Taxonomic and ecologic transitions in Triassic bivalve communities (#105957)

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Taxonomic and ecologic transitions in Triassic bivalve communities

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The Permian–Triassic mass extinction was a pivotal event in shaping marine benthic ecosystems, leading to the rise of mollusks such as bivalves and gastropods as representatives of the Modern Evolutionary Fauna. However, the detailed changes in the ecological structure of these ecosystems throughout the Triassic remain underexplored, particularly in relation to the interrelationship between taxonomic and ecological diversity. Here, we report on bivalve communities from Triassic shallow marine facies in South China to document regional patterns and explore how these patterns connect to global trends. Broad congruence in the timing of taxonomic and ecological shifts was observed in South China, driven by biotic interactions within the region. However, both the South China materials and global data revealed a decoupling of taxonomic and ecological diversity. Substantial variability in taxonomic richness was observed alongside stable ecological diversity. Taxonomic recovery occurred earlier, while ecological diversity did not fully recover until the Anisian. The Carnian stage represents a significant transition in ecosystem structure, characterized by a shift towards infaunal dominance and the expansion of habitat depth. The evolutionary trajectory of Triassic bivalves follows a two-step pattern, with full recovery in the Anisian followed by ecological reorganization in the Carnian.

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Abstract

The Permian–Triassic mass extinction was a pivotal event in shaping marine benthic ecosystems, leading to the rise of mollusks such as bivalves and gastropods as representatives of the Modern Evolutionary Fauna. However, the detailed changes in the ecological structure of these ecosystems throughout the Triassic remain underexplored, particularly in relation to the interrelationship between taxonomic and ecological diversity. Here, we report on bivalve communities from Triassic shallow marine facies in South China to document regional patterns and explore how these patterns connect to global trends. Broad congruence in the timing of taxonomic and ecological shifts was observed in South China, driven by biotic interactions within the region. However, both the South China materials and global data revealed a decoupling of taxonomic and ecological diversity. Substantial variability in taxonomic richness was observed alongside stable ecological diversity. Taxonomic recovery occurred earlier, while ecological diversity did not fully recover until the Anisian. The Carnian stage represents a significant transition in ecosystem structure, characterized by a shift towards infaunal dominance and the expansion of habitat depth. The evolutionary trajectory of Triassic bivalves follows a

two-step pattern, with full recovery in the Anisian followed by ecological reorganization in the Carnian.

Keywords: Triassic; Bivalves; Biotic recovery; Diversification; Taxonomic and ecological diversity.

Introduction

The Permian–Triassic mass extinction (PTME), the most significant biotic crisis in the Phanerozoic, profoundly impacted the ecological structure of global ecosystems (Erwin, 1993; Benton, 1997). This event marked the transition from the Paleozoic Evolutionary Fauna to the Modern Evolutionary Fauna (Sepkoski, 1981, 1984; Bambach, Knoll & Sepkoski, 2002). A noteworthy transition during this interval was the substitution of brachiopods by bivalves as the predominant components of marine benthic ecosystems (Sepkoski, 1984; Hallam & Wignall, 1997; Fraiser & Bottjer, 2007). Consequently, bivalves played a crucial role in the recovery and transformation of marine benthic ecosystems during the Triassic. Bivalves, due to the high preservation chances and ecological versatility, are an ideal group to explore diversity and evolutionary dynamics (Ros & Echevarría, 2011).

However, the timing and pattern of bivalve recovery remain debated. One perspective suggests a prolonged recovery throughout the Early Triassic, with the main phase occurring in the Anisian (Posenato, 2008; Friesenbichler, Hautmann & Hugo, 2021). In contrast, another view proposes a more rapid initial recovery beginning in the Griesbachian (Hautmann et al., 2011; Hofmann, Hautmann & Bucher, 2015; Tu, Chen, & Harper, 2016). Recovery onset is typically marked by widespread rediversification (Erwin, 1988), with increasing genus or species richness signifying the recovery phase. The divergence between these perspectives stems from differences in study scale—whether focusing on regional datasets (Posenato, 2008; Hautmann et al., 2011; Hofmann, Hautmann & Bucher, 2015) or global data (Tu, Chen & Harper, 2016)—as well as methodologies, such as statistical analyses of fossil material (Friesenbichler, Hautmann & Hugo, 2021) versus analyses based on paleobiological databases (Tu, Chen & Harper, 2016).

Ecological diversity, or functional diversity, is another crucial aspect of biodiversity, driving essential ecosystem processes in marine communities (Solan et al., 2004). However, research on the specific patterns of ecological diversity change is scarce. By the Middle Triassic, the ecology of marine benthic communities was undergoing reorganization (Friesenbichler, Hautmann & Bucher, 2021). Some Anisian paleocommunities remained unstable, a reflection of

the ongoing biotic and environmental changes during this period (Dineen, Fraiser & Tong, 2015). Significant diversification of key groups that dominate modern ecosystems had occurred by the Carnian (Dal Corso et al., 2020).

Several studies indicate a decoupling of taxonomic and ecological recovery from the PTME (Edie, Jablonski & Valentine, 2018; Song, Wignall & Dunhill, 2018). However, comprehensive studies on ecological diversity in benthic communities throughout the Triassic—particularly during the Late Triassic—remain lacking, and the relationship between taxonomic and ecological diversity is still unclear.

To better assess the evolution of Triassic bivalve taxonomy and ecology, we adopted two approaches. First, we selected representative stratigraphic sections for fossil collection and conducted observational studies to enable precise quantitative analyses. Second, we statistically analyzed our data and supplemented it with data from global databases to uncover macroevolutionary trends. Our findings reveal that the shifts in taxonomic and ecological structure occurred in concert among Triassic bivalves. Furthermore, a positive correlation is evident between taxonomic and ecological diversity. The evolution of Triassic bivalves demonstrates a two-stage process, comprising fully recovery in the Anisian and a subsequent ecological transformation in the Carnian.

Materials & Methods

Field work

Triassic marine sediments are widely exposed in South China Triassic, comprising a variety of depositional types and sequences. Among these, the Lower-Middle Triassic predominantly features marine deposits, which extend continuously to the Upper Triassic in the western region (Tong et al., 2019). Guizhou is particularly notable for its exceptional Triassic deposits, which have yielded a wealth of information about from Permian-Triassic transition to the Late Triassic. Additionally, the area has yielded rich bivalve fossil records. The shallow facies is rich in benthic fossil fauna, making it an optimal region for investigating the evolution of Triassic bivalves across various time intervals.

In order to ensure comparability of data for each interval, a series of representative shallow facies sections were selected in Guizhou, and thorough studies of the most abundant members were carried out, including systematic field fossil collection, as well as indoor identification, statistical and analytical studies. Each fossil bed was systematically collected until no new fossil

types could be found for a longer time, normally four hours. All bivalve specimens were subjected to thorough examination and rigorous identification. For the purposes of enumeration, fossil specimens exhibiting more than half of their original parts intact were considered a single unit, and articulated bivalve specimens were treated as discrete entities.

Most bivalve fossils were preserved as complete and undamaged valves, and some were articulated, suggesting they are para-autochthonous. We establish Triassic communities by the dominant and characteristic taxa. The fossil communities were analyzed and validated using Q-mode cluster analysis and Bray and Curtis (1957) coefficient to classify samples as similar association in terms of taxonomic composition and abundance, with the similarity threshold set to 1 (Clarke, 1993).

Data collection

The data under analysis can be divided into two principal categories. One data set is that of bivalve fossils from the South China shallow facies, which is derived primarily from species and ecology data constructed from the fossil collections of the South China Triassic key sections (Dataset 1). The second dataset is based on the global data d in the Palaeobiology Database https://paleobiodb.org/#/ (PBDB). PBDB data have been extracted to assess genus-level turnover metrics of bivalves from the Late Permian to the Late Triassic (Dataset 2). Although the primary study interval is Triassic, the dataset was extended to encompass records from the Late Permian Radian to the Early Jurassic Toarcian in order to mitigate edge effects. The original data, downloaded on 17 February 2024, comprised all reliably identified occurrences at the genus-level and was subsequently corrected to include 31,325 taxonomic record occurrences from 654 genera. The information on accepted name, order, family, genus, early interval, late interval and mobility, diet and habit in the downloaded dataset was then selected to integrate and clarify the dataset to form the database for this analysis. The mode of life of each genus in the dataset was carefully checked and corrected to provide a reliable basis for analysis.

To assess ecological diversity, each bivalve genus was assigned to a mode of life (MOL) within the ecospace model modified from Aberhan and Kiessling (2015). Detailed information on the bivalves, along with their respective modes of life, can be found in Dataset 1 and 2.

Statistical analysis

We used a minimum sample size of 30 individuals for inclusion in the analyses, resulting in

a final dataset of 27 samples from South China. To test the influence of this analytical choice we repeated analyses with sample size thresholds of 20 and 40 for analysis. Taxonomic and ecological diversity were calculated separately for the samples, and the metrics included richness (S), evenness (J) and Shannon index (H) (Jost, 2006), which together provide a more complete understanding of the alpha-diversity of South China bivalves. Correlations between taxonomic and ecological diversity were explored using both Pearson correlation coefficient and Spearman rank-order correlation coefficient (ρ), which ranged from -1 to 1, indicating the strength and direction of the correlation.

Two main methods were used to investigate beta diversity. First, a Bray-Curtis similarity matrix was used to identify species that tended to co-occur in samples based on the evaluation of distances between clusters using a Ward's minimum variance method, and samples with similar taxonomic composition were grouped together (Roden et al., 2018). Hierarchical cluster analyses were performed to explore taxonomic and ecological differences between samples (Murtagh & Legendre, 2014). Two-way cluster analysis generated dendrograms for both taxa or function (R-mode) and samples (Q-mode), which reveals changes in the proportion of taxonomy and ecology. Second, non-metric multidimensional scaling (nMDS) was applied to group samples. Stress values of <0.05, <0.1, <0.2 (for 2D plots only) and <0.3 indicated excellent, good, acceptable and unsatisfactory data representation respectively (Clarke & Warwick, 1994). In order to determine the variability of bivalve groupings of different substages, the analysis of similarities (ANOSIM) was used. The R and P values were used as indicators of statistical significance, with P values $\leqslant 0.001$ indicating significance. An R value close to 1.0 indicates dissimilarity between groups, while an R value close to 0 indicates an even distribution of high and low ranks within and between groups. The above studies were conducted using the 'vegan' package (Oksanen et al., 2019).

Species and functional diversity (also referred to as taxonomic and ecological diversity) of fossil material from South China were calculated, and species and functional richness were assessed using range-based data methods (Foote, 2000), as sampling instability precludes the use of modern occurrence-based methods (e.g., Alroy, 2014). We used the Shareholder Quorum Subsampling (SQS) method (Alroy, 2010), valued at 70% and averaged over 1,000 subsampling runs, to standardize sampling and assess corrected diversity patterns. Origin, extinction and net diversification rates were also calculated to provide a more complete picture of trends in diversity evolution. Due to the limitations of the collected fossil material, the same diversity

trend analyses were performed on the global statistical data to explore similarities and differences in the evolution of diversity trends regionally and globally. The above functionality is implemented through the 'divDyn' package (Kocsis et al., 2019).

Data analyses were conducted in the R 4.4.1 (R Core Team, 2024).

Results

Bivalve communities of South China

The lower Triassic is represented by the Liangshuichong section, which is situated in Langdai town, Liupanshui city (Fig. 1). The stratigraphic succession comprises the Yelang and Yongningzhen formations. The lithological and fossil compositions of the Yelang Formation indicate a shallow marine mixed clastic-carbonate facies. The fossil beds are mainly distributed in the clastic lithology, and each fossil bed averages about 0.5 m, which allows important collection and statistical analysis. The lower part (LSC7-19), comprising over 41% *Claraia wangi*, was assigned *Claraia wangi* community in Dienerian-Smithian. The middle part (LSC20-40) comprised over 71% *Claraia*, with *Claraia aurita* representing the most abundant species. Thus, *Claraia aurita* community is thus distinguished, which can be considered to Dienerian-Smithian. The upper part (LSC41-58) contains both *Eumorphotis* and *Unionites*, representing approximately 10% each. This distinguishes the *Unionites canalensis-Eumorphotis multiformis* community, which can be assigned to the Smithian-Spathian (Fig. 2A).

The Anisian is represented by the Maotai section, which is located in Maotai Town, Renhuai City (Fig. 1). The section yields the Guanling and Yangliujing formations, which are characteristic of shallow marine carbonate facies. The fossils are mainly found in the dolomites of the Guanling and Yangliujing formations, with each major fossil layer about 1m thick. The fossils are most abundant in the lower part of the section. The proportion of *Costatoria goldfussi mansuyi* exceeds 31%, while that of *Asoella illyrica* is approximately 13.9% in the lower part (MG78-90). The *Costatoria goldfussi mansuyi-Asoella illyrica* community is distinguished and assigned to the Pelsonian. The proportion of *Costatoria goldfussi mansuyi* exceeds 55.8%, while that of *Unionites spicatus* is approximately 25.8% in the upper part (MG91-129). The *Costatoria goldfussi mansuyi-Unionites spicatus* community is distinguished and assigned to the Pelsonian-Illyrian (Fig. 2B).

The Ladinian is represented by the Gaoqiao section, which is located in Zunyi city and primarily exposes the Guanling and Yangliujign formations. The lithological and facies

characteristics are identical to those of the Maotai section; however, the Yangliujing Formation is thicker and more well-preserved in this section. This study is concerned with the fossils of the Yangliujing Formation, which is approximately 1 m thick and is located primarily in the middle of the section (GQ96-112). The proportion of *Palaeolima subcostata* exceeds 27%, while that of *Costatoria goldfussi* is approximately 22%. The *Palaeolima subcostata-Costatoria goldfussi* community is distinguished and assigned to the Fassanian (Fig. 2C).

The Carnian is represented by the Hehuachi section, which is situated within Langdai town (Fig. 1D). This section uncovers the Late Triassic Laishike Formation and the base of the Banan Formation. The lithological and fossil evidence suggests a shallow marine clastic facies. The studied fossil beds are mainly distributed in the siltstone and mudstone of the Laishike Formation, which is on average 1 m thick. The basal to middle section (HHC1-8) was composed of over 84% *Bositra wengensis*, which was assigned to the *Bositra wengensis* community. The top of the section (HHC10) is composed of approximately 40% of the community. These two communities are assigned to the Julian.

Changes in taxonomic and ecologic composition of South China

Based on the cluster analyses of the South China fossil samples the main groups of samples can be distinguished, both taxonomically and ecologically (Fig. 3). These three groups of samples represent the Early Triassic, Middle Triassic and Late Triassic, respectively. The pattern is robust to changes in sample size thresholds (Figs. S3-S6). The Middle Triassic bivalve community has the greatest variability, with the early Carnian (Julian) having the next greatest variability (Fig. 3). This variability was tested to be not significantly influenced by lithology (Figs. S7-8). There are shifts in the structure of the Anisian and Carnian bivalve communities.

The nMDS of the South China fossil samples also shows the above pattern. In the taxonomic nMDS, the Early Triassic samples are on the right side of the figure, the Middle Triassic samples are on the left, and the Late Triassic samples are in the middle (Fig. 4A). The stress value for the nMDS ordination is 0.03, indicating that the two-dimensional plot accurately represents the sample relationships (Clarke, 1993). Similarly, in the ecological nMDS, Early Triassic samples are on the left, Middle Triassic samples are in the middle and Late Triassic samples are on the right (Fig. 4B). The stress value for the nMDS ordination is 0.14, indicating an acceptable representation of the sample relationships (Clarke, 1993). The distances of the three groups are almost equal, indicating that the variability between these three groups is close.

The Induan samples overlap in both taxonomy and ecology, indicating homogeneity, with the Smithian sample close to the Induan (Fig. 4A), indicating the Early Triassic, with no significant change in bivalve structure, at least until the Smithian. Moreover, the Two-way cluster analysis shows that the difference between the Induan and Olenekian samples is due to limited taxonomic turnover of disaster taxa (i.e. *Claraia*, *Eumorphotis*, *Unionites* and *Promyalina*; Hallam & Wignall, 1997), accompanied by an ecological transition from MOL19 (epifaunal, facultatively motile, byssate, suspension feeders) to MOL4 (epifaunal, stationary, byssate, suspension feeders) (Fig. S2). The Anisian and Ladinian samples show that the disaster taxa that were abundant in the Early Triassic have disappeared from the Anisian, with a markedly altered genus composition (Fig. S2A). Although the Anisian and Ladinian have some overlapping species, the dominant species are different. The Anisian is dominated by *Costatoria* and *Unionites* (Fig. 5), with a dominant ecology of MOL3 (shallow infaunal, facultatively motile, unattached, suspension feeders). The Ladinian is dominated by *Palaeolima* and *Plagiostoma*, with a dominant ecology of MOL4 (Fig. S2). The Carnian samples are far from the Early and Middle Triassic samples. The species composition is relatively distinct, with *Bositra* and *Halobia* represented in the early Julian (Fig. 5), and a rapid increase in taxonomic diversity and a marked increase in evenness in the late Julian (Fig. S2A). The ecology of the early Julian (HHC6-8) was dominated by MOL12 (epifaunal, stationary, unattached, suspension feeders). Later, in late Julian (HHC10), ecological diversity increased with great evenness, MOL15 (shallow infaunal, mobile, suspension feeders) became dominant, and MOL14 (shallow infaunal, facultatively mobile, suspension feeders) began to appear (Fig. S2B). Thus, the Anisian and Carnian are important turning points in Triassic bivalve taxonomy and ecological diversity.

In addition, the ANOSIM method was used to assess the differences between the different substages of the Triassic bivalve communities. The ANOSIM test gave an R value of 0.88 for taxonomy and 0.73 for ecology, indicating a high degree of separation between groups (Table S5). The significance values are 0.001, indicating that the observed differences were statistically significant and not due to random variation (Clarke, 1993). All these results indicate a taxonomic and ecological shift in Triassic bivalves during the Anisian and Carnian.

Thus, the structure of bivalve communities shows consistency in taxonomic and ecological evolution. This pattern is also reflected in other diversity indices, including richness, the Shannon index, and evenness. These indices show a strong linear correlation between taxonomic and ecological diversity (Fig. 6), indicating a positive correlation (Table S1).

Taxonomic and ecologic diversity trends

Diversity trajectories show decoupling both in South China and globally. Diversity calculated from South China materials shows fluctuating taxonomic trends and stable ecological trends (Fig. 7A). The Anisian is characterized by significantly higher species and functional diversity. The corrected diversity curve shows a similar trend (Fig. 7A). The SQS-calculated diversity curve (q=0.7) showed trends in species-level richness that were similar to, but partly different from, the raw data, suggesting that taxonomic diversity was affected to a small extent by sampling standardization, but that the overall pattern was more reliable (Fig. 7A). Through extinction and origination rates, taxonomic and ecologic diversity showed significant recovery during the Anisian, with further diversification during the Carnian (Fig. 7B). Net diversification rates also show similar trends in taxonomic and ecological diversification, with higher net diversification rates in the Anisian and Carnian (Fig. 7B), indicating diversification in the taxonomy and ecology of Triassic bivalves.

The result calculated from the global database shows that genus richness increased from the Olenekian, and functional richness increased from the Anisian (Fig. 7C). Thus, taxonomic diversity recovered before ecological diversity. SQS subsampling diversity (q = 0.7) shows similar trends in genus-level richness to the raw data, suggesting that overall trends in taxonomic diversity were not strongly affected by sampling standardization (Fig. 7C). The turnover rate curves show diversification of genus richness in the Olenekian and diversification of functional richness in the Anisian, supporting the pattern that taxonomic diversity recovered before ecological diversity. And the strong recovery of taxonomic and ecological diversity during the Anisian is also observed (Fig. 8D). Thus, the pattern that taxonomic diversity recovered before ecological diversity is confirmed in the global database.

Notwithstanding fluctuations in taxonomic diversity, ecological diversity demonstrates considerable stability. The raw and subsampled data from both South China and globally demonstrate a trajectory towards functional stability in Triassic bivalves (Fig. 7A, C). However, this can only represent a stability in the ecological diversity of bivalves. Further research has demonstrated that the role of modes of life changes within stages is also an important aspect (Fig. 8). Following PTME, bivalve ecology exhibited a decline in infaunal habitats (MOL2, 3, 11, 14) and an increase in epifaunal (MOL7, 12, 19) and semi-infaunal (MOL16) habitats. However, the overall structure remained largely unchanged (Fig. 8). The Anisian witnessed a notable increase

in diverse modes of life, accompanied by the appearance of novel mode of life (MOL5). The Ladinian bivalve ecology underwent significant changes with the emergence of a diverse range of new lifestyles and a notable prevalence of infaunal types (MOL6, 18, 20). During the Carnian, a reduction in the number of epifaunal species (MOL1, 4, 12, 19) was accompanied by an increase in the proportion of infaunal species (MOL3, 6, 10, 11, 14, 17). This trend has continued since that time, particularly with a sustained increase in the proportion of deep infaunal bivalves (MOL10, 11, 14).

Discussion

South China Pattern

The shift in ecological structure did not parallel changes in bivalve diversity in South China. Structural changes in ecosystems involve the first appearance or replacement of ecologically dominant higher taxa (Droser et al., 2000). Fossil evidence from South China indicates that bivalve communities experienced concurrent taxonomic and ecological transitions from the Permian-Triassic boundary into the Middle Triassic (Posenato, 2008; Hofmann, Hautmann & Bucher, 2015; Song et al., 2019). This pattern is due to interactions between taxonomic and functional diversity (Stanley, 1979; Wahl et al., 2011).

Previous studies have shown that taxonomic and ecological diversity decoupled to some extent in South China. The ecological recovery after the Permian-Triassic mass extinction (PTME) was more complex and protracted than the recovery of taxonomic diversity (Clampham and Bottjer, 2007). Prior research has demonstrated that numbers of mode of life has been increasing since the Phanerozoic (Erwin, Valentine & Sepkoski, 1987; Bambach et al., 2007). Taxonomic and ecological diversity was decoupled after the PTME (Dineen, Fraiser & Sheehan, 2014). One reason for this phenomenon is replacement of specialists with generalists, has likely resulted in the emergence of more generalized functional characteristics (Baker et al., 2021). Another is that functional richness has been demonstrated to exhibit greater stability than species richness (Foster and Twitchett, 2014; Song et al., 2017).

Global pattern

The global bivalve data similarly show a decoupling between genus-level taxonomic and functional diversity, with taxonomic recovery occurring earlier than ecological recovery. This decoupling of taxonomic and ecological diversity has also been widely reported and discussed in

previous research (Foster & Twitchett, 2014; Edie, Jablonski & Valentine, 2018; Song, Wignall & Dunhill, 2018). Despite the PTME, there was no substantial reduction in global functional diversity (Foster & Twitchett, 2014). Both the South China and global data reflect this decoupling, with ecological diversity stabilizing after the mass extinction.

However, the consistency of the taxonomic and ecological structure shifts observed in the South China is challenging. Global patterns are, in part, shaped by regional dynamics, including geographic and environmental (Jablonski, 1998; Bush & Bambach, 2004). Therefore, the pattern of South China and globe didn't show the consistency.

Recovery and transformation of Triassic bivalve

Our South China materials indicate a prolonged recovery of both taxonomic and ecological diversity in bivalves, a trend often observed in benthic ecosystems (Song et al., 2011; Chen & Benton, 2012; Foster & Sebe, 2017). In contrast, global data point to an earlier taxonomic recovery during the Induan (Hautmann et al., 2011; Hofmann, Hautmann & Bucher, 2015; Tu, Chen, & Harper, 2016; Brayard et al., 2017), likely due to local biotic and environmental factors (Brayard et al., 2017). Therefore, this cannot be considered a significant recovery event on a global scale.

Full recovery, defined as a significant increase in both taxonomic and ecological diversity diversification and a return to pre-extinction community-level properties (Erwin, 1998), did not occur until the Anisian. During this stage, both taxonomic and ecological diversification accelerated (Fig. 7), marking the main and final phase of the recovery process (Foster & Sebe, 2017; Hofmann et al., 2014; Friesenbichler, Hautmann & Hugo, 2021). Nutrient influx from volcanic or terrestrial sources may have facilitated this recovery (Cao et al., 2024).

Although Anisian benthic communities fully recovered in South China, functional evenness remained low, indicating ecological instability (Dineen, Fraiser & Tong, 2015). This indicates that benthic community of Anisian has not yet established a stable ecological structure. This process can be attributed to the filling of vacant niches prior to reaching maximum environmental carrying capacity, irrespective of ecosystem structure development (Song, Wignall & Dunhill, 2018). A similar pattern has been observed in modern freshwater systems (Baker et al., 2021).

The timing of the formation of stable benthic communities and the completion of the Paleozoic-type to modern-type remains a topic of ongoing debate. Bivalves underwent a

significant ecological divergence in the post-Paleozoic (Stanley, 1968). They shifted from an epifaunal to an infaunal existence, from a sedentary to a motile state, and from a benthic to a planktonic habitat (McRoberts, 2001; Bonuso & Bottjer, 2008; Mondal & Harries, 2016). By the Late Triassic, infaunal bivalves had surpassed epifaunal genus in diversity (Bonuso & Bottjer, 2008; Ros et al., 2011). This shift is also observed in the Julian stage of South China, where infaunal modes of life (MOL2) became dominant, particularly in the *Palaeoneilo elliptica* community (HHC10) (Fig. S2B). Globally, the increased proportion of infaunal bivalves in the Carnian (Fig.8), coupled with the expansion into deeper niches, was likely driven by the evolution of siphon-feeding (Stanley, 1968). These changes signal the transition towards a modern-type bivalve community.

Conclusion

The transitions of taxonomic and ecological structure occurred in concert in bivalve communities from South China and there is a strong positive correlation between the taxonomic and functional diversity. However, the diversity trajectories observed differ from the structure shifts. In both South China materials and global data, the taxonomic and ecological diversity show a decoupling, due to the relative stability of ecological diversity. This difference can be attributed to the influence of biotic interactions in the region and on a global scale.

Two key stages are identified in the ecological evolution of Triassic bivalves. The first occurred in the Anisian, which marks the full recovery and radiation of both taxonomic and ecological diversity. The second transition took place in the Carnian, a period of ecological change in which bivalves shifted from epifaunal to infaunal dominance, with a corresponding increase in depth of life. The evolution of Triassic bivalves suggests that the emergence of modern-type bivalves can be viewed as a two-step evolutionary leap.

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Figure 1

The Early-Middle Triassic paleogeography of the Nanpanjiang basin and Yangtze platform in Guizhou and Guangxi of South China (after Lehrmann et al., 2005) and the location of the studied sections.

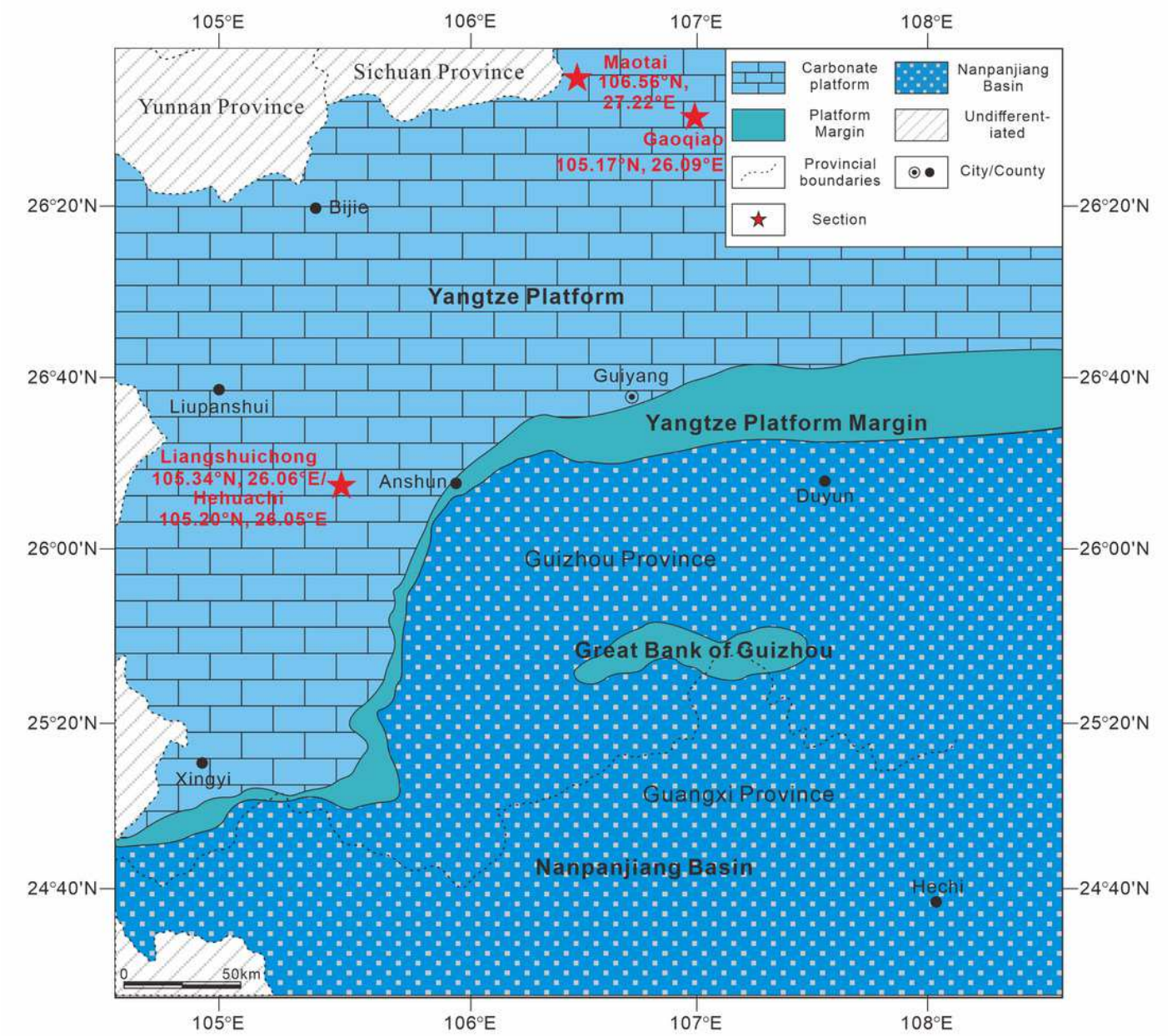


Figure 2

Logs of the studied sections from South China with sample locations for bivalves. (A). Liangshuichong (LSC); (B). Maotai (MG); (C). Gaoqiao (GQ); (D). Hehuachi (HHC).

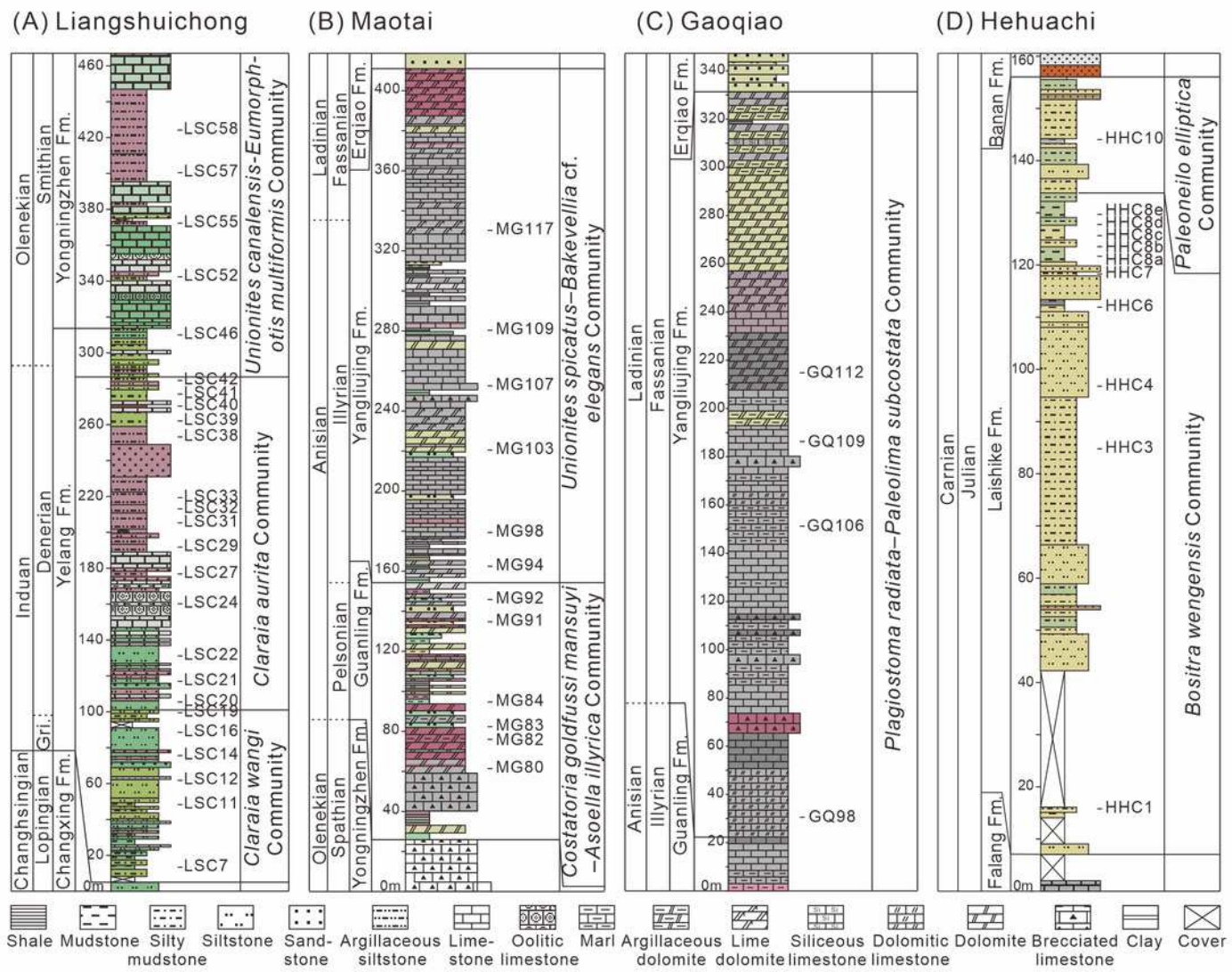


Figure 3

Hierarchical cluster of the samples from South China based on (A) species and (B) modes of life.

Red, Griesbachian; Blue, Dienerian; Green, Smithian; Yellow, Pelsonian; Orange, Illyrian; Brown, Julian. The abbreviations represent the samples in Fig. 2.

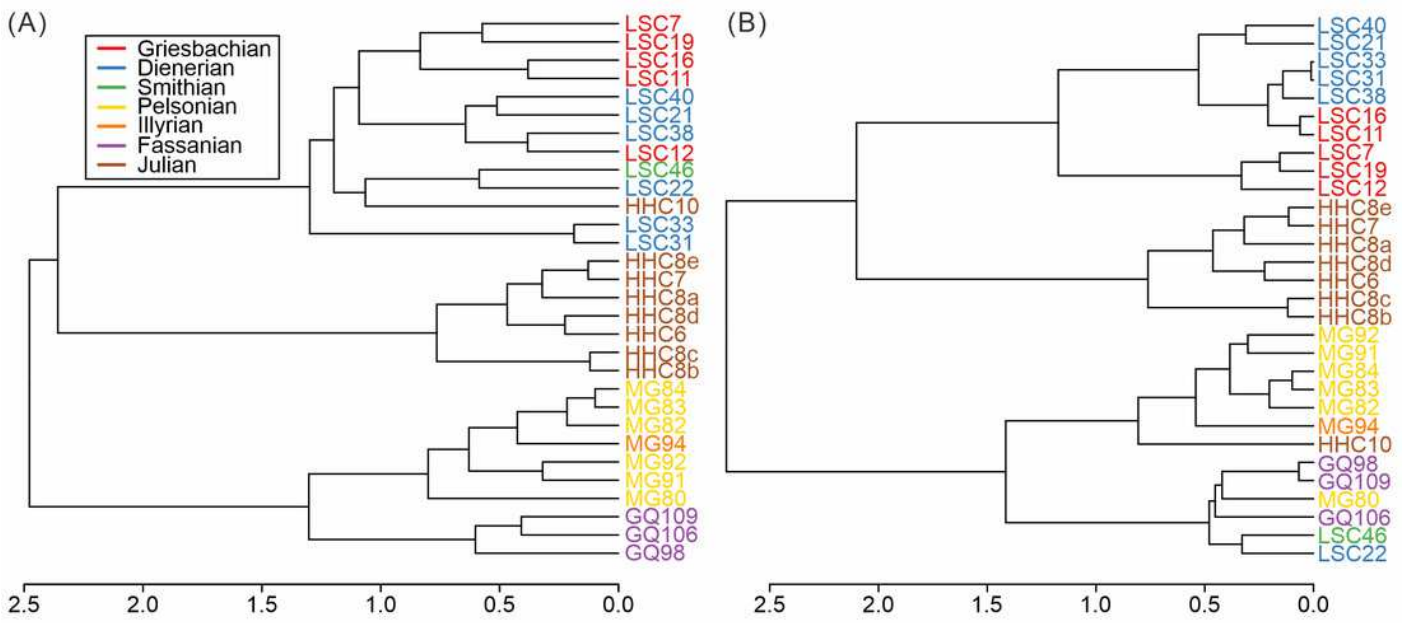


Figure 4

The nMDS ordination of samples from South China based on (A) species and (B) modes of life. The groups were conducted according to the Triassic substages.

1, epifaunal, stationary, cemented, suspension feeders; 2, shallow infaunal, motile, deposit feeders; 3, shallow infaunal, facultatively motile, unattached, suspension feeders; 4, epifaunal, stationary, byssate, suspension feeders; 7, epifaunal, facultatively motile, unattached, suspension feeders; 12, epifaunal, stationary, unattached, suspension feeders; 14, deep infaunal, facultatively motile, suspension feeders; 16, semi-infaunal, stationary, byssate, suspension feeders; and 19, epifaunal, facultatively motile, byssate, suspension feeders. The color and abbreviations are presented in Fig. 3.

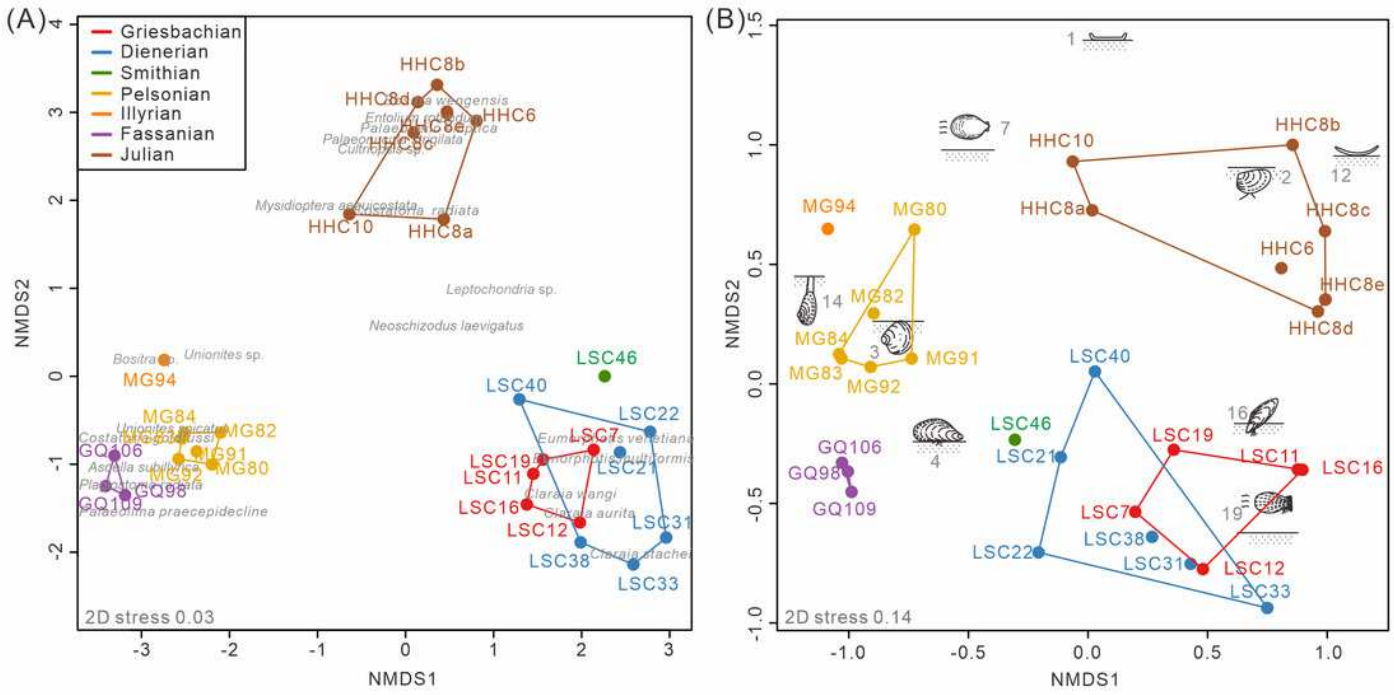


Figure 5

Images of the key species of Triassic bivalves from South China.

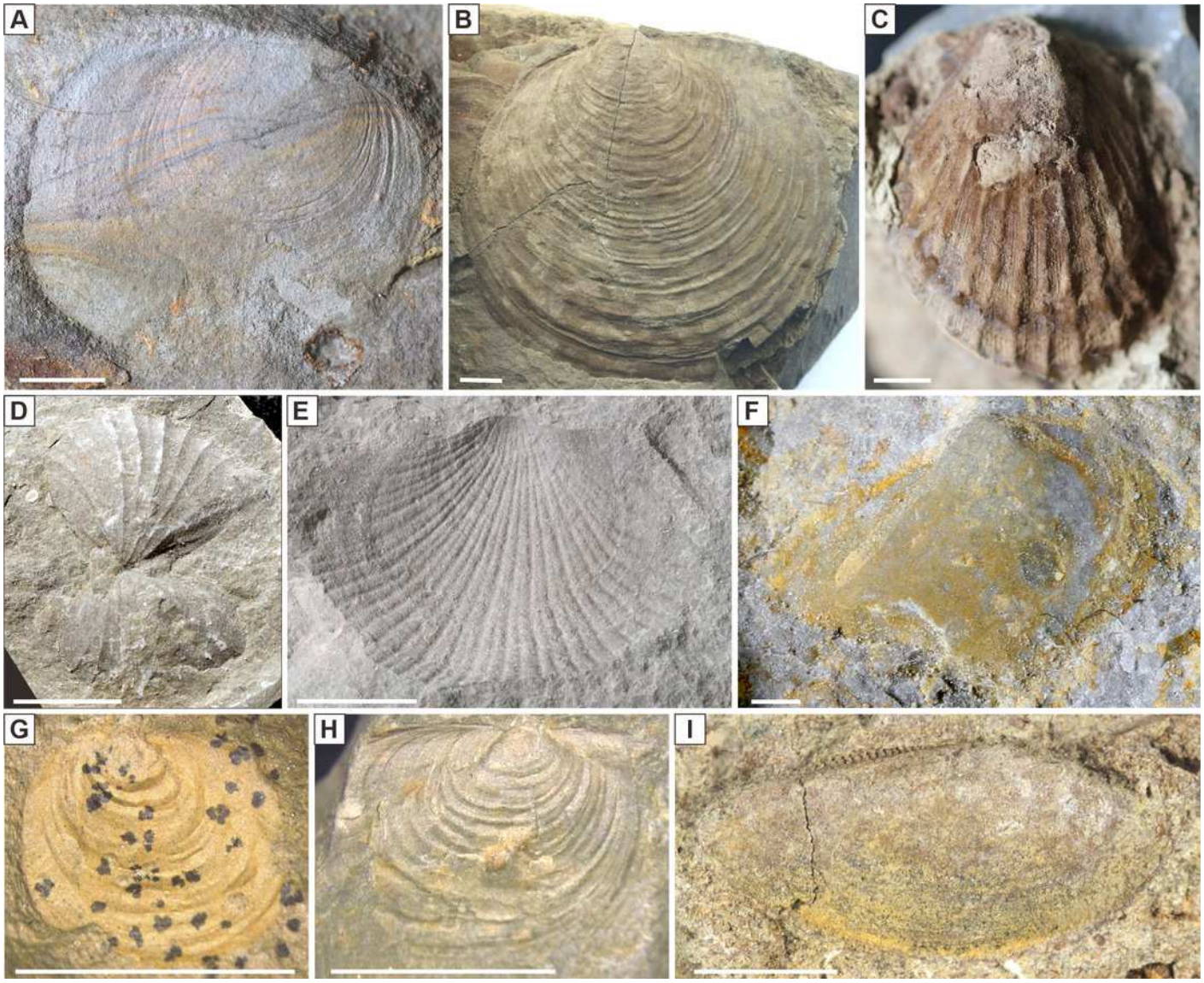


Figure 6

Linear relationship of taxonomic and ecologic diversity metrics in South China. (A) Shannon diversity, (B) species richness and (C) evenness.

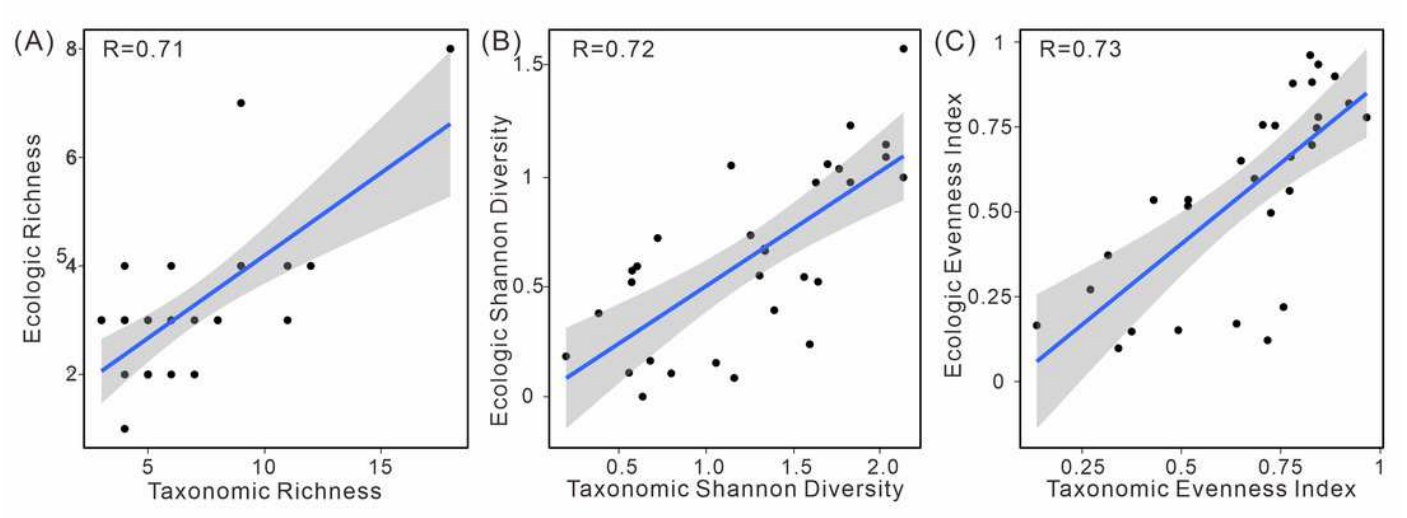


Figure 7

Diversity dynamics of bivalves through the Triassic. (A) Species-level taxonomic and functional diversity in South China. (B) Species-level taxonomic and functional extinction and origination rates in South China. (C) Genus-level taxonomic and functional

Stage abbreviations: Ch or Chg – Changhsingian; In or Ind– Induan; Ole – Olenekian; Ani – Anisian; Lad – Ladinian; Car – Carnian; Nor – Norian; Rha – Rhaetian; He orHet – Hettangian.

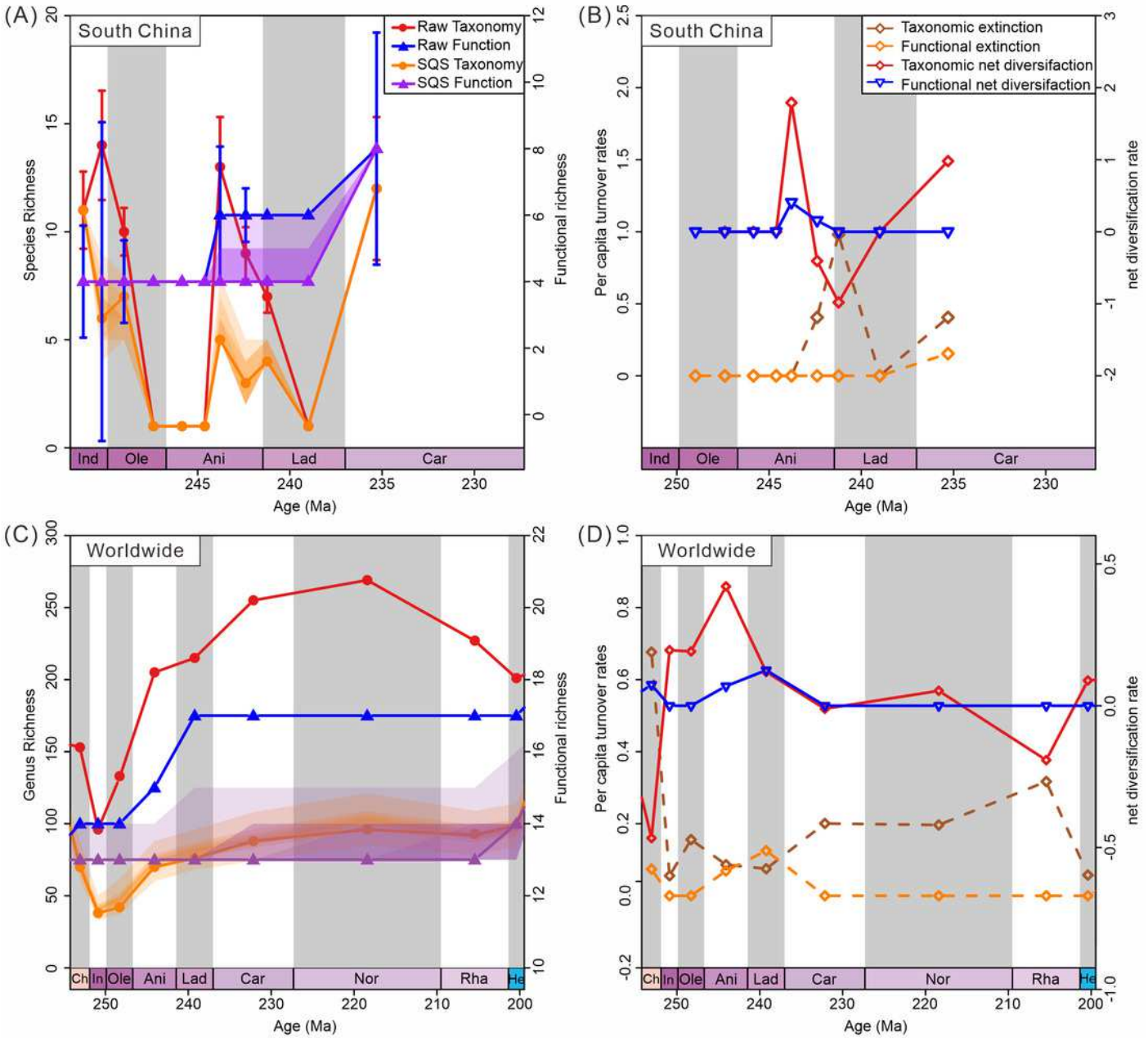
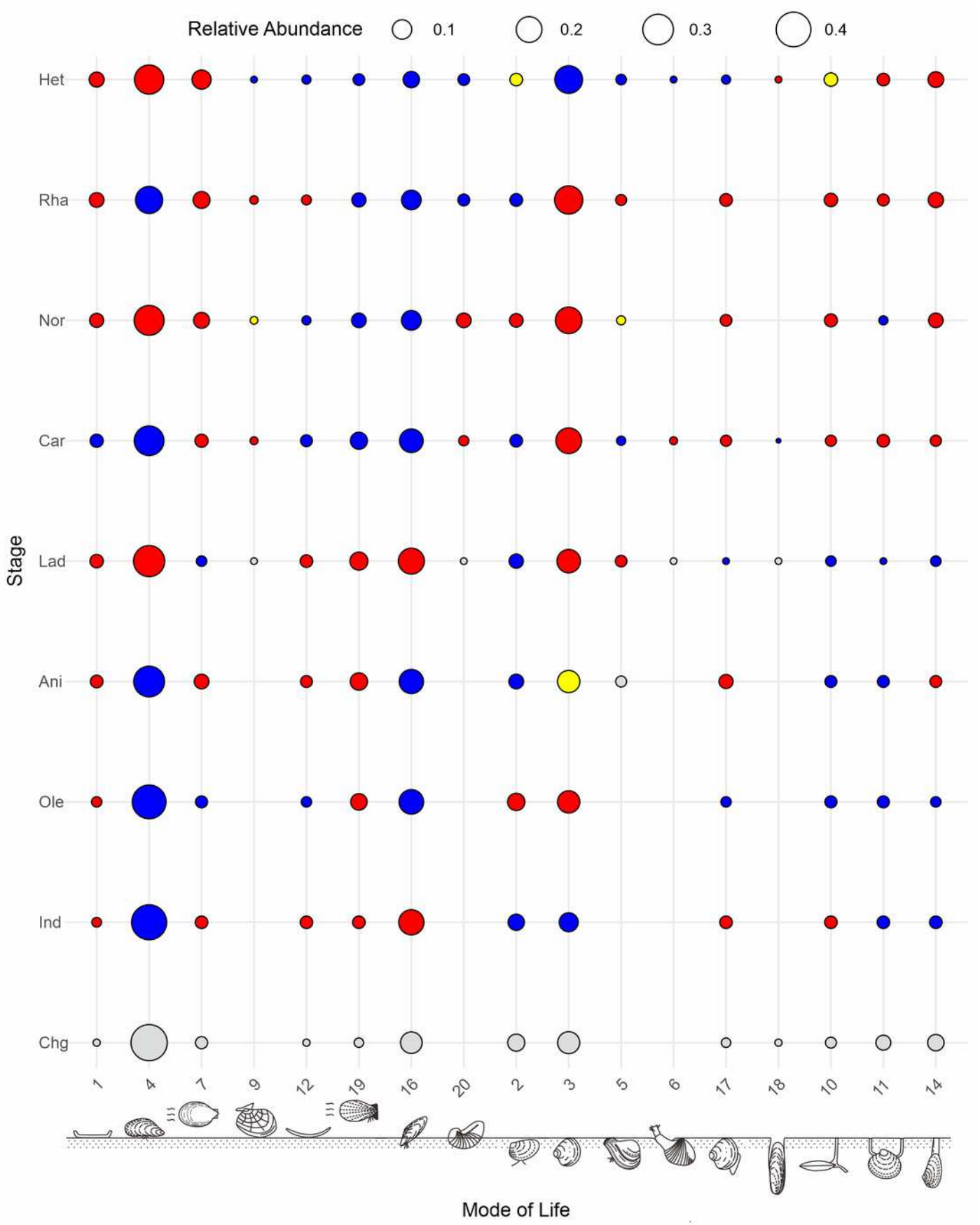

(A)
South China
Raw Taxonomy
Raw Function
SQS Taxonomy
SQS Function
Species Richness
Functional richness
Ind
Ole
Ani
Lad
Car
Age (Ma)
(B)
South China
Taxonomic extinction
Functional extinction
Taxonomic net diversifaction
Functional net diversifaction
Per capita turnover rates
net diversification rate
Age (Ma)
(C)
Worldwide
Genus Richness
Functional richness
Ch
In
Ole
Ani
Lad
Car
Nor
Rha
He
Age (Ma)
(D)
Worldwide
Per capita turnover rates
net diversification rate
Age (Ma)

Figure 8

Relative abundance of genera richness in each mode of life across the studied interval.

Colors indicate changes in proportion of greater than 0.1%: increases (red), decreases (blue) and no change (yellow) from the previous time bin. 1, epifaunal, stationary, cemented, suspension feeders; 2, shallow infaunal, motile, deposit feeders; 3, shallow infaunal, facultatively motile, unattached, suspension feeders; 4, epifaunal, stationary, byssate, suspension feeders; 5, shallow infaunal, facultatively motile, byssate, suspension feeders; 6, shallow infaunal, motile, carnivores; 7, epifaunal, facultatively motile, unattached, suspension feeders; 9, epifaunal, motile, carnivores; 10, deep infaunal, facultatively motile, surface deposit feeders; 11, deep infaunal, facultatively motile, other feeders; 12, epifaunal, stationary, unattached, suspension feeders; 14, deep infaunal, facultatively motile, suspension feeders; 15, shallow infaunal, motile, surface deposit feeders; 16, semiinfaunal, stationary, byssate, suspension feeders; 17, shallow infaunal, motile, suspension feeders; 18, infaunal, stationary, boring, suspension feeders; 19, epifaunal, facultatively motile, byssate, suspension feeders; 20, semiinfaunal, stationary, unattached, suspension feeders; 21, epifaunal, stationary, attached, cemented, other feeders; 22, semiinfaunal, facultatively motile, byssate, suspension feeders The stage abbreviations refer to Fig. 7.


Relative Abundance
0.1
0.2
0.3
0.4
Stage
Het
Rha
Nor
Car
Lad
Ani
Ole
Ind
Chg
1
4
7
9
12
19
16
20
2
3
5
6
17
18
10
11
14
Mode of Life