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Functional Diversity of Regional Marine Paleocommunities After the Permo-Triassic Mass Extinction: Case Studies from Panthalassa and Paleo-tethys

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FUNCTIONAL DIVERSITY OF REGIONAL MARINE PALEOCOMMUNITIES
AFTER THE PERMO-TRIASSIC MASS EXTINCTION: CASE STUDIES FROM
PANTHALASSA AND PALEO-TETHYS

by

Ashley A. Dineen

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August 2015
ABSTRACT

FUNCTIONAL DIVERSITY OF REGIONAL MARINE PALEOCOMMUNITIES AFTER THE PERMO-TRIASSIC MASS EXTINCTION: CASE STUDIES FROM PANTHALASSA AND PALEO-TETHYS

by

Ashley A. Dineen

The University of Wisconsin-Milwaukee, 2015
Under the Supervision of Professor Margaret Fraiser

The Permo-Triassic mass extinction (PTME) was the largest biodiversity collapse in Earth’s history. Published data has been interpreted as indicating that marine ecological devastation following the PTME was protracted and may have lasted 5 million years into the Middle Triassic (Anisian). However, a review of previous literature shows that understanding of biotic recovery is usually based on only a few components of the ecosystem, such as on taxonomic diversity, a single genus/phylum, or shallow water facies. Typically, paleocommunities are considered fully recovered when dominance and diversity are regained and normal ecosystem functioning has resumed. However, to more fully characterize Triassic ecologic restructuring, paleoecologists should take into account ecological proxies, such as functional diversity and marine paleocommunity structure. Functional diversity (i.e., richness and evenness), defined as the abundance and distribution of traits present in a community, has important implications for the functioning of ecosystems in the wake of events of major disturbance. Function richness and evenness was quantified from two post-PTME marine localities (i.e. south China, and the western United States), in addition to previously published datasets using a ten-trait
ecospace model. Data from marine fossil assemblages in all of these localities indicates that paleocommunities had high taxonomic diversity and generally high functional richness, but appear to be functionally uneven. The two case study paleocommunities, the Spathian Virgin Limestone and Anisian Leidapo Member, were numerically and ecologically dominated by one functional group, implying that either resource availability and/or the utilization of resources in these post-extinction paleocommunities was uneven, or strong environmental filtering was in effect. As such, despite deposition in fairly stable ramp paleoenvironments, both of these biotic assemblages would have been very susceptible to biotic and environmental perturbations such as recurrent species invasion or anoxic events. While it is uncertain whether this pattern is typical of all paleocommunities in the aftermath of the PTME, these results imply that some Early and Middle Triassic paleocommunities may not have been as fully restructured as previously thought, and could have been inherently unstable due to the numerous biotic and environmental changes present in the wake of the PTME.
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Chapter I: Introduction

Permo-Triassic mass extinction and its aftermath

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 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.

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 CO2, methane, and sulfides were emitted, leading the atmosphere and ocean to become rich in CO2 and depleted in O2 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.,
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; Twitchett and Oji, 2005; Chen et al., 2005; Nutzel, 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., Fraiser et al., 2011; Brayard et al., 2011b) 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;
Current data support the idea that Early and Middle Triassic oceans were vertically-stratified, with a CO₂-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 ¹³C 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 ¹³C record also indicates that high productivity intervals were followed by productivity crashes (i.e. negative ¹³C excursions), a product of the variable anoxia, CO₂, 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.
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).

Project Goals and Synopsis

Multiple studies have revealed variable and complex spatial and temporal recovery patterns in fossil 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; Meyer et al., 2013; Hofmann et al., 2013a; Benton et al., 2013; Clapham et al., 2013). As such, novel and innovative proxies are needed in order to examine and quantify the differences and/or similarities in regional paleocommunities. The objectives of this study 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 quantifying the nature and patterns of regional marine paleocommunity recovery after the PTME.

Chapter II presents an overview of how recovery in the Triassic has been quantified in previous paleontological studies. Data from modern marine studies is also discussed in order to examine different methods in which recovery from disturbance is quantified. To more fully characterize Triassic recovery, the term “restructuring” is proposed in addition to the use of two novel metrics, functional richness and evenness. Additionally, to test the viability of these metrics, functional diversity is calculated from five previously-published marine paleoecological studies, chosen to represent different stages pre- and post-extinction (i.e., Middle Permian, Early Triassic, and Middle Triassic). Overall, the results from this analysis indicate that taxonomic and ecologic diversity was decoupled after the PTME, in that taxonomic diversity increased quickly in several Early Triassic paleocommunities, but functional diversity did not return to high levels until the Middle Triassic (Anisian).

Chapter III presents a case study using field-collected data from the Middle Triassic (Anisian) Leidapo Member (Qingyan Formation) in Qingyan, south China (Figure 1.1). Previously interpreted to represent a fully restructured paleocommunity in the aftermath of the PTME, results indicate that the fauna of Leidapo Member had high taxonomic diversity and high functional richness, however was functionally uneven. Despite the presence of 24 different functional groups, the paleocommunity was numerically and ecologically dominated by one functional group consisting of mostly
attached epifaunal suspension feeding brachiopods. As such, it is hypothesized that this assemblage would have been very susceptible to biotic and environmental perturbations, such as species invasion and anoxic events.

![Figure 1.1. Map reconstruction of Early to Middle Triassic (~240 ma) paleogeography. Red stars indicate location of the Spathian Lost Cabin Locality in Nevada (Panthalassa) and the Anisian Fossil Hill Locality in south China (Paleo-Tethys). Modified from Colorado Plateau Geosystems, Inc., 2014.](image)

Chapter IV examines another regional case study, this time from the Early Triassic (Spathian) Virgin Limestone Member (Moenkoepi Formation) in southern Nevada (Figure 1.1). While very few paleoecologic studies have been conducted on the Lost Cabin Springs locality, it has been previously hypothesized that fauna found here is representative of a low diversity paleocommunity either under the influence of high environmental stress, or a lack of significant competition. Results indicate that taxonomic and functional richness are moderate, while overall functional evenness is extremely low due to community dominance by two genera of disaster bivalves. It is hypothesized that the Virgin Limestone paleocommunity lacked any significant or prolonged environmental
stresses, however contained high levels of competition in some areas of the available trait space.

Lastly, Chapter V presents a summary of all previously discussed datasets, comparing and contrasting functional diversity levels between regional localities from Panthalassa and Paleo-Tethys. It is presented here that functional diversity, defined as the abundance and distribution of traits present in a community, has vital implications for the functioning of ecosystems in the wake of events of major disturbance. However, additional localities and studies quantifying ecologic restructuring are required in order to fully understand the dynamics and impacts of the Permian-Triassic mass extinction on marine ecosystems.
References


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

Quantifying Recovery

While several researchers have created definitions and/or models of measuring recovery (e.g., Stanley, 1990; Krassilov, 1996; Harries et al., 1996; Erwin, 1996, 1998; Solé et al., 2002, 2010; Twitchett, 2005; Erwin, 2007; Chen and Benton, 2012; Hofmann et al., 2013a; Pietsch and Bottjer, 2014), no single method gives a complete picture of community paleoecology or has been embraced by all paleontologists. Biotic recovery is not linear or systematic; a community may contain some components indicative of high ecosystem functioning, such as high diversity and evenness, but lack others, such as large organism body size, guild diversity, or morphological complexity (e.g., Díaz and Cabido, 2001; McGowan, 2005; Sahney and Benton, 2008). Previous ecologically focused definitions of recovery state that a community can be considered fully recovered when normal ecosystem functioning has resumed and previous abundances and diversity are regained (Erwin, 1996; Krassilov, 1996). However, these definitions lead to a vital and perhaps impossible question: what is “normal” in the aftermath of Earth’s largest mass extinction? And, did Triassic communities return to what would be considered the Permian “normal”?

Proxies used in quantifying recovery

In order to recognize how our current understanding of Triassic recovery is shaped, we completed a literature review of 50 publications (1973-2012) focused on the aftermath of the PTME. In analyzing data from the literature, we took note of the level of
recovery each paleocommunity was interpreted to exhibit (i.e. early phase or fully
completed determined by the author’s conclusions); the stage (e.g., Spathian) recovery
began or was completed; geographic location studied; environments of deposition; biota
quantified; and what metrics or community characteristics were used to quantify biotic
recovery in each publication. Substantial variation was found not only in when recovery
began or was completed after the PTME, but also in the level of recovery. This was
largely because of: 1) geographic location and environment of deposition, and 2) the
biotic component of paleocommunities examined.

Only 34% of studies used comprehensive paleocommunity data (i.e. all
genera/phyla present in a fossil paleocommunity), 40% used only a single taxonomic
group (genus, phylum), 10% used 2 to 3 genera/phyla, 10% used metazoan reefs, and 6%
used only trace fossils to evaluate Triassic post-extinction paleoecology (Figure 2.1).
38% of studies were based on data from global databases, while 62% were regional. Of
the regional studies, 42% were focused in China, followed by the western United States
(23%), northern Italy (10%), Oman (10%), Canada (6%), Australia (3%), Tibet (3%), and
Svalbard (3%). Since marine sections from Gondwana and the Panthalassa Ocean are not
common due to subduction, 36% of studies were from Paleo-Tethys, 18% from
Panthalassa, 10% from Neotethys, and 2% from Boreal sections; 34% of studies
combined all Triassic oceans
Figure 2.1. Literature review results indicating biota measured to quantify recovery after the Permo-Triassic mass extinction. Results expressed as percentage of studies that used comprehensive paleocommunity data (i.e. all genera/phyla present), a single genus/phylum, two to three genera/phyla, reef data, or trace fossil data.

The majority of studies focused on shallow water environments (48%), and only 7% and 9% were from middle shelf and deep water environments, respectively; 36% of studies combined all of these environments. Of the 48% of shallow water studies, 32% of these were based in inner shelf, 5% in nearshore, 5% in reef, 4% in subtidal, and 2% in seamount facies. Overwhelmingly the most utilized metric was taxonomic diversity with 96% of the studies analyzed using it to affirm that high taxonomic diversity equaled a fully or mostly recovered paleocommunity. High numerical abundance (62% of studies), large organism body size (30%), wide environmental or geographic distribution (22%), increased tiering or guild structure complexity (16%), and complex community structure (10%) were also used to determine recovery (Figure 2.2).
Figure 2.2. Literature review results indicating metrics used to quantify or define a recovered community in the Triassic. Results expressed as percentage of studies examined that used that metric in order to measure biologic recovery following the Permo-Triassic mass extinction.

Herein lies a potential problem in understanding Triassic biotic recovery: rediversification and radiation should not be mistaken for full paleoecologic recovery. Schwartz et al. (2000) indicated that communities are not necessarily more stable (i.e. resistant to change) with increasing taxonomic diversity, and that studies need to focus on the distribution of abundances among species in order to determine their stability. In addition, morphological recovery can lag behind taxonomic diversification, thus taxonomic diversity is a poor predictor of the extent of morphological differences between taxa (i.e. disparity) during recovery intervals (McGowan, 2005; Brosse et al., 2013). Paleocommunity ecological components can be decoupled from taxonomic diversity during times of significant environmental stress (McKinney et al., 1998; Droser et al., 2000; McGhee et al., 2004, 2012, 2013; Christie et al., 2013), meaning that while
taxonomic diversity may recover quickly after an extinction event (e.g., Twitchett et al., 2004; Brayard et al., 2009), true ecological recovery, such as the refilling of guilds, the rebuilding of trophic structures, and gaining an even abundance of species, may take much longer (e.g., Schubert and Bottjer, 1995; Sahney and Benton, 2008).

The Triassic: A return to normal?

Intervals after mass extinctions are considered periods of reorganization, with clades invading newly vacated habitats and many survivors quickly evolving into ecological settings they had not previously occupied (Boucot, 1983; Sheehan, 1996). Strong selectivity of the PTME resulted in passive and physiologically unbuffered (i.e. low metabolic rates, limited internal circulation, etc.) taxa suffering much higher extinction rates, thus breaking a pattern of biologic incumbency that had lasted the majority of the Paleozoic (Bambach et al., 2002). The PTME also permanently altered marine community structure, whereby increased ecological complexity and alpha diversity (within-habitat) characterized post-extinction communities compared to those of the Permian (Wagner et al., 2006). Therefore it is clear that Triassic paleocommunities were physiologically and ecologically different from those of the Permian or any other previous time; many clades evolved the ability to live in vacated habitats where they had not previously existed. To examine the context of biotic recovery after the PTME, comparison between the Permian and the Triassic seems problematic since fundamental new ecological processes were established (e.g., Bambach et al., 2002; Wagner et al., 2006; Leighton et al., 2013). Looking for a “return to normal” is not useful or practical in the aftermath of the PTME; focus instead should be directed towards determining
ecosystem complexity and functioning, as well as how ecosystems equilibrated towards the new Triassic “normal”.

Several studies have indicated that after natural disturbances, complex and often indirect interactions (i.e. physiological and behavioral) among species can influence the rate of ecosystem recovery (Gardmark et al., 2003; Peterson et al., 2003; Lotze et al., 2011; Gilmour et al., 2013). Petchey et al. (1999) found that disturbance, in this case climate change, caused complex changes in the marine trophic structure and altered ecosystem functioning by causing reduced top-down control of producers. Marine ecosystems can potentially entrain into alternative stable states after reaching a critical threshold (e.g., Scheffer et al., 2001; Knowlton, 2004; Jones and Schmitz, 2009; Graham et al., 2013). This indicates that after a stochastic event an ecosystem may shift to an alternative stable regime containing different dominant organisms than the previous regime. Palumbi et al. (2008) stated that after deep disturbance, “new ecological players may enter the system, preventing a rapid return to former state”.

Bellwood et al. (2006) experimentally triggered biotic disturbance by simulating overfishing of herbivores on the Great Barrier Reef, resulting in the ecosystem shifting from that of coral and epilithic algae-dominated to macroalgae-dominated due to removal of the ecosystem’s herbivores. The reversal of this state shift and recovery was driven by a single, rare species known as a “sleeping functional group”, one that is capable of performing a certain functional role, but does so only under exceptional circumstances. Rare species have been shown to contribute critical and diverse functional abilities to a community, indicating their importance to ecosystem resilience (Mouillot et al., 2013a). These studies illustrate that high taxonomic diversity doesn’t always offer an ecosystem
protection against state shift and disturbance, and that post-disturbance ecology is often not comparable to that of pre-disturbance.

**Restructuring in the Triassic**

It is clear that the Permo-Triassic mass extinction had a huge influence on the taxonomic and ecologic restructuring of the marine realm, and that Early and Middle Triassic paleocommunity ecology was very different from that of the Permian (e.g., Raup, 1979; Sepkoski, 1981; Valentine, 1986; Bambach, 1993; Bambach et al., 2002; Wagner et al., 2006; Leighton et al., 2013). The stochastic nature of biotic systems confounds and perhaps pre-empts our ability to directly compare pre-extinction ecosystems with those following the disturbance, especially in the case of mass extinction recovery intervals. We propose that instead of the term “recovery”, which implies a return to normal or previous conditions, the term “restructuring” should be used in its place to describe ecological processes during and after the PTME. This term more accurately encompasses the reorganizational and unique nature of ecosystems in the wake of Earth’s largest mass extinction.

Here we suggest and test the use of novel ecologic metrics previously unused in examining the Triassic. Complex and stable ecosystems are likely to have high taxonomic diversity, even assemblages, large body sizes, and high tiering, all of which have been included in previous models of PTME restructuring (e.g., Twitchett, 2005). We propose that fully restructured paleocommunities should include these components as well as high ecological complexity and functional diversity. The use of these has been restricted to mostly vertebrate studies (Benton et al., 2004; Sahney and Benton, 2008),
the development of recovery models (Solé et al., 2002; Bush and Novack-Gottshall, 2012), or other intervals of time (Villéger et al., 2011; Sessa et al., 2012).

Quantifying ecosystem complexity and functioning

Ecological complexity can be determined from such factors as the number of species in the system, the number of interspecific interactions, the magnitude of the interaction among species, and the relative distribution of species abundance in an assemblage (evenness) (Pimm, 1984; DiMichele et al., 2004; Parrott, 2010). In this study we will evaluate ecological complexity by the number of functional groups within a community (Walker, 1995). A functional group is defined as an assemblage of taxonomically distinct organisms that share identical ecological characteristics (i.e. traits) and therefore perform similar functional roles (i.e. producer, predator, engineer, etc.) in the community (Steneck, 2001). The topic of functional diversity has received much attention in the past decade (e.g., Petchey and Gaston, 2006; Villégar et al., 2008, 2011; Mouchet et al., 2010; Mouillot et al., 2013b; Mason and de Bello, 2013) and is widely thought to exert greater influence on ecosystem functioning than taxonomic diversity (Díaz and Cabido, 2001; Hooper et al., 2005; Danovaro et al., 2008; Mouillot et al., 2011).

Similar to taxonomic diversity, which is often split into species richness and evenness, functional diversity can be split into functional richness (i.e. the amount of functional space occupied by an assemblage, i.e. the number of functional groups in a community) and functional evenness (i.e. evenness of abundance distribution across functional groups) (Mouillot et al., 2005; Mouchet et al., 2010). A robust and complex
community is typically characterized by high diversity of functional groups because a community made up of species with a variety of ecological functions is more likely be resilient against environmental disturbance and extinction (Walker, 1995; Bellwood et al., 2004; Solan et al., 2004; Cardinale et al., 2012). As such, the abundance of functional groups present has a large influence on the ecological stability and complexity of ecosystems; loss of functional groups from disturbance and/or extinction often leads to cascading secondary extinction, especially if those lost contain functionally important or ecologically dominant species (Walker, 1995; Naeem, 1998; Petchey et al., 1999; Dunne et al., 2002; Larsen et al., 2005). Therefore, resilience from disturbance and the capacity for recovery depends a great deal on the strength and number of ecological interactions between species within the community (Bernhardt and Leslie, 2013).

The concept of functional evenness addresses how evenly distributed species are within functional groups, akin to ecological overlap (Walker, 1995; Naeem, 1998). A community with high functional evenness would contain a variety of functional groups that have an abundance of species within each group, allowing them to functionally compensate for each other if one member of their group becomes extinct. However, if the majority of these functional groups contain only one species (i.e. low evenness), the loss of one species might result in the disappearance of an entire functional group from the ecosystem. Ecosystem functioning shows substantial changes when entire functional groups are added or lost; high functional evenness can help buffer an ecosystem against disturbance, making it more resilient and stable (Lawton and Brown, 1993; Tilman and Downing, 1994; Micheli and Halpern, 2005; Bellwood et al., 2006; Nystrom, 2006; Mouillot et al., 2013b). Ecosystems with higher functional evenness often show a higher
rate of recovery after community collapse, but if evenness is reduced the ecosystem may be pushed into a state shift (i.e. alternative natural state; Palumbi et al., 2008).

The relationship between taxonomic and functional diversity is dependent upon the community being assessed (e.g., Díaz and Cabido, 2001; Loreau et al., 2001; Fridley, 2001; Enquist et al., 2002). Coral reef ecosystems, for instance, have very high taxonomic diversity but low functional evenness and redundancy, making them highly susceptible to environmental change (e.g., Bellwood et al., 2003, 2004; Micheli and Halpern, 2005; Hoey and Bellwood, 2009; Guillemot et al., 2011; Brandl and Bellwood, 2014). Though the connections between ecosystem functioning and functional diversity are complex (e.g., Fonseca and Ganade, 2001; Naeem, 2002; Mouchet et al., 2010), we argue that evaluating functional richness and evenness of Triassic paleocommunities is vital for understanding restructuring dynamics.

**Assessing Permian and Triassic ecosystem functioning**

One unanswered question concerning mass extinctions is what the dynamics of ecospace filling were like during the ensuing community restructuring (Erwin, 2001; Bush and Novack-Gottshall, 2012; Foster and Twitchett, 2014). Many studies have compared restructuring to the concept of ecological succession (e.g., Walker and Alberstadt, 1975; Krassilov, 1996; Solé et al., 2002), in which the initial pattern is that of a low diversity community consisting of small-sized opportunists or generalists, followed by an increase in diversity, body size, primary production, and colonization and construction of niches, finally resulting in a mature and highly functional community. This has been observed in the fossil record (e.g., Bottjer and Ausich, 1986; Bottjer et al.,
1996; D’Hondt et al., 1998; Roopnarine et al., 2007; Sahney and Benton, 2008; Hull and Darroch, 2013) during the aftermaths of other mass extinctions. Modern ecology studies (e.g., Micheli and Halpern, 2005) report that increased functional diversity coincided with the increase in species diversity following biotic degradation. As such, one would predict that during the Triassic restructuring and rebuilding interval paleocommunities would generally show an increase in functional diversity as community composition transitioned from simple generalists to complex specialists via increased ecospace utilization (Solé et al., 2002).

Here, for the first time, we test the use of functional metrics (i.e. functional richness and evenness) across the Permo-Triassic interval using fossil data from published marine paleoecologic studies. Five paleocommunities from the Middle Permian, Early Triassic, and Middle Triassic (Table 2.1) were chosen because of their extensive sampling and comprehensive paleocommunity lists, and because they represent pre- and post-extinction communities from nearshore-to-middle shelf environments (studies containing all of this information were found to be rare). Data from the primary literature were culled in order to determine the taxonomic composition and ecology of the five paleocommunities; any missing ecological information (i.e. feeding habit, mobility, etc.) that was not found in the literature was supplemented by the Paleobiology Database (www.fossilworks.org). All invertebrate macrofauna listed in the literature, such as brachiopods, molluscs (bivalves, gastropods, cephalopods, etc.), arthropods, echinoderms, sponges, bryozoans, annelids, and corals, was included in the analysis.
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<td>Olenekian</td>
<td>Moenkopi (Virgin LS Member)</td>
<td>Beaver Dam Mountains and Hurricane Cliffs, Utah</td>
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<td>62967-62972, 62974, 62975, 62977, 62981-62984, 62991, 62995-62997, 62999, 63000, 63004-63007, 63009, 63014-63016, 63018, 63021-63023, 63029, 63031-63036, 63143, 63145-63147, 63193, 63198, 63205, 63221, 63280, 63295, 63296, 63298, 63299, 63385, 64680, 64710, 64715, 64719, 65878, 66049, 66113, 122196-122207, 14586, 141588, 141594-141597, 141602-141603, 141606</td>
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<td>Anisian</td>
<td>Qingyan (Leidapu Member)</td>
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Table 2.1. Primary literature and Paleobiology Database (www.paleodb.org) collection numbers used to quantify functional richness and evenness for Permian, Early Triassic, and Middle Triassic paleocommunities.

We applied the framework for quantifying the traits and ecospace of marine fossil genera created by Novack-Gottshall (2007). Compared to other ecospace methods that are three-dimensional (i.e. microhabitat, foraging habit, mobility; e.g., Bambach, 1983),
this method unites morphological and guild models, providing up to 27 different characters in a theoretical ecospace framework. We choose ten functional traits (similar to those used in Villégar et al. 2011) that focused on how marine taxa interacted with and utilized each other and their environment (e.g., mobility, substrate relationship, support, condition of food, etc.). These ten traits, with the exception of body volume, are categorical and can be coded based on separate modalities corresponding to each trait. For example, the trait category of diet is sorted into three separate modalities, 1) carnivore, 2) microbivore, or 3) carnivore and microbivore. Skeletal body volume (in ml) is an ordered category and was calculated with Novack-Gottshall’s (2008) ATD (anteroposterior, transverse, and dorsoventral) metric using data from either the primary literature or the Paleobiology Database. If faunal body size was unknown (or any other trait for that matter) that category was simply coded as “unknown” for that taxon. This method allows for each fossil genus to be classified distinctly according to its adult life characteristics for each of the ten functional traits. For this study, we examined the ecology of 352 fossil genera, assigning 3,520 traits. Genera were then sorted into functional groups based on the condition that they contain identical traits across all ten categories, and therefore perform identical ecological functions in the paleocommunity. This method has previously been used successfully by Villégar et al. (2011) in quantifying functional diversity in Cambrian, Silurian, and Modern fossil communities, but has not been used to examine paleocommunities following the PTME.

Functional evenness was calculated using the taxonomic evenness metric \( H'/H'_{max} \). While this equation is typically used to calculate species abundance distribution within a community, we input the abundance of genera within each
functional group instead of species abundance to get the evenness of distribution across functional groups for each paleocommunity. The Shannon Index ($H'$) thus becomes the measure of the difficulty in predicting the functional group of the next genus collected. The lowest possible value is $H'=0$, while the maximum value can be calculated as $H'_{max} = \ln S$, with $S$ representing the number of functional groups present (Shannon, 1948). Therefore, functional evenness ($Fe$) can be calculated by using the values of the Shannon Index ($Fe = H'/H'_{max}$); a paleocommunity with high evenness would have high values (maximum of $Fe=1$), while low values (minimum of $Fe=0$) would represent low evenness.

This calculation more accurately portrays the evenness of functional groups as opposed to simply dividing the number of genera present by the number of functional groups (e.g., Villégar et al., 2011), which would only be accurate if genera were completely even in their distribution (i.e. $Fe=1$) across functional groups. The use of the functional evenness index ($FEve$), a measure of functional evenness based on a minimum spanning tree (MST) graph (e.g., Villégéar et al., 2008), was not achievable because individual genus abundances were not provided for the majority of the fossil data analyzed. Nonetheless, our calculation is a simple and effective means to estimate functional evenness in fossil paleocommunities.

**Permian and Triassic functional diversity**

We evaluated a total of 61 different functional groups in five Permian and Triassic paleocommunities (Figure 2.3). The pre-extinction Middle Permian (Wordian) Texas paleocommunity contained 125 genera and 34 functional groups, with an evenness
of 0.77 (range of 1 to 37 genera per functional group). Post-extinction, the Early Triassic (Griesbachian) Oman paleocommunity contained 27 genera and 12 functional groups, with an evenness of 0.94 (range of 1 to 5 genera). The Early Triassic (Griesbachian-Dienerian) Wyoming paleocommunity contained 9 genera and 5 functional groups, with an evenness of 0.89 (range of 1 to 4 taxa). The Early Triassic (Spathian) Utah paleocommunity, meanwhile, was composed of 47 genera and 18 functional groups, with an evenness of 0.91 (range of 1 to 7 genera). Lastly, the Middle Triassic (Anisian) China paleocommunity contained 144 genera and 37 functional groups, with an evenness of 0.91 (range of 1 to 14 genera).

Figure 2.3A illustrates loss of functional richness in paleocommunities during the Permo-Triassic mass extinction, the rebuilding of functional ecospace through the Early Triassic, and increasingly higher taxonomic and functional richness in the Middle Triassic. An increase in both taxonomic and functional richness is apparent during the Early to Middle Triassic restructuring interval examined here, from a low of 5 functional groups in the Induan to a high of 37 in the Anisian. This data supports recent work by Foster and Twitchett (2014), which indicates that while global functional diversity remained unchanged across the PTME boundary, local and regional functional richness was significantly reduced. Furthermore, despite previous interpretations that these Early Triassic communities were significantly recovered (e.g., Twitchett et al., 2004; Hofmann et al., 2013b, 2013c; Foster and Twitchett, 2014), we find that functional richness is still fairly low in the communities studied. However it is important to note that the majority of those studies (e.g., Hofmann et al., 2013b, 2013c; Foster and Twitchett, 2014) were based on only a three-trait ecospace model (i.e. tiering, motility, feeding habits), whereas this
study used a ten-trait ecospace model (Novack-Gottshall, 2007) that better quantifies ecological diversity. Additionally, while some communities showed high taxonomic richness after the PTME (e.g., Griesbachian Oman, Olenekian Utah), functional richness remained at low levels. This supports the idea that while taxonomic diversity may rapidly increase following mass extinctions, ecological restructuring may take longer (McKinney et al., 1998; Droser et al., 2000; McGhee et al., 2004, 2012, 2013; Christie et al., 2013).

When examining functional evenness, we found that the Middle Permian paleocommunity contained relatively low evenness (Fe=0.77), indicating a semi-uneven distribution of genera within functional groups (Figure 2.3). Interestingly, evenness increased after the PTME, with all Triassic paleocommunities showing higher evenness than that of the Permian, with the highest being the Griesbachian (Fe=0.94), then the Anisian (Fe=0.91), Spathian (Fe=0.91), and Griesbachian-Dienerian (Fe=0.89). Functional evenness did not increase linearly through time in the Triassic, but varied depending on geographic location. For example, the post-extinction Griesbachian-Dienerian Wyoming paleocommunity had the lowest functional richness (5 functional groups), and the lowest evenness (Fe=0.89) of all the Triassic paleocommunities, but the Griesbachian Oman paleocommunity had moderately high functional richness (27 functional groups) and the highest evenness (Fe=0.94) of all of the Triassic paleocommunities. This further supports the pattern of variable levels of restructuring and functional diversity in different geographic regions (e.g., Foster and Twitchett, 2014), as it appears that the Griesbachian Paleotethyan Oman locality was in a later stage of restructuring than the Griesbachian Panthalassan Wyoming locality.
Figure 2.3. A. Comparison of taxonomic and functional richness for one Permian and four Triassic paleocommunities. B. Comparison of functional evenness for one Permian and four Triassic paleocommunities. Functional richness is represented by the number of functional groups present in the paleocommunity, while evenness is represented by the ratio of $H'/H'_\text{max}$ (Shannon evenness) on a scale of 0 to 1, with higher values indicating that genera is more evenly distributed among functional groups.
Perhaps Middle Permian low evenness was due to the abundance of brachiopod genera. Sixty-three genera of the Middle Permian paleocommunity (125 genera total) were distributed among 32 functional groups, while the other 62 genera were contained within just 2 functional groups. Of these 62 genera, 61 were brachiopods that made up the majority of the 2 functional groups of sedentary, epifaunal, attached, particle filter feeders. These two functional groups (separated only by differing body volumes) comprised half (50%) of the Middle Permian paleocommunity. Brachiopods have less variety of feeding habits and modes of mobility compared to molluscs, and therefore a community dominated by brachiopods could be expected to have lower functional evenness. This could also explain why the Triassic paleocommunities typically show higher functional evenness, as more functionally diverse molluscs became more abundant than brachiopods (Fraiser and Bottjer, 2007). For example, 38 bivalve, gastropod, and cephalopod genera from the Spathian Utah paleocommunity belong to 13 different functional groups, as opposed to 3 brachiopod genera that belong to just 1 functional group. Thus, the switch in taxonomic dominance between brachiopods and bivalves (i.e. Paleozoic EF to Modern EF) could have played a role in the transition from low to high evenness. This hypothesis is in conjunction with Villégar et al. (2011) in which functional richness and redundancy was higher in Modern faunas in comparison to those of the Cambrian and Silurian, suggesting that functional diversity of the marine benthos has increased throughout geologic time.

The high functional evenness values of the Early Triassic paleocommunities (Induan Oman, Fe=0.94; Induan Wyoming, Fe=0.89) indicate that genera were evenly distributed among functional groups. This is contrary to most studies (e.g., Mouillot et
al., 2013b) that show a decrease in functional richness and evenness immediately following disturbance. However, the majority of those studies are on modern time scales, so perhaps this pattern is beyond the resolution of the geologic record. High functional redundancy and evenness lends higher resilience to communities during periods of disturbance (e.g., Harris, 1993; Palumbi et al., 2008). Ecosystems existing in harsher environments are interpreted to have a higher fraction of development capacity (i.e. potential for ecosystem organization) encumbered for functional evenness and redundancy, as these provide ecological “insurance” against frequent disturbance (Walker, 1995; Fonseca and Ganade, 2001; Elmqvist et al., 2003; Bellwood et al., 2004; Hooper et al., 2005). While all four Early and Middle Triassic paleocommunities are interpreted to have developed under normal, well-oxygenated conditions (i.e. Stiller, 1997; Twitchett et al., 2004; Komatsu et al., 2004; Marenco et al., 2012; Hofmann et al., 2013a, 2013b), it is possible that conditions during the PTME and its aftermath did not favor the survival of paleocommunities that lacked high functional evenness.

High functional evenness would contribute to ecosystem resilience by increasing the ability of the group to maintain its function in the face of frequent abiotic and biotic perturbations during and after the PTME (Harris, 1993; Walker, 1995; Loreau et al., 2001; Elmqvist et al., 2003; Mason et al., 2005; Mouillot et al., 2005; Gonzalez and Loreau, 2009). Paleocommunities that contained genera not able to optimize their resources, compete, and/or persist in stressful environmental conditions during the PTME were likely selected against, resulting in highly functionally even communities. While it has been shown that paleocommunities cannot “evolve” in the strict definition of the word (i.e. Bambach and Bennington, 1996), they can change through time and reflect
long-term assembly and diversification processes (Solé et al., 2002). Therefore, it can be hypothesized that Early and Middle Triassic high functional evenness was the result of surviving paleocommunities that developed high resilience to endure abiotic and biotic perturbations during and after the PTME. Perhaps paleocommunities that did not develop high functional evenness were unable to persist or gain stability in the Triassic. This ecological approach to ecosystem rebuilding agrees with recovery models in which species interactions and niche processes are essential aspects of diversification after mass extinctions (e.g., Solé et al., 2002, 2010; Roopnarine, 2006).

Paleocommunities during the Early and Middle Triassic interval likely developed some degree of resilience in order to maintain a desirable state in a variable environment (Elmqvist et al., 2003). Higher functional evenness may have developed in Triassic paleocommunities as a consequence of 1) abiotic and biotic perturbations associated with the PTME, and/or 2) the transition to dominance by functionally diverse molluscs (i.e. the Modern EF). Together these hypotheses suggest the interaction of complex evolutionary and ecological dynamics in the wake of the PTME. Additional research is needed in order to establish global and regional patterns, and its occurrence following other mass extinction intervals.

**Summary**

Herein it was determined that the majority of Early and Middle Triassic paleoecological studies are based on taxonomic diversity, a single genus/phylum, shallow water facies, and combined or limited regional data. We argue that the term “restructuring” be used in place of “recovery” to describe paleoecological processes
following the PTME as it more accurately encompasses the reorganization and distinct nature of the Early and Middle Triassic. Functional richness decreased to low levels in the immediate aftermath of the PTME and increased throughout the Early Triassic with high levels returning in the Middle Triassic (Anisian).

Inversely, functional evenness was higher in the Triassic paleocommunities compared to the Middle Permian paleocommunity. We propose that this was likely the result of 1) brachiopod versus mollusc taxonomic dominance, and 2) abiotic and biotic perturbations associated with the PTME. These results support the idea that taxonomic and ecological diversity can be decoupled after mass extinctions (i.e. Droser at al., 1997; McGhee et al., 2004), such that taxonomic diversity increased quickly after the PTME but functional diversity appears to have taken much longer to reach high levels. The wide geographic range of the paleocommunities examined here suggests that this pattern is possibly a global trend, but future work will involve applying these metrics to other Permian and Triassic paleocommunities. The addition of more comprehensive ecological parameters such as the ones evaluated here will be beneficial in better understanding the complex nature of biotic survival and restructuring in the aftermath of the Permo-Triassic mass extinction, as well as other intervals of global environmental change.
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Chapter III: Low functional evenness in a post-extinction Anisian (Middle Triassic) paleocommunity: A case study of the Leidapo Member (Qingyan Formation), south China

Introduction

Quantifying the functional diversity of a community has recently gained traction in paleoecological studies (e.g. Villégar et al., 2011; Bush and Novack-Gottshall, 2012; Dineen et al., 2014; Foster and Twitchett, 2014). This approach is particularly important in the aftermath of major biologic disturbances, as communities are typically prone to state shifts and ecosystem reorganization (Scheffer et al., 2001). Examining functional diversity gives us insight into the range of organism traits present in a community, and how this might have influenced paleocommunity stability, resilience, and resistance via the utilization of resources.

The Permo-Triassic mass extinction (PTME), approximately 252 Ma, was the largest biodiversity collapse in the Phanerozoic, and thus provides an opportunity to study how functional diversity influenced paleocommunity restructuring and survival in the aftermath of extreme environmental and biologic disturbance. Results from our recent study (i.e. Dineen et al., 2014) that sampled several regional paleocommunities indicated that functional richness (i.e. amount of functional trait space occupied) decreased to low levels in the immediate aftermath of the PTME but reached high levels in the Middle Triassic. In contrast, functional evenness (i.e. evenness of genera distributed across trait space) was found to be very high in all Early and Middle Triassic paleocommunities. Furthermore, similar to the findings from other mass extinction studies (McKinney et al., 1997; McGhee et al., 2004, 2012, 2013; Christie et al., 2013), functional diversity trends were decoupled from those of taxonomic diversity. We proposed that Triassic
paleocommunities with high functional evenness maintained stability and survival in the aftermath of the PTME. In addition, we also proposed new terminology to describe the nature of paleocommunities in the wake of mass extinctions because they are not “recovering”, but instead “restructuring” (i.e. developing new community assembly patterns in comparison to their Permian predecessors).

Here we test our recently published hypothesis on field-collected data from the Middle Triassic (Anisian) Leidapo Member (Qingyan Formation) in south China. The Leidapo Member has been extensively studied in terms of fossil morphology and taxonomy, in part because of its highly fossiliferous sequences and well-preserved calcareous shells (e.g. Stiller, 1997). However, very few paleoecologic studies have been completed on the formation (Stiller, 2001a). As this section has been proposed to contain a fully restructured Anisian paleocommunity after the PTME (e.g. J. Chen et al., 2010a, 2010b), we predicted that functional diversity would be high, as the community should have achieved optimal resource utilization, productivity, and stability 5 my after the PTME if it were truly recovered. For the first time, we quantified taxonomic and functional diversity of the Leidapo Member paleocommunity in order to determine the nature and level of ecosystem restructuring in south China after the Permo-Triassic mass extinction.

**Background Information**

*Geologic Setting*

A highly fossiliferous section of the middle to late Anisian Leidapo Member (Qingyan Formation) is present at the “Fossil Hill” locality (Bangtoupo, Leidapo), and
has been the subject of numerous sedimentological and paleontological studies (e.g. Enos et al., 1997; Stiller, 1997, 2001; Komatsu et al., 2004; J. Chen et al., 2010a, 2010b; Saito et al., 2013). The study area, located near the small town of Qingyan in Guizhou Province, China, was situated on a transitional slope between the vast carbonate Yangtze Platform to the northwest and the deep-water siliciclastic Nanpanjiang Basin to the south (Guizhou Bureau, 1987; Enos et al., 1997, 2006; J. Chen et al., 2010a; Figure 3.1A).

Covering most of the Yangtze Craton, a former tectonic plate that now extends west from beneath the South China Sea, the Yangtze Platform accumulated as much as 4,000 meters of shallow water carbonates in the eastern Tethys during the Early and Middle Triassic (Wei et al., 1996; Enos et al., 2006). While the platform was largely stable through its existence (late Proterozoic-Late Triassic), a small retreat took place in the Anisian, moving the platform margin about 2 km through the shedding of large blocks and skeletal debris (Enos et al., 1997; Payne et al., 2006).

The Qingyan Formation (397 to 1048 m thick) contains basin-margin deposits from the Anisian retreat of the Yangtze Platform platform in addition to input from the more distal Nanpanjiang Basin, resulting in the deposition of interbedded limestone, carbonate breccia, and mudstone (Guizhou Bureau, 1987; Enos et al., 1997, 2006). The Qingyan Formation is composed of five members: the Xiaoshan, Mafengpo, Yingshangpo, Leidapo, and Yuqing members, respectively (Figure 3.1B). Recent biostratigraphic analysis by Stiller and Bucher (2008) places the boundary of the middle and late Anisian in the middle of the Leidapo Member, which is approximately 192 meters thick and characterized by alternating calcareous marl and thinly-beded silty mudstone and shale (Komatsu et al., 2004).
Figure 3.1. A. Map of study area, the Fossil Hill locality, near Qingyan, Guizhou Province, China. B. Middle Triassic (Anisian) stratigraphy in the Qingyan region. Studied member, the Leidapo, is marked with a star.

Fossil biota found in the Leidapo Member are considered some of the most diverse of the Triassic and include brachiopods (Yang and Xu, 1966; Stiller, 1999a; J. Chen et al., 2010a, 2010b), bivalves (Gu et al., 1976; Komatsu et al., 2004; Stiller and Chen, 2004, 2006), gastropods (Yin and Yochelson, 1983a, 1983b, 1983c), ammonoids
(Stiller and Bucher, 2008), corals (Qi and Stanley, 1989), conodonts (Wu et al., 2008; Ji et al., 2011), echinoids (Stiller, 2001b), crinoids (Stiller, 1999b, 2000), sponges (Stiller, 1998), foraminifers (Kristan-Tollmann, 1983), and many others (Stiller, 2001a, 2001c; Enos et al., 2006). However, taxonomic composition of the Leidapo Member appears to be dependent on lithology. For example, the paper bivalves, Daonella and Posidonia, are abundant within the laminated mudstone facies, while a high diversity fossil assemblage (i.e. brachiopods, gastropods, bivalves, crinoids, etc.) can be found within the alternating thin marl limestone beds (Stiller, 1997).

This highly diverse fossil assemblage has previously been interpreted as a shallow water community, but opinions differ on depositional environment. Stiller (1997, 2001a) interpreted the community to represent an in-situ algal meadow community of alternating low and high energy, while others (Komatsu et al., 2004) have suggested that the shallow water community is parautochthonous and was transported to a deeper-water lower slope environment via gravity flows. There seems to be a general consensus that the fossil-rich limestone marl beds were deposited during periods of high energy (i.e. periodic storms, gravity flows), resulting in the rapid burial of taphonomically unaltered fossils that lack abrasion and current-reworking (Stiller 1997, 2001a; Komatsu et al., 2004; J. Chen et al., 2010a). As such, the fossil assemblages of the Leidapo Member are considered to be very well preserved and lacking taxonomic bias (Stiller, 1997). As such, based on field observations and recent studies (e.g. Z.Q. Chen et al., 2010; J. Chen et al., 2010a; Saito et al., 2013), we agree that the Leidapo Member was likely deposited in a slope paleoenvironment, though the fauna was likely transported from shallower water.
Functional Diversity and Ecosystem Functioning

It has been hypothesized that functional diversity, rather than taxonomic diversity, is a better determinant of ecosystem functioning and productivity (Chapin et al., 1997; Diaz and Cabido, 2001; Petchey and Gaston, 2002, 2006; Cadotte et al., 2011; Dalerum et al., 2012; Mason and de Bello, 2013; Song et al., 2014). Functional diversity can be split into functional richness and functional evenness. Functional richness is a measure of the volume of functional trait space filled, while functional evenness indicates the regularity of the distribution of abundance across this volume (Mouillot et al., 2005; Villégar et al., 2008; Mouchet et al., 2010). The nature of relationships between taxonomic diversity and functional diversity is currently uncertain, and can be either correlated or uncorrelated depending on the ecosystem being assessed (Loreau, 2000; Loreau et al., 2001; Hooper et al., 2005; Song et al., 2014). An excellent example is coral reef ecosystems which are known for their high taxonomic diversity but typically have low functional evenness, making them extremely vulnerable to environmental changes (Bellwood et al., 2003; Micheli and Halpern, 2005; Guillemot et al., 2011; Brandl and Bellwood, 2014).

Ecosystem processes and functioning are strongly influenced by changes in species composition as species diversity determines the variety of functional traits present in the community (Chapin et al., 1997; Schwartz et al., 2000; Symstad et al., 2003; Song et al., 2014). This is especially true after events of major disturbance, in which high functional richness and evenness can add stability and complexity to an ecosystem. For example, during an event of high environmental stress, functional groups may be lost via species extinction, leading to loss of ecological function and possibly cascading
secondary extinction (Lawton, 1994; Petchey et al., 1999; Petchey and Gaston, 2002; Larsen et al., 2005). Thus, having a variety and an evenness of ecological functions present in the community can protect and provide resilience in the wake of extinction, as surviving species may be able to compensate for the loss of functionally similar species (Vinebrooke et al., 2003; Cardinale et al., 2012; Bernhardt and Leslie, 2013). The strength and number of ecological interactions between species in a community therefore has important implications for the rate and pattern of recovery following events of major disturbance, particularly mass extinctions (e.g. Hull and Darroch, 2013).

**Methods**

Thirteen bulk samples were collected from the middle Leidapo Member at the Fossil Hill (i.e. Bangtoupo) locality (Figure 3.1). These bulk samples were broken up in the laboratory, and all identifiable invertebrates were counted and identified to the genus level, if possible, from whole and fragmented fossils. Microfossils (e.g. foraminifera) and vertebrates (e.g. conodonts) were excluded from this study. Dorsal and ventral valves for bivalves and brachiopods were identified and the ratio of each was considered in order to avoid over counting of bivalved individuals. The abundance of crinoids, echinoids, and sponges was counted using a presence-absence system due to the uncertain nature of their biomass. For examples, the presence of multiple crinoid ossicles was considered to be equal to one individual in a sample. Organism size was measured in order to calculate skeletal body volume using the ATD (anteroposterior, transverse, dorsoventral) model by Novack-Gottshall (2008).
To quantify taxonomic diversity we calculated the Simpson Index of Diversity (1-D), which takes into account the total number of genera present and the abundance of each (Simpson 1949). Thus, the higher the value of the Simpson Index of Diversity (1-D), the greater the taxonomic diversity of the samples. We also calculated the Shannon Index ($H'$), which is a measure of the difficulty in predicting the species of the next individual collected. The lowest possible value is $H' = 0$, while the maximum value can be calculated as $H'_{\text{max}} = \ln S$ (Shannon 1948). Meanwhile taxonomic evenness ($E = H'/H'_{\text{max}}$) is a measure of how similar the abundances of groups of genera are, while dominance ($D = 1-E$) is the conceptual inverse of this value (Hammer and Harper, 2006); both of these values can be used to determine if genera are evenly distributed in terms of abundance.

To quantify functional diversity we applied the multi-trait ecospace framework for marine fossil genera created by Novack-Gottshall (2007) and used in Dineen et al. (2014). In contrast to the popular three-dimensional ecospace model (i.e. Bambach, 1983), ten functional traits were used in order to focus on how marine taxa interacted with each other and used their environment (e.g. substrate relationship, mobility, body size, and condition of food; Table 3.1). Data from the primary literature and the Paleobiology Database (http://www.paleobiodb.org/) was culled in order to determine the ecology of each genus identified. Genera were then sorted into functional groups based on the condition that they contain identical traits across all ten categories. Functional richness is therefore equal to the number of functional groups present.
Table 3.1. Functional traits and modalities used to characterize functional groups. See Novack-Gottshall (2007) for formal definitions of these traits.

Functional evenness (Fe) was calculated using the taxonomic evenness metric (Shannon Index; $H'/H'_\text{max}$) in which we input the abundance of individuals/genera within each functional group to get the evenness of distribution across functional groups in the paleocommunity. Thus, the lowest possible value (Fe = 0) would indicate uneven distribution of individuals/genera across functional groups, and the maximum possible value (Fe = 1) would indicate an even distribution of individuals/genera across functional groups. We used this metric to look at both the evenness of genera ($F_{\text{gen}}$), similar to the

<table>
<thead>
<tr>
<th>Traits</th>
<th>Modalities</th>
</tr>
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<tbody>
<tr>
<td>1) Skeletal Body Volume</td>
<td>8 ordered categories for size magnitude from 0.001-0.01ml to 10,000-100,000ml</td>
</tr>
<tr>
<td>2) Reproductive Mode</td>
<td>-Sexual</td>
</tr>
<tr>
<td></td>
<td>-Sexual and asexual</td>
</tr>
<tr>
<td>3) Mobility</td>
<td>-Sedentary</td>
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<td></td>
<td>-Passively mobile</td>
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<td></td>
<td>-Facultatively mobile</td>
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<td></td>
<td>-Intermittently mobile</td>
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<td></td>
<td>-Habitually mobile</td>
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<tr>
<td>4) Substrate Composition</td>
<td>-Biotic</td>
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<tr>
<td></td>
<td>-Lithic</td>
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<td></td>
<td>-Fluidic</td>
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<td>5) Substrate Relationship</td>
<td>-Attached</td>
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<td></td>
<td>-Free-living</td>
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<tr>
<td>6) Primary Microhabitat</td>
<td>-Above substrate</td>
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<td></td>
<td>-Below substrate</td>
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<td>7) Support</td>
<td>-Supported</td>
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<td>-Self supported</td>
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<td>8) Diet</td>
<td>-Microbivore</td>
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<td></td>
<td>-Carnivore</td>
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<td></td>
<td>-Microbivore and carnivore</td>
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<tr>
<td>9) Condition of Food</td>
<td>-Solution feeder</td>
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<td></td>
<td>-Particle feeder</td>
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<td>-Bulk feeder</td>
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<td>10) Feeding Habit</td>
<td>-Filter feeder</td>
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<td>-Mass feeder</td>
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<td>-Attachment feeder</td>
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<td>-Raptorial feeder</td>
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</tbody>
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metric used in Dineen et al., 2014) and individuals (Fe$^{\text{indiv}}$) across functional groups in the paleocommunity.

To quantify the most ecologically dominant groups, we calculated mean rank order and breadth of distribution (e.g., Clapham et al., 2006). To determine rank order, the most abundant group receives a rank order of 1, the second most abundant group receives a 2 and so on. To determine the mean rank order, the sum of the rank orders is divided by the number of samples. Breadth of distribution measures the proportion of samples in which each organism was present. Together, these taxonomic and ecologic metrics provide an effective way to determine the nature and level of restructuring in the Anisian Leidapo Member paleocommunity.

**Results and Discussion**

*Taxonomic and Functional Diversity*

We identified 664 marine invertebrates in the Anisian Leidapo Member bulk samples, including brachiopods, bivalves, gastropods, ammonoids, corals, crinoids, echinoids, sponges, ostracods, and microconchids. The packstone-wackestone samples contained 62 genera, with a Simpson Index of Diversity (1-D) of 0.88 and a taxonomic evenness (E) of 0.70. Bivalves were the most taxonomically rich group, with 20 different genera present. This was followed by brachiopods (17 genera), and gastropods (15 genera), respectively. Brachiopods, though, were the most numerically abundant group, consisting of 67% (456 individuals) of the community.

In terms of functional diversity, the Leidapo Member fauna belonged to 24 different functional groups and had an individual functional evenness (Fe$^{\text{indiv}}$) of 0.48 (1
to 441 individuals per functional group) (Figure 3.2). Only brachiopods and crinoids
appeared in all examined shell beds (breadth of distribution = 1.00), although
brachiopods also had a high mean rank order (1.15 followed by bivalves with 2.00, and
gastropods with 2.55, respectively).

![Figure 3.2. Abundance distribution of individuals within functional groups. Functional Group #1 (medium-sized epifaunal attached suspension feeders) was overwhelmingly dominant in the paleocommunity, with 67% of individuals (n = 664).](image)

Low functional evenness in these samples is due to the numerical dominance of
Functional Group #1 (medium-sized epifaunal attached suspension feeders), in which
67% (441 individuals) of the community belonged. Functional Group #2 (4%) and
Functional Group #3 (8%) follow with much lower abundances. The 20 other functional
groups (Functional Groups #4-24) only constituted 21% of the community total.
Functional Group #1 was also the most taxonomically rich, with 13 brachiopod and 5
bivalve genera (18 total); this is followed by Functional Groups #2 and #3, each
containing 5 genera (Figure 3.3). Genera were fairly evenly distributed across functional groups in the community ($F_{\text{genera}} = 0.85$). This result is similar to our previous finding for the Leidapo paleocommunity ($F_{\text{genera}} = 0.91$; Dineen et al., 2014), in which we used taxonomic data from Stiller (2001a).

![Figure 3.3. Number of genera within each functional group. Functional Group #1 contained the most genera, with 13 brachiopod genera and 5 bivalve genera (total of 18).](image)

**Implications for Middle Triassic Restructuring**

Our results indicate that the Anisian Leidapo Member had high taxonomic richness, taxonomic evenness, and functional richness. However, the paleocommunity was functionally somewhat uneven ($F_{\text{indiv}} = 0.48$) in that it was numerically and taxonomically dominated by the individuals of Functional Group #1. The dominance of Functional Group #1 (medium-sized epifaunal attached suspension feeders) was likely
due to the ecological and numerical dominance of brachiopods in the community. Out of 664 invertebrates in the paleocommunity, 456 of these were brachiopods (17 genera).

These results support previous findings (e.g. J. Chen et al. 2010a) that brachiopods dominated in south China during the Middle Triassic, and that the two most common genera found in the Leidapo are *Rhaetina* and *Diholkorhynchia*. As discussed in Dineen et al. (2014), brachiopods are not as functionally diverse as molluscs; for example, brachiopods in the Leidapo Member belonged to only two functional groups, while bivalves belonged to 12 different functional groups, indicating the larger variety of ecospace bivalves were able to exploit. Despite this, brachiopods were the numerical and ecological dominant. This finding supports previous studies that have shown brachiopod ecological dominance locally in the Early and Middle Triassic (Clapham and Bottjer, 2007; Greene et al., 2011). It is thus clear that the previous notion of a transition from brachiopod-dominated Paleozoic Evolutionary Fauna (EF) to the bivalve-dominated Modern EF at the PTME boundary is more complex than previously thought. While not as taxonomically diverse as bivalves in the Anisian, brachiopods appear to have been the most important group in the Leidapo Member in terms of ecology.

The overwhelming numerical and taxonomic dominance of Functional Group #1 has implications for restructuring after the Permo-Triassic mass extinction. The high taxonomic and functional richness of the Leidapo Member indicates that the paleocommunity occupied a large amount of the functional trait space available, and was likely deposited in a fairly stable paleoenvironment. However, functional uneveness of the Leidapo shows that some resources in the ecosystem were over-utilized, as communities that are dominated by species with a set of particular traits (low functional
evenness) tend to use some resources more completely than others (Mouillot et al., 2005; Mouchet et al., 2010). In other words, some parts of the Leidapo functional space were densely occupied (Functional Groups #1-3), while others were mostly empty (Functional Groups #4-24). As such, the Leidapo paleocommunity would have been highly sensitive to species loss and invasion of new species, which would result in a possible decrease in the system’s productivity (Mason et al., 2005). And while Functional Groups #4-24 were not numerically dominant (e.g. consisting of only 21% of the paleocommunity), these 20 groups together comprise the majority of functional richness in the paleocommunity and were likely very important in maintaining ecosystem function (Mouillot et al., 2013). It could also be speculated that low functional evenness of the paleocommunity may have been a result of uneven resource availability, but this interpretation would require additional biogeochemical data in order to determine what primary productivity was like in the shallow shelf Leidapo paleoenvironment.

A recent study (Saito et al., 2013) indicated that the lower slope paleoenvironment of the Leidapo Member was likely euxinic, signaling that deeper water anaerobic conditions that expanded and contracted during the Middle Triassic. While it is uncertain what the paleoredox conditions were like further up on the shallow water shelf (the source of the parautochthonous Leidapo assemblage), one can speculate that conditions were well-oxygenated due to the high taxonomic and functional richness of the Leidapo assemblage. Because of this, it seems likely that the Leidapo assemblage’s paleoenvironment was mostly stable, although prone to stressful events (i.e. storms, anoxic or euxinic pulses). The shallow water shelf may have provided a “refuge” of sorts for members of the Leidapo fauna, particularly Functional Group #1 (majority
brachiopods), which appears to be the favored lifestyle. These environmental conditions plus the low functional evenness ($Fe^{\text{indiv}} = 0.48$) of the assemblage indicate possible environmental or niche filtering may have been in effect. The niche filtering hypothesis assumes that “coexisting species are more similar to one another than would be expected by chance as environmental conditions act as a filter” (Mouillot et al., 2007). The process of niche filtering typically yields communities with functionally similar species, as species with traits poorly adapted to the ecosystem are excluded (Cornwell et al., 2006; Mouchet et al., 2010). However, it is extremely difficult to discriminate community assembly rules in modern biologic communities, let alone those over the vast temporal scales of paleocommunities (e.g. Bretsky and Klofak, 1986; Pandolfi, 1996; Jablonski and Sepkoski, 1996; Belyea and Lancaster, 1999; Webb et al., 2002; Kraft et al., 2007; Olszewski, 2012).

The overall high taxonomic and functional diversity of the Leidapo paleocommunity supports that the paleoenvironment was mostly stable though prone to periodic environmental perturbations (i.e. deep-water euxinic pulses; Saito et al., 2013). Given the uneven distribution of individuals across functional groups in the paleocommunity, the Anisian Leidapo assemblage was likely highly susceptible to intermittent environmental changes. As such, despite previous interpretations that the Leidapo Member was fully restructured (e.g. J. Chen et al., 2010a, 2010b), these results indicate that this Anisian paleocommunity had not achieved optimal resource utilization and likely had fairly low resistance to biotic and environmental perturbations. This implies that marine paleocommunities during the Middle Triassic may have not been as inherently stable and fully restructured as previously thought. Further research is ongoing
to determine if this pattern is only seen in the local paleocommunities of eastern Paleo-Tethys (i.e. south China) or in other paleo-oceans as well.

**Conclusions**

Here, for the first time, the taxonomic and functional diversity of the Anisian Leidapo Member from south China was quantified. The fossil assemblage was found to have very high taxonomic richness and evenness, as well as high functional richness. However, functional evenness was low, with 66% of the paleocommunity’s individuals belonging to a single functional group, consisting mainly of attached epifaunal suspension-feeders. Bivalves were the most taxonomically diverse group present, however brachiopods were overwhelmingly the ecological and numerical dominant. This agrees with previous research that indicates the ecological dominance of branchiopods well into the Triassic, and highlights the importance of assessing ecological traits during periods of restructuring.

The shallow shelf paleoenvironment of the Leidapo fauna is interpreted to have provided an ideal “refuge” for members of the dominant Functional Group #1 (i.e. majority brachiopods). The overwhelming dominance of one functional group in the paleocommunity indicates that either some resources in the ecosystem were over-utilized, or the general resource availability in the paleoenvironment was uneven. Either of these scenarios would result in functional unevenness (i.e. uneven occupation of functional space available), of which we found to be present in the Leidapo Member. As such, while the Leidapo paleoenvironment is interpreted to have been mostly stable, this Anisian paleocommunity was likely very sensitive to biotic and environmental stresses and thus
may be interpreted to represent an assemblage that may have been unstable. In addition, while three functional groups (Functional Groups #1-3) were the numerical and ecological dominants of the paleocommunity, the remaining functional groups (Functional Groups #4-24) protected vulnerable functions in the community and were thus highly important to ecosystem functioning. However, additional localities are needed in order to determine if this type of pattern is regional or global, and if numerical dominance of a paleocommunity by one functional group is the norm in the aftermath of the PTME or other mass extinctions. Consequently, the reorganization of ecosystems after the PTME was highly complex, and its understanding requires the application of novel and innovative ecological metrics in order to determine the multifaceted biotic and environmental patterns present.
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Chapter IV: Functional diversity of the Early Triassic Virgin Limestone Member (Moenkoepi Formation) at Lost Cabin Springs, southern Nevada

Introduction

The Permo-Triassic mass extinction (PTME), approximately 250 million years ago, was devastating to terrestrial and marine organisms alike, resulting in the largest loss of biodiversity in Earth’s history (Raup and Sepkoski, 1982; Payne and Clapham, 2012). As a consequence, a long-dominant Paleozoic pattern of incumbency was broken, resulting in structure of the marine realm becoming permanently altered (Bambach et al., 2002; Bush and Bambach, 2004; Wagner et al., 2006). The PTME also facilitated a shift in taxonomic and ecological dominance of marine faunas, from the Paleozoic Evolutionary Fauna (EF) (i.e., rhynchonelliform brachiopods, crinoids, rugose and tabulate corals, etc.) to the Mesozoic EF (i.e., bivalves, gastropods, echinoids) (Gould and Calloway, 1980; Sepkoski, 1981; Fraiser and Bottjer, 2007a; Greene et al., 2011). This shift in dominance is a strong indication that Triassic paleocommunities are ecologically and physiologically different from those of the Permian, as previous Permian ecological structures were completely reorganized in several unique ways, including the emergence of new community types and stable relationships (Bambach et al., 2002).

Numerous studies have shown that the Early Triassic marine realm also endured variable and recurrent environmental stresses, such as periods of high anoxia, hypercapnia, hydrogen sulfide, and acidification, in addition to elevated temperatures and continental weathering, resulting in an extremely hostile setting for surviving marine faunas (e.g., Wignall and Hallam, 1992; Renne et al., 1995; Knoll et al., 1996, 2007; Payne et al., 2004; Fraiser and Bottjer, 2007b; Meyer et al., 2008, 2011; Sun et al., 2012;
Grasby et al., 2013; Dustria et al., 2013; Black et al., 2014; Sedlacek et al., 2014; Zhang et al., 2015). As such, marine invertebrate paleocommunities of the Early Triassic are generally classified as having low taxonomic diversity, small body sizes, and reduced tiering levels (Schubert and Bottjer, 1995; Twitchett, 2007; Rego et al., 2012). Although regional paleocommunities of the Early and Middle Triassic have been shown to vary considerably, with the extent of these spatial and temporal patterns largely being dependent on regional location, environmental setting, and even the clade studied (e.g., Knoll et al., 2006; Wignall et al., 1998; Twitchett et al., 2004; Beatty et al., 2008; Jacobsen et al., 2011; Greene et al., 2011; Hautmann et al., 2011; Chen and Benton, 2012; Hofmann et al., 2013a, 2015; Pietsch and Bottjer, 2014). In addition, evidence suggests that ecologic and taxonomic dominance are often decoupled during periods of extreme environmental stress, such as the Triassic (McKinney et al., 1998; Droser et al., 2000; McGhee et al., 2004, 2012, 2013; Greene et al., 2011; Christie et al., 2013). Together, this suggests that regional taxonomic and ecologic restructuring after the Permo-Triassic mass extinction is extremely mercurial and may fluctuate depending on the paleocommunity and/or region assessed.

Recently there has been a surge in publications using functional diversity of paleocommunities as a proxy for deep-time ecosystem functioning (i.e., fluxes of energy and material through biotic and abiotic components of an ecosystem) (e.g., Villégar et al., 2011; Foster and Twitchett, 2014; Dineen et al., 2014; Roopnarine and Angielczyk, 2015). This concept comes from modern biologic research, which in recent years has emphasized that functional diversity (i.e., identity and dominance patterns of trait composition in a community) is more important to community stability and productivity
than the number or abundance of species (Petchey and Gaston, 2002, 2006; Cadotte et al., 2011; Dalerum et al., 2012; Mason and de Bello, 2013; Song et al., 2014; Gagic et al., 2015). Functional diversity is defined as the range of traits present in a community, and can be split into functional richness (i.e., volume of traits space filled) and functional evenness (i.e., regularity of distribution of abundance across this volume) (Mouillot et al., 2005; Villégar et al., 2008; Mouchet et al., 2010). A loss of functional diversity has been shown to have a mostly negative effect on the functioning of a community, particularly if the functional groups lost utilize resources in different ways (i.e., niche complementarity) (Loreau et al., 2001; Mason et al., 2005; Hewitt et al., 2008). Most theoretical models predict that greater resource use complementarity leads to more efficient use of resources and subsequently, greater productivity and ecosystem reliability (Tillman et al., 1997; Loreau 1998; Diaz and Cabido, 2001; Petchey and Gaston, 2006). Thus determining the functional richness and evenness of marine paleocommunities has important implications for ecosystem processes, dynamics, and stability.

Here we examine the functional and taxonomic diversity of the Spathian Virgin Limestone Member (Moenkoepi Formation) at the Lost Cabin Springs locality in southern Nevada. While many studies have focused on the Virgin Limestone Member, most of these are based in nearshore localities in southern Utah, such as the Beaver Dam Mountains or Hurricane Cliffs (e.g., McGowan et al., 2009; Hofmann et al., 2013a, 2013b). Very few studies have examined invertebrate taxonomic diversity of the offshore Virgin Limestone at Lost Cabin Springs (e.g., Schubert and Bottjer, 1992, 1995; Marenco et al., 2012), and even fewer have examined any ecological parameters (e.g., Pietsch et al., 2014). For the first time, we quantified taxonomic and functional diversity of the
Virgin Limestone Member at the Lost Cabin Springs locality in order to determine the level of ecosystem restructuring in a Spathian offshore paleoenvironment after the PTME.

**Background Information**

**Stratigraphy**

The study locality, Lost Cabin Springs (located near Las Vegas, Nevada), contains an excellent Lower Triassic (Spathian) mixed carbonate-siliciclastic sequence (Figure 4.1). During the Early Triassic the interior of the western United States was flooded by several marine incursions from Panthalassa, resulting in a broad, shallow seaway spanning from southern Idaho to southern Arizona (Blakely, 1972; Marzolf, 1993). These transgressive events (Griesbachian, Nammalian, and Spathian in age), were the outcome of subsidence and global sea level increases that resulted in the deposition of shallow-water carbonates and mixed carbonate-siliciclastic beds punctuated by periodic red beds (Stewart et al., 1972; Rief and Slatt, 1979; Stewart, 1980; Paull and Paull, 1986).

While nomenclature is different depending upon study area, the Early Triassic sequence in southern Nevada is represented by the Moenkopi Formation, and consists of the Timpoweap, Lower Red, Virgin Limestone, Middle Red, Schnabkaib, and Upper Red Members (lowest to highest stratigraphically) (Stewart, 1980). The Moenkopi Formation, specifically, signifies deposition through both the Nammalian and Spathian transgressions (Stewart et al., 1972; Rief and Slatt, 1979; Dean, 1981). The Virgin Limestone Member (Spathian) was chosen for this study due to its complete stratigraphic
sequence and paleontological record (e.g. Schubert and Bottjer, 1995; Boyer et al., 2004; Pruss et al., 2005; Pruss and Payne, 2009; McGowan et al., 2009).

![Map of study area, Lost Cabin Springs, in the Spring Mountains, near Las Vegas, Nevada.](image)

Figure 4.1. Map of study area, Lost Cabin Springs, in the Spring Mountains, near Las Vegas, Nevada.

The Virgin Limestone Member was deposited in a variety of shelf paleoenvironments during the regionally extensive Spathian transgression and highstand (Reif and Slatt, 1979; Schubert and Bottjer, 1995; Pruss and Payne, 2009). At the Lost Cabin Springs locality, the member is composed of interbedded limestone, mudstone, siltstone, and sandstone units deposited on a west-dipping middle to lower steep carbonate ramp on the edge of the eastern Panthalassan Ocean (Stewart et al., 1972; Reif and Slatt, 1979; Pruss et al., 2006; Mata and Bottjer, 2011). Several unusual facies have
also been reported, including microbial reef/sponge mounds and spheroids, flat-pebble conglomerates, and wrinkle structures interpreted to represent periodic deposition in a storm-dominated subtidal paleoenvironment (Blakey, 1974; Pruss and Bottjer, 2004; Pruss et al., 2004, 2005, 2006; Pruss and Payne, 2009; Mata and Bottjer, 2011; Marenco et al., 2012). Mata and Bottjer (2011) identified eight shallowing-upward, flooding-surface bound parasequences in the Virgin Limestone at Lost Cabin Springs, reflecting recurrent paleoenvironmental change within the member from offshore ramp to subtidal deposition.

**Virgin Limestone Fauna**

Typical marine invertebrate fossils at the Lost Cabin Springs locality include rhynchonelliform brachiopods, bivalves, crinoids, echinoids, gastropods, scaphopods, and sponges (Stewart et al., 1972; Schubert et al., 1992; Schubert and Bottjer, 1995; Boyer et al., 2004; Twitchett et al., 2005; McGowan et al., 2009; Pietsch et al., 2014). Containing a large quantity of parautochthonous shell beds deposited below wave base, the Virgin Limestone Member has previously been interpreted to represent a low-diversity paleocommunity in the process of recovery from the PTME (Schubert and Bottjer, 1995; Boyer et al., 2004; Pruss and Bottjer, 2004; McGowan et al., 2009). However, causes for the low faunal diversity have been debated, and have been attributed to either repeated environmental stress (e.g., Boyer et al., 2004; Pruss and Bottjer, 2004a, 2004b; Pruss et al., 2004, 2007; Mata and Bottjer, 2011; Marenco et al., 2012; Pietsch et al., 2014) or intrinsic controls (e.g., McGowan et al., 2009; Hofmann et al., 2013a, 2013b).
For example, several studies have suggested that the region was subject to the periodic upwelling of deep anoxic waters onto the shelf, resulting in the deposition of laminated mudstones lacking infaunal traces common throughout the Virgin Limestone (e.g., Boyer et al., 2004; Pruss and Bottjer, 2004b; Woods, 2009; Mata and Bottjer, 2011; Pietsch et al., 2014). In addition, it has been previously hypothesized that stromatolites and microbialites present at Lost Cabin were formed during anomalous conditions such as enhanced anoxia and alkalinity (Pruss and Bottjer, 2004a; Pruss et al., 2005; Mata and Bottjer, 2011). However, a geochemical study by Marenco et al. (2012) indicated that anoxia was most likely not prevalent or sustained in the area, though does not exclude the possibility that the deleterious conditions were short-lived or periodic.

Conversely, a study by Hofmann et al. (2013a) proposed that the Virgin Limestone paleocommunity lacks any characteristics of typical post-extinction faunas under the influence of environmental stress (i.e., small body size, low taxonomic diversity, faunal homogeneity). Instead, they suggest that the Virgin Limestone paleocommunity is in the early stages of recovery, and that the low beta diversity present is an indication of low competition among paleocommunity members. As such, it seems clear that additional ecologically-focused studies are needed to establish if the Virgin Limestone biota represents a paleocommunity hindered by periodic harmful environmental conditions or possibly a lack of significant competition for resources.

**Methods**

At the Lost Cabin Springs locality, bulk samples of fossiliferous beds (2-15 cm in width) were collected at 20-25 meter intervals over a 100 meter stratigraphic section in
order to assemble a wide range of depositional environments within the member (Figure 4.3). A stratigraphic section of the middle to upper Virgin Limestone was measured in detail in order to match the samples in stratigraphic context, and also to ensure collection from multiple parasequences and depositional environments. Using the parasequences identified in Mata and Bottjer (2011) and Pietsch et al. (2014), we sampled four parasequences in the middle to upper part of the Virgin Limestone (i.e., parasequences 3, 4, 5, and 6 (53-146 m) from Mata and Bottjer, 2011), each separated by flooding surfaces and containing proximal offshore (low energy) to offshore transition (high energy) depositional environments.

From Parasequence 1, two sampling horizons were combined to represent Level 1, deposited in low energy paleoenvironments. In Parasequence 2, three sampling horizons were combined to represent Level 2, from high energy depositional environments. From Parasequence 3, only one horizon was sampled (Level 3), representing a high energy depositional environment. From Parasequence 4, three sampling horizons were sampled and combined from low energy paleoenvironments (Level 4), and one sampling horizon was collected from a high energy paleoenvironment (Level 5). Poor preservation limited the ability to collect from all depositional environments in each parasequence, however all parasequences in the middle to upper Virgin Limestone are represented as well as both low energy (Levels 1 and 4) and high energy (Levels 2, 3, and 5) depositional environments in four different continual parasequences.

Samples were mechanically disaggregated in the laboratory into 2-5 cm³ fragments, and all identifiable invertebrates were count and identified to the genus level
from whole and fragmented fossils. The abundance of crinoids and echinoids was counted using a presence-absence system due to the uncertain nature of their biomass. For example, the presence of multiple crinoid ossicles was considered to be equal to one individual in a sampling horizon. Shell size of each individual were also measured in order to calculate skeletal body volume using the ATD (anteroposterior, transverse, dorsoventral) model by Novack-Gottshall (2008). Due to the poor fossil preservation at Lost Cabin Springs, we combined our fossil abundance data with that of Pietsch et al. (2014) if the samples were found to have been collected at comparable stratigraphic intervals. We feel that the combination of our data with that of Pietsch et al. (2014) allows for a more comprehensive and detailed assessment of the paleocommunities present at Lost Cabin Springs. This also allows every level to have more than than 25-50 individuals, which has been has been identified as the minimum number of individuals needed to effectively represent a true paleocommunity signal (Forcino, 2012). The only exception is Level 3 (n = 24), in which no comparable stratigraphic interval could be found with Pietsch et al. (2014); though this level falls just short of the 25-50 individuals recommended.

We applied the multi-trait ecospace framework for marine fossil genera created by Novack-Gottshall (2007) and used in Dineen et al. (2014) to quantify paleocommunity functional diversity. This framework employs the use of ten functional traits to focus on how marine taxa interacted their environment and each other, thus influencing ecosystem functioning (e.g. substrate relationship, mobility, body size, and condition of food) (Table 4.1). The use of ten functional traits, as opposed to only three or four, allows for a more accurate representation of functional diversity. For example, if only a few functions are
considered, then the level of functional unevenness might be biased and appear to be higher than it actually is (e.g., Fonseca and Ganade, 2001). Data from the primary literature and the Paleobiology Database (www.paleobiodb.org/) was culled in order to determine the ecology of each genus identified. Genera were then sorted into arbitrarily numbered functional groups based on the condition that they contain identical traits across all ten categories in each level. This also allows genera to change functional group occupation based on an increase or decrease in skeletal body volume between levels, in order to more accurately portray functional diversity changes through time.

<table>
<thead>
<tr>
<th>Traits</th>
<th>Modalities</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) Skeletal Body Volume</td>
<td>8 ordered categories for size magnitude from 0.001-0.01ml to 10,000-100,000ml</td>
</tr>
<tr>
<td>2) Reproductive Mode</td>
<td>-Sexual</td>
</tr>
<tr>
<td></td>
<td>-Sexual and asexual</td>
</tr>
<tr>
<td>3) Mobility</td>
<td>-Sedentary</td>
</tr>
<tr>
<td></td>
<td>-Passively mobile</td>
</tr>
<tr>
<td></td>
<td>-Facultatively mobile</td>
</tr>
<tr>
<td></td>
<td>-Intermittently mobile</td>
</tr>
<tr>
<td></td>
<td>-Habitually mobile</td>
</tr>
<tr>
<td>4) Substrate Composition</td>
<td>-Biotic</td>
</tr>
<tr>
<td></td>
<td>-Lithic</td>
</tr>
<tr>
<td></td>
<td>-Fluidic</td>
</tr>
<tr>
<td>5) Substrate Relationship</td>
<td>-Attached</td>
</tr>
<tr>
<td></td>
<td>-Free-living</td>
</tr>
<tr>
<td>6) Primary Microhabitat</td>
<td>-Above substrate</td>
</tr>
<tr>
<td></td>
<td>-Below substrate</td>
</tr>
<tr>
<td>7) Support</td>
<td>-Supported</td>
</tr>
<tr>
<td></td>
<td>-Self supported</td>
</tr>
<tr>
<td>8) Diet</td>
<td>-Microbivore</td>
</tr>
<tr>
<td></td>
<td>-Carnivore</td>
</tr>
<tr>
<td></td>
<td>-Microbivore and carnivore</td>
</tr>
<tr>
<td>9) Condition of Food</td>
<td>-Solution feeder</td>
</tr>
<tr>
<td></td>
<td>-Particle feeder</td>
</tr>
<tr>
<td></td>
<td>-Bulk feeder</td>
</tr>
<tr>
<td>10) Feeding Habit</td>
<td>-Filter feeder</td>
</tr>
<tr>
<td></td>
<td>-Mass feeder</td>
</tr>
<tr>
<td></td>
<td>-Attachment feeder</td>
</tr>
<tr>
<td></td>
<td>-Raptorial feeder</td>
</tr>
</tbody>
</table>

Table 4.1. Functional traits and modalities used to characterize functional groups. See Novack-Gottshall (2007) for formal definitions of these traits.
Functional richness is therefore equal to the number of functional groups present within each level. Functional evenness (Fe) was calculated using the taxonomic evenness metric (Shannon Index; H'/H’max) in which we input the abundance of individuals/genera within each functional group to get the evenness of distribution across functional groups in the paleocommunity. Thus, the lowest possible value (Fe = 0) would indicate uneven distribution of individuals/genera across functional groups, and the maximum possible value (Fe = 1) would indicate an even distribution of individuals/genera across functional groups. We used this metric to look at both the evenness of genera (Fe^genera; similar to the metric used in Dineen et al., 2014) and individuals (Fe^indiv) across functional groups in the paleocommunity.

To quantify the most ecologically dominant groups, we calculated mean rank order and breadth of distribution. To determine rank order, the most abundant group receives a rank order of 1, the second most abundant group receives a 2 and so on. To determine the mean rank order, the sum of the rank orders is divided by the number of samples. Breadth of distribution measures the proportion of samples in which each organism was present. To quantify taxonomic diversity we calculated the Simpson Index of Diversity (1-D), which takes into account the total number of genera present and the abundance of each. Thus, the higher the value of the Simpson Index of Diversity (1-D), the greater the taxonomic diversity of the samples. The Shannon Index (H’) was also calculated, which is a measure of the difficulty in predicting the species of the next individual collected. The lowest possible value is H’ = 0, while the maximum value can be calculated as H’max = ln S (Shannon 1948). Meanwhile taxonomic evenness (E = H’/H’max) is a measure of how similar the abundances of groups of genera are, while
dominance (D = 1-E) is the conceptual inverse of this value. All together, these taxonomic and functional diversity metrics provide a systematic and effective way to determine the level of restructuring in the Spathian Virgin Limestone.

Results

We identified 188 marine invertebrates from the Spathian middle to upper Virgin Limestone Member bulk samples, which coupled with 453 invertebrates from Pietsch et al. (2014) brought the overall total abundance to 641 individuals. Fauna identified include brachiopods, bivalves, gastropods, crinoids, echinoids, and scaphopods, belonging to 21 genera. The Simpson Index of Diversity (1-D) varied depending on level sampled, ranging from a high of 0.86 (Level 5), to a low of 0.75 (Level 2 and 3) (Table 4.2). Similarly, taxonomic evenness (E) varied from 0.79 (Level 5), to 0.64 (Level 2) (Table 4.2 and Figure 4.2).

Bivalves were the overwhelmingly the most taxonomically diverse and numerically abundant group of the paleocommunity, with 12 genera consisting of 92% (589 individuals). This is followed by gastropods (4 genera, 4% of individuals), brachiopods (2 genera, 1%), crinoids (1 genus, 1%), echinoids (1 genus, 1%), and scaphopods (1 genus, 1%), respectively. As such, bivalves had the highest mean rank order (1.00), followed by gastropods (2.20), and crinoids (3.00). Bivalves, gastropods, crinoids, and echinoids appeared in all levels, with a breadth of distribution of 100%, followed by brachiopods with 60% and scaphopods with 20%. While bivalves are the most ecologically dominance biota, it is also important to note the high numerical abundance of echinoderm debris throughout the section. Though these are not
taxonomically diverse, with only one genus of crinoid and echinoid each present.

Regardless, this data supports previous studies which note the numerical dominance of both bivalve and crinoidal debris in the Virgin Limestone (e.g., Boyer et al., 2004; Hofmann et al., 2013b; Pietsch et al., 2014).

<table>
<thead>
<tr>
<th></th>
<th>Level 1</th>
<th>Level 2</th>
<th>Level 3</th>
<th>Level 4</th>
<th>Level 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abundance (N)</td>
<td>138</td>
<td>223</td>
<td>24</td>
<td>122</td>
<td>134</td>
</tr>
<tr>
<td>Number of Genera</td>
<td>17</td>
<td>17</td>
<td>8</td>
<td>15</td>
<td>17</td>
</tr>
<tr>
<td>Simpson Diversity (1-D)</td>
<td>0.83</td>
<td>0.75</td>
<td>0.75</td>
<td>0.81</td>
<td>0.86</td>
</tr>
<tr>
<td>Taxonomic Evenness (E)</td>
<td>0.77</td>
<td>0.64</td>
<td>0.77</td>
<td>0.75</td>
<td>0.79</td>
</tr>
<tr>
<td>Functional Richness</td>
<td>10</td>
<td>9</td>
<td>7</td>
<td>7</td>
<td>12</td>
</tr>
<tr>
<td>$F_e^{\text{genera}}$</td>
<td>0.88</td>
<td>0.88</td>
<td>0.98</td>
<td>0.92</td>
<td>0.96</td>
</tr>
<tr>
<td>$F_e^{\text{indiv}}$</td>
<td>0.62</td>
<td>0.50</td>
<td>0.61</td>
<td>0.63</td>
<td>0.76</td>
</tr>
</tbody>
</table>

Table 4.2. Taxonomic and functional diversity metrics for Levels 1-5 for the Virgin Limestone Member, Lost Cabin Springs, Nevada.

Figure 4.2. Graph illustrating changes in taxonomic evenness (E) and functional evenness ($F_e^{\text{indiv}}$ and $F_e^{\text{genera}}$) from Level 1 (oldest) to Level 5 (youngest) of the Virgin Limestone Member, Lost Cabin Springs. Evenness values range from the lowest possible value (0), indicating uneven distribution of individuals/genera, to the maximum possible value (1.00), indicating even distribution of individuals/genera.
For functional diversity, fauna of the Virgin Limestone Member belong to 17 different functional groups (Figure 4.3). Functional richness varied between levels, with the highest belonging to Level 5 (12 functional groups), followed by Level 1 (10 functional groups) Level 2 (9 functional groups), and Level 3 and 4 (7 functional groups each). Generic functional evenness ($F_{\text{genera}}$) was mostly even in all levels, ranging from a high in Level 3 ($F_{\text{genera}} = 0.98$) to a low in Levels 1 and 2 ($F_{\text{genera}} = 0.88$) (Table 4.2).

Individual functional evenness however, was much lower, with the highest value belonging to Level 5 ($F_{\text{indiv}} = 0.76$) and the lowest value to Level 2 ($F_{\text{indiv}} = 0.50$). This low functional evenness was largely due to the numerical dominance of Functional Group #9 (medium-sized (0.1-1 ml), sedentary, free-living, epifaunal suspension feeders), which constituted 57% of Level 1, 69% of Level 2, 67% of Level 3, and 57% of Level 4, respectively (Figure 4.3A). The only exception is Level 5, in which Functional Group #9 becomes the second most numerically dominant, with 24% of individuals in the level, and the most numerically dominant becomes Functional Group #13 (large-sized (1-10 ml), sedentary, free-living, epifaunal suspension feeders) with 25%; therefore, the only difference in these two functional groups is body size. This is largely due to the bivalve, *Eumorphotis*, previously a member of Functional Group #9 in Levels 1-4, increasing in body size, and thus becoming an occupant of a different functional group (FG #13) in Level 5.
Figure 4.3. Detailed stratigraphic section of the Virgin Limestone Member at Lost Cabin Springs. Sampling horizons are marked with stars, and grouped based on proximity and paleoenvironment into 5 Levels. A) Abundance distribution of individuals within functional groups. B) Distribution and number of genera within each functional group.
Implications for Early Triassic Restructuring

Our results indicate that the offshore Virgin Limestone paleocommunity at Lost Cabin Springs had low taxonomic richness, though moderately high levels of taxonomic evenness (E). In general, these values increase up section, with the upper parasequence Level 5 containing the highest taxonomic diversity. Similarly, while functional richness was generally low throughout the section, Level 5 contained the highest functional richness. Thus, taxonomic and functional richness in the Virgin Limestone appear to have increased throughout time, with the highest values belonging to the uppermost parasequence (i.e., Level 5). Conversely, there does not appear to be a statistically significant difference in the average taxonomic and functional richness (p > 0.05) between depositional environments (low vs. high energy), indicating that the amount of time after the PTME was likely the more important factor in the level of restructuring seen in the offshore Virgin Limestone.

Another important factor appears to have been the distribution of traits in the paleocommunity. For example, genera were evenly distributed across functional groups (Fe\(^{\text{genera}}\)), however distribution of individuals was highly uneven (Fe\(^{\text{indiv}}\)). Therefore fauna seem to be clustered in trait space, with the majority of biota belonging to a single functional group (i.e., Functional Group #9), thus occupying one region more heavily. The dominance of this functional group is largely due to the numerical abundance of two bivalve genera, *Leptochondria* and *Eumorphotis*. For example, out of the 641 individuals present in this section of the Virgin Limestone, 60% were either *Leptochondria* or *Eumorphotis*. Additionally, it is important to note that these two bivalve genera belong to
the same functional group in each level with the exception of Level 5, in which *Eumorphotis* moved up a size category (i.e., Functional Group #13).

Furthermore, the high abundance of *Leptochondria* and *Eumorphotis* suggests the presence of intrinsic and/or extrinsic stresses at Lost Cabin, as both of these cosmopolitan genera are regarded as disaster taxa and likely opportunistic (e.g., Hallam and Wignall, 1997). Schubert and Bottjer (1995) previously noted the abundance of generalist cosmopolitan taxa present in the Virgin Limestone, such as disaster bivalves and microgastropods. The large microbial reef mounds and stromatolites that occur in several horizons of the Virgin Limestone have also been suggested to represent disaster forms, albeit ones that likely flourish in normal marine conditions due to a lack of competition from benthic invertebrates (Schubert and Bottjer, 1992). Coupled with geochemical data from Marenco et al. (2012) that found no indication of persistent anoxia, this suggests that paleocommunity development at Lost Cabin Springs was not hindered by any unusual or sustained extrinsic (i.e., environmental) stresses.

However, the numerical dominance of one functional group, along with the low overall functional richness and dominance of generalist disaster taxa throughout the section indicates that this paleocommunity was not yet functioning at a high level (i.e., not utilizing all available ecospace). As such, it seems likely that uneven exploitation of available trait space and/or distribution of resources was occurring, allowing high competition in some areas of trait space while almost none in other areas (Mouillot et al., 2005; Mouchet et al., 2010). Previous studies have predicted that after mass extinctions, one would expect to find a low diversity community consisting of small-sized opportunists or generalists, with fairly low primary production and a general lack of
colonization and construction of niches (e.g., Walker and Alberstadt, 1975; Krassilov, 1996; Solé et al., 2002). This is interpreted to be the case in the Virgin Limestone at Lost Cabin Springs, in that the dominance of generalist disaster taxa skewed the abundance distribution in trait space and resulted in a paleocommunity with low functional diversity, despite a lack of prolonged environmental stresses.

As such, the dominant intrinsic processes behind this pattern are open to interpretation given that these and other community assembly rules can be extremely difficult to distinguish in fossil paleocommunities (e.g., Bretsky and Klofak, 1986; Pandolfi, 1996; Jablonski and Sepkoski, 1996; Belyea and Lancaster, 1999; Webb et al., 2002; Kraft et al., 2007; Olszewski, 2012). Although these results appear to be in accordance with some of the predictions made by a recent generalized recovery model (i.e., Hofmann et al., 2013a, 2013b; Hautmann, 2014), in that there seems to be a low level of competition in some regions of trait space in the Virgin Limestone; however this was not homogenous, as competition for resources was extreme in some functional groups. This interpretation is not in accordance with the model which postulates a low level of competition throughout the entire paleocommunity, thus indicating that utilization of ecospace and trait space after mass extinctions is likely not always be linear or systematic. Additionally, the overall pattern of low functional evenness could suggest that strong niche or environmental filtering was in effect, as it is hypothesized that species with traits poorly adapted to the ecosystem are excluded resulting in an assemblage of functionally similar species (Cornwell et al., 2006; Mouillot et al., 2007; Mouchet et al., 2010). However this is merely speculation, as such intrinsic patterns are extremely difficult to distinguish in fossil paleocommunities as previously discussed.
Conclusions

For the first time, we quantified the taxonomic and functional diversity of the Virgin Limestone Member at the offshore Lost Cabin Springs locality in Nevada. Our results indicate that the Virgin Limestone paleocommunity had moderate taxonomic diversity and functional richness, although functional evenness was very low. Functional Group #9 was the most numerically abundant, dominating in every level and consisting of the two disaster bivalves, *Leptochondria* and *Eumorphotis*. Bivalves were the most taxonomically diverse and ecologically dominant group, though crinoids were also extremely abundant. Taxonomic and functional diversity generally increase up section, with Level 5 containing the greatest values. Additionally, there does not appear to be a significant difference in the taxonomic and functional diversity of levels deposited in either low or high energy paleoenvironments, suggesting that time after the PTME was a more important factor in restructuring of the section.

The overwhelming dominance of one functional group in the offshore Lost Cabin Springs locality indicates that either some resources in the ecosystem were over-utilized, or that general resource availability in the paleoenvironment was uneven. As such, the Spathian Virgin Limestone Member in Nevada had not achieved optimal resource utilization and was not yet functioning at a high level in that all available ecospace was not being exploited. This is in contrast to results from more onshore localities of the Virgin Limestone (i.e. Beaver Dam Mountains or Hurricane Cliffs), which suggest either advanced stages of recovery (e.g., McGowan et al., 2009; Hofmann et al., 2013a, 2013b) or that prolonged anoxia significantly hindered fauna (e.g., Boyer et al., 2004; Mata and Bottjer, 2011). Though we cannot exclude the possibility of periodic environmental
stresses (i.e., Marenco et al., 2012), these were apparently not prolonged enough to
significantly limit benthic paleocommunity development as fauna achieved moderate
taxonomic diversity and functional richness at the Lost Cabin Springs locality.

Nonetheless, the functionally uneven Virgin Limestone paleocommunity likely
lacked resilience to invasion or any periodic environmental stresses that may have been
present. Strong niche or environmental filtering may have been in effect, and competition
was extremely high in some areas of trait space while almost non-existent in others. It can
thus be hypothesized that the ecological structure of the post-PTME Virgin Limestone
was largely influenced by functionally similar generalist species and that extreme
reorganizational nature of the PTME had significant effects on the inherent structure of
ecosystems well into the Early Triassic. Consequently, these results have important
implications for the pattern of functional diversity during restructuring from mass
extinctions events, suggesting a convergence of genus traits and uneven resource
exploitation via a lack of competition in some areas of available trait space. The complex
and variable nature of the Triassic restructuring thus necessitates the need for regional
studies that employ novel and quantifiable proxies in order to determine if this pattern is
present in other local paleocommunities.
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Chapter V: Triassic Restructuring and Functional Diversity

A review of the literature shows that our 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 richness, a single genus or phylum, shallow water facies, and combined or limited regional data. In addition, Early Triassic paleocommunities previously have been considered fully recovered when prior dominance and diversity were regained. Considering that the PTME permanently altered the marine realm and resulted in Triassic paleocommunities that were physiologically and ecologically different than that of the Permian, the term “recovery” is not applicable for that of the Triassic (e.g., Bambach et al., 2002; Wagner et al., 2006). Instead, the term “restructuring” is suggested, as it more completely encompasses the reorganizational and distinctive nature of marine ecosystems in the wake of Earth’s largest mass extinction.

Previous studies have shown that high taxonomic diversity does not always offer an ecosystem protection against disturbance or environmental stresses (e.g., Schwartz et al., 2000; Symstad et al., 2003; Song et al., 2014). As such, it is of extreme importance to consider both taxonomic and ecological biotic factors in order to determine the level of restructuring in the wake of mass extinctions. Novel proxies, such as functional diversity (i.e., the number and distribution of traits), offer a more complete and accurate view of ecosystem functioning after disturbance, as it has been shown to have a large and vital influence on the ecological stability and complexity of communities following events of major disturbance (e.g., Vinebrooke et al., 2003; Cardinale et al., 2012; Bernhardt and Leslie, 2013; Hull and Darroch, 2013).
It is thus suggested that functional diversity represents an excellent proxy for ecosystem functioning after the PTME, and can be quantified in order to determine paleocommunity processes and dynamics. In order to test the viability of this metric, functional richness (number of functional groups) and functional evenness (distribution of abundance across functional groups) was quantified in several regional pre- and post-PTME paleocommunities. A novel method for quantifying ecospace was used, in that 10 functional traits (e.g., body size, mobility, diet) were considered in order to more accurately represent how marine taxa interacted with and utilized each other and their environment. Using these methods, the functional diversity of Permian, Early Triassic, and Middle Triassic paleocommunities was determined from previously published literature, as well as field-collected data in two different regional localities (Table 5.1).

<table>
<thead>
<tr>
<th></th>
<th>Number of Genera</th>
<th>Functional Richness</th>
<th>$F_e^{\text{genera}}$</th>
<th>$F_e^{\text{indiv}}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wordian</td>
<td>Texas Word Fm</td>
<td>125</td>
<td>34</td>
<td>0.77</td>
</tr>
<tr>
<td>Induan</td>
<td>Oman Al Jil Fm</td>
<td>27</td>
<td>12</td>
<td>0.94</td>
</tr>
<tr>
<td>Induan</td>
<td>WY Dinwoody Fm</td>
<td>9</td>
<td>5</td>
<td>0.89</td>
</tr>
<tr>
<td>Olenekian</td>
<td>Utah Moenkopi Fm</td>
<td>47</td>
<td>18</td>
<td>0.91</td>
</tr>
<tr>
<td>Olenekian</td>
<td>NV Moenkoepi Fm</td>
<td>21</td>
<td>15</td>
<td>0.92</td>
</tr>
<tr>
<td>Anisian</td>
<td>China Qingyan Fm</td>
<td>144</td>
<td>37</td>
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<tr>
<td>Anisian</td>
<td>China Qingyan Fm</td>
<td>62</td>
<td>24</td>
<td>0.85</td>
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</tbody>
</table>

Table 5.1. Comparison of quantified functional diversity metrics for regional Permian, Early Triassic, and Middle Triassic paleocommunities. Studies in blue represent field-collected data.

Results indicate that functional richness was high in the pre-extinction Permian paleocommunity, decreased to low levels in the immediate aftermath of the PTME, and increased throughout the Early Triassic with high levels returning in the Middle Triassic. This indicates loss of functional richness and rebuilding of ecospace in regional
paleocommunities in the aftermath of the PTME, agreeing with previous models of ecosystem restructuring that suggests a decoupling of taxonomic and ecologic diversity, in that taxonomic diversity increased quickly but ecological restructuring took much longer to reach high levels (e.g., Droser et al., 1997; McGhee et al., 2004). In addition, functional evenness of genera ($F_{\text{genera}}$) was found to be high in all of the pre- and post-extinction paleocommunities studied, suggesting that genera were evenly distributed across functional groups. The distribution of individuals within functional groups ($F_{\text{indiv}}$) however, was only able to be quantified in paleocommunities in which the number of individuals present was available; thus only the two field-collected case studies could be calculated. Nonetheless, results indicate that the evenness of individuals across functional groups ($F_{\text{indiv}}$) was very low in the Spathian Virgin Limestone Member of Nevada and the Anisian Leidapo Member of China. Both paleocommunities were numerically dominated by one functional group; the Panthalassa Virgin Limestone paleocommunity was dominated by a functional group consisting of two disaster bivalve genera, while the Paleo-Tethys Leidapo Member was dominated by a functional group consisting of two brachiopod genera.

High evenness of genera distribution across functional groups ($F_{\text{genera}}$) in all of the paleocommunities studied may indicate that these ecosystems existed in harsher paleoenvironments, as they likely had a high fraction of development capacity (i.e., potential for ecosystem organization) encumbered for generic functional evenness and redundancy, as these provide ecological insurance in the wake of disturbances. However there is a lack of evidence for prolonged environmental stresses (i.e., high anoxia, alkalinity, temperatures) in the majority of the studied paleocommunities during
deposition; although periodic or recurrent stresses cannot be ruled out. Yet, the low individual functional richness ($F_{\text{indiv}}$) and numerical dominance of certain functional groups in the two case study paleocommunities suggests that not only were these ecosystems not yet operating at a high level of functioning, but that resource utilization and/or distribution across trait space was uneven (Figure 5.1). It could also be hypothesized that strong environmental or niche filtering may have been in effect in the Virgin Limestone and Leidapo Member paleocommunities. The niche filtering hypothesis assumes that “coexisting species are more similar to one another than would be expected by chance as environmental conditions act as a filter”, and typically yields communities with functionally similar species (Mouillot et al., 2007). However, this community assembly process can be extremely difficult to detect, and the level of restructuring and functioning present in each paleocommunity appears to vary depending on geographic region and depositional environment.

Regardless, it is hypothesized here that the high evenness of genera across functional groups ($F_{\text{genera}}$) may have been a long-term intrinsic paleocommunity survival strategy, allowing some level of ecological insurance and resistance for post-PTME assemblages in the wake of Earth’s largest mass extinction. The low individual functional evenness ($F_{\text{indiv}}$), though, was likely a mostly extrinsic factor of certain individuals taking advantage of the overabundance of certain resources or the fairly open areas of trait space. It appears that some of the dominant functional groups were generalists and likely opportunistic, a survival strategy that may have been due to strong environmental or niche filtering. Overall, this pattern of functional dominance indicates while paleocommunities were mostly stable and lacked evidence for prolonged
environmental stresses, they likely would have lacked much resistance to any periodic biotic and environmental perturbations (i.e., invasion, migration, anoxia, etc.). It is unknown, however, if these are common survival strategies after the PTME or if these patterns are the norm during intervals of restructuring (Figure 5.1). Nonetheless, it appears that functional diversity and the inherent ecological structure of the paleocommunity played a large and dynamic role in determining which communities survived and flourished during the Triassic reorganizational interval.

Figure 5.1. Simplified theoretical model of multidimensional (10 trait) functional space after the Permo-Triassic mass extinction. Colors represent different functional groups, while the size of the circle represents the abundance of individuals present in that functional group (larger the circle, the more individuals).

Despite previous results indicating ecosystem functioning was high and that select paleocommunities were significantly recovered after the PTME (e.g., Twitchett et al., 2004; Chen et al., 2010; Hofmann et al., 2013; Foster and Twitchett, 2014), our results
indicate that the distribution of individuals in trait space was uneven in both Panthalassa and Paleo-Tethys localities studied, despite high to moderate taxonomic and functional richness. As such, paleocommunities do not appear to have obtained a high level of ecosystem functioning and complexity, even 5 million years after the PTME in the Anisian. This documents a previously unknown pattern of functional diversity and ecological complexity after the PTME, and has important implications for the nature of biotic survival following extremely large environmental disturbances. It is thus clear that novel proxies, such as functional diversity, are of the upmost importance in understanding and quantifying how marine systems were restructured following the Permo-Triassic mass extinction.
References


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EDUCATION
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2011  Molding/mapping of vertebrate trackways, screen-washing/identification of vertebrate bones and teeth in the Jurassic Morrison Formation, Dinosaur National Monument, Utah (GSA GeoCorp Internship)
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