

MODELING THE ROLE OF PRIMARY PRODUCTIVITY DISRUPTION IN END-PERMIAN EXTINCTIONS, KAROO BASIN, SOUTH AFRICA

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Abstract—The end-Permian mass extinction is well-known as the most severe mass extinction of the Phanerozoic. Terrestrial communities appear to have been strongly affected by the event, but the cause of the extinction remains enigmatic. Here we explore whether primary producer disruption (e.g., extinction of terrestrial plants) could have led to a collapse of end-Permian terrestrial ecosystems, using models of probabilistic trophic networks. Based on a trophic network reconstructed for the *Dicynodon* Assemblage Zone community of the Karoo Basin, we show that late Permian terrestrial communities were vulnerable to collapse brought about by the disruption of primary producers. However, relatively high levels of primary producer loss are needed to account for observed levels of extinction among consumers in the *Dicynodon* zone fauna. Depending on network parameters, we predict that a shutdown of 69% to 87% of primary producers would be needed to generate observed extinction levels. A disruption of this magnitude is not unreasonable, given that terrestrial floras underwent a major turnover at the end of the Permian, and our predictions can be tested by further scrutiny of floras from this time.

INTRODUCTION

The end-Permian mass extinction is the largest extinction event of the Phanerozoic, with evidence suggesting that up to 80% of marine animal species and 74% of terrestrial animal families disappeared at this time (Erwin et al., 2002, Benton and Twitchett, 2003; Benton et al., 2004; Ward et al. 2005). Although the extinction has been the subject of much scrutiny, its ultimate cause remains enigmatic. A variety of scenarios have been proposed, including extraterrestrial impact (Retallack et al., 1999; Becker et al., 2004), catastrophic release of oceanic methane (Erwin, 1993; Krull and Retallack 2000), and global warming caused by Siberian flood basalt volcanism (Bowring et al., 1998; Wignall, 2001), but none is supported by conclusive evidence.

The uncertainty surrounding the trigger for the end-Permian event reflects the fact that very few unique mechanisms have been associated definitively with mass extinctions, the notable exception being the asteroid impact at the end of the Cretaceous (Alvarez et al., 1980). However, regardless of their ultimate causes, it is clear that episodes of mass extinction represented times of severe ecological crisis, during which ecological community functions were disrupted or shifted into new states. Many of the species that became extinct during intervals of mass extinction therefore probably did not succumb to the direct effects of abiotic triggers, but rather were victims of the resultant ecological crises and failing communities (Roopnarine, in review). The disruption of primary production is cited often as a proximal cause of ecological crises during times of mass extinction (Vermeij, 1995; Martin, 1996; Allmon, 2001), because it is predicted to unleash avalanches of secondary extinctions at higher trophic levels (Borrvall et al., 2000; Vermeij, 2004). 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 species diversity, functional or guild diversity, the pattern and relative strengths of trophic links between species, and the comparative species richnesses of guilds of similar trophic function but different composition (e.g., herbivorous insects and tetrapods) (Roopnarine et al., 2004).

Here we use a model of probabilistic trophic networks to explore how the disruption of primary producers may have affected end-Permian terrestrial ecosystems, focusing on the well-studied communities of the Karoo Basin of South Africa. We are interested specifi-

cally in patterns of secondary extinction as primary producer disruption is increased, as well as predicting the levels of disruption that would be necessary to cause observed end-Permian terrestrial extinctions. Previous simulations indicate that secondary extinctions do not scale linearly with primary producer disruption (Roopnarine et al., 2004; Roopnarine, in review). Instead, a threshold exists beyond which communities collapse and high levels of secondary extinction are observed. Our current models suggest that a range of levels of primary producer disruption could have caused the observed Permian secondary extinctions, but the inferred levels depend critically on details of the reconstructed trophic networks.

RECONSTRUCTING PALEO-TROPHIC NETWORKS

An important issue that must be considered in an analysis such as ours is the fact that very little can be stated precisely about the mechanisms by which disruptions of primary production might cause secondary extinctions in ancient communities. This is because the mechanisms must operate through complex trophic pathways and systems of sometimes poorly known species diversities, interactions, and linkages. Data that are difficult to obtain, both neontologically (Goldwasser and Roughgarden, 1997) and paleontologically, dictate to a large extent the possibility of reconstructing paleo-trophic networks. For example, interactions between fossil species often are obscure (Leighton, 2004), and even those interactions that are inferred with great confidence (e.g. 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. Therefore, we must 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 trophic network theory, such as trophic species and connectance (Williams and Martinez, 2000), that cannot be quantified and applied with measurable precision in paleoecological contexts.

Constructing probabilistic networks on the basis of known properties and distributions of Recent trophic networks (Havens, 1992; Martinez, 1992; Montoya and Solé, 2002) allows us to explore the responses of paleo-trophic networks to varying levels of primary producer perturbation and extinction, without having to know all the exact details of the network in question (Roopnarine, in review). For example, species with similar potential interactions can be grouped into

guilds on the basis of morphology, phylogenetic affinity, and comparison to extant organisms. Links between species in different guilds, and the properties of links (e.g., interaction strengths), are specified not as fixed vector quantities, but instead are assigned randomly to members of a guild based on distributions derived from reasonable inferences from organismal and autecological data. By constructing a large number of trophic networks that are based on the same parameters, but differ stochastically in the specific properties assigned to each member of the included guilds, and subjecting these networks to primary producer disruption, it is possible to estimate how a particular paleontological community likely would have responded to such a disturbance. A detailed description and justification of the approach used in this paper can be found in Roopnarine (in review).

EXTINCTION IN PALEO-TROPHIC NETWORKS

Figure 1 shows a simple three guild schematic network with each guild representing a set of species sharing the same sets of potential prey. This means that, for example, while the specific prey of two predators are not known precisely, we still can identify the guilds to which the prey most likely belonged. Each species within a consumer guild possesses an in-degree, or number of incoming trophic links, or prey species. Therefore, there are detailed species-level directed networks embedded within the higher-level schematic network. Let g represent the number of guilds ($= 3$ in Fig. 1), and N_i be the diversity of the i^{th} guild, G_i . If ρ_i is the frequency (estimated probability) of primary extinction, and φ_i the frequency of secondary extinction in G_i , then

$$E(\psi_i) = (\rho_i + \varphi_i) N_i$$

where $E(\psi_i)$ is the expected level of total extinction, ψ_i , in guild G_i .

Suppose that a species' survival in a trophic network relies solely upon having at least one trophic (food) resource. Then from Figure 1, if the bottom-level of perturbation to G_i (i.e., the disruption of primary productivity) is ω , then the probability of secondary extinction of a taxon in guild G_2 is

$$(\varphi_2 | \omega, r_2) = \binom{N_1 - r_2}{\omega - r_2} \binom{N_1}{\omega}^{-1} = \frac{\omega! (N_1 - r_2)!}{N_1! (\omega - r_2)!}$$

where r_2 is the in-degree of the taxon. Then

$$E(\psi_2 | \omega) = (\rho_2 + \sum_{r_2=\omega}^{r_2=N_1} [(\varphi_2 | \omega, r_2) P(r_2)]) N_2$$

where $P(r_2)$ is a density function describing the in-degrees of taxa in G_2 . Similarly,

$$E(\psi_3 | \omega, \psi_2) = (\rho_3 + \sum_{r_3=\psi_2}^{r_3=N_2} [(\varphi_3 | \omega, r_3) P(r_3)]) N_3$$

The summations on the right hand side of the formulae have limits at ω and ψ_2 successively because

$$\left. \begin{aligned} 0 < (\varphi_i | \psi_{i-1}, r_n) \leq 1 & \text{ for } \psi_{i-1} \geq r_n, \\ (\varphi_i | \psi_{i-1}, r_n) = 0 & \text{ for } \psi_{i-1} < r_n \end{aligned} \right\}$$

and consumer species are immune to secondary extinction if extinction in the prey guild is not greater than their in-degree.

This basic model is made more realistic by permitting a taxon's populations to become extinct prior to the loss of all in-links (r), ac-



FIGURE 1. A schematic three guild trophic network. Each guild represents a set of species sharing the same sets of potential prey, and arrows point in the direction of energy transfer between guilds. M represents units of primary production; N_1 represents the diversity of guild 1; N_2 represents the diversity of guild 2.

knowledging that the loss of resources stresses population sustainability. For example, if the carrying capacity of a population is considered to be a function of incoming energy and the state of the community, then carrying capacity and hence population size decline as the number of food sources decreases. Population size eventually reaches a lower threshold where stochastic factors make extinction inevitable (Lande et al., 2003), even though $r \gg 0$. Approaching an extinction threshold therefore can be described as changes in carrying capacity resulting from the loss of trophic resources. Given a threshold T , the probability of secondary extinction now follows the rules

$$\left. \begin{aligned} 0 < (\varphi_i | \psi_{i-1}, r_n) \leq 1 & \text{ for } \psi_{i-1} \geq r_n(1 - T_i), \\ (\varphi_i | \psi_{i-1}, r_n) = 0 & \text{ for } \psi_{i-1} < r_n(1 - T_i) \end{aligned} \right\}$$

Varying thresholds among guilds serves to distinguish guilds of similar trophic function (e.g., carnivores), but differing in other ecological impacts and susceptibilities (e.g., body size).

Finally, 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 is at least balanced by incoming energy. The energy 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. The model so far considers the loss of an in-link to represent 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, i.e. 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 ω goes to N_1 . 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

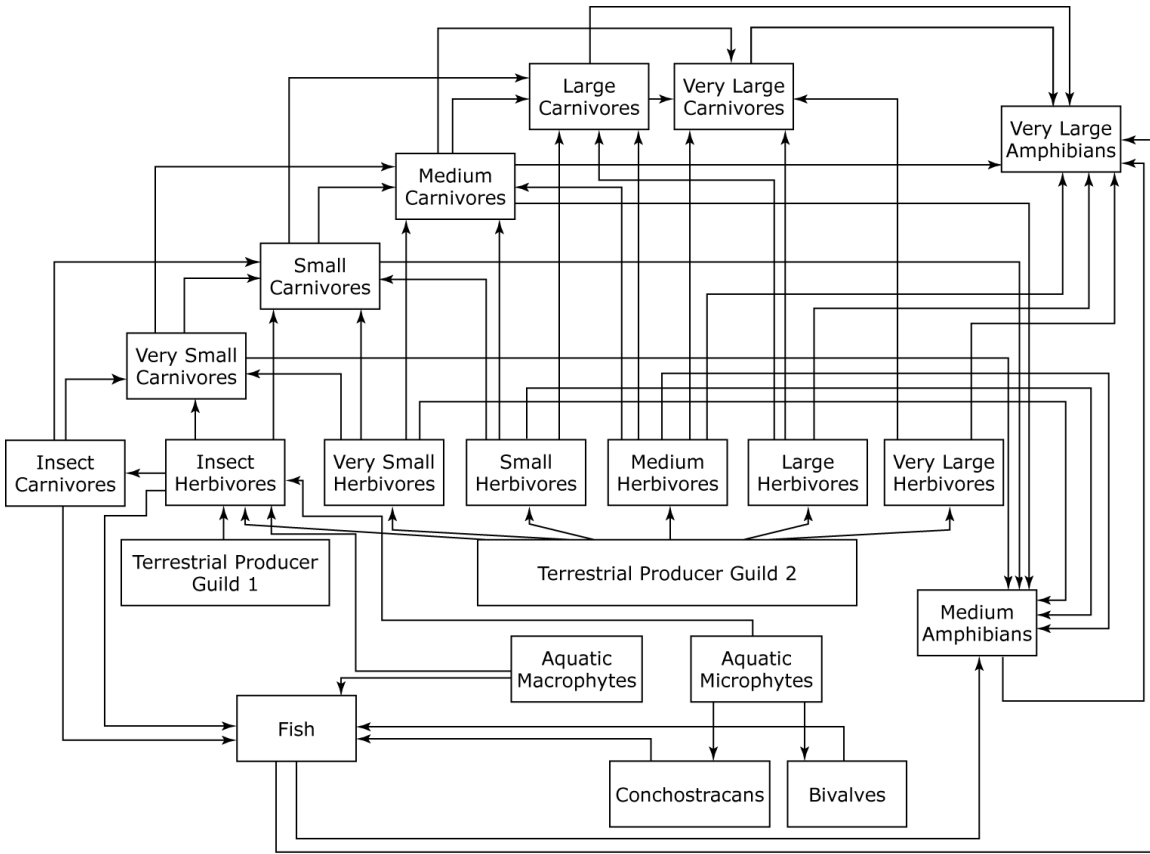


FIGURE 2. Trophic network used in the FPM. Each guild represents a set of species sharing the same sets of potential prey, and arrows point in the direction of energy transfer between guilds. Terrestrial Producer Guild 1 represents primary production accessible only to insect herbivores; Terrestrial Producer Guild 2 represents primary production accessible by all terrestrial herbivores.

remaining links. Such compensation, though, has a negative impact on prey species, since it increases the rate at which prey species approach their effective extinction thresholds. The result is additional extinction of prey species, followed possibly 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. The model can now be summarized as

$$E(\psi_{2,\tau}|\omega) = N_2 \cdot f(N_1, \omega, \rho_2, P(r_2))$$

Feedback from the consumers of guild G_2 , i.e. guild G_3 , is incorporated as

$$E(\psi_{2,\tau}|\omega) = N_2 \cdot f(N_1, \omega, \rho_2, P(r_2), P(S_{3,\tau-1}))$$

where $P(S_{3,\tau-1})$ is the distribution of link strengths in G_3 at time τ . τ is an approximately single-valued subdivision of the larger (stratigraphic) time interval t , e.g. organismal generations, with $\tau \ll t$. Given consumer compensation for lost links,

$$P(S_{3,\tau-1}) = f(P(r_3), N_{2,\tau-1})$$

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

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

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

$$E(\psi_{2,\tau+2}|\omega) = N_{2,\tau+2} \cdot f(N_1, \omega, \rho_2, P(r_2), P(r_3), N_{2,\tau}, (\psi_{2,\tau}|\omega))$$

PRIMARY PRODUCER DISRUPTION AND EXTINCTION IN END-PERMIAN TERRESTRIAL ECOSYSTEMS

A second issue that must be addressed is whether there is evidence of large-scale primary producer disruption in end-Permian terrestrial ecosystems. Even if the effects of primary extinction *could* cascade through these trophic networks, such a scenario would be unlikely if terrestrial plants pass through the Permo-Triassic transition largely unscathed. However, a number of data sources suggest that primary production in terrestrial ecosystems was disrupted at the Permo-Triassic boundary. For example, data from the plant and pollen fossil records, as well as fossil soils, indicate that a major floral turnover associated with environmental changes occurred at the Permo-Triassic boundary (e.g., Retallack, 1995, 1999; McLoughlin et al., 1997; Lozovsky, 1998; Retallack and Krull, 1999; Looy et al., 1999; 2001; Tiwchett et al., 2001; Retallack et al., 2003). This turnover coincides with a worldwide hiatus in coal formation (Faure et al., 1995; Retallack et al., 1996; McLoughlin et al., 1997), and a spike in fungal spores that likely corresponded to large-scale plant die-offs (Eshet et al., 1995; Visscher et al., 1996; Steiner et al., 2003; although see Foster et al., 2002). Changes in sedimentary deposition observed in Russia, Australia, and South Africa also are consistent with increases in erosion and runoff that would occur during a large-scale shutdown of terrestrial plants (Smith, 1995; Newell et al., 1999; Ward et al., 2000; Michaelson, 2002; Benton et

al., 2004). Finally, dramatic, global shifts in carbon isotope ratios are observed at the end of the Permian (e.g., MacLeod et al., 2000; Erwin et al., 2002; de Wit et al., 2002; Benton and Twitchett, 2003), indicating that some type of large perturbation to the global carbon cycle occurred at this time. Taken together, these observations suggest that regardless of the ultimate cause of the end-Permian mass extinction, disruption in primary production had the potential to at least contribute to observed extinctions on land. We therefore seek to estimate the minimum level of disruption that would have been necessary to cause the observed extinctions.

METHODS

Data Collection

The trophic network modeled in our analysis is based on the fauna of the Late Permian-age *Dicynodon* Assemblage Zone of the Karoo Basin of South Africa. The *Dicynodon* zone is the youngest of six Middle to Late Permian-age terrestrial faunal assemblages found in South Africa, and ends at the Permo-Triassic boundary (e.g., Rubidge, 1995; Smith and Ward, 2001; Ward et al., 2005). Because detailed faunal lists and precise correlations are not yet available for all *Dicynodon* zone localities (although see Kitching, 1977), we treated all taxa reported from the assemblage zone as a single paleoecological community. This is a simplification, however, because not all taxa reported from the zone have stratigraphic ranges spanning the entire zone (Rubidge, 1995; Smith and Ward, 2001; Ward et al., 2005).

We compiled a fauna of 101 animal genera for the *Dicynodon* zone, based on a variety of published references (e.g., Rubidge, 1995; van Dijk and Geertsema, 1999; Damiani and Rubidge, 2003). The genus level was chosen for this work because taxonomic uncertainty surrounds the species level for many groups of Permo-Triassic vertebrates, making the genus level a more conservative estimate of taxonomic diversity. The fauna includes one bivalve genus, one conchostracan, seven fish, 54 tetrapods, and 40 insects, which were binned into a total of 17 guilds (lists of taxa in each guild available from KDA upon request). Tetrapods were divided into 12 guilds based on body size (using maximum skull length as a proxy) and diet (herbivore vs. carnivore, based on cranial and dental morphology); bivalves, conchostracans, and fish are represented by one guild each. Insects were divided into two guilds (carnivores and herbivores) with equal diversity. We did not attempt a more precise division of insects because most of the included taxa are known only from wings, and some are members of groups whose extant members include both carnivores and herbivores. Because the fossil record provides an incomplete representation of the diversity of organisms alive at any one time, we multiplied the observed diversity of each guild by a factor of two for use in our modeled trophic network (i.e., the total diversity of the modeled network was 202 taxa).

Paleo-trophic Network Construction and Perturbation

Links between guilds were assigned based on three factors, diet, body size, and likely habitat. Diet determined whether a consumer's links would include primary producers, other consumers, or a combination of the two. Body size did not affect incoming trophic links to primary consumers, but did affect secondary consumers; each secondary consumer guild was constrained to feed on primary and secondary consumer guilds of equal body size or the next two smaller body size increments. Habitat reflected whether the guild in question likely was terrestrial or aquatic. Terrestrial guilds fed on other terrestrial guilds, whereas aquatic guilds fed on other aquatic guilds. The main exceptions to this rule were the insects and amphibians, reflecting the fact that these groups straddled terrestrial and aquatic systems (e.g., many terrestrial insects have aquatic larvae). A schematic diagram of the modeled food web is shown in Figure 2. The in-degree (number of incoming trophic links) of each species within a guild was drawn randomly from a truncated power law distribution. Power law distribu-

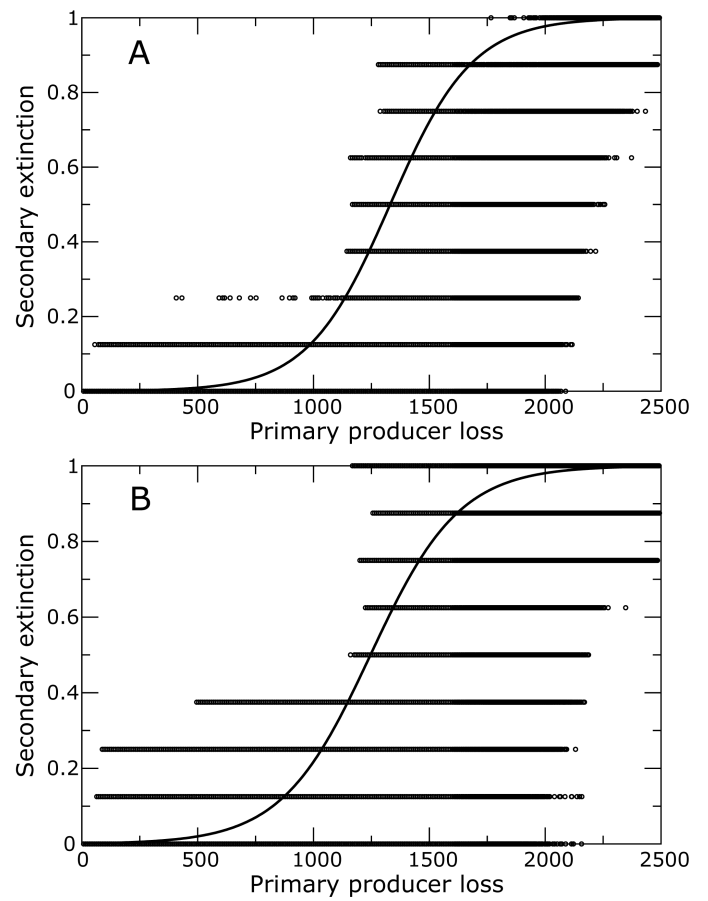


FIGURE 3. Examples of the best-fit logistic curves used to estimate primary producer loss implied by observed levels of consumer extinction in the Karoo Basin. Part **A** shows the curve for the very small herbivore guild based on data from the FPM. Part **B** shows the curve for the large carnivore guild based on data from the FPM. Estimated minimum primary producer loss for **A** and **B** are approximately 86% and 94%, respectively. Units for x-axis are units of primary production; y-axis represents secondary extinction within the guild.

tions took the form $P(r) = M\gamma^{-1}r^{-\gamma}$ (with $\gamma = 2$), where M is the species richness of the prey node(s).

The complete feedback model was simulated in the following way: When a consumer loses some of its in-links because of prey extinction, it compensates by increasing the strength of its remaining links, so that individual link strength is always a function of current in-degree ($= 1/r$). This increases stress on prey taxa, thereby accelerating their approach to extinction. Increased stress is ameliorated to some degree in the model by the inclusion of within-guild competitive rankings among taxa. Competitive ranks were determined by random ordering of species within nodes, yielding a uniform distribution. Extinction of a species' competitors makes more resources available, and could 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 is now re-formulated as

$$p(e) = 1 \text{ when } T > 1 - \frac{1}{2} \left(\frac{S_0 - S_i}{S_0} + \frac{R_0 - R_i}{R_0} \right)$$

where $p(e)$ is the probability of extinction, S_i is predation intensity and R_i is competitive rank within a guild when $i = \zeta_j = !$. S_0 and R_0 are predation intensity and competitive rank respectively when $! = 0$. The extinction of competitors should serve to slow a population's approach to its extinction threshold.

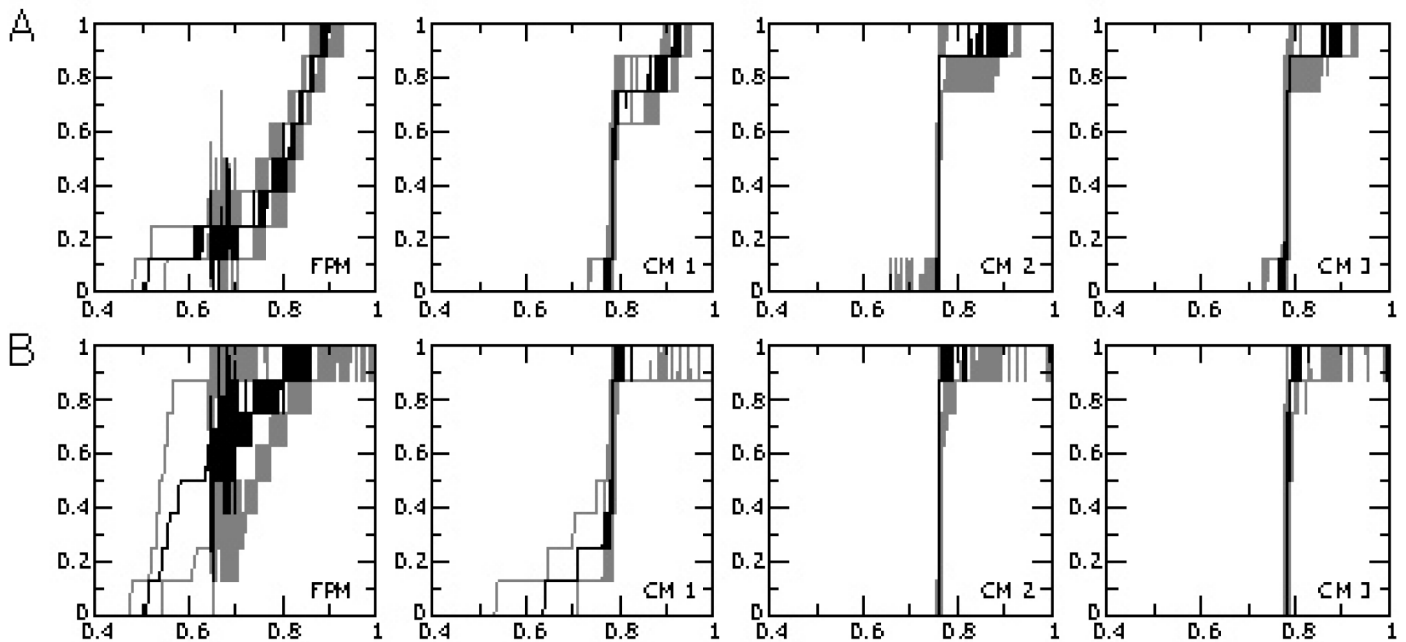


FIGURE 4. Example curves showing responses of guilds to increasing levels of primary producer loss. Part **A** shows the response of the very small herbivore guild in the FPM and Control Models 1 – 3. Part **B** shows the response of the large carnivore guild in the FPM and Control Models 1 – 3. Black lines represent median secondary extinction value for a given increment of primary producer loss; gray lines represent 25th and 75th percentiles. X-axis in each plot represents primary producer loss; y-axis represents secondary extinction within the guild.

Each network was subjected to disruption of primary production by eliminating a fixed number of units of primary production (see below), and assessing the number of consumer species (at all trophic levels) that became extinct as a consequence (secondary extinction). The magnitude of the disruption, $\omega!$, ranged from 0 to M (the maximum level of primary production). Top-down feedback was never allowed to propagate to the primary producer guilds in order to distinguish the effects of bottom-up primary production perturbation and top-down cascades of secondary extinction.

Five hundred simulations were performed for each parameter set (see below) and food web. Simulation programs were written in standard C++, and are available upon request from PDR. All simulations were run on a 16 CPU Pentium Xeon Linux cluster at the California Academy of Sciences. Subsequent statistical analyses were performed with Stata for Linux, and scripts written in Octave and R. The scripts are also available upon request from PDR (Octave) and SCW (R).

Units of Primary Production

Paleoproductivity usually is expressed indirectly as the temporal and/or spatial variation of proxy measurements (e.g., $\delta^{13}\text{C}$). 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. Yet given that for any paleocommunity of consumers that we observe, there must have been sufficient levels of primary production to support them, we can parameterize the model on the basis of initial consumer demand (i.e., when $\omega! = 0$).

The major factor controlling a consumer's demand for production is body size. Larger animals consume relatively greater amounts of food (i.e., metabolic requirements scale positively with increasing body size) (Peters, 1983), and hence larger individuals are more sensitive to interruptions of supply (e.g., Roopnarine, 1996). Larger consumers also generally have lower population densities, and larger range requirements (Brown, 1995), and therefore higher probabilities of extinction.

On the other hand, larger consumers also tend to have broader dietary repertoires as a function of larger size, due for example to larger and more efficient digestive systems, or the ability to handle a wider array of prey. Large consumers in our model therefore have more sensitive extinction thresholds, although large secondary consumers also have more incoming links (i.e., more potential prey).

The number of available units of primary production was fixed at 10 times the maximum number of primary consumers among the networks. This function reflects the general thermodynamic scaling of energy transfer among trophic levels. The units of primary production were subdivided into primary producer guilds according to the proportions of primary consumers of particular trophic habits. Primary consumers of a particular trophic habit were divided among guilds that reflect binning according to body size, with five bins per habit per network. The range of an appropriate truncated power law distribution was therefore also binned in accordance with body size, and the link distribution of a species in any particular bin was drawn randomly from the range of the power law distribution encompassed by the bin. Thresholds served to discriminate among guilds comprising species of similar trophic habit but different body sizes; larger species have more sensitive extinction thresholds, with thresholds ranging from 0.1 to 0.5.

The fully parameterized model (FPM) therefore comprised 17 consumer guilds with varying extinction thresholds. A control model with thresholds fixed at 0.1 for all guilds was also simulated. FPM also possessed four guilds of primary producers, including suspended aquatic organics, aquatic macrophytes, terrestrial plants accessible to all herbivores, and terrestrial plants accessible only to insect herbivores. Terrestrial tetrapods were not linked to the latter guild because we considered a significant fraction of terrestrial plants to have been beyond the physical reach of those animals. A control model making these plants accessible to terrestrial tetrapods was also simulated (i.e., three producer guilds present). Therefore, a total of four models were simulated; FPM, a control model with three producer guilds and varying thresholds (CM 2), a control model with four producer guilds and fixed thresholds (0.1) (CM 3), and a control model with three producer guilds and fixed thresholds (0.1) (CM 4).

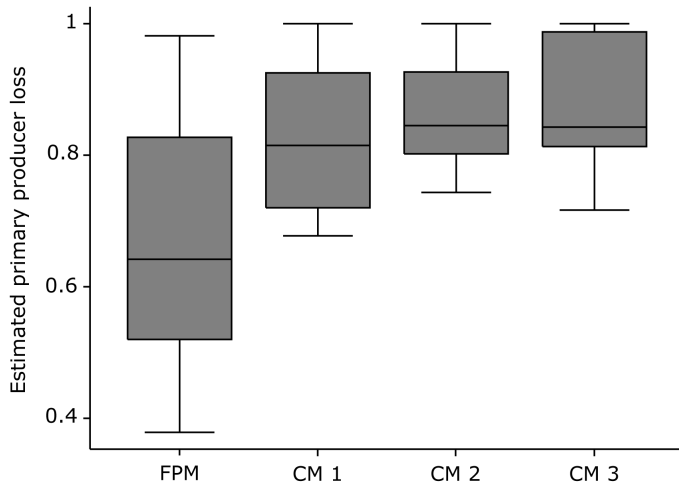


FIGURE 5. Boxplot showing estimates of primary producer loss for the four models. The horizontal line in each box is the median estimate based on the 17 consumer guilds. Boxes mark the 25th to 75th percentiles of data values, and whiskers mark the 5th to 95th percentiles.

Estimating Levels of Primary Producer Disruption

As noted above, one of the goals of this study was to estimate the amount of primary producer disruption that would generate observed levels of extinction among consumers. To make these estimates, the proportion of consumer genera going extinct in each guild was plotted against the units of primary production loss for each of the simulated network models. We then fitted a logistic curve to each plot to summarize the relationship between secondary extinction and primary producer loss for each guild (Fig. 3). Using the best-fit curves, we estimated the level of primary producer loss necessary to cause the observed level of secondary extinction in each guild. For instance, the actual extinction level among genera of very small herbivores was 100%. From the best-fit curve for the FPM, the minimum level of primary producer loss needed to cause 100% secondary extinction among very small herbivores was 86% (Fig. 3a). Likewise, the estimate based on large carnivores was 94% (Fig. 3b). Repeating this procedure for each consumer guild gave us 17 estimates of the level of primary producer loss. We further repeated this procedure for all guilds under the remaining three sets of network parameters.

Observed levels of consumer extinction for each guild were calculated by taking the proportion of genera reported from the *Dicynodon* Assemblage Zone that also occur in the overlying *Lystrosaurus* Assemblage Zone. This procedure resulted in overestimates of extinction for some lineages (e.g., cynodonts show 100% extinction, even though some members of the clade must have survived), but it avoids making assumptions about the unsampled diversity of ghost lineages.

RESULTS

Effects of Primary Producer Disruption on Guilds

The effects of primary producer loss for two example guilds (very small herbivores and large carnivores) under the four models are summarized in Figure 4. Several important features are demonstrated by these plots. First, secondary extinction is initiated in both guilds when at least one species falls below its extinction threshold. The patterns of secondary extinction are approximately linear in the FPM between initiation and 100% extinction, but display very rapid increases in the control models. All the patterns though display a mathematically catastrophic behavior, where small incremental increases in primary producer shutdown generate very sudden shifts in state (Roopnarine, in review).

Second, the guilds do not respond uniformly to a given amount

of primary producer loss. In the examples shown in Figure 4, the very small herbivores generally show a lower amount of secondary extinction for a particular loss of primary producers than do the large carnivores. This variation stems mainly from differences in how each guild responds to top-down feedback in the models; top-down consumer feedback generates feedback loops that exacerbate responses to the loss of primary production, and such loops are more pronounced in consumer guilds with multiple predatory guilds, as well as high-level predatory guilds that are themselves subject to their own predatory compensation. Moreover, when guilds that consistently display catastrophic thresholds are compared, the exact placement of the catastrophe varies from guild to guild, based on the number of prey and predator guilds to which the guild is linked.

Finally, some variation in response to primary producer shutdown is apparent if the behavior of a particular guild is compared from model to model (e.g., compare the FPM and control models for the very small herbivore guild). In general, the control models are consistent in their predictions of the amount of secondary extinction caused by a given loss of primary producers. The FPM shows a somewhat different response in that it sometimes requires the loss of a relatively smaller amount of primary production to cause a given amount of secondary extinction. This response is based on the presence of a noisy region in many of the curves that occurs at moderate levels of secondary extinction. Within this noisy region small changes in primary extinction can result in large changes in secondary extinction. In some cases this can lead to the complete extinction of a guild at relatively low levels of primary producer loss. For example, in the FPM it is possible to approach 100% extinction of large carnivores at 65-70% primary producer loss because of this noisy region, whereas in the control models similar levels of secondary extinction do not occur until nearly 80% primary producer loss.

Predicted Levels of Primary Producer Disruption in the Karoo Basin

After calculating estimates of the primary producer shutdown needed to cause observed levels of consumer extinction using all 17 consumer guilds in the four models, we calculated a median value for each model to serve as our best estimate of the level of primary producer disruption predicted by the model (Fig. 5). The three control models were highly consistent in both the median estimate and range of predicted primary producer loss. The median for CM 1 was 85% (range 68% - 100%), the median for CM 2 was 86% (range 74% - 100%), and the median for CM 3 was 87% (range 72% - 100%). In contrast, the estimates from the FPM were somewhat lower, with a median of 69% and a range of 38% - 98%. The lower median value for the FPM stems from the earlier onset of secondary extinction in many of the guilds in this model, whereas the wider range results from the fact that some guilds do not show a strong catastrophic effect. These factors do not come into play in the control models, in which the responses of nearly all guilds show a distinct threshold effect and relatively little noise.

DISCUSSION

Taken together, our results imply that the end-Permian terrestrial ecosystem of the Karoo Basin was susceptible to collapse brought on by the shutdown or extinction of primary producers. This result is significant because it suggests that it may be unnecessary to invoke an abiotic trigger for terrestrial animal extinctions at the time. Instead, a proposed kill mechanism need only affect non-marine primary producers for the resulting extinctions to be propagated throughout the trophic network. Moreover, the behavior of the system is distinctly non-linear, with small to moderate losses of primary producers causing little secondary extinction, but higher levels of producer loss resulting in the complete or near complete extinction of many guilds. Thus, the observed levels of extinction require relatively high levels of primary

producer loss. Such levels of extinction are not unrealistic, however, because many lines of evidence suggest that a major floral turnover took place at the end of the Permian in South Africa and elsewhere in Gondwana, with the Permian glossopterid-dominated flora being replaced by floras with greater representation of peltasperms, corystosperms, lycopsids, and conifers (e.g., Anderson and Anderson, 1985; Retallack, 1995; McLoughlin et al., 1997; Retallack et al., 2003).

The fully parameterized model (FPM), with variable extinction thresholds and functionally diverse guilds of terrestrial producers, was favored *a priori* given its greater realism. However, it produced results that were the least consistent among the four classes of models. In general, uniformly lower consumer extinction thresholds (T), and functionally less diverse producer guilds, confer greater resistance to secondary extinction on the community. This is explained easily since the lower thresholds allow consumer species to lose more sources of prey before becoming extinct, as well as the fact that the functionally less diverse networks generate less intense top-down predatory feedback. The control models, however, are highly unpredictable in the sense that the patterns of secondary extinction are very catastrophic, with the transition from no secondary extinction to extremely high levels of secondary extinction being separated by very small increments of primary producer shutdown. Though this feature is also present in the FPM, the transitions from zero secondary extinction are generally more incremental.

Intriguingly, many of the FPM guilds become unstable at moderate levels of primary producer shutdown, but then stabilize at increasing levels, and continue the incremental increase of secondary extinction. This instability at moderate levels of shutdown means that the FPM is capable of generating results consistent with observed levels of

extinction at levels of shutdown lower than those in the control models (though FPM also will generate results consistent with those models at increasingly greater levels of shutdown). The implication, though currently unexplored in our simulations, is that the responses of this general class of probabilistic paleo-trophic networks to primary producer disruption may bifurcate, and generate multiple states of community collapse.

The overall greater resistance of the FPM model also suggests roles for functional composition and diversity in ecosystem resistance to extinction, with the presence of tetrapod herbivores of greater feeding capabilities in the control models adding greater resistance. Given that there has been an overall increase in trophic functional diversity through the Phanerozoic, one must question if resistance to secondary extinction has also increased. Mass extinction events present unique opportunities to address this question, particularly if selectivity on the basis of trophic characteristics was involved in taxon extinction or survival. Currently, our database of Karoo Permian taxa is not complete enough to address this question in detail. Additional information is required regarding producer composition, diversity, and extinction, as well as additional consumer information (e.g., insects). Our simulations, however, do present potential levels of producer disruption, and these levels can be tested both on the basis of enhanced information for further simulations, as well as independent methods for assessing primary productivity and producer diversity.

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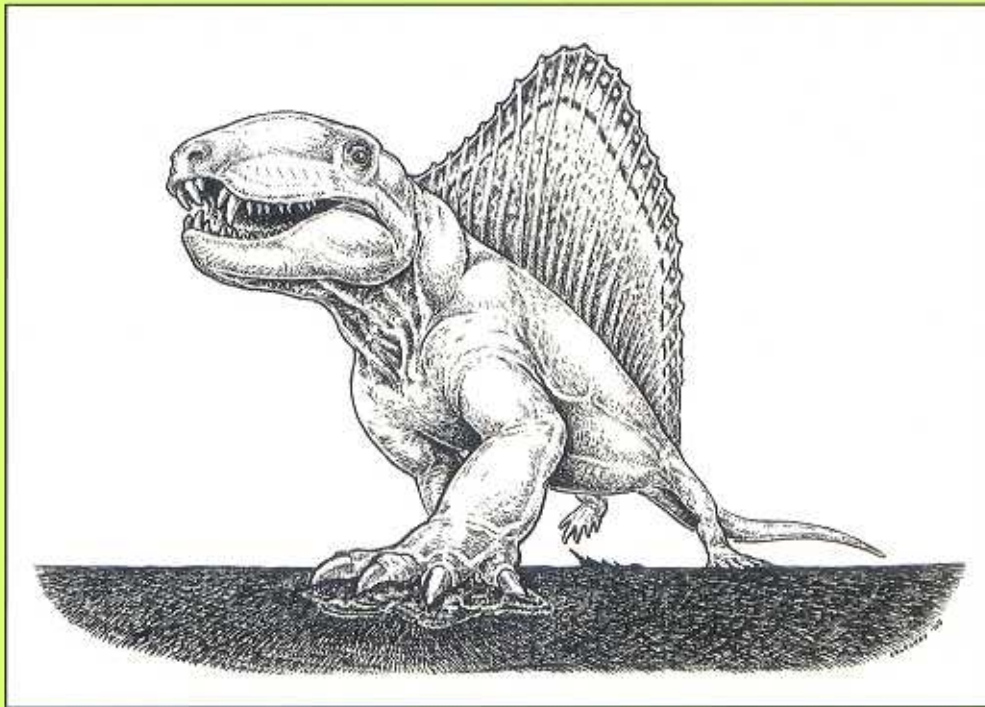
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