et al. 2012), which has supported and extended results based on deterministic models. Here I focused on deterministic dynamics to simplify the analysis, but future work should incorporate predator switching and stochastic environmental variation to investigate if and/or how these factors influence extinction cascades or species persistence in the face of direct competitive exclusion amongst basal species, or higher trophic levels when direct competition exists. For example, it would be interesting to establish under what conditions the storage effect (Chesson and Warner 1981, Chesson 1994) could promote coexistence following primary species deletion, —0.25) also tends to generate P(Ext) results more similar to diffuse competition (results not shown; see Moen 1989 and Kokkoris et al. 2002 for further discussion). Goldberg and Barton (1992) analysed the available literature on plant field experiments, and found no evidence that interspecific competition was weaker than intraspecific competition, which suggests that even when including relatively stronger interspecific competition, food web models such as those examined here may still underestimate the impact of competitive exclusion on ecosystem stability.

More complex approaches to modelling food webs have incorporated predator switching and/or included allometric relationships that constrain food web structure (Kondoh 2003, Quince et al. 2005, Staniczenko et al. 2010, Blanchard 2011, but see Naisbit et al. 2012). Recent work has also investigated the impact of stochastic environmental variation on community extinction patterns (Enberg et al. 2006, Ruokolainen et al. 2007, Borrall and Ebenman 2008, Ruokolainen and Fowler 2008, Kaneryd et al. 2012), which has supported and extended results based on deterministic models. Here I focused on deterministic dynamics to simplify the analysis, but future work should incorporate predator switching and stochastic environmental variation to investigate if and/or how these factors influence extinction cascades or species persistence in the face of direct competitive exclusion amongst basal species, or higher trophic levels when direct competition exists. For example, it would be interesting to establish under what conditions the storage effect (Chesson and Warner 1981, Chesson 1994) could promote coexistence following primary species deletion,
reducing the probability of secondary extinction cascades. Likewise, recent work examining communities assembled with qualitatively different species level dynamics (Fowler 2009, Fowler et al. 2012) demonstrates that including such dynamical variation can generate novel diversity–stability relationships at the community level. Including species with high growth rates (leading to cyclic or more complex dynamics in the absence of species interactions) represents another avenue for future research in extinction cascades. Other future research should also include mutualistic or parasitic species interactions in the food web structure (Fontaine et al. 2011).

Assumptions about the form of direct competition between species on any trophic level should be based on the best available knowledge from empirical studies. Much research effort has so far been focussed on characterising the number and strength of trophic (consumer–resource) links in food webs (Berlow et al. 2004, Kéfi et al. 2012). The results presented here show that the form of direct competition amongst species, e.g. diffuse or asymmetric, has important effects on the patterns of secondary extinction cascades in food webs, and should be also considered in future studies examining ecosystem responses to perturbation.

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