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Quantifying functional diversity in pre- and post-extinction paleocommunities: A test of ecological restructuring after the end-Permian mass extinction

Ashley A. Dineen [a,*], Margaret L. Fraiser [a,b], Peter M. Sheehan [a,b]

[a] Department of Geosciences, University of Wisconsin-Milwaukee, 3209 N. Maryland Ave, Milwaukee, WI 53201, USA
[b] Geology Department, Milwaukee Public Museum, 800 W. Wells St, Milwaukee, WI 53233, USA

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ABSTRACT

A review of the literature shows that understanding of biotic restructuring following the Permo-Triassic mass extinction (PTME) is typically based on only a few components of the ecosystem, such as taxonomic diversity, and that Early Triassic paleocommunities previously have been considered fully recovered when previous dominance and diversity were regained. To more fully characterize Triassic ecologic restructuring, we propose herein that paleoecologists take into account functional diversity (i.e. abundance distribution of genera in functional space). To test the viability of this metric, we quantified here for the first time functional richness (number of functional groups) and functional evenness (distribution of abundance across functional groups) in five different local paleocommunities from classic Permian and Triassic sections using a quantitative ten-trait ecospace model. Functional richness was low in local paleocommunities immediately after the PTME, but increased to high levels by the Middle Triassic. In contrast, functional evenness was low in the Middle Permian, but high in all of the Triassic paleocommunities. Overall, the results of this analysis indicate that taxonomic and ecological diversity was decoupled after the PTME, in that local taxonomic diversity increased quickly in several Early Triassic paleocommunities, but local functional diversity did not return to high levels until the Middle Triassic (Anisian).

Contents

1. Introduction

The topic of recovery from environmental disturbance has become increasingly necessary in ecology and conservation today. This concern is driven by the present crisis in ecosystems, including substantial degradation of communities on relatively short timescales, resulting in the extinction of species at an alarming and unprecedented magnitude (IPCC, 2007). Accordingly, interest in recovery after periods of disturbance or environmental stress in the fossil record has increased in the past few decades, especially in the intervals after mass extinctions. Garnering considerable attention is the Permo-Triassic mass extinction (PTME) and subsequent recovery, perhaps the most spectacular

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* Corresponding author. Tel.: +1 414 2293952.
E-mail addresses: aadineen@uwm.edu (A.A. Dineen), mfraiser@uwm.edu (M.L. Fraiser), sheehan@mpm.edu (P.M. Sheehan).

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example of biologic devastation and reestablishment in Earth's history (e.g., Payne and Clapham, 2012). However, despite an abundance of research, the complex nature of ecologic recovery after the PTME has not been completely established.

Recent studies have revealed multiple spatial and temporal recovery patterns in marine communities during the Early and Middle Triassic aftermath (e.g., Algeo et al., 2011a, 2011b; Greene et al., 2011; Song et al., 2011, 2012; Chen and Benton, 2012; Benton et al., 2013; Chen et al., 2013; Clapham et al., 2013; Hofmann et al., 2013a; Meyer et al., 2013; Foster and Twitchett, 2014). The objectives of this paper are to 1) examine how ecologic recovery is defined, 2) propose the use of two additional metrics (functional richness and evenness) for examining the ecological effects of extinction events, and 3) demonstrate their use in understanding the nature and patterns of marine community recovery after the PTME.

2. The Permo-Triassic mass extinction and its aftermath

The Permo-Triassic mass extinction occurred approximately 252 Ma and was the largest global biodiversity collapse in the Phanerozoic. Devastating both the marine and terrestrial realms, up to 78% of marine genera and ~70–80% of terrestrial families did not survive into the Triassic (Raup and Sepkoski, 1982; Maxwell, 1992; Benton et al., 2004; Clapham et al., 2009; Payne and Clapham, 2012). Biotic structure of the oceans was vastly altered; the PTME helped facilitate a shift in taxonomic and numerical dominance from that of the Paleozoic Evolutionary Fauna (EF) (i.e. rhynchonelliform brachiopods, crinoids, rugose and tabulate corals) to the Modern EF (i.e. bivalves, gastropods, demosponges, echinoids) (Gould and Calloway, 1980; Sepkoski, 1981; Bambach et al., 2002; Fraiser and Bottjer, 2007a; Stanley and Helmle, 2010). Evidence suggests that the eruption of the Siberian Traps igneous province triggered a combination of environmental stresses that proved deadly to the large majority of the Permian fauna (Campbell et al., 1992; Kamo et al., 1996; Benton and Twitchett, 2003; Knoll et al., 2007; Bottjer, 2012). Huge amounts of CO_2, methane, and sulfides were emitted, leading the atmosphere and ocean to become rich in CO_2 and depleted in O_2 at the end of the Permian (Renne et al., 1995; Knoll et al., 1996; Kiehl and Shields, 2005; Payne and Kump, 2007; Reichow et al., 2009; Svensen et al., 2009; Black et al., 2012; Grasby et al., 2013). This facilitated global warming which, in turn, helped induce development of dysoxia/anoxia in the deep ocean and expansion into shallow water environments (Wignall and Hallam, 1992; Joachimski et al., 2012; Sun et al., 2012; Winguth and Winguth, 2012; Algeo et al., 2013; Dustria et al., 2013). Rising temperatures and continued volcanic emissions are proposed to have also facilitated severe hypercapnia, ocean acidification, and hydrogen sulfide toxicity (Fraiser and Bottjer, 2007b; Payne and Kump, 2007; Hinojosa et al., 2012; Schobben et al., 2013; Black et al., 2014).

Following the PTME, invertebrate body sizes were small (Schubert and Bottjer, 1995; Twitchett, 2007; Wade and Twitchett, 2009; Metcalfe et al., 2011; Rego et al., 2012), anachronistic facies such as wrinkle structures and calcimicrobialites were present (Bottjer et al., 1996; Wignall and Twitchett, 1999; Pruss et al., 2004, 2006; Baud et al., 2007; Lehrmann et al., 2007; Marenco et al., 2012), and an intricate pattern of decoupling existed between pelagic and benthic marine environments (Isozaki, 1997; Payne et al., 2011; Chen and Benton, 2012). For example, nektonic organisms such as ammonoids and conodonts (e.g., McGowan, 2005; Brayard et al., 2006, 2009; Orchard, 2007; Stanley, 2009; Brosse et al., 2013) generally showed rapid taxonomic and morphological diversification <1–2 myr after the PTME, while mainly benthic groups (e.g., bivalves, brachiopods, foraminifers, gastropods, etc.) did not show rapid taxonomic diversification until 2–5 myr later (Schubert and Bottjer, 1995; McRoberts, 2001; Chen et al., 2005; Nutzel, 2005; Twitchett and Oji, 2005; Payne et al., 2006; Forel et al., 2011; Hofmann et al., 2013b). Sponge-microbial patch reefs have been reported from the Smithian, while scleractinians appeared in the Anisian, though both do not appear to play a role in major reef-building until the Late Triassic (Flügel, 2002; Stanley, 2003; Payne et al., 2006; Stanley and Helmle, 2010; Brayard et al., 2011a; Marenco et al., 2012).

The temporal and spatial extent of these patterns is the subject of much debate (e.g., Brayard et al., 2011b; Fraiser et al., 2011) as a result of the variation to which Triassic clades, regions, and environmental settings were impacted by the PTME and subsequent aftermath processes (e.g., Knoll et al., 1996; Wignall et al., 1998; Wignall and Newton, 2003; Twitchett et al., 2004; Beatty et al., 2008; Posenato, 2008; Jacobsen et al., 2011; Hautmann et al., 2013; Hofmann et al., 2013b; Pietsch and Bottjer, 2014). Hypotheses attribute Early Triassic biotic recovery patterns to either intrinsic (i.e. ecosystem dynamics) or extrinsic (i.e. physical environment) processes. The most prevalent extrinsic hypothesis is that PTME environmental stresses (i.e. high temperatures, anoxia, euxinia) lasted several million years into the Triassic, adversely affecting the development of benthic ecosystems (e.g., Hallam, 1991; Payne et al., 2004; Fraiser and Bottjer, 2005, 2007b; Sun et al., 2012; Winguth and Winguth, 2012; Clapham et al., 2013; Grasby et al., 2013; Pietsch and Bottjer, 2014). Current data support the idea that Early and Middle Triassic oceans were vertically-stratified, with a CO_2-rich Oxygen Minimum Zone (OMZ) that periodically expanded to shallow shelves (Wignall and Hallam, 1992; Woods et al., 1999; Woods and Bottjer, 2000; Woods, 2005; Algeo et al., 2007). An expansion of the Panthalassan OMZ vertically and horizontally after the PTME was likely driven by 1) increasing global temperatures (Sun et al., 2012), 2) higher productivity zones due to upwelling in Panthalassa and nutrient-trapping in Tethys (Meyer et al., 2008; Winguth and Winguth, 2012), and/or 3) enhanced sediment flux into the oceans after devastation of plant life during the extinction (Algeo and Twitchett, 2010). Several studies (e.g., Korte et al., 2003; Sephton et al., 2005; Algeo and Twitchett, 2010; Algeo et al., 2011) have indicated that continental weathering increased during and after the PTME, resulting in destructive siltation and eutrophication that increased turbidity and smothered benthic organisms. The increased flux of nutrients into the ocean enhanced marine productivity, a scenario which has been invoked as a potential source of the positive ^{13}C excursions evident in models and bulk carbonate sediment data from the Triassic (Payne et al., 2004; Grard et al., 2005; Meyer et al., 2008, 2011; Algeo et al., 2011a, 2011b; Algeo et al., 2013). The Triassic ^{13}C record also indicates that high productivity intervals were followed by productivity crashes (i.e. negative ^{13}C excursions), a product of the variable anoxia, CO_2, and sediment influx at this time (Kidder and Worsley, 2004; Payne and Kump, 2007; Dornbos et al., 2012; Grasby et al., 2013; Meyer et al., 2013). New evidence supports that these environmental stresses appear to have varied spatially and temporally (i.e. Twitchett et al., 2004; Beatty et al., 2008; Hautmann et al., 2011; Hofmann et al., 2011; Proemse et al., 2013; Pietsch and Bottjer, 2014).

The intrinsic process hypothesis attributes Triassic recovery patterns to the magnitude of the PTME and ensuing reduced biotic competition (e.g., Erwin, 2001, 2007; Hofmann et al., 2013a, 2013b, 2013c). Low beta-diversity (between-habitat) after the PTME could be a result of low taxonomic diversity, which led to a low degree of competition for niche space (i.e. ecosystem undersaturation) (Hofmann et al., 2013a, 2013b, 2013c). Beta diversity increases when new taxa (via origination and/or immigration) enter the community, saturating the ecosystem and increasing niche space competition between species. Thus, an increase in speciation rate and subsequently the rate of interactions between species would result in an increasing rate of diversification (Solé et al., 2010; Hautmann, 2014). Paleocommunities with low beta diversity have been identified in Early Triassic paleocommunities in the western US (e.g., McGowan et al., 2009; Hofmann et al., 2013a).

3. Quantifying recovery after the Permo-Triassic mass extinction

While several researchers have created definitions and/or models of measuring recovery (e.g., Stanley, 1990; Erwin, 1996, 1998; Harries