Late Cretaceous restructuring of terrestrial communities facilitated the end-Cretaceous mass extinction in North America

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The sudden environmental catastrophe in the wake of the end-Cretaceous asteroid impact had drastic effects that rippled through animal communities. To explore how these effects may have been exacerbated by prior ecological changes, we used a food-web model to simulate the effects of primary productivity disruptions, such as those predicted to result from an asteroid impact, on ten Campanian and seven Maastrichtian terrestrial localities in North America. Our analysis documents that a shift in trophic structure between Campanian and Maastrichtian communities in North America led Maastrichtian communities to experience more secondary extinction at lower levels of primary production shutdown and possess a lower collapse threshold than Campanian communities. Of particular note is the fact that changes in dinosaur richness had a negative impact on the robustness of Maastrichtian ecosystems against environmental perturbations. Therefore, earlier ecological restructuring may have exacerbated the impact and severity of the end-Cretaceous extinction, at least in North America.

dinosaur diversity | extinction selectivity | paleoecology | trophic cascade | cascading extinctions on graphs

The end-Cretaceous mass extinction was a pivotal event in Earth history with effects still observable today (1). As the only major mass extinction with a well-supported ultimate cause (2, 3), the end Cretaceous has received intense scrutiny. However, why this impact resulted in a mass extinction and other significant abiotic events sometimes did not (4), and why some clades and ecological guilds suffered more than others, remain open questions. We reconstructed Late Cretaceous terrestrial food webs from North America to determine whether changes in community structure, including apparent declines in nonavian dinosaur richness during the Late Cretaceous, may have made these communities more prone to cataclysmic extinction. How richness is divided among functional groups (guilds) in a community influences the propagation of perturbations through a community and how those perturbations cause extinction (5). Dynamic changes to the relative richness of different guilds can occur both by evolution on long time scales and community assembly on ecological time scales (6). Therefore, if ecosystem restructuring is found to be widespread and/or frequent, it may help explain why it is so hard to predict mass-extinction survivorship based on previous background extinction rates (7).

Food-web models have been used previously to explore and simulate how the structures of modern (8–10) and ancient (11–13) ecosystems influence their responses to perturbations. The end-Cretaceous mass extinction is an ideal candidate for study because one of the proximate causes of the extinction [cessation or extreme disruption of terrestrial primary productivity (14)] is readily assessed via simulations. Further, the North American terrestrial record includes numerous, well-sampled localities that are amenable to the use of food-web analysis for exploring hotly debated questions concerning the tempo and mode of community change. We compared the robustness of Campanian and

Maastrichtian communities to test whether disturbances could cause extinctions more easily in Maastrichtian communities than earlier Campanian ones by using a food-web model, cascading extinctions on graphs (CEG) (12, 13, 15), that is specifically designed to accommodate the uncertainties of fossil data. We chose 17 well-sampled Late Cretaceous locations (22–95 taxa each; *SI Materials and Methods*) and nine formations, and subjected a total of 2,600 species-level food webs drawn randomly from the entire pool of potential webs to varying primary productivity disruptions (see *Materials and Methods*, and *SI Materials and Methods* for details; Fig. 1*A* shows the pattern of secondary extinction at varying perturbation levels for 100 food webs at a single example site. Fig. 1*B* compares the median secondary extinction patterns for all 17 sites; see *SI Materials and Methods* for complete secondary extinction at each site). By focusing on locations and formations that are exceptionally rich and well-sampled, we mitigated some of the biases that often plague paleobiological investigations.

Many current macroevolutionary hypotheses are tested through the use of richness curves, diversification rates, or patterns of disparity, yet regularly postulate ecological scenarios specific to those hypotheses. Our goal is to assess macroevolutionary patterns by using well-established ecological and evolutionary principles that underlie all historical scenarios, regardless of historical contingencies (6). However, understanding ecosystem dynamics in deep time requires a more inferential approach than is used in studies of extant communities where interactions can be observed directly (16). Our method uses uniform assumptions based on measures of modern food-web topology such as how links are distributed between taxa, or how productivity scales with herbivore richness, creating model outputs that differ solely as a result of the input data, rather than assumptions of different ecological functioning at different times. A major advantage of explicit models such as CEG is that all assumptions about mechanisms and parameters are laid bare, rendering them far more open to direct testing than verbal models.

The terrestrial record of North America is the best sampled and most often studied portion of the global Late-Cretaceous terrestrial record (17, 18). However, reliance on North America to understand global patterns has produced arguments for a more gradual, less catastrophic decline of dinosaurs at the end of the Cretaceous (19, 20). This debate over the tempo and mode of nonavian dinosaur extinction traditionally focused on trajectories

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Fig. 1. (*A*) Primary productivity perturbation versus secondary extinction for 100 species-level networks generated for the Bone Butte Quarry (see *SI Materials and Methods* for other locations), with the threshold perturbation marked by the red line. (*B*) Median secondary extinction at each perturbation for the Campanian (blue) and Maastrichtian (red) sites. (*C* and *D*) Boxplots showing the range of variation in PC1 (*C*) and PC2 (*D*) for species-level networks at each of the 17 sites, ordered by decreasing sample size, with the pooled median values for each stage represented by the red (Maastrichtian) and blue (Campanian) dashed lines. Community robustness decreases with increasing PC scores for both components. Locality abbreviations are explained in Table S1.

of dinosaur richness through time (21–24). Recent work has shifted from concerns specifically about nonavian dinosaur richness to potential causes of the apparent decline, particularly the importance of geological biases and tectonic influences on richness and the fidelity of the fossil record (17, 25). CEG provides an ideal vehicle to test for a relationship between apparent differences in dinosaur richness and possible changes in ecosystem structure in North America.

Results and Discussion

Our results support pronounced differences in the dynamics of Campanian and Maastrichtian communities at the sites examined, with markedly less robust communities in the Maastrichtian given uniform assumptions of several ecological parameters (e.g., how insect richness and primary productivity are modeled; *Materials and Methods* and *SI Materials and Methods*). We quantified robustness using the level of extinction resulting from 15, 25, 35, and 45% perturbations of primary production and the collapse threshold (perturbation that resulted in the largest, often abrupt increase in extinction; Fig. 1*A*). We explored the differences between responses using a principal components (PC) analysis of summary statistics (percentages normalized using arcsine–double square root transformation) to extract the two major axes of variation (91% of the variance). High values on the first principal component (72% of the variance) corresponded to high secondary extinction at each of the four specified perturbation levels and a low

threshold; whereas, high values on the second PC (19% of the variance) corresponded to low perturbation values for the collapse threshold. These components are therefore complementary measures of community robustness, with high scores of a community on either component representing food-web topologies prone to extinction at low perturbation levels. Maastrichtian food webs are overall less robust than Campanian ones (Kolmogorov–Smirnov test, $P < 0.001$ for both PC1 and PC2), although there is considerable within-site variation stemming from inherent uncertainty in the fossil webs (Fig. 1*A*), and between-site variation based on differences in taxonomic composition (Fig. 1*B–D*) and guild richness (*SI Materials and Methods*). Nevertheless, both nested MANOVA of PC scores using stage and site as factors, and multiple individual t tests, show highly significant differences between Campanian and Maastrichtian food webs along the first two axes (P values < 0.0001, with Bonferroni inequality correction applied to t tests). Although food webs constructed from whole-formation aggregated assemblages returned similar results (with the Maastrichtian and Campanian differing significantly for PC1 and PC2; MANOVA, $P < 0.001$), these results include a greater amount of temporal, spatial, and paleoenvironmental averaging (*SI Materials and Methods*).

We selected our Campanian sites for their high richness, temporal range, and environmental breadth (they encompass the full range of terrestrial ecosystems present across North America during the approximately 13 million years of the stage). The more geographically and temporally restricted Maastrichtian sites,

however, have greater variance than Campanian sites along the first two principal components (0.027 versus 0.016 for PC1, F test, $P < 0.0001$; 0.010 vs. 0.004 for PC2, F test, $P < 0.0001$). This would not be predicted given the greater environmental heterogeneity of the Campanian sites and is explained best by differences between the two stages in the response of food webs to increasing richness, even when sample size is considered (Fig. 2). This strongly suggests that fundamental community structure differed between stages. Moreover, at least one guild comprising dinosaurs only (very large herbivores) played a significant role in determining community response to perturbation. Multiple regression of PC1 and PC2 scores on guild richness shows that increasing richness in the very large herbivores guild (average richness at sites in the Campanian = 2.5, Maastrichtian = 3.28), as well as in the very small omnivores (4.5, 8, respectively) and very small herbivores (2.5, 3.57, respectively) guilds, significantly decreases network robustness (*SI Materials and Methods*; PC1, F = 97.96, $R^2 = 0.39$, $P < 0.0001$; PC2, F = 53.66, $R^2 = 0.39$, $P < 0.0001$).

Given that the Chicxulub impact caused mass extinctions in both the marine and terrestrial realms, it cannot be doubted that it would have precipitated a mass extinction in the Campanian as well. However, the magnitude of the extinction and, importantly, the ways in which different guilds were affected may not have been the same because the ecological framework in which extinctions occur influences the loss of richness in guilds. Similarly, whether a clade becomes extinct or survives depends on its distribution among the ecosystem's guilds (i.e., its functional diversity). Our results show that in the Maastrichtian of North America not only were more taxa driven to extinction than would have been the case in a hypothetical Campanian extinction, but the guilds that were most strongly affected, and thus the clades that were hit hardest, also differed. Localities in the two intervals differ in the taxon richness of several guilds, including the very large herbivores (*SI Materials and Methods*). This guild was highly influential because of its high number of connections in the food web: very

large herbivores would have been prey of small predators (or juvenile larger predators) when young, moderately sized predators when juveniles, and top predators during adulthood. Therefore, removing a single species of very large herbivore, such as *Triceratops*, would have affected carnivore species distributed among several guilds. The removal of such highly connected species can have disastrous effects on communities (11) so the impact of the complete removal of guilds such as the very large herbivores can ripple through the food web in myriad ways. Nevertheless, it is important to stress that we documented ecological restructuring stemming from changes in a variety of taxa and guilds, ranging from smaller-bodied vertebrates and invertebrates to dinosaur-dominated guilds.

Extending these results to other realms (terrestrial vs. marine) and other continents, as well as determining how extreme the modeled restructuring is between the Campanian and Maastrichtian relative to other stage boundaries remain important avenues for future research. Between the Campanian and the Maastrichtian, North America saw a massive change in terrestrial ecosystems in the form of the retreat of the Western Interior Seaway (26), with sites from the Maastrichtian representing only recently coalesced ecosystems. Therefore, our observed restructuring, and many other patterns related to the end-Cretaceous extinction in the terrestrial realm, may be a provincial effect, albeit an interesting and important one. In support of this, our data show that although the total richness of nonavian dinosaurs decreased from the Campanian to the Maastrichtian in North America, much of this decline between the two stages can be attributed to changes in how richness was partitioned at the α and β levels. The Campanian had higher β-diversity (proportionally more endemic taxa, e.g., *Medusaceratops* and *Chasmosaurus*), whereas the Maastrichtian had higher α-diversity (proportionally more cosmopolitan taxa, e.g., *Triceratops*). This is reflected in our model: average dinosaur richness is higher at our individual Maastrichtian sites, but the total number of distinct dinosaur taxa is higher when summed over our Campanian localities (*SI Materials and Methods*). This shift in geographic richness partitioning, from high β-diversity to high α-diversity, and the associated restructuring of trophic networks, explains the apparent North American decline in dinosaur richness without invoking intrinsic properties of dinosaurs collectively as a clade, and is concordant with previous findings (27) and the documented decrease in regional provinciality (26).

Our precise quantitative results concerning higher extinctions and lower collapse thresholds only hold if our uniform assumptions (e.g., consistent food-web distributions and scaling of herbivory with primary productivity) are within reason. However, the qualitative conclusion that terrestrial ecosystems underwent a dramatic shift over this interval is inescapable. The consistency of response across the entire series of Campanian localities, spanning 13 million years and numerous environments, stands in stark contrast to the highly variable, and fundamentally different, reactions of the Maastrichtian communities, which span a mere 2 million years and are from a more homogeneous environment. Our analyses, however, are agnostic toward the potential cause of the ecological restructuring from the Campanian to the Maastrichtian.

Given that our model infers biotic interactions among extinct taxa in ancient communities, we note the concordance between our modeled results and observed data from the fossil record in two instances. First, the CEG model produces simulation results concordant with observations of another mass extinction, the end-Permian event. The CEG model predicts that in the immediate aftermath of the end-Permian extinction in the Karoo Basin of South Africa, the earliest Triassic *Lystrosaurus* assemblage zone community would have been demographically and compositionally unstable in the face of continued environmental perturbations (13, 28). Model instability in this case is the result
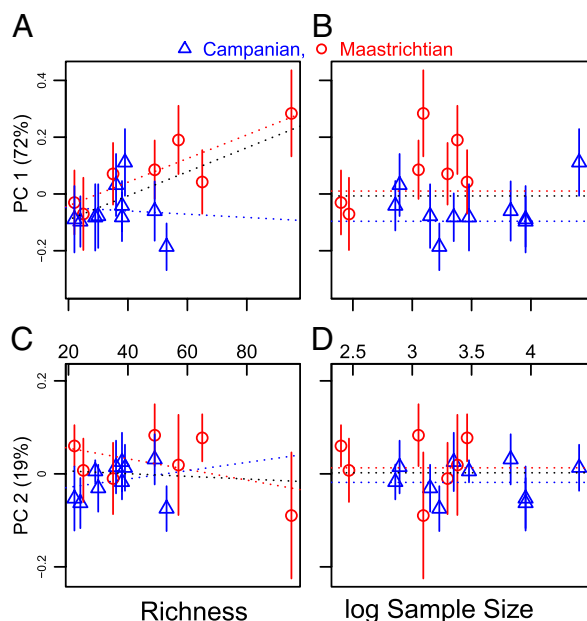

Fig. 2. Mean and SE of PC1 (high secondary extinction before threshold value) and PC2 (early threshold) regressed against site richness (A and C) and the log of sample size (B and D) for the Campanian (blue) and Maastrichtian (red). Dotted lines represent the best fit for each stage, and for the aggregate dataset (black). Only the Maastrichtian line for richness against PC1 has a slope significantly different than zero, with increasing richness resulting in increased proportions of early secondary extinction.

of the near extinction of large-bodied tetrapod herbivores coupled with a dramatic diversification of medium-sized tetrapod predators, leading to structurally unstable food webs. Empirical evidence has been presented recently supporting this model prediction by showing that many *Lystrosaurus* zone species exhibited dramatic demographic fluctuations (29).

Second, we used the Paleobiology Database (PBDB) to estimate the observed extinction levels for each consumer guild, and then compared those levels to our simulations to assess how well the simulations matched reality. Our fit metric is exceedingly conservative, as we used the global extinction level, despite the fact that many taxa may have been extirpated locally yet survived globally, and we only considered perturbations that produced simulated extinction levels below that observed in each guild, thus further precluding local extinction (Fig. 3). In addition, we do not take into account important secondary characteristics of taxa in guilds with high survivorship, such as low metabolism or high reproductive output, which further constrains the model. The practical implications of this metric are that guilds with extremely low extinction levels [e.g., freshwater guilds (30)] place rigid upper bounds on the perturbation magnitude possible that does not exceed their low extinction fraction. This upper bound of the perturbation is usually low enough to dramatically underestimate dinosaur extinction levels, driving the mismatch between the simulated extinction and the observed extinctions. Despite this rigid methodology, our results show that CEG produces largely concordant results between different locations, across multiple orders-of-magnitude differences in sampling intensity (21% of species were misclassified as surviving). Nevertheless, there is a considerable amount of the end-Cretaceous extinction that is unaccounted for by the simulated disruptions of primary productivity, implying that other impact-related kill mechanisms, such as cooling, were also important in the terrestrial realm.

Food-web models have repeatedly shown utility in understanding dynamics in modern (8–11) and ancient (6, 12, 28, 29, 31) communities. Our results paint a picture of Late Cretaceous North America in which pre–mass-extinction changes to terrestrial ecosystems, likely driven by a combination of tectonic (26), environmental (17), and purely biological factors, created communities that either underwent a radical shift in functionality or became significantly more fragile in the face of environmental catastrophe. In particular, our results provide evidence that earlier

ecoevolutionary changes may have affected the richness trajectories of dinosaurs, among other taxa, and facilitated the extraordinary impact the extinction had on guilds dominated by nonavian dinosaurs. Guild-based assessments of extinction risk may prove useful in understanding differential extinction across the many taxonomic and environmental realms decimated by the end Cretaceous, but extrapolation of broad ecological restructuring, such as that to marine communities, will require further research. Given our current spiral into an anthropogenically driven mass extinction (32), using mechanistic models to understand how subtle ecological changes and massive environmental events influence the propagation of extinctions is of increasing importance (7, 8). We have an urgent need to understand how our alteration of modern food webs may shape ecological responses to future catastrophes (32), and potentially exacerbate extinctions. The fossil record provides a unique opportunity to quantitatively test the accuracy of ecological methods for predicting extinctions and responses to environmental changes.

Materials and Methods

CEG analyses begin with the partitioning of taxa within each locality into guilds on the basis of ecological function (5, 12, 15), with taxa assigned to guilds based on body size, trophic habit (e.g., carnivore, herbivore), and habitat. Trophic links between guilds are assigned on the basis of these ecological characteristics (*SI Materials and Methods*) (5, 12, 15). There is a finite ensemble of species-level food webs consistent with the assigned links between guilds. The species-level food webs vary in the distribution of interspecific trophic links, which we stochastically generated by applying mixed exponential–power-law link distributions uniformly to all our communities, consistent with the hyperbolic distributions typical of modern food webs (5) and other complex networks (33). This method of stochastically assigning links using an empirically derived power-law distribution allows our model to capture the structure and spatiotemporal variation of a real food web in the ensemble. In general, this variation does not generate significant differences of dynamics among food webs in the ensemble, being constrained and dictated by the higher-level guild organization and interaction of the community (6). To sample the food-web ensembles of our locality food webs, we stochastically generated 100 food webs consistent with each partitioned community and obtained average pictures of each community's response to perturbations. We simulated bottom–up extinctions by incrementally reducing primary productivity (Fig. 1A; see *SI Materials and Methods* for details), and recorded the resulting secondary extinction (the proportion of consumers that become extinct at a given perturbation level). Unlike many food-web models, extinction is not purely topological; CEG permits top–down interactions and trophic cascades resulting from bottom–up perturbations by recalculating interaction strengths of species when some of their resources or predators go extinct (5, 15).

To properly simulate a food web, primary productivity and insect richness must be taken into consideration. Unfortunately, it is often difficult to directly assess these parameters at localities that preserve vertebrates, especially among a large enough sample of sites to draw reasonable conclusions. Further, the inherent biases in estimates of both parameters between sites are exceedingly difficult to compare or assess. To circumvent these issues, we modeled primary productivity as a function of herbivore diversity (*SI Materials and Methods*), as has been done previously (12, 15). For insect richness, we used a selection of six diverse fossil insect faunas from around the world and through the Phanerozoic to fit a linear model relating the richness in each deposit and the richness and trophic variation of insectivores found in the same, or nearby, deposits ($R^2 = 0.66$, $P < 0.02$). This method is uniformly biased, which means that uncertainty in the relationships and richness are applied evenly to all deposits, making comparisons between sites valid, a point confirmed by sensitivity analyses for insect richness (*SI Materials and Methods*) and productivity (13).

Using stratigraphic ranges in the PBDB for the taxa included in our analysis, we calculated the proportion of taxa in each guild that went extinct during the end-Cretaceous event. The vector of guild-specific extinctions used is provided in the *SI Materials and Methods*, and agrees well with previously published analyses of tetrapod extinction (30), with exceptionally low extinction in freshwater groups, and a noticeable size bias. We then searched all 100 food webs at each Maastrichtian site, and found the perturbation that minimized the distance between the simulated secondary extinction in each tetrapod guild with that observed from the fossil record. Euclidean distance (sum of the squared differences) was computed between the simulated
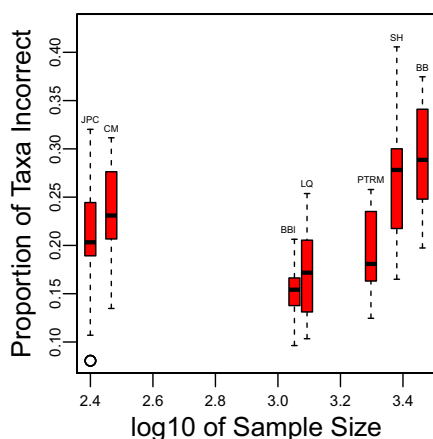
Fig. 3. Number of species incorrectly assigned divided by the total number of species at each Maastrichtian locality, arranged by the $\log_{10}$ of sample size for that location. It is notable that despite not allowing local extinction, nor taking secondary survival characteristics into account, our model correctly assigned an average of 78.4% of taxa. Locality abbreviations are explained in Table S1; additional explanation of analysis is presented in *SI Materials and Methods*.

and observed extinction vectors for tetrapods. We constrained the analysis to only examine perturbation levels that produced extinction vectors where the simulated extinction for each guild fell below that observed. For an example of this analysis, consider a hypothetical site with two guilds, one with 50% observed extinction and one with 100% observed extinction. In our analysis, we found the perturbation of each of our 100 food webs (per community) that was closest to, but did not exceed, 50% extinction in the first guild, and then calculated the distance (square root of the sum squared differences) between the simulated extinction at that perturbation (<50%, ≤100%) and the observed vector (50% and 100%). This allowed us to evaluate the "fit" of our model to the different sites in an absolute sense by giving us the number of species the

model incorrectly found surviving the extinction, which we transformed by the total richness of the site to get the percentage misclassified (Fig. 3, *SI Materials and Methods*).

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