

Trophic network models explain instability of Early Triassic terrestrial communities

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Studies of the end-Permian mass extinction have emphasized potential abiotic causes and their direct biotic effects. Less attention has been devoted to secondary extinctions resulting from ecological crises and the effect of community structure on such extinctions. Here we use a trophic network model that combines topological and dynamic approaches to simulate disruptions of primary productivity in palaeocommunities. We apply the model to Permian and Triassic communities of the Karoo Basin, South Africa, and show that while Permian communities bear no evidence of being especially susceptible to extinction, Early Triassic communities appear to have been inherently less stable. Much of the instability results from the faster post-extinction diversification of amphibian guilds relative to amniotes. The resulting communities differed fundamentally in structure from their Permian predecessors. Additionally, our results imply that changing community structures over time may explain long-term trends like declining rates of Phanerozoic background extinction

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1. INTRODUCTION

Mass extinctions represent times of severe ecological crisis in the Earth's past. The history of mass extinctions documented in the fossil record is one of the geosciences' crucial contributions to the assessment of human impact on the Earth today (May 2001). Although numerous studies have focused on distinguishing background from mass extinctions, measuring extinction magnitudes, identifying primary abiotic causes, searching for clade-based selectivity and examining biotic recovery (Sepkoski 1996; Solé *et al.* 2002; Benton & Twitchett 2003; Wang 2003; Lockwood 2004; Jablonski 2005), less attention has been paid to the role of community structure in the propagation of or resistance to perturbative mechanisms. Understanding the influence of community structure on responses to extinction mechanisms is important because many of the species that went extinct during these episodes probably did so in response to cascading secondary effects on their ecological communities (Vermeij 2004; Angielczyk *et al.* 2005; Roopnarine 2006). Moreover, even if the physical nature of mechanisms that cause mass extinctions varied little during the Phanerozoic, the structures and compositions of affected communities and ecosystems have changed significantly (Vermeij 1977; Bambach 1993; McGhee *et al.* 2004; Wagner *et al.* 2006).

The largest mass extinction recorded in the fossil record is the end-Permian mass extinction (approx. 251 Myr ago). It has been estimated that at least 80% of all marine invertebrate animal species and up to 74% of

terrestrial animal families disappeared at this time (Erwin *et al.* 2002; Benton & Twitchett 2003; Benton *et al.* 2004; Ward *et al.* 2005), and the post-extinction Early Triassic world was characterized by degraded terrestrial and marine ecosystems (Looy *et al.* 1999; Pruss & Bottjer 2004). We investigated the potential role of community structure in this event using a numerical network simulation model (cascading extinction on graphs, CEG) to examine the extent to which food-web topology promotes or inhibits the propagation of disruptions through a community (Roopnarine 2006). We measure community resistance as the number of secondary extinctions resulting from a specific disruption or perturbation, with secondary extinction defined as the extinction of a species owing to the elimination of dependencies on at least one other species within the community.

We applied the CEG model to three terrestrial, tetrapod-dominated palaeocommunities from the Late Palaeozoic and Early Mesozoic of the Beaufort Group, Karoo Basin, South Africa: the Middle Permian *Eodicynodon*, end-Permian *Dicynodon* and the Early Triassic *Lystrosaurus* biostratigraphic assemblage zones (Wordian, Changhsingian and Induan–Olenekian stages, respectively; Rubidge 1995, 2005). The *Dicynodon* and *Lystrosaurus* zones occur immediately before and immediately after the end-Permian mass extinction, respectively. We focused on bottom-up disruptions of primary productivity for three reasons. First, considerable evidence indicates widespread declines in primary production during several major biodiversity crises, including the end-Permian and Cretaceous–Tertiary extinctions (Zachos *et al.* 1989; Knoll *et al.* 1996; Looy *et al.* 2001). Second, the modern biodiversity crises, comprising primarily the loss of species of high trophic levels owing

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