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PALEONTOLOGY

Resilience of infaunal ecosystems during the Early Triassic greenhouse Earth

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The Permian-Triassic mass extinction severely depleted biodiversity, primarily observed in the body fossil of well-skeletonized animals. Understanding how whole ecosystems were affected and rebuilt following the crisis requires evidence from both skeletonized and soft-bodied animals; the best comprehensive information on soft-bodied animals comes from ichnofossils. We analyzed abundant trace fossils from 26 sections across the Permian-Triassic boundary in China and report key metrics of ichnodiversity, ichnodisparity, ecospace utilization, and ecosystem engineering. We find that infaunal ecologic structure was well established in the early Smithian. Decoupling of diversity between deposit feeders and suspension feeders in carbonate ramp-platform settings implies that an effect of trophic group amensalism could have delayed the recovery of nonmotile, suspension-feeding epifauna in the Early Triassic. This differential reaction of infaunal ecosystems to variable environmental controls thus played a substantial but heretofore little appreciated evolutionary and ecologic role in the overall recovery in the hot Early Triassic ocean.

INTRODUCTION

The body fossil record across the Permian-Triassic (P-Tr) mass extinction, the largest biocrisis of Phanerozoic life, shows severely devastated biodiversity of animals (1, 2), with variable environmental and temporal recovery afterward (3, 4). Trace-making animals (mostly soft-bodied or poorly skeletonized) also variably flourished after this mass extinction (5–8). Compared with skeletonized animals, which are well studied, the behavior, architectural components, and ecosystem engineering of trace-making animals (soft-bodied animals) are poorly understood. Understanding all organisms in the marine ecosystem and especially the roles of deep burrowers in generating opportunity is crucial in understanding the recovery of the ecosystem from crisis.

The history of life can be viewed as a process of colonization, which, in turn, might reflect the exploitation of empty or underused ecospace (9). Trace fossils therefore provide unique information on colonization patterns, behavioral styles, ecologic categories, and paleoenvironmental trends of ancient trace-making animals (10–13). In particular, infaunal ecosystem engineering behaviors could have affected the carbon cycle by increasing the provision and use of organic matter in deeper levels of the sediment, which may have resulted in a positive feedback on biodiversity, increasing the utilizable ecospace, and resource availability (14–17). Bioturbation also increases the complexity of geochemical gradients in sediments and recycles nutrients such as nitrogen and phosphorus, which, in turn, can greatly increase microbial biomass, attracting further bioturbators and expanding the habitable zone, showing a strong positive feedback effect on biodiversity of skeletonized animals (18–21). Whether the behavioral and ecologic diversifications of trace-making animals

facilitated the initial recovery of skeletonized animals during the Early Triassic has been debated (15, 16, 22). When and where infauna flourished in this Early Triassic greenhouse world (23) and potential environmental controls remain poorly understood (7, 24–28).

Here, we report a quantitative evaluation of infaunal behavioral and ecologic diversities using four ichnologic measures (ichnodiversity, ichnodisparity, ecospace utilization, and ecosystem engineering) conducted on abundant trace fossils collected from 400 horizons in 26 sections in South China and adjacent regions, spanning the uppermost Permian to topmost Lower Triassic strata and from shelf-slope-basin to lower shoreface, ramp, carbonate platform, brackish, and lacustrine settings (fig. S1; for more details, see the Supplementary Materials) to examine the potential environmental selectivity on behaviors and ecology of trace-making animals during the Early Triassic greenhouse regime. To assess the relationship of behavioral and ecologic diversification between soft-bodied and skeletonized animals over the P-Tr transition, several ecologic categories of the trace fossil and body fossil records were analyzed in half-substage time bins from the studied sections and the whole of South China, respectively.

RESULTS

Environmental selectivity in behavioral and ecologic categories of infauna and potential controls

During the P-Tr transition, trace fossil metrics of ichnodiversity, ichnodisparity, ecospace utilization, and ecosystem engineering varied in each environmental setting. In terrestrial lacustrine settings, trace fossils are rather sporadically present, and all metrics are coupled as they all declined across the P-Tr extinction and remained at low levels until the early Spathian, when all ecologic indices recovered to their pre-extinction levels (Fig. 1 and figs. S2 and S3). In brackish habitats, trajectories of all metrics show a pronounced decline from Griesbachian to Dienerian, an increase in the early Smithian, and, lastly, a modest decline across the Smithian-Spathian boundary. In carbonate platform settings, all measures seemed to experience modest declines in the P-Tr extinction, remained low

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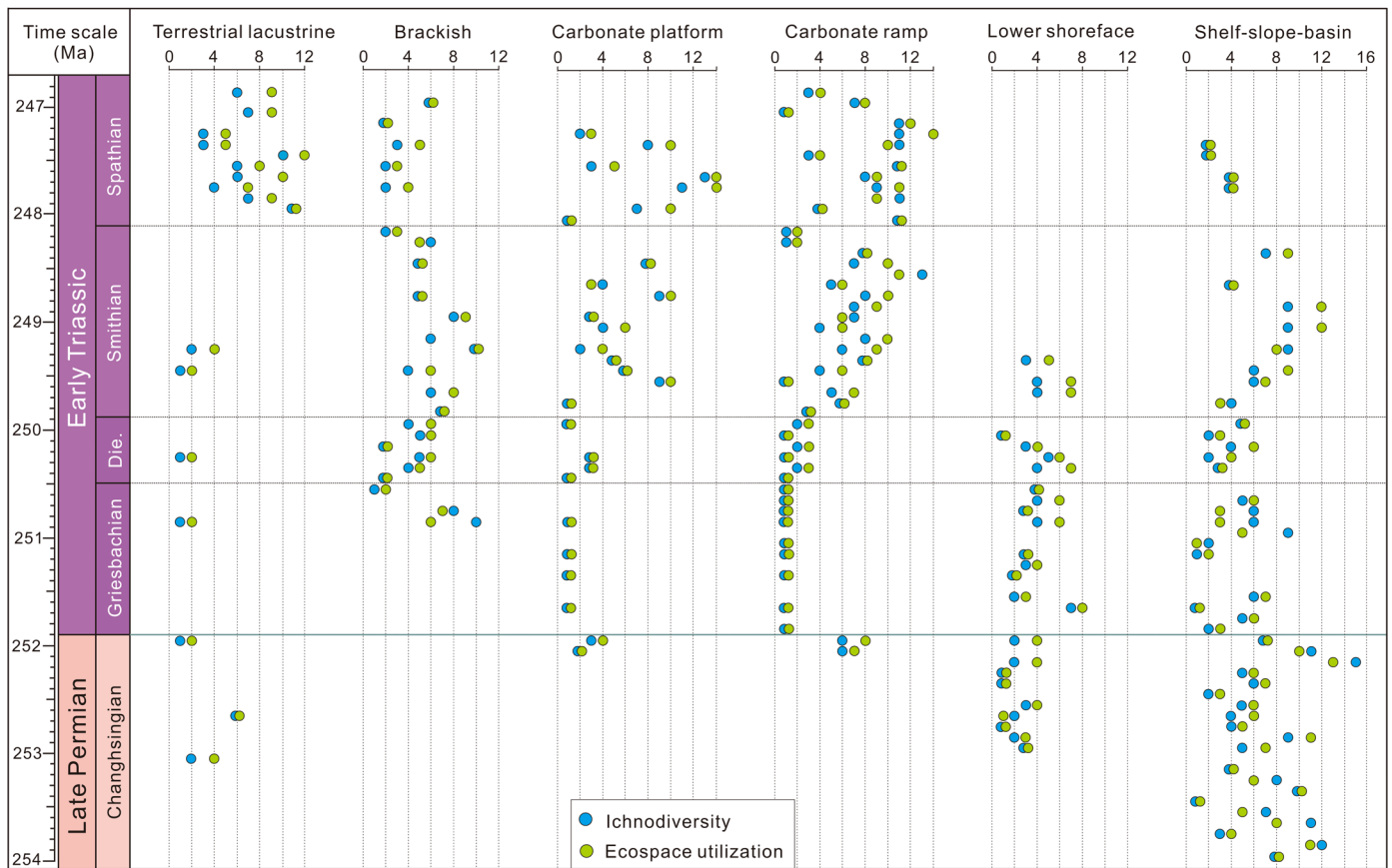


Fig. 1. Behavioral evolution of marine animals through the P-Tr mass extinction and Early Triassic recovery. Stratigraphic plots showing two ichnologic metrics (ichnodiversity and ecospace utilization) in six environmental settings, in South and North China. Raw data for each horizon were compiled from the original trace fossil records examined horizon by horizon in the studied sections and were combined into 0.1-million year (Ma) time bins. Time scale follows (44). Numbers on the x axis represent raw counts of ichnogenera (blue) and occupied ecospace modes (green) from each time bin. Stratigraphic distributions of another two metrics (ichnodispersity and ecosystem engineering) are illustrated in fig. S2. Die., Dienerian.

through the late Griesbachian-Dienerian, increased in the early Smithian, and exceeded pre-extinction levels to form a pronounced plateau toward the early Spathian (Fig. 1 and figs. S2 and S3). In carbonate ramp settings, all measures probably declined across the P-Tr extinction, remained at low levels in the late Griesbachian-Dienerian, peaked in the late Smithian, and then, experienced a minor decline (Fig. 1 and fig. S4). Lower shoreface facies sections record increases of metrics across the P-Tr extinction and in the Dienerian and declines in the early Smithian (Fig. 1 and fig. S3). In shelf slope to basin settings, all metrics underwent rebounds in the late Griesbachian and showed pronounced recovery in the early Smithian (Fig. 1 and fig. S5). Thus, bioturbating behavior varied by environment during the P-Tr interval. After the extinction, infaunal behavioral and ecologic diversities declined somewhat to the early Griesbachian and fully recovered in the early Smithian in marine settings. In the terrestrial realm, recovery does not seem to occur until the early Spathian (Fig. 1).

Comparisons were made among these four ichnologic metrics and between ichnologic metrics and environmental proxies (C, S, and O isotopes; further detailed in the Supplementary Text) in carbonate ramp-platform and shelf-slope-basin environmental settings to determine whether these ichnologic metrics covaried before and after the P-Tr mass extinction, as well as whether the ichno-ecologic variations might be explained by temporal variations in carbon cycles

(C isotopes), marine redox conditions (S isotopes), and sea surface temperature (indicated by conodont oxygen isotopes) (Fig. 2 and figs. S6 and S7). These environments were chosen for their superior coverage (Fig. 1). The four ichnologic measures of ichnofossil records covaried before and after the P-Tr extinction (Fig. 2 and fig. S2), which suggests that the behavioral and ecologic strategies of trace-making animals responded consistently during the Early Triassic hothouse regime. Although strictly statistical correlation between ichno-average and isotopic data were rather low (figs. S6 and S7), elevated temperatures and extended anoxia coincided with low values of behavioral and ecologic diversities across the P-Tr boundary, Dienerian, and latest Smithian, while cooling intervals and reduced anoxia were coupled with increased behavioral and ecologic diversities in the early Spathian (Fig. 2).

Ecologic categories of infauna and skeletonized animals from carbonate ramp-platform and shelf-slope-basin environments

Sixteen of 90 potential infaunal ecospace categories (modes of life) were occupied in the Changhsingian, based on the combined data in half-substage time bins from carbonate ramp-platform and shelf-slope-basin environmental settings, which have better temporal coverage (fig. S8). The number of modes of life declined across the

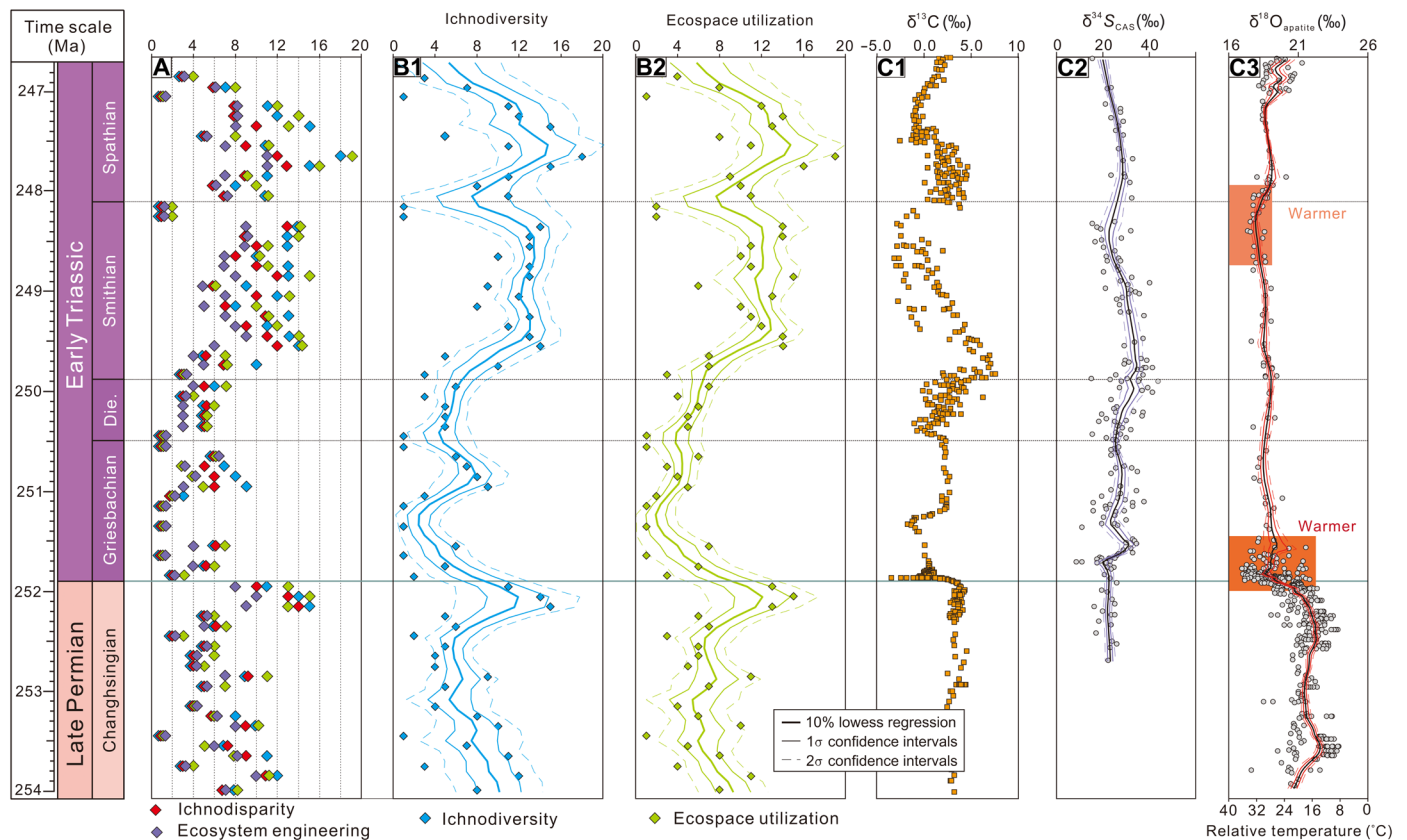


Fig. 2. Marine animal evolution and key environmental indicators through the P-Tr mass extinction and Early Triassic recovery. Stratigraphic plots of four ichnologic metrics in carbonate ramp-platform and shelf-slope-basin environmental settings from the Changhsingian to Spathian in South and North China and their comparisons with compiled $\delta^{13}\text{C}$, $\delta^{34}\text{S}$, and $\delta^{18}\text{O}$ datasets. (A) Combined plot of all four ichnologic metrics. Numbers on the x axis represent raw counts of ichnogenera (blue), ichnodispersity (red), ecospace utilization (green), and ecosystem engineering (purple) from each time bin. (B1 and B2) The ichnologic metrics (ichnodiversity and ecospace utilization) extracted from (A) with 10% LOWESS (locally weighted scatterplot smoothing) regression. (C1 to C3) Compiled plots of $\delta^{13}\text{C}$, $\delta^{34}\text{S}$, and $\delta^{18}\text{O}$ datasets of marine environmental settings from South China. The 10% LOWESS regressions are shown in (C2) and (C3). Isotopic datum sources are from (23, 50–53).

P-Tr extinction, followed by a tiny increase in the late Griesbachian and then a sharp decrease across the Griesbachian-Dienerian boundary, and exceeded pre-extinction levels in the early Smithian-Spathian (fig. S8). Ecospace utilization shows a decrease in occurrence across the P-Tr extinction, especially for the shallow- and deep infaunal tiers, and rebounded in the early Smithian (Fig. 3A). Ecologic categories of facultatively motile, suspension feeders and freely motile, non-specialized deposit feeders of the shallow infaunal tier from trace fossil records rebounded in the Dienerian and became very common through the rest of the Early Triassic (number codes 9 to 11 in Fig. 3A and fig. S8). In contrast, most other ecologic categories of semi-infaunal to intermediate infaunal tiers were rather sporadic in the Griesbachian-Dienerian and rebounded in the early Smithian (Fig. 3A). Ecologic categories of deep infaunal tiers rebounded in the early Smithian but did not exceed their pre-extinction levels through the Smithian-Spathian (number codes 23 to 26 in Fig. 3A and fig. S8).

Of all potential combinations of mechanisms of substrate interaction and sediment modification (ecosystem engineering), 10 occurred in the late Changhsingian, 5 in the early Griesbachian, and returned to pre-extinction levels in the Smithian-Spathian (fig. S8). Thus, pronounced losses in the number of ecosystem engineering modes occurred across the P-Tr extinction in carbonate ramp-platform and shelf-slope-basin environmental settings. The occurrence of ecosystem

engineering modes rebounded to pre-extinction levels in the early Smithian and formed a plateau in all tiers in the Smithian-Spathian (Fig. 3B). Shallow tier sediment conveyors that interacted with sediment through backfilling (number code 7 in Fig. 3B) and deep tier gallery biodiffusers that interacted with sediment through compression (number code 13 in Fig. 3B), as well as regenerators that interacted with sediment through excavation (number code 15 in Fig. 3B), were most common in the late Changhsingian. Their occurrence reached pre-extinction levels in the early Spathian (Fig. 3B).

The time series of ichnofauna from carbonate ramp-platform and shelf-slope-basin environmental settings show that all four metrics display a broad “W” pattern of variation through the Changhsingian to Smithian, with a marked decrease across the P-Tr extinction, followed by a conspicuous increase in the late Griesbachian and then a sharp decrease across the Griesbachian-Dienerian boundary (Fig. 4A). All four metrics peaked in the early Smithian and formed plateaus through the late Smithian, then followed by a decrease in the Spathian, while the number of ecosystem engineering modes remained at relatively high levels when compared with Griesbachian-Dienerian data (Fig. 4A and fig. S8). Deposit-feeding infauna was relatively scarce through the late Changhsingian to Dienerian, followed by a conspicuous increase through the Smithian to early Spathian in shallow carbonate ramp-platform environmental settings (Fig. 4C).

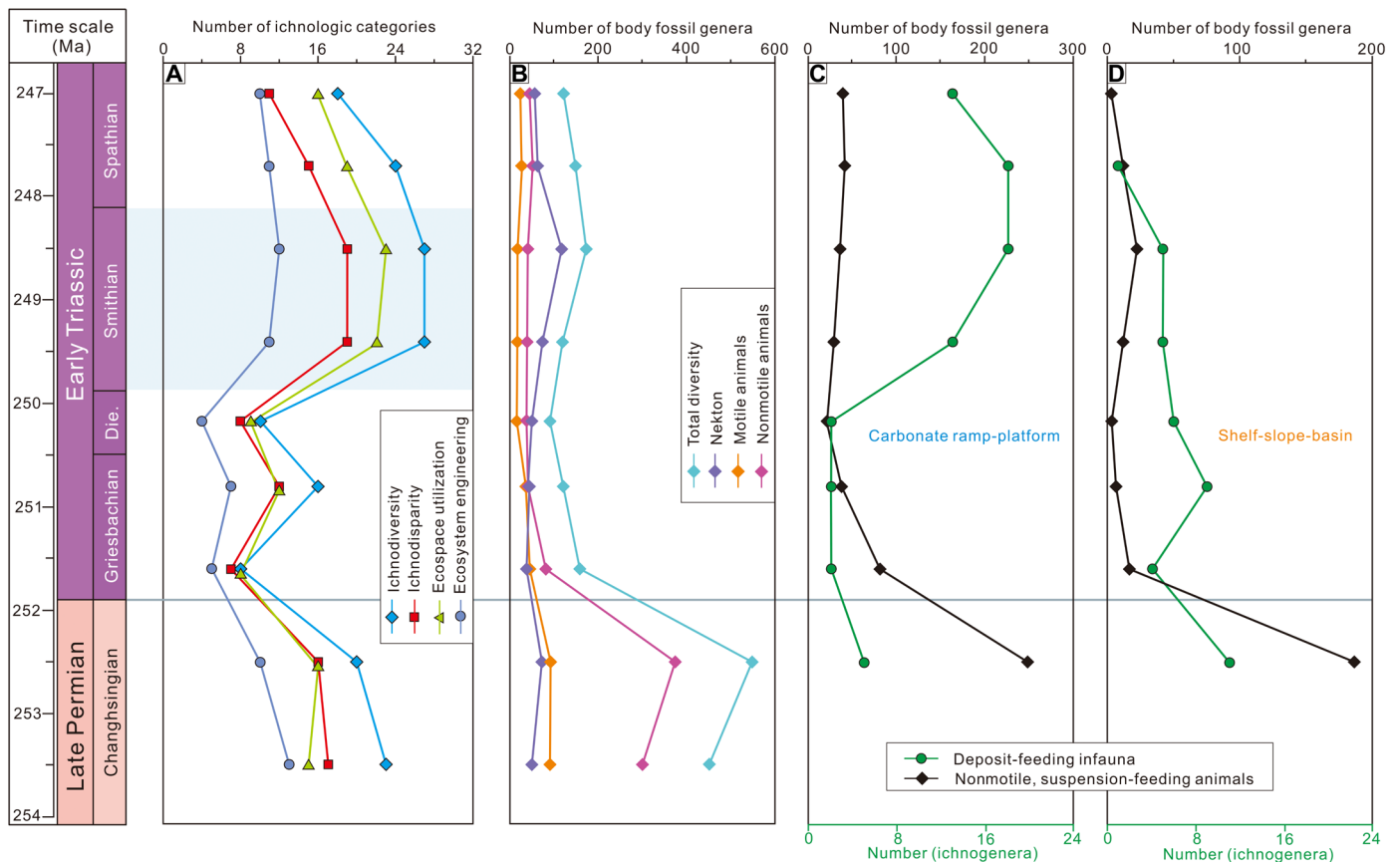


Fig. 4. Behavioral and ecologic richnesses of infauna and generic richness of different functional groups of skeletonized animals in carbonate ramp-platform and shelf-slope-basin environmental settings within half-substages in the latest Permian and Early Triassic. (A) Variations of ichnodiversity, ichnodispersity, ecospace occupation, and ecosystem engineering of infauna (trace fossils). Numbers on the x axis represent raw counts of ichnogenera, ichnodispersity, ecospace utilization, and ecosystem engineering modes from each time bin. The shaded blue box shows when all ichnologic metrics reached a plateau in the Smithian. (B) Generic richness variations of total, nekton, motile, nonmotile animals (body fossils). (C) Generic richness variations of nonmotile, suspension-feeding animals and ichnogenic richness of deposit-feeding infauna in carbonate ramp-platform environments. (D) Generic richness variations of nonmotile, suspension-feeding animals and ichnogenic richness of deposit-feeding infauna in shelf-slope-basin environments.

sporadic as well (Fig. 3). Abundant freely motile, nonspecialized deposit feeders colonized the shallow-tier ecospace (number code 11 in Fig. 3A), acting as sediment conveyor modifiers and interacting with the sediment through backfilling (number code 7 in Fig. 3B). Thus, infaunal ecospace in the Griesbachian-Dienerian functioned much like a ship manned by a skeleton crew; most posts were occupied but with only a few taxa or behavioral programs (31). The early Smithian saw not only a full recovery of behavioral and ecologic diversities but also the nearly identical occurrences of these ecologic styles (Figs. 3 to 5E and fig. S8). Such an ecologic structure is characterized by the appearance of a wide repertoire of behavioral strategies, reflecting the interactions of newly developed, distinctive body plans with the substrate, increased trophic structure complexity, and a reorganization of the occupation of infaunal ecospace and more complex ecosystem engineering (Figs. 3 and 5). Thus, the four ichnologic metrics all indicate that infaunal ecologic structure was well established in the early Smithian, ~3 million years (Ma) after the P-Tr extinction (Figs. 4A and 5).

As ecosystem engineers, bioturbators can have both negative and positive feedback effects on biodiversity. Bioturbation increases the complexity of geochemical gradients in sediments by changing

the rate of redox cycling through biomixing and bioirrigation (32, 33). Biomixing (diffusive solid phase sediment mixing) and bioirrigation (nonlocal solute mixing) tend to have opposite impacts on sedimentary biogeochemistry, as biomixing tends to increase oxygen consumption and bioirrigation tends to oxygenate the sediment (33). Ecologically, this is critical, as biomixers and bioirrigators may have opposite impacts on biodiversity and the structure of benthic and infaunal communities. Increased levels of biomixing throughout Earth history have been linked to ocean anoxia and global warming (34), while increased levels of bioirrigation fuel productivity by recycling nutrients such as nitrogen (16) and phosphorus (21). Ultimately, the combined effects of biomixing and bioirrigation do not have unidirectional impacts on nutrient cycling and are likely also a function of environmental conditions (21, 34).

Although the modes of life of benthic marine invertebrate genera (body fossils) show no significant loss in functional diversity and the subsequent Early Triassic marine ecosystems were not ecologically depauperate (31), all functional groups of benthic fauna compiled from carbonate ramp-platform and shelf-slope-basin environments from South China show significant drops in generic richness (Fig. 4B). The small peak of total generic diversity is driven



Fig. 5. Reconstruction of marine ecosystems before and after the P-Tr mass extinction in China. (A) Pre-extinction marine ecosystem in the latest Permian, showing diverse nekton, benthic animals, and burrowing animals. (B) Marine ecosystem in early Griesbachian (early Induan) after the mass extinction, showing only few nekton, simple horizontal burrows, and the development of microbialites. (C) Marine ecosystem in late Griesbachian, showing the flourishing of burrowing animals in some habitats. (D) Marine ecosystem in Dienerian, which is similar to early Griesbachian. (E) Marine ecosystem in Smithian, showing more diverse nekton and motile benthic animals, and a well-established infaunal ecologic structure. (F) Marine ecosystem in Spathian, which is similar to Smithian but with the emergence of reptiles. The reconstruction is largely based on the carbonate ramp environment. The artistic illustrations were designed by authors X.F., Z.-Q.C., and M.J.B. and drawn by Y. Jiang, who is a graduate student of art.

largely by the diversification of the nekton in the Smithian (Fig 4B). Nekton suffered relatively little during the P-Tr extinction probably because of their free-moving ability, which brought them a wider fundamental niche (4) or ability to disperse to refugia of suitable environmental conditions. The recovery of nekton occurred at the same time as the full rebound of infaunal ecosystem engineering activities (Fig. 4A and B). We cannot fully determine from our data whether this reflects the positive feedback effects of ecosystem engineering on biodiversity because the recovery of nektonic diversity to pre-extinction levels is probably not attributable to the activities of infaunal ecosystem engineers. However, a fair amount of evidence has demonstrated that bioturbating animals in shallow marine environments can promote benthic-pelagic coupling by increasing nutrient exchange between the sediment and water column (10). Bioturbation influences the distribution of planktonic organisms by controlling the dormancy of resting/larval stages of planktonic organisms and thus essentially influences the base of the food web in a marine ecosystem (20). “Bottom-up control” mechanism of ecosystem cascades connects nutrient concentrations to primary producers to first-order consumers and has positive feedbacks on higher-order consumers such as nekton (35). Both peaks of the diversity of infaunal ecosystem engineers and nekton in the Smithian may also be a result of the amelioration of environmental conditions in the aftermath of the extinction.

For infaunal communities, motile deposit feeders were relatively scarce in the late Changhsingian, but they acted as important components of marine benthic ecosystems through the Smithian-Spathian in shallow carbonate ramp-platform environmental settings (Fig. 4C). This functional group is generally decoupled from nonmotile, suspension feeders in generic diversity through the late Changhsingian to late Early Triassic (Fig. 4C). This is probably because a trophic group amensalism phenomenon (a biologic interaction in which one species is inhibited or destroyed and the other is unaffected) occurred in such shallower environments, where the biological bulldozing activities of motile, deposit-feeding infauna may have destroyed the fragile ecologic habitats on the seafloors, destabilized the substrate, and clogged the filtering structures of nonmotile, suspension-feeding animals during the Early Triassic (36–38). This may have been responsible, in part, for the so-called “suppressed” recovery of nonmotile, suspension-feeding animals during the Early Triassic (4). The decoupling in diversity of these two functional groups may also indicate that ecosystem engineering of bioturbators can have negative feedback effects on biodiversity in ancient carbonate ramp-platform settings. However, another explanation could be that skeletal organisms were selected against by the environment in a way that nonskeletonized trace fossil-making animals were not, in light of feedbacks between life and the environment and the complexity of ecologic interactions. In addition, the decoupled relationship of these two

functional groups was not conspicuous or evidenced in deeper shelf-slope-basin environmental settings (Fig. 4D), which is more probably because of less detrital “fuel” for deposit feeders but better ecologic advantage for suspension feeders in deeper waters, thus resulting in limited trophic group amensalism.

Thus, a well-established infaunal ecologic structure developed in the late Early Triassic, which was earlier than full restoration of the epifauna-dominated ecosystem in the Middle Triassic (Fig. 5). Some pioneering ecosystem engineers cultivated the seafloor and filled vacant ecospace, which may have had negative feedback effects on the recovery of nonmotile, suspension-feeding animals during the late Early Triassic. Although the recovery of nekton occurred at the same time as the full rebound of infaunal ecosystem engineering activities, their positive feedback effects remain partly undetermined. However, phylogenetic study of coeval fishes and marine reptiles has shown that explosive diversification occurred in the Early Triassic (39, 40). These innovations and diversification were part of the opportunistic refilling of ecospace after the mass extinction (41, 42). Molecular and fossil evidence also demonstrate that the Early Triassic was a time of origination and diversification of the nonskeletal ancestors of many major Mesozoic skeletal groups (43). Thus, the flourishing of soft-bodied (nonskeletal) animals in the late Early Triassic from our trace-fossil evidence may support the hypothesis that soft-bodied bioturbating ecosystem engineers triggered the evolutionary innovations and radiations to some extent (43). This study therefore provides new insights into how ecosystem engineering by soft-bodied, bioturbating animals may increase resilience to extinction in different environmental settings, as well as how ecosystem engineering may have played a role in benthic ecosystem recovery after severe mass extinctions.

MATERIALS AND METHODS

Age model

Radiometric ages for the time scale follow (44). The time scale in this study is constrained by correlation of 18 conodont zones over the 7 Ma (254 to 246.7 Ma) of the Changhsingian (latest Permian) and four Early Triassic substages, namely, Griesbachian, Dienerian, Smithian, and Spathian (fig. S1). These biozones, together with high-resolution carbon isotopic profiles and reliable radiometric dates, provide precise correlation and reliable time control for compilation of regional trace fossil records and conodont oxygen, sulfur, and carbon isotope dataset.

Trace fossil data

Trace fossils used in our study are primarily based on field observations and specimens collected during the past 10 years. Most of the fossil localities have been visited more than three times to collect specimens and take photos, ensuring the best possibilities to excavate enough fossil materials. It always took about 5 days or 1 week to work on the fossil-bearing successions through the Late Permian to Early Triassic for most studied sections, and the time spent on fossil collection was about 2 days at each locality. When a studied section has more complete strata, the time spent on fossil collection was longer. Some data are cited from earlier publications, but the localities have been revisited, the materials have been reexamined, and taxonomic evaluation of some ichnotaxa has been undertaken. We originally recorded the fossils horizon by horizon, and because of the uneven distribution of trace fossils in the stratigraphic units,

we then standardized the data from different sections in 0.1-Ma time bins by division of thickness of the fossil-bearing formation and age of that formation (table S1 and data file S1). Here, we treated the sedimentation rate of the successions in one formation or in several formations of the same section as constant according to shared same environmental backgrounds. Last, to reconstruct and compare the four ichnologic metrics along six environmental settings across the P-Tr mass extinction and the Early Triassic, we binned the collection data into a series of nine half-substage time intervals. Subdivisions are primarily based on biostratigraphic data and chemostratigraphic data when available. These bins are early Changhsingian, late Changhsingian, early Griesbachian, late Griesbachian, Dienerian, early Smithian, late Smithian, early Spathian, and late Spathian (tables S2 to S4 and data file S2).

Range-through data may be used to ameliorate the effects of a patchy body fossil record because species cannot re-evolve and so must be present between their first and last appearances (12). However, trace fossils are different from body fossils in this regard: A variety of organisms can make the same ichnotaxon by performing the same behavior, and the same organism can make different ichnotaxa by performing different behaviors. Hence, ichnotaxa are generally broadly defined and long ranging, so it is usually assumed that their absence does not indicate poor sampling but true absence (12). Thus, raw counts of trace fossils were used in our analysis to identify patterns of behavioral strategies and ecologic styles of trace-making animals. In addition, to accommodate sampling bias, we used rarefaction analysis using ichnogenus richness versus occurrences of ichnofossils from carbonate ramp-platform and shelf-slope-basin environments, indicating that sampling is sufficient in all sampling intervals (fig. S10A and table S7).

Body fossil data

We compiled a dataset of all known marine invertebrate genera by using range-through data spanning the Late Permian to the end of the Early Triassic from South China in half-substage bins (data file S3). The dataset was derived largely from the database constructed in (4) with revisions of some genera and further subdividing the Smithian and Spathian each in two (i.e., early Smithian, late Smithian, early Spathian, and late Spathian), as well as a further dividing of environmental settings (data file S3). We use the ecospace model of marine animals used before (45, 46) as a basis for the quantitative analysis of the ecology of all known late Permian to Early Triassic benthic marine genera. Some parameters of tiering, motility level, and feeding strategy of the original model have been combined to make the model more simplified and better for comparison with trace fossils (tables S8 to S10). Rarefaction analysis is also used to test sampling bias using generic richness versus occurrences of body fossils through the Late Permian to Early Triassic (fig. S10B), indicating that sampling is sufficient in all time bins.

Behavioral diversification

Analysis of behavioral diversification is based on comparisons of ichnodiversity and ichnodisparity. Ichnodiversity is a measure of ichnotaxonomic richness. Ichnotaxa are biogenic sedimentary structures that are produced by behavioral interactions between organisms and their inhabited substrates. We counted the number of ichnogenera for ichnodiversity. Ichnodisparity is a measure of the variability of trace fossil morphological plans, quantified as the number of architectural designs such as simple horizontal trails or

vertical unbranched burrows (29). Several ichnotaxobases, including configuration, orientation, and position with respect to stratification, were given priority to define categories of architectural designs of trace fossils. Configuration consists of the spatial arrangements of the trace fossil components, revealing what is typically visualized at first sight. Orientation reflects the overall disposition with respect to bedding (i.e., vertical, inclined, and horizontal). Position with respect to stratification is an equivalent of toponomy, so defining whether a trace fossil is preserved as full relief or epirelief (29). There is a detailed list for the categories of architectural designs, and each ichnogenus was included in one category of architectural design in previous work (29). Categories of architectural designs are summarized in table S2.

Ecospace utilization

The calculation of ecospace utilization of infauna follows established methods (12, 13). The amount of occupied ecospace is quantified as the number of modes of life, categorized by three parameters: (i) tiering, subdivided into surficial, semi-infaunal, shallow infaunal, intermediate infaunal, and deep infaunal tiers; (ii) motility, subdivided into motile, facultatively motile, and nonmotile types; and (iii) feeding mode, subdivided into suspension feeders, nonspecialized deposit feeders, specialized deposit feeders, predators, chemosymbiosis, farming, and trapping. Ecospace utilization is summarized in tables S1 and S3.

Tiering refers to the level of an animal vertically in the sediment when it is in its regular life position. For a trace fossil to form, an animal must interact with a substrate. Trace fossils provide direct information on the life positions of animals, so it is possible to be rather precise regarding infaunal tiering levels (13, 47). The system adopted here comprises a shallow infaunal tier for depths up to 6 cm below the substrate-water interface, an intermediate infaunal tier for depths of 6 to 12 cm, and a deep infaunal tier for depths greater than 12 cm. This allows for the differentiation of an intermediate tier and a truly deep tier of infaunal animals. Thus, for tiering, each trace fossil was classified as surficial, semi-infaunal (0 to 0.5 cm), shallow (0.5 to 6 cm), intermediate (6 to 12 cm), or deep (>12 cm) (10, 48).

Motility is subdivided into motile, facultatively motile, and nonmotile (12). Most trace-making animals have some degree of motility. In general, any organism capable of producing temporary bioturbation structures that reflect continuous movement is considered motile. Animals that are generally stationary but are capable of movement are included in the category of facultatively motile.

The mode of feeding is constrained to five categories: suspension feeding, nonspecialized deposit feeding, specialized deposit feeding, predation, chemosymbiosis, farming, and trapping (12). Suspension feeders are those that obtain and capture food particles from the water column. Deposit feeders are those that actively ingest particles of food from a substrate. Deposit feeders are categorized by their trace fossil morphology into nonspecialized deposit feeders with nonpatterned and overcrossing trails and specialized deposit feeders with exploration and non-overcrossing locomotory burrows. Predators are those trace-makers inferred to have been able to capture prey. Chemosymbiosis involves animal endosymbiosis with chemotrophic bacteria, such as downward radiating burrows of *Chondrites*. Farming involves the culturing of suitable bacteria or fungi for feeding purposes, which can take place on large internal surfaces of burrows or chambers, whereas trapping refers to the passive capture of

migrating meiofauna or other microorganisms such as complex, regular, patterned, meandering, spiral, radiating, and network trace fossils known as graphoglyptids (12).

Ecosystem engineering

The calculation of ecosystem engineering of infauna follows (12). Ecosystem engineering is classified by three proxies: (i) tiering, (ii) mode of sediment interaction, and (iii) mode of sediment modification (summarized in tables S1 and S4). Tiering categories have been documented in ecospace utilization. The styles by which trace-making animals interact with the substrate (mode of sediment interaction) consist of intrusion, compression, backfilling, and excavation. Intrusion refers to displacement of sediments as the animal moves through, but the sediment closes up behind it (12). Compression is composed of movement and compaction of sediments around the trace-making animal as it passes through. Backfilling is the process of active backward movement of sediments around the animal. Excavation refers to active loosening of sediments from one location to another. Each ichnogenus was assigned one of four sediment interaction modes. There is a detailed list for the sediment interaction modes of most ichnogenera in previous works (12).

Mode of sediment modification is evaluated by categorizing trace fossils according to how their makers affected and reworked sediment (13). This scheme is adapted from the conceptual framework of marine benthic ecology (49). Sediment modification can be classified into four types: biodiffusion, gallery biodiffusion, conveyor, and regenerator (12). Biodiffusion is the movement of sediment particles over short distances, whereas gallery biodiffusion involves the rapid redistribution of sediment particles from one part of the sediment profile to another. Upward and downward conveyors are subsumed within the simpler concept of conveyors, with animals also able to convey sediment laterally. This category refers to animals that actively transport sediment particles across and within tiers. Regenerators are animals that actively move sediment to the surface from below, where it may be transported away by physical sedimentary processes such as currents (12). Each ichnogenus was assigned one of the above sediment interaction and sediment modification modes based on previous descriptions and divisions (12).

SUPPLEMENTARY MATERIALS

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