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Restructuring in benthic level-bottom shallow marine communities due to prolonged environmental stress following the end-Permian mass extinction

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Abstract

Because the end-Permian mass extinction was the largest mass extinction since the Cambrian, numerous studies have focused on taxonomic changes and patterns immediately before and after the Permian/Triassic boundary. This synthesis of paleoecological data demonstrates that the end-Permian mass extinction and the Early Triassic aftermath were ecologically, as well as taxonomically, significant events in the history of life. A variety of short-term and long-term structural changes in ecosystems and paleocommunities were facilitated by deleterious environmental conditions that persisted through the Early Triassic. **To cite this article: M.L. Fraiser, D.J. Bottjer, C. R. Palevol 4 (2005).**

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Résumé

Restructuration des communautés benthiques de mers peu profondes induite par un stress environnemental prolongeant la crise biologique de la fin du Permien. Les extinctions massives qui se sont produites vers la fin du Permien se rattachent à la crise biologique la plus importante depuis le Cambrien. Aussi de nombreuses études ont-elles porté sur les changements taxonomiques intervenus immédiatement avant et après la limite Permien–Trias, ainsi que leurs modalités. La présente synthèse des données paléocéologiques établit que la crise de la fin du Permien et ses répercussions pendant le début du Trias constituent des événements capitaux de l'histoire de la vie, tant sur le plan écologique que taxonomique. Un ensemble de changements structuraux, à court et à long terme, affectant à la fois les écosystèmes et les paléocommunautés, fut entretenu par des conditions environnementales hostiles, qui persistèrent durant tout le début du Trias. **Pour citer cet article : M.L. Fraiser, D.J. Bottjer, C. R. Palevol 4 (2005).**

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1. Introduction

The end-Permian mass extinction signifies the largest decrease in global biodiversity in the Phanerozoic [48]; several causes for this biotic crisis have been proposed, including hypercapnia (CO₂ poisoning) [33], global marine anoxia [28,29,66], extraterrestrial impacts [5], and intense volcanism [49]. Physiological and chemical stresses likely linked to the end-Permian mass extinction pulsed throughout its aftermath during the Early Triassic (Scythian), as evidenced by isotopic [2,35,44] and sedimentologic [68] data; hypercapnia and marine anoxia are the most widely cited mechanisms for the prolonged environmental stress [35,59,65,66]. A taxonomic pattern, the extinction of a significant proportion of the world's biota in a geologically insignificant period of time [28] was the first signal that a major change in paleocommunities occurred approximately 250 Myr ago. Thus, numerous studies subsequently have focused on taxonomic changes and patterns at the Permian/Triassic boundary to determine the timing of the extinction [56,57], and throughout the Early Triassic aftermath, to determine the nature of taxonomic recovery [17,24,43,62].

However, taxonomic data alone are insufficient for discerning ecological patterns and processes [15,42]. Furthermore, the most significant results of mass extinctions actually may be the establishment of the new ecological patterns that arise during the aftermath [14,15]. Bottjer et al. [6] determined that the entire Early Triassic aftermath of the end-Permian mass extinction experienced severe ecological degradation; ecospace utilization had been reset to the level of the Late Cambrian/Early Ordovician because of prolonged environmental stresses. The short- and long-term consequences of the Latest Permian/Earliest Mesozoic environmental perturbations on paleocommunity structure are still being deciphered, but mounting research indicates that the aftermath of the end-Permian mass extinction was as crucial as the mass extinction in shaping the evolutionary history of life on Earth. A current synthesis of the short-term and long-term structural changes in benthic level-bottom shallow marine paleocommunities that

occurred during the Early Triassic, as well as evidence that these structural changes resulted from the environmental stresses during the Paleozoic-Mesozoic transition, is presented here.

2. Proxies for assessing structural changes in benthic level-bottom shallow marine paleocommunities

Structural changes within benthic level-bottom shallow marine paleocommunities during the aftermath of the end-Permian mass extinction are indicated by various types of paleoecological data. Included in this synopsis are data on alpha diversity, taxonomic dominance, relative abundance, tiering, Bambachian megaguilds, and biosedimentary fabrics (ichnofabrics, shell beds, and wrinkle structures). Except in the discussions of Early Triassic tiering and Bambachian megaguilds, body fossils and trace fossils are treated separately because trace fossils represent behavior of organisms; tiering and Bambachian megaguilds are paleoecological gauges that evaluate the combined epifaunal and infaunal characteristics of paleocommunities to assess broad-scale changes in adaptive strategies.

2.1. Taxonomic patterns

2.1.1. Biodiversity and taxonomic dominance among the Early Triassic skeletonized invertebrate fauna

Taxonomic patterns, such as alpha diversity (species richness) and taxonomic evenness/dominance, are useful as the initial indicators of change in community structure [3,45,56]. In Early Triassic benthic level-bottom marine communities around the world, alpha, beta, and gamma diversity were very low. Mollusks, brachiopods, and echinoderms are the only higher taxa with known macroscopic benthic fossil representatives [54], even in regions interpreted to have experienced rapid recovery [64]. Compared to the Late Permian and the Late Triassic, taxonomic diversity among these skeletonized groups remained low throughout much of the

Early Triassic around the world [10,17,54]. Alpha diversity of Early Triassic macroinvertebrate paleocommunities was low (average = 13) [54] and more closely resembled that of Lower Paleozoic paleocommunities than typical Upper Paleozoic or other Mesozoic paleocommunities [6]. Global pre-extinction taxonomic diversities did not appear until the Middle Triassic (Anisian) [17]. Low alpha, beta, and gamma diversity among the skeletonized macroscopic biota during the Early Triassic represents a short-term structural change in benthic level-bottom shallow marine communities.

A shift among the taxonomic dominants in benthic level-bottom marine paleocommunities was also facilitated by the end-Permian mass extinction and the Early Triassic aftermath, and represents a long-term structural change in paleocommunities that persisted for the remainder of the Phanerozoic. Rhynchonelliform brachiopods were taxonomically dominant during the Ordovician to the Permian and dominated the Paleozoic Evolutionary Fauna for nearly 500 Myr, but the Mesozoic and Cenozoic are dominated by gastropod and bivalve taxa, the major constituents of the Modern Evolutionary Fauna [56]. Despite this Evolutionary Fauna pattern, bivalves and rhynchonelliform brachiopods were taxonomically dominant in certain marine environments during the Paleozoic [36] and Mesozoic [52], respectively. However, the end-Permian mass extinction precipitated the global abrupt phyletic switch from the Paleozoic Fauna to the Modern Fauna [22,56].

2.1.2. Ichnogeneric diversity

Changes in ichnofossil taxonomic patterns after the end-Permian mass extinction are not long-term and last only during the Early Triassic. Early Triassic ichnogeneric diversity in low paleolatitudes is low compared to Uppermost Permian strata but increases through the Early Triassic [44,59,61]. While ichnogeneric diversity remained high in high paleolatitudes (see references in Pruss and Bottjer [46]), in oldest Lower Triassic (Griesbachian) strata deposited at low paleolatitudes in western Paleotethys, the horizontal trace fossil *Planolites* is commonly the only ichnofossil present [59]. The reappearance of *Diplocraterion* in the Late Griesbachian/Early Dienerian and of *Rhizocorallium* in the Smithian/Spathian may be somewhat synchronous around the world in low paleolatitudes [59,61]. *Thalassinoides*, which has been used as an indication of a return of 'normal' marine conditions, reappears in

latest Griesbachian-Dienerian age strata deposited in high paleolatitudes [61,67] and in upper Lower Triassic (Spathian) strata deposited in low latitudes [46], indicating that recovery was not uniform around the world [46,61]. *Planolites*, *Arenicolites*, and *Diplocraterion* are the most common ichnogenera in Lower Triassic strata around the world [54,59,67].

2.2. Paleoecologic patterns

2.2.1. Relative abundance of Early Triassic skeletonized invertebrates

The most abundant members of a community, ecological dominants, may be more important than species richness in governing energy flow, trophic structure, and species composition of communities [12,23,58]. Therefore, determination of the most abundant organisms in Early Triassic paleocommunities provides a more complete understanding of short-term and long-term changes in community structure after the end-Permian mass extinction.

Ecological dominance among the skeletonized biota in benthic level-bottom marine paleocommunities can be assessed from the fossil record using distinctive biofacies, shell bed composition, and relative abundance data [11]. Relative abundance data and shell bed surveys indicate that Early Triassic paleocommunities from a wide range of level-bottom benthic marine environments around the world were numerically dominated by very few taxa. Worldwide during the Griesbachian, many paleocommunities in nearshore to middle shelf marine environments were numerically dominated by the inarticulate brachiopod *Lingula* [49]. Intermittently throughout the Griesbachian, Dienerian, and Smithian, paleocommunities from low paleolatitudes around the world are dominated by large numbers of three species of microgastropods (gastropods < 1 cm in height) [20] that commonly form a microgastropod biofacies unique to the Lower Triassic [21]. Bivalves, however, are the most numerically dominant group in Early Triassic benthic level-bottom shallow marine paleocommunities [20,54] and primarily only three genera (*Eumorphotis*, *Promyalina*, *Unionites*) are responsible for the group's numerical dominance [18]. Abundant crinoids and echinoids are only found at some intervals in the late Early Triassic [38,53]. Comparisons to Modern communities and paleocommunities throughout the Phanerozoic indicate that, in terms of

ecological dominance, Early Triassic paleocommunities around the world are non-actualistic and anomalous (see references in [20]). The numerical dominance of *Lingula*, microgastropods and bivalves in Early Triassic paleocommunities has been attributed to opportunistic behavior of these organisms; opportunistic behavior subsided by the latest Early Triassic [20,21,51].

A long-term, permanent change among the ecological dominants in level-bottom benthic marine paleocommunities also occurred at the Permian/Triassic boundary. An ecologic switch in benthic level-bottom marine environments between rhynchonelliform brachiopods, which numerically dominated Paleozoic paleocommunities, and bivalves, which dominated post-Paleozoic paleocommunities, was triggered by the end-Permian mass extinction and facilitated by conditions during the Early Triassic aftermath [18]. Though bivalves and rhynchonelliform brachiopods are present in large numbers (and even dominant) in certain environments during the Paleozoic [36] and the Mesozoic [52] respectively, the Early Triassic marks the first time in Earth's history that bivalves are numerically dominant globally in nearly all marine environments [18].

2.2.2. Extent of bioturbation (ichnofabric indices)

Though not directly correlative to determining the relative abundance of body fossils, determining the cumulative amount or extent of bioturbation in Lower Triassic strata using ichnofabric indices [13] provides an indication of the amount of infaunal activity during the aftermath of the end-Permian mass extinction. Very little data on extent of bioturbation is available from Permian and Middle Triassic strata, but general patterns that resulted from the end-Permian mass extinction are discernible from the present literature. The extent of bioturbation decreases from ii5–6 in the Upper Permian [60,63] to ii2 in the immediate aftermath of the end-Permian mass extinction in eastern Panthalassa [54], western Paleotethys [60], and the Boreal ocean [63]. Like ichnodiversity, the decrease in extent of bioturbation was short-term and the extent of bioturbation increased throughout the Early Triassic, so that beds with ii5 and ii6 are characteristic of the Spathian [46,59,61].

2.2.3. Tiering

Tiering, the vertical subdivision of space by organisms above and below the benthic boundary layer, is

useful for evaluating paleocommunity structure because it reflects resource and space partitioning by organisms [1]. Epifaunal and infaunal tiering were reduced as a result of the end-Permian mass extinction, and reestablishment of the highest and deepest tiers varied throughout the Early Triassic. During the earliest Early Triassic (Griesbachian, Nammalian), epifaunal tiering, primarily by bivalves, microgastropods, and the inarticulate brachiopod *Lingula*, was confined to the 0 to +5 cm tier in low paleolatitudes around the world [6,54]. The reappearance of crinoids during the Smithian in Japan [30] added the +5 to +20 cm tier back in some paleocommunities, but this tier was not characteristic of benthic level-bottom shallow marine paleocommunities until the late Early Triassic (Spathian), at least in low paleolatitudes (with the reappearance of abundant crinoids) [9,27,53]. Infaunal tiering in pre-extinction strata, indicated by trace fossils, occupied the 0 to –6 cm, the –6 to –12 cm, and the –12 to –100 cm tiers [67]. Infaunal burrowers, including the *Arenicolites* and *Diplocraterion* tracemakers, only occupied the 0 to –6 cm tier during the Griesbachian in eastern Panthalassa and western Paleotethys [46,50,63]; by the Dienerian in western Paleotethys and by the Smithian in eastern Panthalassa, *Arenicolites* and *Diplocraterion* tracemakers occupied the –6 to –12 cm tier [6,54,59,61]. The reappearance of higher tiers (due to the reappearance of crinoids) in Neotethys during the Griesbachian has been used as an indication of rapid recovery in this region [61]. Early Triassic reductions in epifaunal and infaunal tiering were short-term structural changes in benthic level-bottom shallow marine communities.

2.2.4. Benthic Bambachian megaguilids

In addition to tiering, another method of evaluating the short- and long-term changes in ecospace utilization during the Early Triassic is by determining which combinations of mode of life and feeding type, or Bambachian megaguilids (cf. [14]), were present and/or absent. Of 17 possible benthic Bambachian megaguilids [BBMs], only four were occupied during the Early Triassic [7]: bivalves and rhynchonelliform brachiopods occupied the epifaunal-attached-low-suspension-feeding megaguilid; crinoids occupied the epifaunal-attached-erect-suspension-feeding megaguilid; echinoids and gastropods occupied the epifaunal-mobile-herbivore megaguilid; and bivalves and inarticu-

late brachiopods occupied the infaunal-shallow-passive-suspension-feeding megaguild. The attached-erect-suspension-feeding megaguild, occupied by crinoids, reappeared during the Smithian in western Panthalassa [30], during the Spathian in eastern Panthalassa and western Paleotethys [9,53], and during the Griesbachian in Neotethys [64], indicating that ecospace refilled at different times around the world. Ecospace remained fairly empty only for the Early Triassic; eight BBMs were occupied during the Middle Triassic [54]. However, more BBMs were occupied during the Mesozoic and Cenozoic than during the Paleozoic [4], suggesting that conditions during the Paleozoic/Mesozoic boundary also had a long-term effect on ecospace utilization.

2.3. Biosedimentary structures

2.3.1. Shell beds

Shell beds, densely packed accumulations of biological hardparts [31], accurately record broad-scale ecological changes and therefore serve as proxies for structural changes in marine communities, particularly in patterns of dominance and abundance through geologic time [8,20,21,31,32,34]. Shell beds are abundant throughout Lower Triassic strata around the world [8,21] and therefore depict the restructuring that occurred in benthic level-bottom shallow marine communities during the aftermath of the end-Permian mass extinction. The majority of Lower Triassic shell beds range from mm-scale pavements to 20 cm-thick beds; amalgamated shell beds can reach up to 2 m in thickness [8,21]. The majority of Lower Triassic shell beds are numerically and taxonomically dominated by members of the Modern Evolutionary Fauna [8,21,56]. Lower Triassic shell beds are more similar to shell beds from the Paleozoic, though, in thickness and geometry [8]. Therefore, Lower Triassic shell beds represent a transition from archaic-style shell beds characteristic of the Paleozoic to modern-style shell beds characteristic of the post-Jurassic [8].

2.3.2. Wrinkle structures

Wrinkle structures have been found in shallow subtidal siliciclastic paleoenvironments in Lower Triassic strata in the western United States and in northern Italy [47]. Wrinkle structures are a type of microbially-mediated sedimentary structure found commonly in

Proterozoic–Cambrian siliciclastic strata deposited in intertidal to deep-sea marine environments, the formation of which has been attributed to the stabilization of the substrate by microbial mats [25,26,40,41]. In the post-Cambrian, wrinkle structures have been restricted to supratidal, intertidal and deep-sea siliciclastic environments because of the increase in levels of bioturbation and consequent mixed-layer development during the Ordovician [26]. Therefore, subtidally-deposited Lower Triassic wrinkle structures likely formed because of decreased bioturbation during the aftermath of the end-Permian mass extinction [47]. The proliferation of subtidal microbial mats was limited to the Early Triassic and represents another short-term structural change in benthic level-bottom shallow marine communities.

3. Restructuring in benthic level-bottom shallow marine communities due to prolonged environmental stress following the end-Permian mass extinction

Data from a variety of paleoecological approaches presented here indicate that benthic level-bottom shallow marine communities were restructured during the Early Triassic (Fig. 1). Using the system of four paleoecological levels which Droser et al. [14] developed as a comparative approach to assess major ecological changes in Phanerozoic life, Bottjer et al. [7] showed that the structural changes in Early Triassic paleocommunities can be classified as level-2 (major structural changes within an ecosystem), level-3 (community-type level changes within an ecosystem), and level-4 (community-level changes) changes. Some aspects of the community restructuring (i.e., decrease in biodiversity and the numerical dominance of few taxa) produced a non-actualistic ecology that lasted only during the Early Triassic, while other aspects of benthic level-bottom shallow marine communities were permanently altered (i.e., switch in taxonomic and ecologic dominants). This synopsis also reveals that taxonomic and ecologic recovery from the end-Permian mass extinction was decoupled and was geographically and temporally varied.

What facilitated the temporary and permanent structural changes in benthic level-bottom shallow marine paleocommunities during the Paleozoic/Mesozoic transition? The short-term ecological restructuring during

		benthic skeletonized invertebrate marine fauna			soft-bodied marine ichnofauna		biosedimentary structures				
		alpha diversity	taxonomic dominants	ecologic dominants	extent of bioturbation	epifaunal tiering	infaunal tiering	benthic Bambachian megaguilids	shell beds	wrinkle structures	
post-Early Triassic		35	bivalves and gastropods	bivalves	ii 6	all tiers	all tiers	17	modern style	supratidal and intertidal	
247 mya	Early Triassic (Cycythian)	13	bivalves	bivalves	ii 3-6	0 - +5 cm +5 - +20 cm	0 - -6 cm -6 - 12 cm	4	characteristics of archaic and modern styles	supratidal, intertidal, and subtidal	
											Spathian
											Smithian
											Dienerian
252.6 mya	Upper Paleozoic	23	rhynchonelliform brachiopods	rhynchonelliform brachiopods	ii 5	all tiers	all tiers	12	archaic style	supratidal and intertidal	
											Griesbachian

Fig. 1. Generalized short-term and long-term structural changes among skeletonized invertebrates and infauna in benthic level-bottom shallow marine paleocommunities before, during, and after the Early Triassic aftermath of the end-Permian mass extinction. In this figure: (1) alpha diversity indicates mean number of species in paleocommunities from variable nearshore and from open marine environments (data from [3,6,54]); (2) data on taxonomic and ecologic dominants refers to the general pattern (data on taxonomic dominants from [22,56]; data on ecologic dominants from [18,20,21,49,54]); (3) ichnofabric indices for the Upper Paleozoic and post-Early Triassic represent our best estimates; ichnofabric indices for the Early Triassic represent characteristic bioturbation of each stage/substage; data from low paleolatitudes only (data from [46,54,59-61,63]); (4) epifaunal and infaunal tiering refers only to characteristic tiering (data from [1,6,9,27,30,46,50,53,54,59,61,67]); (5) benthic Bambachian megaguilids refers to number of megaguilids occupied (data from [4,7]); (6) shell bed data from [8,32]; (7) wrinkle structure data from [25,26,47]. Ichnogeneric diversity was omitted because it varies greatly with latitude and because more comparative studies need to be done. Date of 252.6 ± 0.2 Myr represents the age of the end-Permian mass extinction [39] and 247 Myr is the most recent age for the Early–Middle Triassic boundary [37].

Fig. 1. Vue globale des changements structuraux, à court et à long terme, intervenus chez les invertébrés à squelettes et chez l'endofaune faisant partie des paléocommunautés benthiques de mers peu profondes, avant, pendant et après l'intervalle de temps répercutant, au début du Trias, les effets de la crise de la fin du Permien. Dans cette figure : (1) la diversité alpha indique le nombre moyen des espèces des paléocommunautés des domaines littoraux et des environnements marins du large (données d'après [3,6,54]) ; (2) les données concernant les groupes dominants d'un point de vue taxonomique et écologique se rapportent à des modèles généraux (données d'après [22,56] pour les dominants taxonomiques, données d'après [18,20,21,49,54] pour les dominants écologiques) ; (3) les indicateurs de la biostructuration du Paléozoïque supérieur et postérieurs au début du Trias nous paraissent la meilleure approximation ; les indicateurs de la biostructuration du début du Trias consistent en des phénomènes de bioturbation propres à chaque étage ou sous-étage ; les données correspondent uniquement aux basses latitudes (données d'après [46,54,59-61,63]) ; (4) l'étagement de l'épifaune et de l'endofaune se rapporte uniquement à des étagements caractéristiques (données d'après [1,6,9,27,30,46,50,53,54,59,61,67]) ; (5) les mégaguilides de Bambach sont des associations benthiques correspondant au nombre de mégaguilides représentées (données d'après [4,7]) ; (6) les données sur les bancs coquilliers proviennent de [8,32] ; (7) les données sur les figures de froissement (*wrinkle structures*, d'origine microbienne) proviennent de [25,26,47]. La diversité générique des ichnofossiles n'a pas été figurée, car elle varie beaucoup avec la latitude ; de plus, des analyses comparatives sont encore nécessaires. L'âge de 252,6 ± 0,2 Ma est celui des extinctions de la fin du Permien [39], tandis que 247 Ma est l'âge le plus récemment avancé pour la limite Trias inférieur/Trias moyen [37].

the Early Triassic has been underscored in the literature because it indicates that recovery from the end-Permian mass extinction and the return to 'normal' marine communities did not occur until 5–6 Myr after the extinction [37,39]. Three mechanisms to explain Early Triassic non-actualistic paleoecology and the apparent delayed biotic recovery have been hypothesized (cf. [17]): (1) physiologically harsh environmen-

tal conditions persisted long after the end-Permian mass extinction, inhibiting 'normal' community development; (2) Earth's biota needed an exceptionally long time to rewrite community assembly rules after marine ecosystems were profoundly disrupted by the end-Permian mass extinction; and (3) a preservation and sampling bias indicates that Early Triassic non-actualistic paleoecology is more apparent than real and

makes the biotic recovery following the end-Permian mass extinction only appear to be delayed.

Several lines of data support the hypothesis that physiologically harsh environmental conditions persisted long after the end-Permian mass extinction. Though no proposed mechanism is widely accepted as its definitive cause, ever-increasing sedimentological [35,47,68] and isotopic [35,44] data from around the world indicate that deleterious environmental conditions affected marine ecosystems for 5–6 Myr after the end-Permian mass extinction. This prolonged environmental stress is likely linked to the end-Permian mass extinction and facilitated the ecological degradation and short-term restructuring observed in benthic level-bottom shallow marine Early Triassic paleocommunities [20,51,54,59]. The long-term, permanent changes in paleocommunities (i.e., phyletic and ecologic switches) also were facilitated by the harsh environmental conditions that prevailed during the Earliest Mesozoic. The hypothesis that the magnitude of the extinction so disrupted normal communities that the biotic recovery from the end-Permian mass extinction was delayed [16,17] is not completely unsupported. According to Erwin and Pan [17], if ecospace restructuring caused the delayed recovery, then the length of time it took for the recovery to occur would be controlled by the extent of community collapse. However, the severe ecological degradation [6] and restructuring of paleocommunities during the Early Triassic were largely controlled by the deleterious environmental conditions of the time.

The hypothesis that the entire Early Triassic is afflicted by a preservation gap [16,17,55] is not well-supported. Indeed, there is a dearth of silicified faunas from the Lower Triassic and Early Triassic faunas consist mainly of neomorphs and molds [19]. However, a recent evaluation of Early Triassic environmental and ecological characteristics indicates that fossil preservation likely was not significantly decreased during the Early Triassic. The widespread occurrence of assemblages dominated by small fossils (microgastropod biofacies [21]), the lack of extensive bioturbation, and periodic increases in alkalinity that built up in Early Triassic oceans due to bacterial sulfate reduction indicate that shells typically may not have been preferentially dissolved and molds may not have been destroyed in the early diagenetic environment [19]. Therefore, though silicification is not extensive in Lower Triassic strata,

the body fossils and molds that are present are useful and valuable at least for paleoecologic studies, if not for detailed taxonomic studies. The decrease in ichnogenetic diversity and in the depth and extent of bioturbation during the Early Triassic are also excellent proxies for ecological degradation independent of the fossilization process and falsify the hypothesis that the taxonomic and ecologic patterns during the Early Triassic are more apparent than real. Furthermore, the taxonomic and ecologic patterns that characterize the Early Triassic herald the taxonomic and ecologic patterns that characterize the remainder of the Phanerozoic; these long-term changes would not have persisted if Early Triassic patterns were merely the result of a preservation bias. Short-term structural changes in Early Triassic paleocommunities are not merely artifacts of taphonomic bias as previously suggested [16,17], but are primary signals of non-actualistic paleoecology during the aftermath of the end-Permian mass extinction.

The end-Permian mass extinction and its aftermath are ecologically, as well as taxonomically, significant events in the history of life. The end-Permian mass extinction was only one result of deleterious environmental conditions affecting the Late Paleozoic/Early Mesozoic. Rather than concentrating solely on the end-Permian mass extinction, future studies, such as paleocommunity and onshore/offshore pattern analyses, should focus on pre- and post-extinction ecologic patterns to gain a more complete view of the consequences of this environmental stress on evolutionary history. Examining ecologic as well as taxonomic parameters will also aid in constraining the cause of the end-Permian mass extinction and will reveal what aspects of paleocommunities are resilient to severe environmental stress.

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