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Extinction cascades and catastrophe in ancient food webs

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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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