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Extinction cascades and catastrophe in ancient food webs

Peter D. Roopnarine

Abstract.—A model is developed to explore the potential responses of paleocommunities to disruptions of primary production during times of mass extinction and ecological crisis. Disruptions of primary production are expected to generate bottom-up cascades of secondary extinction, and these are predictable given species richnesses, functional diversity, and trophic link distributions. If, however, consumers are permitted to compensate for the loss of trophic resources by increasing the intensities of their remaining biotic interactions, top-down driven catastrophic increases of secondary extinction emerge from the model. Both bottom-up and top-down effects are themselves controlled by the geometry of the food webs. The general Phanerozoic trends of increasing taxonomic and ecological diversities, as well as the varying strengths of biotic interactions, have led to food webs of increasing complexity. The frequency of catastrophic secondary extinction increases as food web complexity increases, but increased complexity also serves to dampen the magnitude of the secondary extinctions. When intraguild competitive interactions are included in the model, competitively inferior taxa are observed to possess greater probabilities of survival if the guilds are embedded in simple subnetworks of the overall food web. The result is the emergence of post-extinction guilds dominated by those inferior taxa. These results are congruent with empirical observations of ‘‘disaster taxa’’ dominance after some mass extinction events, and provide a mechanism for the reorganization of ecosystems that is observed after those events. The model makes the testable prediction that dominance by disaster taxa, however, should be observed only when bottom-up disruptions have caused ecosystems to collapse catastrophically.

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Introduction

Many of the species that became extinct during intervals of mass extinction probably did not succumb to the direct effects of abiotic triggers, but rather were victims of the resultant ecological crises and failing communities. The disruption of primary production is often cited as a proximal cause of such crises (Vermeij 1995; Martin 1996; Allmon 2001; Benton and Twitchett 2003), because it is predicted to unleash avalanches of secondary extinctions at higher trophic levels (Borrvall et al. 2000; Vermeij 2004). If an ecological community is viewed as an Eltonian pyramid of connected trophic levels (Elton 1927), then the effects of an interruption of primary production are driven from the ‘‘bottom up,’’ while the responses of consumer activities are propagated ‘‘top down.’’ Secondary extinction of a species may occur as a direct result of bottom-up perturbations to, or top-down impact from, other species to which it is linked trophically or is otherwise dependent upon (Quince et al. 2005). The simulation model presented here combines bottom-up and top-down processes to provide a theoretical basis for understanding secondary extinctions in fossil communities during times of mass extinction, within the context of community change during the Phanerozoic.

An ecological community may also be viewed as a directed energy transfer network among species, in which energy fixed by autotrophic species is transferred with thermodynamically decreasing efficiency to other species in the network (Lindeman 1942). Primary production is interrupted by the extinction of primary producers, their temporary shutdown, or even their switch to a heterotrophic lifestyle during stressful times. Ecological theory suggests that the effective reduction of primary production should have impacts elsewhere in the community network (Vermeij 2004), including the loss of consumer species as a response to the loss of autotrophic resources. Evidence supporting disruptions of primary production during episodes of extinction includes anomalous excursions of carbon stable isotope ratios at the end of the

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Permian through Early Triassic (Knoll et al. 1996; Benton and Twitchett 2003) and the end of the Cretaceous (Zachos et al. 1989), the loss of abundant or dominant photosynthetic species at the end of the Cretaceous (Sheehan and Hansen 1986; Falkowski et al. 2004; Vajda and McLoughlin 2004; Wilf and Johnson 2004), fungal spikes at the Cretaceous/Tertiary boundary (Vajda and McLoughlin 2004) and possibly the Permo-Triassic boundary (Eshet et al. 1995; Visscher et al. 1996; Benton and Twitchett 2003; but see Foster et al. 2002), and on a more regional scale, massive yet selective species extinctions in marine ecosystems during the Pliocene in the tropical western Atlantic (Vermeij and Petuch 1986; Roopnarine 1996; Anderson 2001; Allmon 2001; Todd et al. 2002). Whether this type of bottom-up perturbation results in the extinction of consumers, and whether such secondary extinctions propagate as trickles or entire avalanches through a trophic network, might depend on several parameters of the network. These include taxonomic richness, functional or guild diversity, the pattern and relative strengths of trophic links between species, and the comparative species richnesses among guilds of similar trophic function but different composition (for example, protistan phytoplankton and benthic macrophytes).

Very little can be known directly of the mechanisms and pathways by which disruptions cause specific secondary extinctions in any particular ancient community, because the mechanisms must operate through complex trophic pathways and systems of sometimes poorly known species diversities, interactions, and linkages. What we do know, however, is that ancient ecosystems have changed dramatically over time with the evolution of major new ecological roles (for example heterotrophy) (Knoll and Bambach 2000), with the variation of species diversity both in total and within guilds (Bambach 1977; Sepkoski 1981), with the secular increase in the energetics of biotic interactions (Vermeij 1987), and with the evolution of species with increased metabolic rates and complexity (Bambach 1993).

I propose that by modeling the general functional structure of community trophic systems, it is possible to compare the relative effects of disruptions of primary productivity among communities of varying complexity. Based on this premise, the numerical model presented herein assesses the magnitude and extent of secondary extinction and extinction cascades that were initiated in paleocommunities under varying levels of interruptions of primary production. Interruptions of productivity in the model take the form of the deactivation of primary producers, as might be expected under hypothesized physical conditions prevailing during episodes of mass extinction. The model is based on the trophic network (food web) representation of ecological communities (Elton 1927; May 1973). It focuses specifically on the changing susceptibility of paleoecosystems to secondary extinction during the Phanerozoic as species richness, ecological/functional diversity, and trophic network complexity have varied. I also account for the fact that there are many details of community relationships that are unknowable for fossil species and paleocommunities (Olszewski and Erwin 2004), and that there are parameters of modern food web theory, such as trophic species and connectance (Williams and Martinez 2000), that cannot be quantified and applied with measurable precision in paleoecological contexts. The model is therefore a probabilistic construct based on necessary abstractions and estimates of community ecological parameters.

Basic Model.—The proposition that disruptions of primary production result in bottom-up cascades of secondary extinction was examined by subjecting several hypothetical paleocommunities to press perturbations of primary producers. Figure 1 shows a simple three-node network with each node representing a guild of species sharing the same sets of potential prey and predators. This means that, for example, although the specific prey of two species are not known precisely, we can still identify the guilds to which their prey most likely belonged. Each species within a consumer node possesses an in-degree, or number of incoming trophic links, or prey species. The in-degree of any particular species within a node is derived from a probability distribution $P(r)$ that describes the in-de-

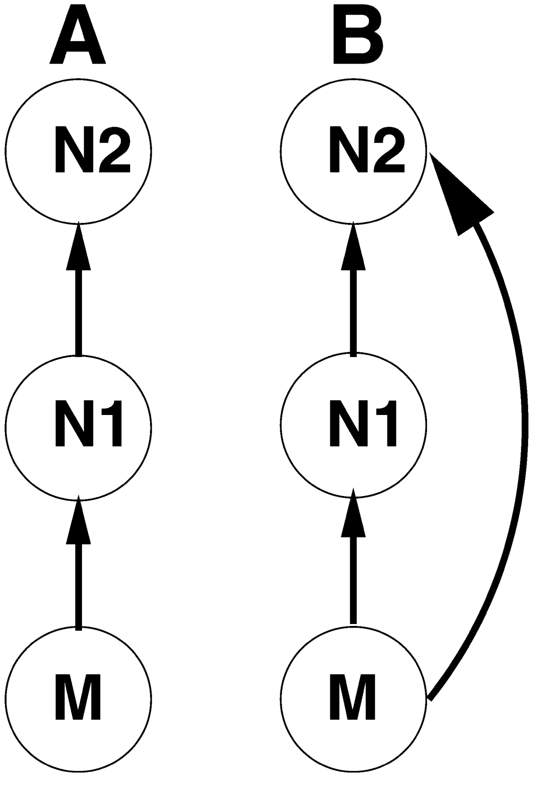

FIGURE 1. Simple three-node statistical trophic network. Each node represents a set of species that share the same sets of potential prey and predators. *M*, primary producers; *N1*, primary consumers; *N2*, secondary consumers. Node designations also represent species richness (see text formulae). Network on right designates node *N2* as a set of omnivorous species.

grees of all the node's species. Suppose that a species' survival in a trophic network relies solely upon having at least one trophic (food) resource (ignoring top-down effects such as predation). Then from Figure 1, if the level of perturbation to M (that is, the disruption of primary productivity) is ω, then the probability of secondary extinction of any primary consumer (node *N1*) as a consequence of extinction of all its trophic resources in node M is

$$p(e_{r_1}|\omega) = \binom{M - r_1}{\omega - r_1}\binom{M}{\omega}^{-1} = \frac{\omega!(M - r_1)!}{M!(\omega - r_1)!} \quad (1)$$

where $P(e_{r_1}|\omega)$ is the probability of extinction of a *N1*-taxon of in-degree r_1 given that primary producer shutdown is ω species out of M (see Appendix). The equation describes the number of ways in which it is possible for a consumer with r prey to lose all those prey when prey extinction is $\omega \geq r$. The expected (average) number of secondary extinctions in *N1*, ψ_1, is therefore

$$\psi_1 = E(e_{r_{N1}}|\omega) = \sum_{i=r_{N1_{\min}}}^{i=\omega} [p(e_{r_i}|\omega)P(r_1)]N_1$$

$$= \frac{N_1\omega!}{M!} \sum_{i=r_{N1_{\min}}}^{i=\omega} \frac{(M - r_i)!}{(\omega - r_i)!} p(r_i) \quad (2)$$

where $P(r_1)$ is a probability density function describing the in-degrees of taxa in node *N1*, and $p(r_i)$ is the probability of an *N1*-taxon having in-degree r_i (Appendix). The equation implies that secondary extinction is a predictable function of primary producer extinction. Secondary extinctions may propagate further to the top-level node *N2*, where the expected level of extinction, ψ_2, given ω and ψ_1, is

$$\psi_2 = E(e_{r_{N2}}|\omega, \psi_1)$$

$$= \frac{N_2\psi_1!}{N_1!} \sum_{i=r_{N2_{\min}}=1}^{i=\psi_1} \frac{(N_1 - r_i)!}{(\psi_1 - r_i)!} p(r_i) \quad (3)$$

and $p(r_i)$ is the probability of an *N2*-taxon having in-degree r_i. Increasing the functional complexity of a food web is accommodated simply by extending the combinatorial bases of the formulae. For example, if *N2* is instead a node of omnivores (Fig. 1B), expected extinction becomes

$$\psi_2 = E(e_{r_{N2}}|\omega + \psi_1)$$

$$= \frac{N_2(\omega - \psi_1)!}{(M + N_1)!} \sum_{i=r_{N2_{\min}}}^{i=(\omega+\psi_1)} \frac{(N + N_1 - r_i)!}{(\omega + \psi_1 - r_i)!} p(r_i). \quad (4)$$

The summations on the right-hand side of the formulae have limits at ω and ψ_1 successively because

$$0 < p(e_{r_i}|\omega, \psi_1) \leq 1 \quad \text{if } \psi_1 \geq r_i,$$

and

$$p(e_{r_i}|\omega, \psi_1) = 0 \qquad \text{if } \psi_1 < r_i$$

meaning that consumer species are immune to secondary extinction if extinction in the prey guild is not greater than the consumers' in-degrees.

Extinction Thresholds.—The realism of the basic model can be increased in two ways, first by recognizing a non-zero probability of extinction before a species or population loses all of its trophic resources, and second by incorporating biotic interactions (Quince et al. 2005), namely competitive interactions and top-down consumer effects. Permitting a species' populations to become extinct prior to the loss of all in-links (r) acknowledges that the loss of resources stresses population sustainability. For example, if the carrying capacity of a population, K, is considered to be a function of incoming energy and the state of the community, then K and hence population size decline as the number of food sources decreases. Population size reaches a lower threshold eventually where depensation (Allee effects) and stochastic factors make extinction inevitable (Lande et al. 2003), even though $r > 0$. Approaching an extinction threshold can therefore be described as changes in carrying capacity resulting from the loss of trophic resources. If $\omega > 0$, then the probability of losing a fraction n links (resources) out of r is given by the hypergeometric probability (compare to eq. 1)

$$p(n|\omega) = \binom{r}{n}\binom{M-r}{\omega-n}\binom{M}{\omega}^{-1} \tag{5}$$

and the expected value of n for any r and ω is simply the hypergeometric mean value $(r\omega)/M$. Given a threshold T, extinction is therefore most likely to occur when

$$T \geq \frac{K_n}{K_r} \equiv T \geq 1 - \frac{n}{r} \tag{6}$$

where K_i is the carrying capacity given i in-links. That is, when $n = 0$, $n/r = 0$, and expected extinction is also zero (T always $> n/r$). The probability of secondary extinction now follows the rules

$$0 < p(e_{r_i}|\omega) \leq 1 \quad \text{if } \omega \geq r_i(1-T),$$

and

$$p(e_{r_i}|\omega) = 0 \qquad \text{if } \omega < r_i(1-T).$$

Given the hypergeometric relationship between n and ω, extinction is now most likely when the expected relationship between the extinction threshold T and primary productivity disruption ω is

$$T \geq 1 - \frac{\omega}{M} \tag{7}$$

(see Appendix).

Top-Down Feedback and Competition.—The model is completed by incorporating top-down effects and competitive interactions. Top-down effects are generally mediated by consumption (Hairston et al. 1960), and different species within a guild or node may compete for resources. Assuming that the community is in equilibrium when $\omega = 0$, then the amount of energy lost by a population to predation and denied to it by competitors is at least balanced by incoming energy. The energy being lost to predation is measured by the out-degree of the species, or number of out-links (consumers), and the strength or intensity of those links. Because the basic model considers link strengths to be single-valued and static, the loss of an in-link represents a net loss of energy to the consumer. Expanding the model allows consumers to compensate for lost in-links by increasing the strength of remaining in-links, that is, increasing the intensity of predation. Without the ability to compensate by altering the strength or intensity of in-links, consumer extinction would increase steadily to 100% as $\omega \rightarrow M$. Compensation, however, is accomplished by increasing the intensity of remaining biotic interactions, and a consumer may maintain its energy budget by continuously increasing the strength of remaining links. Such compensation though has a negative impact on prey species, because it increases the rate at which prey species approach their effective extinction thresholds. One possible result is the additional extinction of prey species, followed by additional extinction of any consumers who subsequently lose all in-links, and further intensification of the link strengths of consumers who have lost some in-links. Thus, a positive feedback loop is initiated between consumers and prey (Appendix).

Although the model considers a consumer's link strengths to be single-valued, some empirical data and theoretical considerations of the distribution of interaction intensities of modern taxa suggest that the distribution of a species' link strength may be skewed, with a predominance of weak or intermediate link strengths (Paine 1992; Goldwasser and Roughgarden 1993; McCann et al. 1998). Link strength here, however, was measured as a fraction of the consumer species' in-degree or dietary diversity ($1/r$), with the initial predation intensity on a prey species being

$$S = \sum_{i=1}^{i=d} \frac{1}{r_i} \tag{8}$$

where d is the number of predators (out-degree of prey) and $1/r_i$ is the link strength of the i^{th} predator. All of a consumer's links are therefore of equal strength, though this strength varies among consumers as the number of food sources (r) varies.

The effect of competitive interactions may be modeled similarly by determining a species' relative rank among its competitors (that is, competitive rank normalized by the diversity of competitors). Extinction of a species' competitors makes more resources available, and would offset the subsequent increase in the predation intensity by a predator common to both the species and its extinct competitors. Combining energy lost to predation and competitors, the threshold for extinction may now be reformulated as

$$p(e) = 1 \quad \text{when}$$
$$T \geq 1 - \frac{1}{2}\left(\frac{S_\omega - S_0}{S_0} + \frac{R_0 - R_\omega}{R_0}\right) \tag{9}$$

where S_i is predation intensity and R_i is competitive rank within a guild when $i = \omega$. S_0 and R_0 are predation intensity and competitive rank respectively when $\omega = 0$. The extinction of competitors should serve to slow a population's approach to its extinction threshold. Note that the combinatorial formulae relating ω and secondary extinction are no longer present. The above formula, however, is a simulation rule that ensures the interaction of the network parameters (diversities, link distributions), T, S, and R (Appendix).

The model is parameter-rich, reflecting the multivariate character of food webs (de Ruiter et al. 2005). The parameters for any given simulation comprise the input parameters of guild diversities, the level of primary producer disruption (ω), trophic link distribution coefficients (γ), guild extinction thresholds (T), as well as variable but dependent parameters, namely link strengths (S) and competitive rank (R). The model is not deterministic, however, because of the stochasticity involved in assembling individual food webs (see ''Methods''), and several interesting and unexpected phenomena emerge from the simulations (see ''Results and Discussion''), notably top-down driven extinctions caused by bottom-up perturbations, catastrophic increases of secondary extinction in response to incremental increases of primary producer disruption, and the sometimes biased nonrandom survival of taxa of low competitive ranks.

Methods

Analysis of the model proceeded by constructing probabilistic paleocommunities with trophic connections, applying the formulae and rules described in the previous section, and simulating extinction by the random removal of links to primary producers. Computer simulations were used to evaluate the model in lieu of alternative approaches (for example, systems of differential equations; Appendix) mostly because the simulations permit the collection of data on individual taxa (see below), in addition to visualization of the ensemble behavior of guilds and communities. The intuitive nature of computer simulations also make them more accessible to a broader audience.

Model Networks.—Constructing probabilistic networks on the basis of known properties and distributions of existing trophic networks (Havens 1992; Martinez 1992; Montoya and Solé 2002) allows us to explore paleo-trophic network response to varying levels of primary producer perturbation and shutdown. Data that are difficult to obtain both neontologically (Goldwasser and Roughgarden 1997) and paleontologically, however, dictate to a large extent the reconstruction of paleotrophic networks. For example, no single stratigraphic sample, nor necessarily even a series of laterally contemporaneous samples, can be considered as the sole basis for network construction. The networks must be the result of regionally integrated sampling, which in turn measures the temporally and geographically stable pools of species from which the components of local communities were assembled. Species interactions are also frequently obscure (Leighton 2004). These interactions can only be inferred for fossil species, and even those interactions that are inferred with great confidence, for example the direct evidence of predation via skeletal scars or gut contents, are representative of an essentially unknowable set of potential interactions among large numbers of species. Interaction strengths are likewise difficult to specify and are rarely considered even in neoecological studies (Goldwasser and Roughgarden 1993). Finally, certain important food web components often preserve very poorly in the fossil record, for example skeletogeneous phytoplankton with skeletons that are highly soluble under certain conditions, benthic macrophytes with few or no hardparts, and top-level consumers with small population sizes and hence relatively lower fossilization rates. Although these data cannot always be obtained for fossil species, potential prey and predators can often be identified by relying upon morphology, geographic and sedimentological proximity, phylogenetic affinity, and uniformitarian comparison to extant taxa. Species may therefore be grouped into guilds or nodes on the basis of similar potential interactions. Links between species, and the properties of links (for example, interaction strengths), cannot be specified as scalar quantities, but instead should be based on distributions, which are in turn derived from reasonable inferences of organismal and autecological data.

Hypothetical communities were therefore constructed on the basis of the simple three-node network model illustrated earlier, as well as Bambach's megaguild characterization of Cambrian, post-Cambrian Paleozoic, and Mesozoic–Cenozoic marine communities (Bambach 1983) (Fig. 2), in turn derived from Sepkoski's evolutionary faunas (Sepkoski 1984). These characterizations are distinguished from each other by the increasing diversity of megaguilds during the Phanerozoic (Bambach 1983), as well as the increasing number of trophic connections between megaguilds, and serve as a first approximation of community changes in shallow marine communities during the Phanerozoic. Species richnesses were assigned to reflect the relative diversity of higher taxa within megaguilds, but were held approximately constant within trophic levels among the three networks (subsequent analyses based on varying relative species richnesses produced results differing very little from the present results). The three-node network was assigned diversities of 1000 primary producer species (M), 100 primary consumers ($N1$), and ten secondary consumers ($N2$), with secondary consumer species diversities being scaled and reduced overall by a factor of ten relative to total primary consumer diversity. Node diversities were assigned to the model megaguild paleocommunities as follows: Cambrian, PS-100, ES-400, ED-300, EH-200, SIS-100, SID-200, PC-65, SIC-65; Paleozoic, PS-96, ES-640, ED-128, EH-160, SIS-128, SID-128, DID-32, PC-52, EC-52, SIC-26; Mesozoic, PS-81, PH-54, ES-513, ED-54, EH-135, SIS-162, SID-108, DIS-135, DID-54, PC-45, EC-45, SIC-36, DIC-9 (see Fig. 2 for an explanation of node designations). Primary producer diversity (or level of productivity) was set at 2600 for each parameter set. Primary consumer species diversities were scaled and reduced overall by a factor of two relative to total primary producer diversity, and diversity in each subsequent trophic level was reduced as a factor of ten relative to the next lowest trophic level. Deposit feeders were linked directly to primary producers, because on the timescales considered here, as well as the potentially short trophic distance between many deposit feeders and primary production (Levinton 1996), the effects of primary producer extinction would not be expected to differ greatly between primary herbivores and deposit feeders.

The webs illustrated in Figure 2 are therefore summary schematics, within which are embedded detailed species-level directed networks. The connections of each network vary from one simulation to the next (described below) but conform to the specific distributions determined by guild diversities and link distributions.

Numerical Simulations.—The in-degree (number of incoming trophic links) of each species within a node was drawn randomly from a

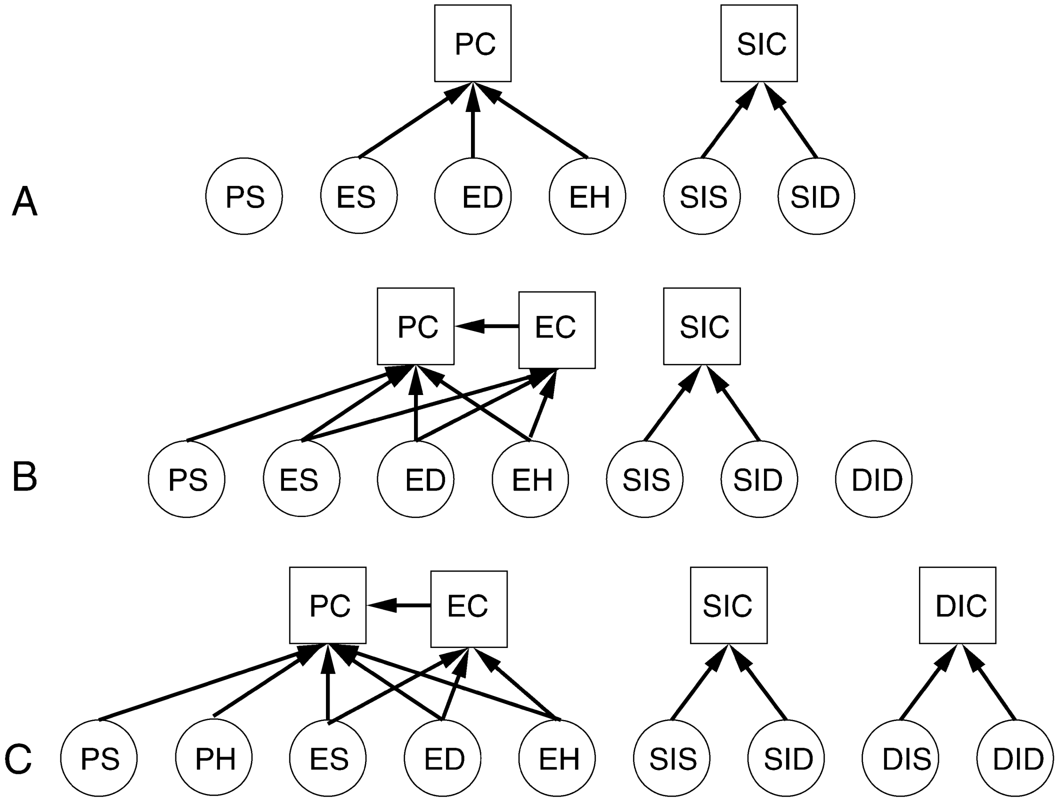

FIGURE 2. Hypothetical model marine food webs based on megaguild scheme. Each node represents a set of species of particular trophic habit, and arrows indicate possible trophic links. Primary producers are not illustrated but occupy a level lower than the primary consumers (circles). A, Cambrian food web. B, Paleozoic food web. C, Mesozoic food web. Megaguilds: PS, pelagic suspension feeders; ES, epifaunal suspension feeders; ED, epifaunal deposit feeders; EH, epifaunal grazers; SIS, shallow infaunal suspension feeders; SID, shallow infaunal deposit feeders; PC, pelagic carnivores; SIC, infaunal carnivores; DID, deep infaunal deposit feeders; EC, epifaunal carnivores; PH, pelagic herbivores; DIS, deep infaunal suspension feeders; DIC, deep infaunal carnivores.

truncated power law distribution. Arguments support the presence of both exponential and power law distributions in empirical modern food webs (Martinez 1992; Williams and Martinez 2000; Camacho et al. 2002), but some recent observations suggest that exponential distributions occur more frequently (Dunne et al. 2002). This may be a factor of the relatively small sizes of the currently measured food webs. Contemporary theory, on the other hand, suggests the ubiquity of power law distributions, as a result both of growth processes that should be involved in the assembly and growth of food webs (Albert et al. 2000), and of the fact that power law distributions encompass a broad range of specialist to generalist consumers. Both distributions were used in the simulations, but results did not differ qualitatively and thus only results from power law distributed networks are reported here. Power law distributions took the form $P(r) = M^{\gamma-1}r^{-\gamma}$ (with $\gamma = 2$), where M is the species richness of the prey node(s).

Measuring productivity in the geological record is very difficult, and it is usually expressed as the temporal and/or spatial variation of proxy measurements (e.g., $\delta^{13}C$). The network nature of the model, however, specifies actual trophic links of primary consumers (herbivores) to producers. Compiling diversity data for producers is difficult for most paleocommunities and carries a high degree of uncertainty. Nonetheless, given that for any paleocommunity of consumers that we observe, levels of primary production must have been sufficient to support them, we can parameterize the model on the basis of initial consumer demand (i.e., when $\omega = 0$). The major factors controlling a consumer's demand for production are body size and trophic level. Larger animals consume relatively greater amounts of food (that is, metabolic requirements scale positively with increasing body size) (Peters 1983), and hence larger individuals are more sensitive to interruptions of supply (for example, Roopnarine 1996). Larger consumers and those at higher trophic levels also generally have lower population densities, larger range requirements (Brown 1995), and therefore higher probabilities of extinction. Extinction thresholds therefore serve to discriminate among guilds comprising species of similar trophic habit but different body sizes, or of different trophic levels. Differences of body size were not treated explicitly in the current simulations (but see Angielczyk et al. 2005), but megaguilds were differentiated on the basis of trophic level. Two sets of simulations were conducted, the first with extinction thresholds T fixed at 0.1 for all species, and the second with T ranging [0.3,0.5] for carnivores, dependent upon the number of carnivorous guilds. The results were essentially identical, suggesting that the model is fairly robust under variation of this parameter; therefore, only results from simulations with varying thresholds are reported below. Competitive ranks were determined by the random ordering of species within nodes, yielding a uniform distribution. Simply put, each taxon within a megaguild was assigned an integer ranging randomly from one to the maximum number of taxa within the megaguild; greater value equaled higher competitive rank and therefore advantage.

Each simulated network was subjected to disruption of primary production by eliminating a fixed number of randomly selected producer species, and assessing the number of consumer species (at all trophic levels) that became extinct as a consequence (secondary extinction). The magnitude of the disruption, ω, ranged from 0 to M (the maximum diversity of primary producers). Link strengths of each consumer were calculated during each round of an extinction cascade in progress, and were adjusted to compensate for links lost because of prey extinction. Simulations of the three-guild network were conducted under the basic conditions outlined by equations (1–4), the extinction threshold condition outlined in equations (5–7), and in the presence of varying link strength, competitive interactions, and top-down feedback (eq. 9). Secondary extinction in the hypothetical Bambachian megaguild food webs was simulated only under the final, fully parameterized conditions (eq. 9).

Thirty simulations were performed for each parameter set and food web. Simulation programs were written in standard C++ and are available upon request from the author. All simulations were run on a 16 CPU Pentium Xeon Linux cluster at the California Academy of Sciences. Load-balancing, using openMosix (http://openmosix.sourceforge.net/), distributes the computations across the cluster, allowing multiple schematic networks to be simulated simultaneously. Currently, however, each network simulation runs as a single process, and therefore only one simulated network per schematic is disrupted at any given time. This bottleneck is currently being addressed with parallelization of the existing code, which will permit multiple schematic and simulated networks to be examined simultaneously.

Results

The three-guild network responds to primary producer extinction in the predicted linear fashion under conditions of the basic model (Fig. 3). The onset of secondary extinction (as $\omega \rightarrow M$) is a simple linear function of primary producer disruption (increasing in increments of two species in these simulations) and the link distribution of the consumers. Secondary extinction is eventually complete as primary extinction nears M, and the rate at which 100% secondary extinction is approached is also a function of consumer link distribution parameters. Addition of a population extinction threshold, T, below which extinction of a species is considered inevitable (eq. 7) causes both the earlier onset of secondary extinction and 100% secondary extinction at lower values of ω. Secondary extinction is initiated in the threshold model when at least one consumer loses all its prey species. The shape of the response curve is perhaps expected when one considers that the threshold

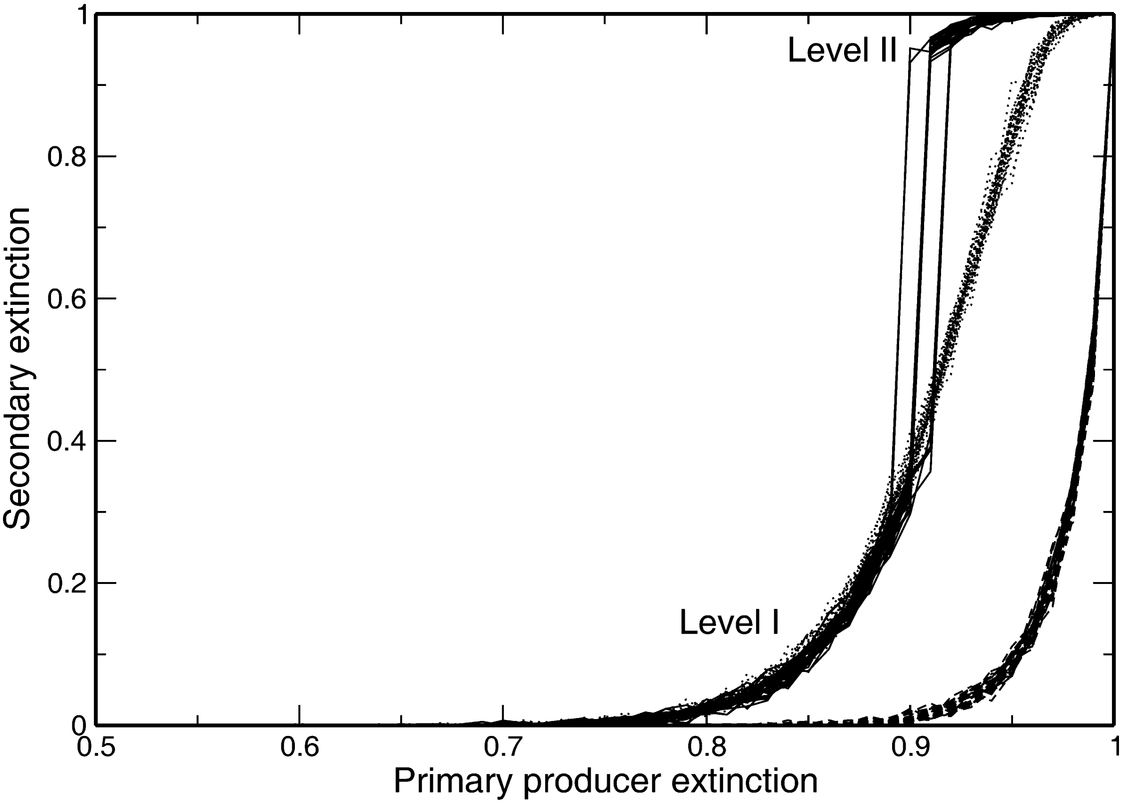

FIGURE 3. Response of the three-guild network (Fig. 1) to disruption of primary producers. Dashed lines, simple model; dotted lines, threshold model; solid lines, model with top-down feedback. Each model was simulated 30 times.

model could be rewritten as a logistic function if individual species properties are ignored (Appendix), meaning that there would be an initially rapid and nearly exponential increase of secondary extinction as consumers with fewer trophic links are lost, followed by a more gradual approach to total secondary extinction, because remaining species have greater in-degrees and hence are more resistant to complete loss of in-links.

The addition of top-down consumer feedback via the variation of link strengths, and the inclusion of competitive interactions, is expected to alter the basic model (including extinction thresholds T) in the following way: increasing the strength of consumer links will accelerate a prey species' approach to T, while the extinction of competitors will delay approach to T. The actual response is a nonlinear and mathematically catastrophic increase of secondary extinction (Fig. 3), marking a departure from the smooth expectation of the threshold model, and stemming from the addition of positive feedback via predator compensation. The result is an initially low level of expected secondary extinction (referred to here as Level I extinction) that is separated from significantly increased Level II extinction by a very small increment in the level of primary producer disruption. Beyond this catastrophic increase, Level II extinction increases slowly to 100% as a function of increasing primary producer disruption.

The three Bambachian paleontological model food webs produce similar results under the feedback model (Fig. 4). These networks exhibit both Level I and Level II extinctions, separated by a catastrophic increase in the magnitude of secondary extinction. Onset of secondary extinction occurs at a slightly lower level of primary producer shutdown in the Cambrian model in contrast to the post-Cambrian models. Level II extinction also takes a different form in the three webs; after

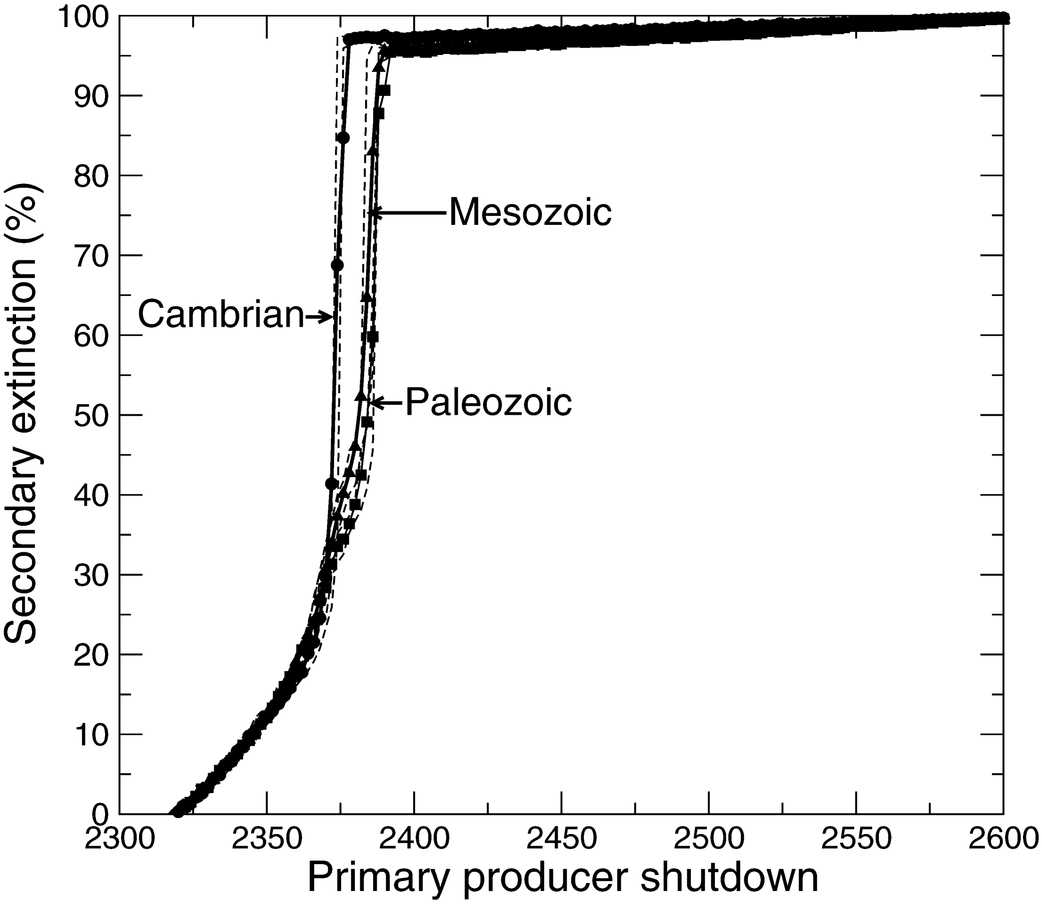

FIGURE 4. Responses of the hypothetical paleontological food webs to disruption of primary producers, using the model with top-down feedback. Circles, Cambrian food web. Squares, Post-Cambrian Paleozoic. Triangles, Mesozoic. Solid lines with symbols represent the mean of 30 simulations, while dashed lines show 25% and 75% quartile ranges.

the catastrophe, secondary extinction tends to be lower in the post-Cambrian models relative to the Cambrian model, at any given level of primary producer shutdown.

Detailed examination of the responses of individual megaguilds to primary production disruption in each simulation explains the summary differences noted above. Figure 5 illustrates the results for three individual megaguilds in the three models. The responses of pelagic suspension feeders vary very little among the models (Fig. 5A–C), even though the trophic relationships vary; pelagic carnivores prey on pelagic suspension feeders in the post-Cambrian models only. This means that the dynamics of this particular megaguild are controlled primarily by its response to bottom-up perturbation. The impact of predation in the post-Cambrian models is minimized by the broad diets assigned to pelagic carnivores in those models. The responses of carnivore guilds, on the other hand, are functions of the relative taxonomic diversities of predators and prey, as well as the complexity of the trophic connections assigned to the predators. For example, Cambrian infaunal carnivores (Fig. 5D) exhibit low levels of Level I secondary extinction, followed by a significant catastrophic increase that results both from bottom-up generated prey extinctions and top-down feedback from the carnivores themselves. Epifaunal carnivores, which are not present in the Cambrian model, exhibit more complicated response patterns in the post-Cambrian models (Fig. 5E,F). This group exhibits an initial catastrophe at the point at

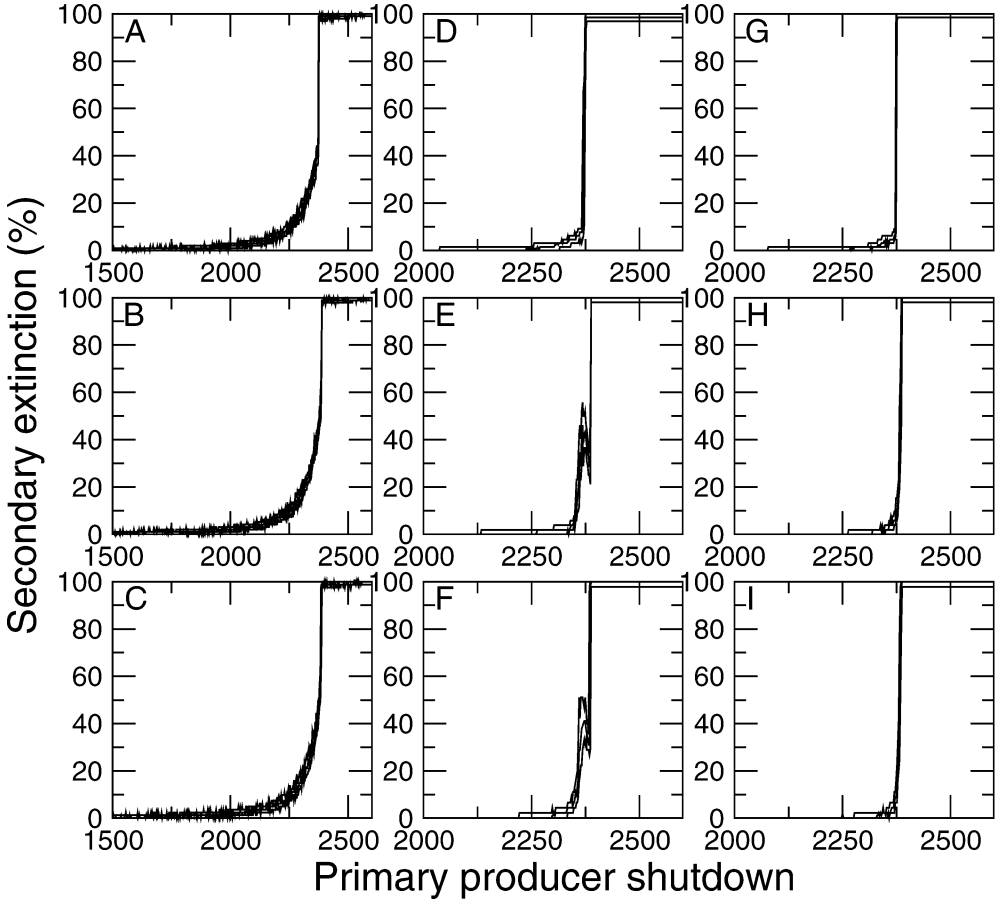

FIGURE 5. Responses of specific megaguilds to disruption of primary producers, using the model with top-down feedback. A, D, G, Cambrian food web. B, E, H, Post-Cambrian Paleozoic. C, F, I, Mesozoic. A–C, Pelagic suspension feeders. D, Shallow infaunal carnivores. E, F. Epifaunal carnivores. G–I, Pelagic carnivores. Lines on each plot represent the median and 25 and 50 percentile points of results from 30 simulations per food web.

which most of the community is collapsing (that is, transitioning from Level I to Level II extinction) (Fig. 4), but this is only a local maximum, and secondary extinction actually decreases at higher levels of primary producer disruption. The decrease is most likely a result of the fact that the epifaunal carnivores are intermediate carnivores and experience some ''release'' from top-down pressure with the catastrophic Level II extinction of their own pelagic carnivorous predators (Fig. 5H,I). Increasing primary producer shutdown does eventually generate another catastrophic increase to a global maximum. Pelagic carnivores are top carnivores in all three models, and exhibit similar patterns of secondary extinction. Extinction is nearly complete at Level II because these carnivores are themselves subject to their own compensatory feedback loops. It is interesting to note, however, that Level I secondary extinction is initiated at higher levels of primary producer shutdown in the post-Cambrian models relative to the Cambrian.

Finally, data were collected to evaluate the competitive ranks of surviving taxa after the Bambachian food webs were subjected to varying levels of primary production disruption. Megaguilds differ in their responses, sometimes significantly, suggesting that the trophic nature of the communities would be altered after extinction. Figure 6 illustrates the detailed responses of the three megaguilds examined previously in Figure 5. These figures are empirical cumulative probability plots, where the ''cumulative frequency'' axis may

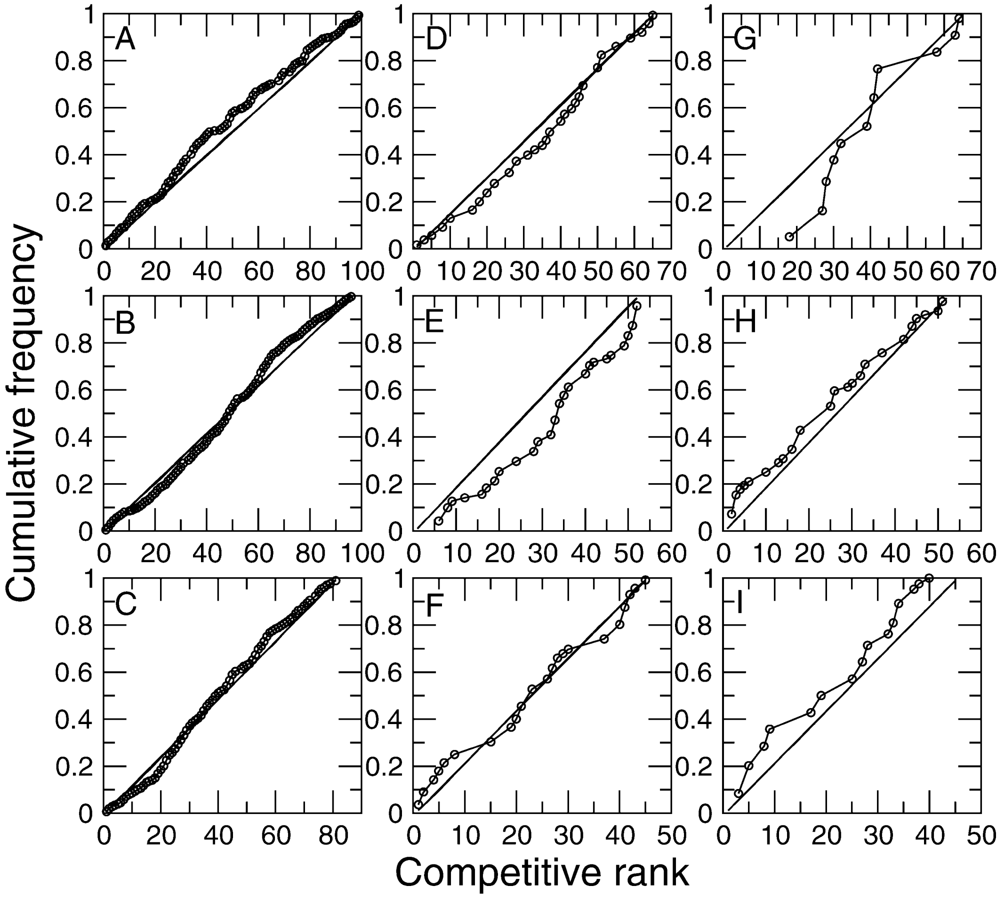

FIGURE 6. Distributions of competitive rank for specific megaguilds at varying levels of primary producer disruption. Higher values (x-axis) indicate higher competitive rank. Arrangement of food webs and megaguilds follows that in Figure 5. Levels of primary producer disruption are given in the text. Plots (lines) are mean cumulative frequencies, at a given competitive rank, from 30 simulations.

be interpreted as the proportion of the underlying distribution that is less than or equal to a particular competitive rank. Each distribution in this case describes competitive ranks in a megaguild. The slope of a plot measures the rate at which observations accumulate as competitive rank is increased, indicating the general shape of the underlying probability density. For example, the straight diagonal lines on all the plots mean that observations are accumulating uniformly, suggesting underlying uniform distributions. This is indeed the case for the starting distributions of competitive ranks in the simulations. Upward-curving (concave up) plots indicate the slow accumulation of taxa, and hence underlying distributions weighted toward competitively superior taxa, whereas concave down plots indicate distributions with a predominance of competitively inferior taxa. Three plots are given for each megaguild, showing the distributions of competitive rank at the following levels of primary producer disruption: 2080 (80%), 2340 (90%), and 2418 (93%). These three points capture low levels of secondary extinction, increasing Level I, and Level II secondary extinction respectively.

There is very little deviation from uniformity, or variation among the models, for pelagic suspension feeders (Fig. 6A–C). Cambrian shallow infaunal carnivores likewise exhibit little departure from uniformity (Fig. 6D), suggesting that members of these megaguilds have roughly equal probabilities of surviving ecosystem collapse, regardless of competitive abilities. The situation is different for epifau-

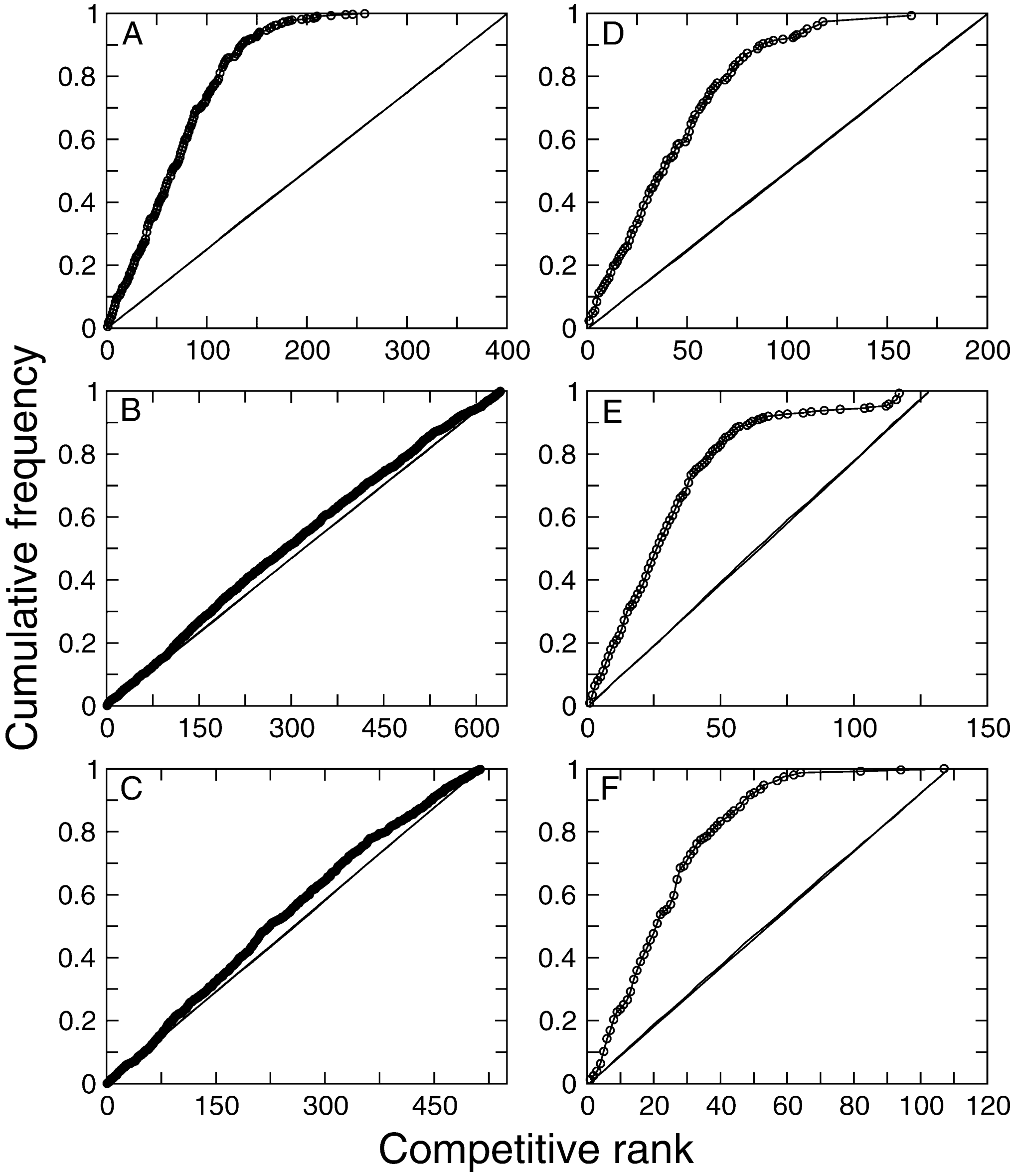

FIGURE 7. Distributions of competitive rank of two additional megaguilds. A–C, Epifaunal suspension feeders. D–F, Shallow infaunal deposit feeders. A, D, Cambrian food web. B, E, Post-Cambrian Paleozoic. C, F, Mesozoic. Significant convexity of cumulative frequency plots indicates predominance of competitively inferior taxa.

nal carnivores in the post-Cambrian models, however, with a greater survivorship of competitively superior taxa in the Paleozoic model (Fig. 6E), but greater survivorship of taxa of low to intermediate abilities in the post-Paleozoic model (Fig. 6F). Pelagic carnivores are likewise variable, with distinctly greater survivorship of competitive superiors in the Cambrian model (Fig. 6G), but slightly greater survivorship of competitive inferiors in the post-Cambrian models (Fig. 6H,I).

Relative survivorship of competitors was examined in detail for two additional megaguilds, epifaunal suspension feeders and shallow infaunal deposit feeders (Fig. 7), both because of the good representation of these taxa in the fossil record and because they serve to demonstrate the variability among the models. The dramatic plot in Figure 7A shows that Level II extinction generates a distribution peaked at low competitive rank. The guild of epifaunal suspension feeders should be dominated by competitively inferior taxa after a Level II extinction within a Cambrian community (Fig. 7A), but would have only a slight predominance of taxa of intermediate competitive rank in post-Cambrian communities (Fig. 7B,C). Level II shallow infaunal deposit feeder survivors, however, are dominated by taxa of relatively low competitive rank in all the models (Fig. 7D–F).

Discussion

Predictions of bottom-up driven cascades of secondary extinction (Quince et al. 2005), combined with observations that primary production is often disrupted severely during times of mass extinction, suggest that such disruption could account for significant proportions of the diversity lost during those intervals of extinction. Studies of perturbation of modern ecosystems further suggest that cascades probably do not follow simple linear rules of cause (loss of primary production) and effect (consequential loss of consumers) (Williams et al. 2002), but rather that the consequences of a loss of productivity are emergent from the complex networks of trophic and other biotic interactions. The model presented in this paper combined bottom-up (production) and top-down (consumption) interactions (Worm and Duffy 2003), as well as intraguild competitive interactions, with very general hypotheses of food web variation through the Phanerozoic, to examine how disruption of primary production affects secondary extinction and extinction cascades. In spite of critical information that can be difficult to obtain for fossil communities, for example the specific details of intimate biotic interactions, our growing understanding of the nature and distributions of interactions in modern communities serves as a guide.

The model simulations were parameterized using reasonable inferences, based on current paleoecological knowledge, of taxonomic richness and of guild and functional diversities. Specifying parameter values when those parameters might range broadly raises concerns of overparameterization and model specificity (May 2004). A partial solution is the broad exploration of parameter sets and combinations in order to evaluate, at least qualitatively, the impact of parameter values on the model. That is essentially the approach adopted in this paper, as well as by Angielczyk et al. (2005) in an empirical application of the model to specific Late Permian terrestrial communities. An alternative approach, which also requires extensive empirical data, is the inference of model parameters from the data themselves (see below). Nevertheless, the following interesting observations emerge from the exploratory application of the model to the hypothetical Bambachian food webs.

Increasing the level of primary production disruption (ω) increases the magnitude of secondary extinction in all food webs. The main cause of secondary extinction is the loss of primary consumers as they are increasingly deprived of their sources of food. This loss is propagated through the trophic network to secondary and higher consumers, but reasonable assumptions of consumer behavior suggest that those consumers should compensate for the loss of a trophic resource or prey taxon by increasing the intensities of their interactions with remaining prey taxa. The result is top-down exacerbation of the stress experienced by prey taxa, thereby accelerating their approach to extinction thresholds. This positive top-down feedback elevates the level of secondary extinction caused by any particular level of disruption of primary production to the point where a positive feedback-loop among the trophic levels causes a catastrophic increase of secondary extinction. Therefore, two distinct forms of secondary extinction may exist for any guild within the network: Level I, where secondary extinction is largely the result of bottom-up propagation, and Level II, where positive top-down feedback contributes to catastrophic increases in secondary extinction.

The level of secondary extinction that results from any given magnitude of ω depends ultimately on the general complexity of the trophic network, that is, the number of megaguilds and the geometry of the trophic connections among them. This is illustrated clearly by comparing the hypothetical Cambrian and post-Cambrian networks. The absence of direct predation, or a limited number of predators on a consumer guild, such as pelagic suspension feeders, means that secondary extinction, both Level I and II, is largely a function of the increasing loss of primary producer resources (ω) (Fig. 5A–C). The addition of predation, however, and the top-down compensatory feedback of predators, can result in variable and complicated patterns of Level I and Level II secondary extinction. Epifaunal carnivores exhibit such patterns in the post-Cambrian models (Fig. 5E,F). There are two maxima of secondary extinction: after an initial and rapid increase, the secondary extinction response declines drastically, only to increase catastrophically at a yet higher level of primary producer disruption.

Overall, the increasing number of connections among megaguilds during the Phanerozoic, representing increases in functional diversity, serve to delay the onset of secondary extinction and catastrophic cascades of extinction. For example, compare the carnivores among the three models. The onset of secondary extinction occurs at increasingly higher levels of primary producer shutdown through the Phanerozoic in both the epifaunal carnivores (Fig. 5E,F) and pelagic carnivores (Fig. 5G,H). This would suggest increasing community resistance to such extinctions through the Phanerozoic (Tang 2001). Community stability also increases, if one defines stability as a transition among different community ''states,'' because the top-down driven transition to Level II, though it occurs in all megaguilds in all the models, can sometimes be dampened (for example, in the post-Cambrian epifaunal carnivores).

One potential mechanism opposing the top-down feedback loop is the extinction of intraguild competitors. For any consumer species, the loss of a competitor might ameliorate the impact of the loss of trophic resources and increasing predation intensity. This mechanism was examined in the model networks by ranking members of each megaguild uniformly and allowing the extinction of competitive superiors to restrain a species' approach to extinction thresholds. The inclusion of competitive interactions in the model does not alter the occurrence of catastrophic secondary extinction, implying that those interaction terms are overwhelmed by the bottom-up perturbations and top-down feedback in the simulations. Interesting patterns of differential survival do, however, emerge from the simulations. In several megaguilds, top-down compensatory feedback interacts with competition to result in the increased probability of survival of competitively inferior taxa. This result can be understood qualitatively if one considers that for a competitively superior species, the loss of a fellow guild member has little or no offsetting effect on the acquisition of trophic resources, whereas for an inferior species, the loss of a competitive superior releases otherwise unavailable resources, allowing it to expand its realized niche (Hutchinson 1957). The only groups that display this result, however, are those prey guilds involved in simple predator-prey networks, that is, having a single predatory guild. For example, epifaunal suspension feeders are preyed upon solely by pelagic carnivores in the Cambrian model, and the distribution of Level II survivors is one dominated by competitively inferior taxa. The pattern is not present in the post-Cambrian models where epifaunal suspension feeders are involved in more complex trophic networks, involving intermediate epifaunal carnivores. Shallow infaunal deposit feeders, on the other hand, remain in essentially isolated sub-communities in all three models involving predation solely by top shallow infaunal carnivores. The preferential survival of competitively inferior taxa is persistent in this megaguild.

The predominance of such taxa in cohorts of survivors in the simulations is very reminiscent of empirically observed post-extinction ''disaster'' taxa (Schubert and Bottjer 1992). Disaster taxa have been described as opportunistic generalists because of their increased representation and ranges after mass extinction events. These taxa would be recognized on ecological timescales as early colonizers and perhaps ''weedy'' species. Their emergence from the simulations might be important validation of the model and is not without precedent in studies of modern communities

(Nielsen and Navarrete 2004). Interestingly, skewed survivor distributions, with a predominance of inferior competitors, has also been observed in terrestrial plant communities of the Permo-Triassic (Looy et al. 2001) and is consistent with models of extinction in modern plant communities (Tillman et al. 1994; Loehle and Li 1996). The model presented here suggests that the dominance of such taxa in post-Level II extinction communities is largely a function of their pre-extinction trophic ecologies and their trophic connectedness. The model therefore predicts that such differential patterns of survival among various megaguilds (for example, compare epifaunal suspension feeders and infaunal deposit feeders in the post-Cambrian webs) should be observed only when bottom-up driven, Level II ecosystem collapse was the mechanism of secondary extinction. Furthermore, Level II secondary extinction is one possible mechanism for generating the ecosystem-replacing Category I extinctions described by Droser et al. (2000) (see also McGhee et al. 2004).

Parameter Determination.—The parameter ranges of the numerical model define a broad parameter space, and exploration of these ranges should yield additional insight into secondary extinction in ancient communities. For example, the effect of nonrandom extinctions or perturbations of primary producers could provide insight into similar perturbations of modern ecosystems, or the use of a wider range of power law distributions for determining the in-degrees of species would result in different ranges of trophic specialization. As mentioned earlier, however, even if parameter ranges could be limited by reliable ecological insight, exploring the possible sets of parameter combinations would still require a prohibitively large number of simulations. It is tempting to use a forward model such as this one to search for and tune parameter sets that produce observed extinction data. Given the complexity of the model, however, and the complexity of the systems that it seeks to describe, it is quite likely that different parameter sets are capable of producing similar results. Exploration of parameter ranges as a search tool for an extinction level is therefore neither feasible nor desirable, unless very specific empirical sample-level paleocommunity data were available. In that case, one alternative would be to use data comprising pre- and postextinction measures of ecosystem composition, along with the model, to estimate parameter posterior probability densities. Bayes' formula would be used to explore the parameter space of the model and data, estimating the posterior distribution of extinction parameters for the feedback model. A Bayesian formulation of the feedback model may be written as

$$p(\theta \mid \Psi) = \frac{p(\Psi \mid \theta)p(\theta)}{p(\Psi)} \tag{10}$$

where ψ is a vector of the observed within-guild extinction data, θ are the model parameters ($=\mathbf{N}$, $\bar{\gamma}$, $\bar{\omega}$) (Appendix), of which $\bar{\gamma}$ and $\bar{\omega}$ and are unknown, and $p(\psi) = \int p(\psi \mid \theta)p(\theta)\, d\theta$ is the normalizing constant. $\mathbf{N}$ is a vector of guild taxonomic diversities, $\bar{\gamma}$ is a vector of degree distribution (power law) coefficients, and $\bar{\omega}$ is a vector (or scalar) denoting levels of primary producer disruption. Both $\mathbf{N}$ and $\bar{\gamma}$ are of a size equal to the number of guilds. An explicit solution of the formula is impossible given the high dimensionality of θ and the complexity of the problem, but evaluation should be possible via stochastic simulation of $p(\theta \mid \psi)$, for example using Markov Chain Monte Carlo sampling or other types of Metropolis-Hastings sampling algorithms (Metropolis et al. 1953; Marjorum et al. 2003).

Recovery.—The catastrophic shift between Level I and II extinctions, in response to the perturbation of primary production, may bear implications for the subsequent recovery of ecosystems that experience Level II extinction. It has been hypothesized that ecosystems which undergo a dramatic shift in state as a result of environmental perturbation will show hysteresis patterns of recovery (Scheffer et al. 2004; van Nes and Scheffer 2004). In other words, simple reversal of the perturbation past the point of catastrophe will not reverse the state of the system, but reversal must instead extend to some point that triggers another dramatic shift, this time back to the pre-perturbation state. If this is the case for Level I to II transition, then ecosystems would be expected to display extended periods of recovery from mass extinctions that involved ecosystem collapse (Looy et al. 1999; Benton et al. 2004; Pruss and Bottjer 2004). Level II extinction would also then be a potential explanation of the ecosystem-destroying Category I extinctions defined by McGhee et al. (2004). Recovery would depend upon the recovery of primary production, the evolution of additional taxa from the survivors, and the assembly of new ecosystems. These issues could be explored by coupling output from the current model with models of ecosystem recovery (Solé et al. 2002) and evolution (Drossel et al. 2001; Quince et al. 2005).

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Appendix

1. There is a set of links, R, mapping consumers to prey resources in the set M. The number of links (size of R) is denoted as $\#(R) = r_1$, with $0 < r_1 \leq \#(M)$. Let $\#(M) = M$. ω resources are eliminated randomly from M, with $0 < \omega \leq M$. If W is the set of eliminated resources, then $W \subset M$ and $\#(W) = \omega$. The probability that $R \rightarrow W$, that is, the set of consumer links all correspond to eliminated resources is

$$\begin{aligned} p(e_{r_1} | \omega) &= \binom{M - r_1}{\omega - r_1}\binom{M}{\omega}^{-1} \\ &= \frac{(M - r_1)!}{(\omega - r_1)!(M - r_1 - \omega + r_1)!}\,\frac{\omega!(M - \omega)!}{M!} \\ &= \frac{\omega!(M - r_1)!}{M!(\omega - r_1)!}. \end{aligned}$$

2. The expected, or mean, number of secondary extinctions (ψ) given the above probability is

$$\psi = \sum_{r_1=1}^{\omega} p(e_{r_1} | \omega) p(r_1) N_1$$

where $p(r_1)N_1$ is the expected number of consumer taxa with r_1 in-links. ψ is the summation of expected extinctions given consumer taxa with $0 < r_1 \leq \omega$, and is reduced algebraically as follows:

$$\psi = \sum_{r_1=1}^{\omega} \binom{M - r_1}{\omega - r_1} \binom{M}{\omega}^{-1} p(r_1) N_1$$

$$\Rightarrow N_1 \sum_{r_1=1}^{\omega} \frac{\omega!(M - r_1)!}{M!(\omega - r_1)!} p(r_1) \Rightarrow \frac{N_1 \omega!}{M!} \sum_{r_1=1}^{\omega} \frac{(M - r_1)!}{(\omega - r_1)!} p(r_1).$$

3. The hypergeometric formula describes the number of different ways that, given M potential prey, r consumer links, and a prey extinction level of ω, exactly n of the consumer's links will be lost. Because the mean of the resulting hypergeometric distribution in this case is $r\omega/M$, then equation (6) may be derived as follows. Define an extinction threshold T ranging between 0 and 1, and set extinction to occur when the ratio of the carrying capacity of the population with n links to carrying capacity with r links falls below T. Because both T and the ratio have a maximum value of 1, and carrying capacity is equivalent to the number of incoming links, this definition can be expressed as

   $$p(e \,|\, \omega) = 1 - \frac{n}{r}.$$

4. The feedback loops cannot be formulated explicitly, but they can be summarized symbolically as follows. Up until this point, the model has operated at geological timescales, above the ecological and generational scales of organisms. The basic model (eq. 2) can be expressed as

   $$E(\psi_{1,\tau} \,|\, \omega) = N1 \cdot f[M, \omega, P(r_{N1})].$$

   That is, expected extinction in guild $N1$ is the product of diversity in that guild and a function of available primary production (M), primary producer shutdown (ω) and the probability distribution of $N1$'s trophic links. Feedback from the consumers of guild $N1$, those are species in guild $N2$, is incorporated as

   $$E(\psi_{1,\tau} \,|\, \omega) = N1 \cdot f[M, \omega, P(r_{N1}), P(S_{N2,\tau}), P(C_{N1})]$$

   where $P(S_{N2,\tau})$ is the distribution of link strengths in $N2$, and $P(C_{N1})$ is the distribution of competitive ranks in $N1$, at time τ. τ is an approximately single-valued subdivision of the larger (geologic) time interval t, e.g. organismal generations, with $\tau \ll t$. Given consumer compensation for lost links,

   $$P(S_{N2,\tau-1}) = f[P(\mathrm{r}_{N2}), N1_{\tau-1}]$$

   and expressing guild diversity at a point in time as a function of earlier diversity, where

   $$N1_{\tau-1} \approx N1_{\tau-2} - E(\psi_{1,\tau-2} \,|\, \omega),$$

   then network-mediated extinction with positive feedback may be expressed as

   $$E(\psi_{1,\tau+2} \,|\, \omega) = N1_{\tau+2} \cdot f[M, \omega, P(r_{N1}), P(r_{N2}), N1_{\tau}, (\psi_{1,\tau} \,|\, \omega)].$$

5. The basic model can be expressed as an ordinary differential equation if we assume a simple linkage relationship between consumers and prey. Let N be the number of consumer species, ω the number of prey extinctions, and ψ the resulting number of secondary consumer extinctions. Then $\psi = N(\omega)$ when $\omega > 0$ means that secondary extinction is a function of the number of consumers and the level of prey extinction. This leads to the rate relationship

   $$\frac{d\psi}{d\omega} = \lambda\psi$$

   which yields the general solution

   $$\psi = \psi_0 e^{\lambda\omega}$$

   where λ is a constant, and ψ_0 is the initial level of secondary extinction. Setting the latter value to one, then when $\omega = M$ (complete extinction of prey), and therefore $\psi = N$ (complete secondary extinction), we derive

   $$N = e^{\lambda M} \Rightarrow \ln(N) = \lambda M \Rightarrow \lambda = \ln(N)/M.$$

   Therefore, a general solution of the basic model is

   $$\psi - \exp\left[\frac{\omega}{M} \ln(N)\right]$$

   which is qualitatively similar to the probabilistic basic model. The differential equation model cannot be extended easily, however, to accommodate individual guild and species properties such as varying link distributions, extinction thresholds, and compensatory feedback.

6. List of notation

   P—probability of event
   $p(e \,|\, x)$—probability of taxon extinction given the occurrence of x
   ω—level of primary producer shutdown or extinction
   r—taxon's in-degree, or number of incoming trophic links
   ψ_i—level of secondary extinction in guild i
   E—expected, or mean level
   $P(x)$—probability density of x
   T—taxon's extinction threshold based on population size, or number of available trophic resources (prey taxa)
   K_i—taxon's carrying capacity given i trophic resources
   S—predation intensity on a taxon, measured as the sum of predators' link strengths
   R—competitive rank of a taxon within its megaguild
   γ—exponential coefficient of power law distribution
   $p(\theta \,|\, \Psi)$—posterior probability of extinction model θ given observed extinction data Ψ
   $p(\Psi \,|\, \theta)$—likelihood of observed extinction data Ψ given extinction model θ
   $p(\theta)$—prior probability of extinction model θ