

Article

Retreat, Resilience, and Reorganization: Decoding the Post-Paleozoic Evolution of Brachiopods

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Abstract

The Paleozoic–Modern Evolutionary Fauna transition is defined by the ecological replacement of brachiopods by bivalves. However, it remains debated whether post-Paleozoic brachiopods experienced a simple, continuous global decline or a complex macroevolutionary reorganization. Previous studies are often limited by ecological mismatches, uncorrected sampling biases, and single taxonomic scales. To resolve this, this study presents a high-resolution analysis of brachiopod evolution from the Triassic to the Quaternary. Using Paleobiology and Geobiodiversity Database records, I applied coverage-based standardization and, for guild-level comparisons, strict ecological filtering, comparing brachiopods only to ecologically equivalent bivalves and echinoderms. Results reveal three major patterns. First, regional and global diversity decoupled: global diversity showed Mesozoic diversification pulses, whereas the Chinese record exhibited a sustained post-Triassic collapse, showing global aggregates mask regional extirpations. Second, brachiopods displayed strong hierarchical resilience: environmental crises drastically pruned species richness (causing generic monotypy), yet family-level diversity remained remarkably stable. Third, brachiopods underwent a macroecological reorganization, retreating from carbonate reefs and shifting poleward to establish their modern anti-tropical distribution. Ultimately, the post-Paleozoic history of brachiopods is not a passive decline, but a multi-dimensional reorganization driven by regional habitat loss, geographic redistribution, and deep-lineage survival.

Keywords: Brachiopoda; macroevolution; Paleobiogeography; diversity dynamics; Mesozoic–Cenozoic; ecological filtering; sample coverage; PBDB; GBDB

1. Introduction

The Phanerozoic history of marine invertebrates is punctuated by major shifts in taxonomic and ecological dominance. Among the most iconic of these macroevolutionary transitions is the transition from the Paleozoic Evolutionary Fauna to the Modern Evolutionary Fauna, epitomized by the ecological replacement of brachiopods by bivalves [1–5]. Brachiopods dominated benthic suspension-feeding communities throughout much of the Paleozoic and persisted through all five major Phanerozoic mass extinctions [6–10]. However, their post-Paleozoic trajectory stands in stark contrast: in modern oceans, they are relegated to ~400 species occupying restricted, often marginal, ecological niches [11]. Explaining how and why this transition occurred remains a central question in paleobiology. Specifically, a critical theoretical dichotomy remains unresolved: Did brachiopods undergo a simple, monotonic global decline during the Mesozoic–Cenozoic, or is their history better characterized as a complex, long-term macroevolutionary reorganization?



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While numerous hypotheses have been proposed—including competitive displacement (e.g., Thayer [12,13], though recently challenged by macroevolutionary modelling [14]), escalating predation during the Mesozoic Marine Revolution [10,15–17], and long-term environmental perturbations [10,18]—current empirical evidence remains insufficient to fully resolve this transition.

The first major limitation is ecological confounding. Throughout their Phanerozoic history, brachiopods have remained overwhelmingly epifaunal suspension feeders, whereas post-Paleozoic bivalves diversified extensively into infaunal, motile, and even non-suspension-feeding niches [19–21]. Consequently, whole-clade comparisons are ecologically asymmetrical. Meaningful tests of evolutionary replacement require restricting comparisons to a shared ecological guild [12,14]. This necessity is underscored by the Early Triassic ecological turnover, where bivalves rapidly radiated into niches vacated by brachiopods [22].

A second limitation is spatial heterogeneity and sampling artifacts. Global diversity syntheses are frequently distorted by uneven rock outcrop area, inconsistent taxonomy, and geographic biases (e.g., the “Pull of the Recent”) [23–26]. Moreover, global aggregates often obscure distinct regional signals: high-resolution records from China, for example, may exhibit evolutionary trajectories that differ markedly from the global pattern. Without rigorous coverage-based standardization, it remains difficult to determine whether regional diversity collapses are genuine biological signals or sampling artifacts.

Finally, prior studies often overrely on a single taxonomic scale. Most macroevolutionary studies evaluate brachiopod history using genus- or family-level richness curves. However, higher taxa may exhibit considerable evolutionary resilience, while species-level dynamics can be extremely volatile [27,28]. Diversity curves alone are therefore insufficient to capture the severity of environmental filtering, such as when surviving genera are stripped of their species to near-monotypy. To overcome these limitations and directly address the “decline versus reorganization” debate, this study presents a high-resolution, integrated macroevolutionary analysis of Brachiopoda spanning the Triassic to the Quaternary. Occurrence data from the global Paleobiology Database (PBDB) [29] and the regional Geobiodiversity Database (GBDB) [30] were cross-calibrated to reconstruct diversity trajectories at both standard geological stages and 10-Myr intervals. To mitigate sampling biases, stringent coverage-based rarefaction and extrapolation methodologies (CR/E [31,32]) were implemented. Crucially, a strict ecological standardization protocol was applied to extract an ecologically equivalent guild of comparative clades (Bivalvia and Echinodermata) to ensure functional parity.

Furthermore, because taxonomic diversity alone provides an incomplete view of macroevolution—where profound ecological reorganizations can often occur without corresponding changes in global richness [33]—this study incorporates explicit spatial and environmental dimensions to complement the temporal diversity trajectories [34,35]. Using this integrated framework, three overarching hypotheses are tested:

H1 (Spatial Decoupling). *Regional diversity trajectories (e.g., the Chinese fossil record) can decouple significantly from global patterns, demonstrating that major regional collapses do not inherently signify global extinctions, and that global aggregates may mask substantial spatial heterogeneity.*

H2 (Hierarchical Resilience). *Macroevolutionary volatility is highly scale-dependent. Diversity fluctuations are extreme at the species level but become progressively dampened at higher taxonomic ranks (families), reflecting the deep-lineage resilience of higher clades under severe environmental pressure (e.g., resulting in generic monotypy).*

H3 (Spatiotemporal Reorganization). *The post-Paleozoic trajectory of brachiopods was not a passive decline, but rather a systematic macroecological reorganization. This reorganization was characterized by ecological niche displacements (e.g., retreating from carbonate reefs) and a major paleolatitudinal migration toward an anti-tropical, temperate-centered modern geographic distribution—a long-term shift consistent with documented changes in their Phanerozoic latitudinal diversity gradient [36,37].*

2. Materials and Methods

2.1. Data Acquisition and Compilation

Fossil occurrence data for Brachiopoda, Bivalvia, and Echinodermata spanning the Mesozoic and Cenozoic (Triassic–Quaternary) were compiled from PBDB [29] and the GBDB [30].

Global occurrences were downloaded from the PBDB API using a paginated protocol, with separate queries for each clade and geological period. Marine fossil records spanning the last 252 million years were retrieved from the GBDB as pre-compiled CSV files for each clade (accessed 5 June 2026).

The raw datasets were merged and filtered independently. All PBDB downloads were combined into a single occurrence matrix, while GBDB records were restricted to the target geological periods, and molluscan records were constrained to Bivalvia. The cleaned datasets were exported as separate occurrence matrices for downstream processing.

2.2. Taxonomic Standardization and Synonymy Resolution

For Brachiopoda, records containing open nomenclature (e.g., *cf.*, *aff.*, *indet.*, *sp.*, and questioned assignments) were removed. An automated standardization protocol was then applied using a fuzzy matching algorithm based on the Jaro–Winkler distance metric (threshold = 0.1 [38]) to resolve alternative spellings and unrevised synonymies. Synonymous pairs and typographical variants were mapped to their valid generic names as defined by the PBDB taxonomic hierarchy. This standardization was propagated across both the PBDB and GBDB datasets. The same cleaning and standardization steps were applied to Bivalvia and Echinodermata.

2.3. Stratigraphic Alignment and Spatiotemporal Deduplication

After merging PBDB and GBDB records for Brachiopoda into a unified occurrence table, temporal resolution was standardized by calculating the midpoint age for each record based on its maximum and minimum estimated ages. These midpoint ages were subsequently assigned to strict international geological stages using the chronostratigraphic framework provided by the R package *divDyn* (version 0.8.3) [39].

To eliminate redundant records across the two databases, occurrences were flagged as duplicates when they shared the same accepted genus, standardized stage, and modern geographic coordinates rounded to 0.1° resolution. PBDB records were prioritized in cases of overlap, and redundant GBDB entries were removed. The same deduplication was applied to Bivalvia and Echinodermata after merging.

Data processing statistics are provided in Table S1. After deduplication and removal of non-marine records, the ecologically unfiltered brachiopod dataset comprised 27,883 occurrences (961 genera, 3425 species, 145 families; PBDB: 27,408, GBDB: 475). Following ecological filtering to epifaunal stationary suspension feeders, the guild-level comparison dataset retained 27,209 occurrences (902 genera, 3375 species, 145 families). The ecologically unfiltered dataset was used for Sections 3.1 and 3.3–3.6; the ecologically filtered subset was used only for comparisons with bivalves and echinoderms (Section 3.2).

2.4. Ecological Standardization and Comparative Clade Selection

To ensure that diversity comparisons reflected genuine evolutionary patterns rather than inconsistencies in ecological terminology, ecological attributes were harmonized across the PBDB and GBDB datasets, broadly following the theoretical ecospace framework for marine benthos [33]. Dietary categories were harmonized by converting “Filter/suspension” to “suspension feeder”. For motility, non-motile and stationary variants (“Non-motile/attached”, “Non-motile/unattached”, “stationary”, “stationary, attached”, and “stationary, attached, epibiont”) were merged into “stationary”. Life habit categories were standardized by grouping epifaunal variants (“Surficial”, “Erect”, “epifaunal”, “low-level epifaunal”, and “epifaunal, gregarious”) as “epifaunal”, and shallow/semi-infaunal categories as “infaunal”. Remaining categories were retained unchanged.

For Brachiopoda, occurrences with a suspension-feeding diet, stationary motility, and epifaunal life habit were retained. Records with missing ecological data were retained unless explicitly assigned to non-target habits. Only taxa with confirmed infaunal life habits were removed.

For Bivalvia and Echinodermata, an ecologically equivalent subset was extracted using genus-level imputation. All genera exhibiting the target ecological traits (suspension feeder, stationary, epifaunal) in the combined PBDB–GBDB dataset were identified, and all occurrences assigned to these genera were retained, including records lacking ecological annotations. This approach balances data completeness against biases from incomplete metadata. It assumes ecological conservatism at the genus level, which is reasonable for this guild [40].

2.5. Temporal Binning and Data Partitioning

Occurrences were analyzed using two temporal binning strategies: standard international geological stages and equal-duration 10-Myr intervals. For the latter, occurrences were binned by the midpoint ages of their stratigraphic ranges, spanning a 260-Myr window from the present to the base of the Triassic. Within each bin, occurrences were transformed into genus-level occurrence matrices [25,26]. To investigate regional signals and test Hypothesis H1, the dataset was partitioned into three subsets: a global dataset, a global dataset excluding Chinese records, and a regional dataset restricted to China.

2.6. Coverage-Based Diversity Standardization

To mitigate biases from heterogeneous sampling and the “Pull of the Recent” [24], coverage-based rarefaction and extrapolation (CR/E [31,32]) was applied using the R package iNEXT (version 3.0.2) [41]. This method standardizes diversity estimates by sample completeness (Sample Coverage, SC), which represents the proportion of the assemblage represented by sampled genera.

Temporal bins exhibiting poor sampling—defined as an SC below 0.6 in all regional subsets (global, global excluding China, and China)—were excluded from both raw and standardized analyses. Informal stages (e.g., “Early Jurassic”, “Middle Triassic”) were additionally omitted. For the retained temporal bins, standardized genus richness (Hill number of order $q = 0$ [31,42]) was calculated at two distinct thresholds to verify the robustness of diversity trajectories:

1. Fixed Coverage ($C = 0.95$): Representing near-complete sampling via extrapolation.
2. Minimal Shared Coverage: The lowest SC value observed among all valid bins, ensuring conservative interpolation across comparative datasets (results presented in Figures S2 and S3).

For visualization, a protocol for connecting temporal data points was implemented: valid data points were plotted as distinct markers, and where temporal continuity was

interrupted, gaps were bridged by dotted lines. While 95% confidence intervals were generated using bootstrap resampling (30 iterations) to verify the statistical robustness of diversity shifts, they were omitted from the main temporal plots to maintain visual clarity.

2.7. Taxonomic Scale Dependence of Diversity Dynamics

Hypothesis H2 was evaluated using raw richness for species, genera, and families in each 10-Myr bin using the global dataset. Species were identified from fully qualified *accepted_name* entries; records lacking a species epithet were excluded. Genus- and family-level richness were derived from the respective taxonomic fields. Richness curves were superimposed to visualize variation across hierarchical levels, and the species-to-genus ratio was computed for each bin.

2.8. Ecological Niche and Paleolatitudinal Distribution

To complement the diversity curves, shifts were examined in ecological niche occupation and paleolatitudinal distribution for Brachiopoda. Occurrences were assigned to geological periods by their midpoint age. The environment field was classified into three mutually exclusive categories using a keyword-based scheme: Deep Marine (e.g., slope, basin, abyssal, bathyal), Carbonate/Reef (e.g., reef, shoal, lagoonal, perireef), and Shallow/Open Shelf (e.g., shelf, ramp, shore, coastal). Records that could not be assigned to these categories were excluded. Niche proportions were calculated and visualized as stacked bar charts. Paleolatitudinal data, derived from modern coordinates using the GPlates rotation model [43], were used to generate density ridge plots with median indicators for each geological period. These analyses enabled the assessment of latitudinal range shifts and biogeographic reorganization accompanying diversity changes.

2.9. Paleogeographic Mapping

To visualize the spatial distribution of brachiopod occurrences through time, paleogeographic maps were constructed for five key time slices representing the Triassic (230 Ma), Jurassic (170 Ma), Cretaceous (100 Ma), Paleogene (50 Ma), and Neogene (15 Ma). Paleocoastlines were obtained from the PALEOMAP Paleocoastlines v7 dataset [44], which provides global coastline reconstructions at 5 Myr intervals based on the paleogeographic models of Scotese [45]. For each time slice, the coastline shapefile closest to the target age was selected. All brachiopod occurrences assigned to the corresponding geological period (i.e., all Triassic, Jurassic, etc., records) were plotted onto the paleogeographic base map using their paleolatitude and paleolongitude coordinates, which had been reconstructed from modern coordinates using the GPlates rotation model of Müller et al. [43]. This approach allows the full temporal span of each period to be represented, while the coastline provides a representative paleogeographic framework for the interval.

3. Results

3.1. Global Stage-Level Brachiopod Diversity

Raw and coverage-standardized richness followed broadly similar macroevolutionary trajectories throughout the post-Permian interval (Figure 1, Tables S2 and S3). Following the end-Permian mass extinction, richness increased rapidly during the Early and Middle Triassic, reaching peak values in the Late Triassic (~235–225 Ma). Following the Late Triassic peak, diversity declined through the Early Jurassic but experienced a notable resurgence during the mid-Cretaceous, where genus richness reached levels comparable to Jurassic values in standardized curves. After this Cretaceous peak, richness declined gradually into the Cenozoic. At the species level, diversity followed a broadly consistent but far more volatile trajectory; while recovering strongly in the Triassic, species richness experi-

enced its most extreme diversification pulse during the Middle–Late Jurassic (160–170 Ma), spiking to over 1000 standardized species before suffering a severe, long-term collapse (Tables S2 and S3). While standardized estimates generally yielded higher values than raw richness due to corrections for sampling incompleteness, the temporal patterns remained robust across both 10-Myr bins and geological stages (Figure S1).

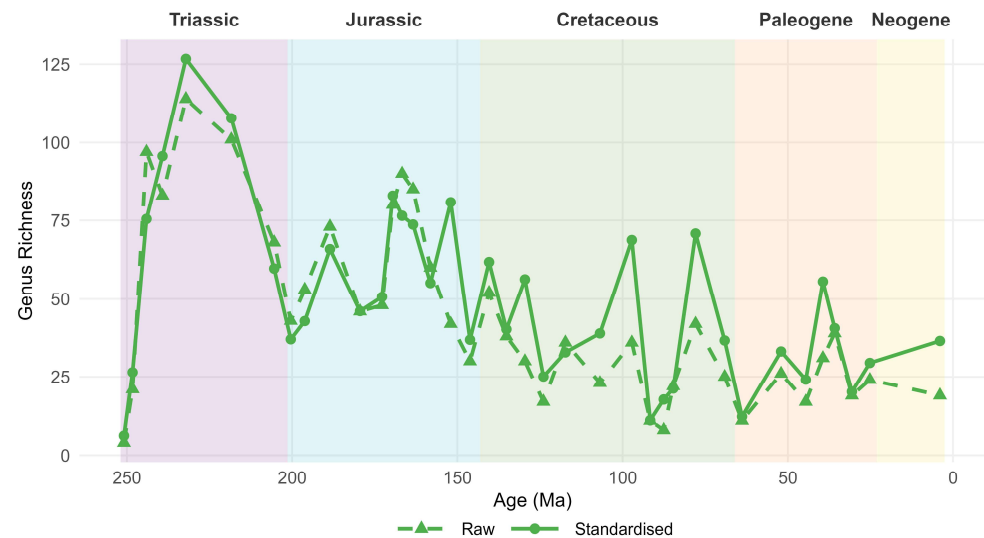


Figure 1. Global stage-level genus richness of the unfiltered brachiopod dataset from the Triassic to the Neogene. The plot illustrates the macroevolutionary diversity trajectory of Brachiopoda based on unified occurrence data from the Paleobiology Database (PBDB) and Geobiodiversity Database (GBDB). Coverage-standardized genus richness (Hill number order $q = 0$, extrapolated to a fixed coverage of $C = 0.95$) is denoted by the solid green line with triangular markers, while raw genus richness is represented by the dashed green line with circular markers. Data are binned by standard international geological stages, with background shading indicating major geological periods.

3.2. Regional Stage-Level Genus Richness Trajectories

Coverage-standardized stage-level genus richness ($q = 0$, $C = 0.95$) of the ecologically filtered dataset revealed clear regional differences in brachiopod diversity between China and the global dataset excluding China (Figure 2). Both datasets exhibited a rapid increase in richness following the end-Permian mass extinction, with diversity recovering throughout the Early and Middle Triassic. However, their diversity trajectories diverged markedly after the Late Triassic. These regional divergence patterns remain highly robust when standardized to the minimum shared sample coverage across all valid stages, confirming they are not artifacts of the chosen extrapolation threshold (Figures S2 and S3).

In the global dataset excluding China, brachiopod richness remained comparatively high and dynamic throughout much of the Mesozoic. Following the Late Triassic diversification, a second major pulse occurred during the Middle Jurassic (~170–160 Ma), followed by fluctuations through the Late Jurassic and Cretaceous before declining into the Cenozoic. In contrast, the Chinese record showed a pronounced reduction near the Triassic–Jurassic boundary. After this decline, richness remained low throughout the Jurassic, Cretaceous, and Cenozoic, rarely exceeding 10 genera, whereas the global dataset maintained substantially higher richness with repeated diversification pulses.

In contrast, ecologically filtered bivalves displayed a different pattern (Figure 2). Global bivalve richness was comparatively stable with repeated fluctuations through the Jurassic and Cretaceous, including a prominent Late Cretaceous diversification pulse. Chinese bivalves, rather than declining at the Triassic–Jurassic boundary, increased to a

Late Jurassic peak (~150 Ma) before declining near the Jurassic–Cretaceous transition and remaining low thereafter.

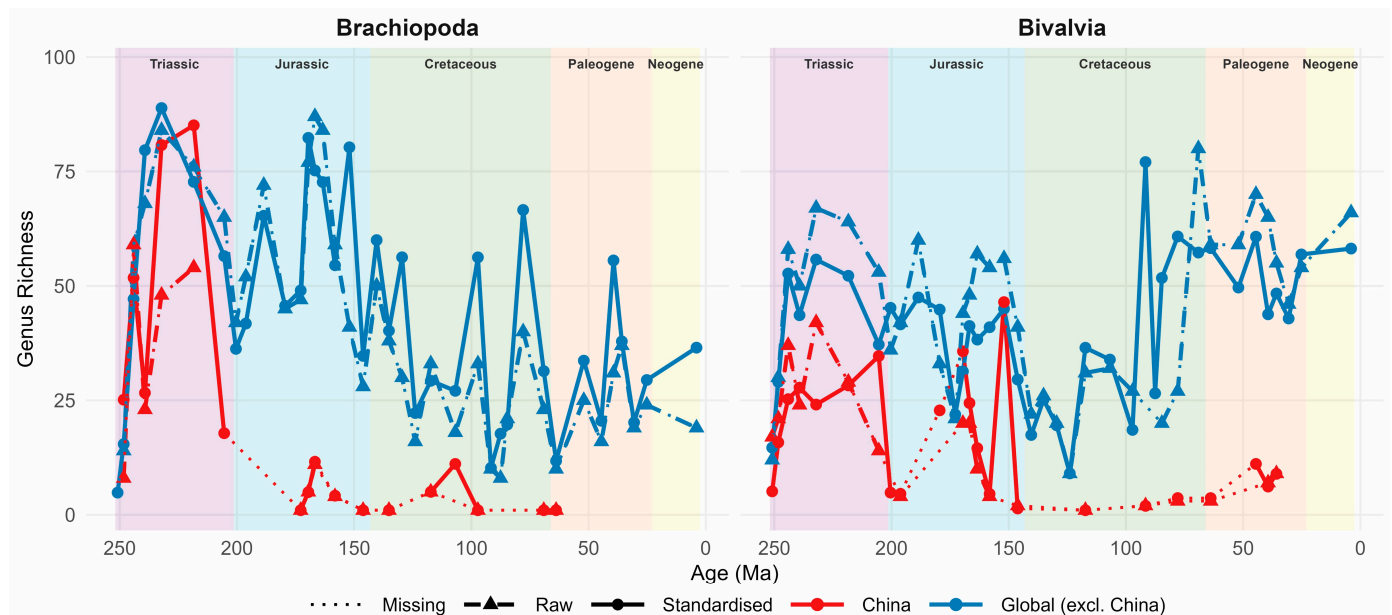


Figure 2. Regional stage-level genus richness trajectories for ecologically filtered Brachiopoda and Bivalvia. The panels contrast the macroevolutionary dynamics of Brachiopoda (**left**) and Bivalvia (**right**) restricted to an ecologically equivalent guild (epifaunal, stationary suspension feeders). Red curves represent the regional Chinese dataset, while blue curves denote the global dataset excluding China. Coverage-standardized genus richness (Hill number order $q = 0$, extrapolated to a fixed coverage of $C = 0.95$) is shown as solid lines with circular markers, plotted alongside raw genus richness (dashed lines with triangular markers). Dotted lines bridge temporal gaps where intervening stages were excluded from the analysis due to insufficient sample coverage ($SC < 0.6$). Background shading corresponds to major geological periods.

Analyses based on 10-Myr time bins produced diversity trajectories broadly consistent with stage-level results, indicating robustness to temporal binning (Figure S4). Ecologically filtered echinoderms exhibited similar regional trends but were represented by substantially fewer occurrences, resulting in reduced temporal continuity and greater uncertainty (Figure S5).

3.3. Taxonomic Scale Dependence of Brachiopod Macroevolution

To test whether macroevolutionary patterns were sensitive to taxonomic rank (Hypothesis H2), raw richness trajectories at the species, genus, and family levels were compared across 10-Myr bins (Figure 3).

The results demonstrate significant variance in volatility across taxonomic ranks. Species-level richness exhibited extreme fluctuations, ranging from a minimum of 62 species (40–50 Ma) to a peak of over 800 species during the Middle–Late Jurassic (160–170 Ma). Generic richness displayed a substantially dampened trajectory (32 to 204 genera), while family-level richness remained stable throughout the 260-Myr interval, fluctuating only from 18 to 56 families.

The species-to-genus ratio provides additional evidence for this hierarchical pattern (Figure 3, bottom panel). The ratio reached a maximum of 4.5 during the Middle–Late Jurassic (160–170 Ma), coinciding with the species richness peak. During the Late Cretaceous decline (70–90 Ma), the ratio collapsed to approximately 1.06. Values approaching 1.0 indicate severe generic monotypy, where nearly every surviving genus is represented by a single species.

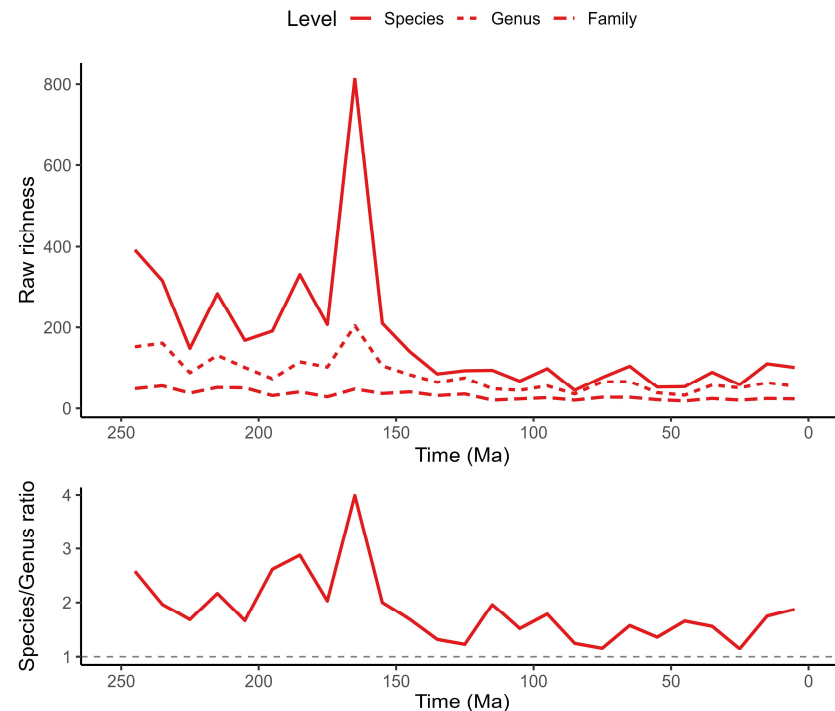


Figure 3. Taxonomic scale dependence of global brachiopod macroevolution (Triassic–Quaternary). The upper panel compares raw richness trajectories at the species (solid line), genus (dashed line), and family (dot-dash line) levels, calculated within equal-duration 10-Myr temporal bins. The lower panel displays the species-to-genus ratio across the same interval. The horizontal dashed line at 1.0 represents a state of absolute generic monotypy, illustrating the severe macroevolutionary bottleneck observed during the Late Cretaceous.

This family-level stability, however, was accompanied by substantial taxonomic turnover. Throughout the Mesozoic, dominant families included Rhynchonellidae, Zeilleriidae, and several others that varied by period (Table S4). Several Paleozoic-holdover groups (e.g., Spiriferinidae, Athyrididae) disappeared by the Jurassic–Cretaceous boundary. By the Paleogene and Neogene, the fauna was dominated by Terebratulidae, Cancellothyrididae, Terebratellidae, and Megathyrididae; notably, many formerly dominant Mesozoic families (including Tetrahyndiidae and Cyclothyrididae) are absent from the Cenozoic record. At the genus level, the most abundant Neogene survivors are *Terebratula* (140 occurrences), *Argyrotheca* (95), and *Terebratulina* (72), followed by *Notosaria*, *Magasella*, *Discinisca*, *Megerlia*, and others (Table S4). This phylogenetic winnowing indicates that deep-lineage resilience was concentrated within a limited number of terebratulide and cancellothyridid clades.

Among the five most abundant post-Paleozoic families, all had some occurrence in deep-marine environments (Table S5): Lobothyrididae (16.1% of records), Zeilleriidae (11.6%), Tetrahyndiidae (9.5%), Rhynchonellidae (3.9%), and Cyclothyrididae (3.2%). The consistent presence of these families in slope and basinal settings indicates that many dominant clades possessed broad depth tolerances, which may have buffered them against shallow-water perturbations and contributed to the observed family-level resilience.

3.4. Ecological Niche Displacement

The proportional representation of brachiopod ecological niches underwent substantial compositional shifts from the Triassic through the Neogene (Figure 4). Throughout the Mesozoic (Triassic–Cretaceous), brachiopods primarily occupied Shallow/Open Shelf environments, consistently accounting for over half of all occurrences. Within this interval, Carbonate/Reef settings maintained a stable and substantial secondary presence, consti-

tuting roughly 30% to 40% of the assemblages. Deep Marine habitats represented only a minor fraction, peaking transiently at approximately 10% during the Jurassic.

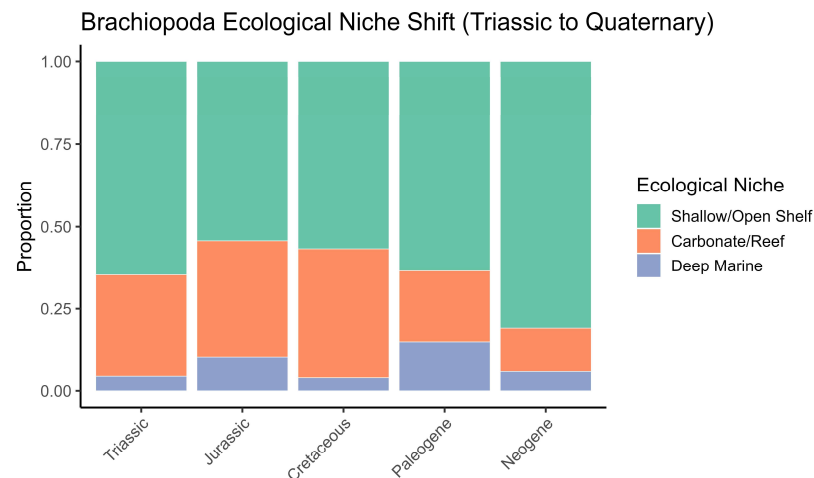


Figure 4. Proportional shifts in brachiopod ecological niche occupation by geological period. The stacked bar charts illustrate the relative frequency of brachiopod occurrences across three mutually exclusive environmental categories: Shallow/Open Shelf (green), Carbonate/Reef (orange), and Deep Marine (purple). The timeline demonstrates the stable dominance of Shallow/Open Shelf habitats, the significant post-Mesozoic contraction of Carbonate/Reef occupancy, and the transient expansion into Deep Marine settings during the Paleogene.

Beginning in the Paleogene, Carbonate/Reef occupation declined steadily, falling to ~10% by the Neogene. Shallow/Open Shelf habitats expanded to dominate the Neogene landscape (~80% of occurrences). Deep Marine environments reached their maximum proportional representation during the Paleogene (~15%) before decreasing slightly in the Neogene.

3.5. Spatiotemporal Shifts in Paleolatitudinal Distribution

The paleolatitudinal distribution of brachiopods revealed a major geographic reorganization from the Triassic to the Neogene (Figure 5). During the Triassic, occurrences were broadly distributed, exhibiting a multimodal pattern with a primary density peak in the low northern latitudes (~15° N). Throughout the Jurassic and Cretaceous, this range contracted significantly, becoming predominantly concentrated in the Northern Hemisphere; the primary density core shifted poleward from ~30° N to ~40° N, while Southern Hemisphere representation diminished.

The Cenozoic marked the emergence of a distinct anti-tropical (bimodal) distribution. In the Paleogene, the northern mid-latitude dominance (~40° N) persisted, and a secondary density peak appeared in the southern mid-latitudes (40° S–50° S). By the Neogene, this bimodal pattern was clearly established, with near-complete absence from equatorial regions and highest densities in temperate-to-high latitudes of both hemispheres.

3.6. Paleogeographic Distribution

Paleogeographic maps confirm the spatial reorganization of brachiopod occurrences (Figure 6). Triassic records were broadly distributed across the Tethyan realm, but through the Jurassic and Cretaceous the distribution contracted poleward and became concentrated in Northern Hemisphere mid-latitudes. By the Paleogene, a bimodal pattern emerged, with northern and southern temperate clusters separated by an equatorial gap. These spatial trends are consistent with the latitudinal shifts quantified in Figure 5.

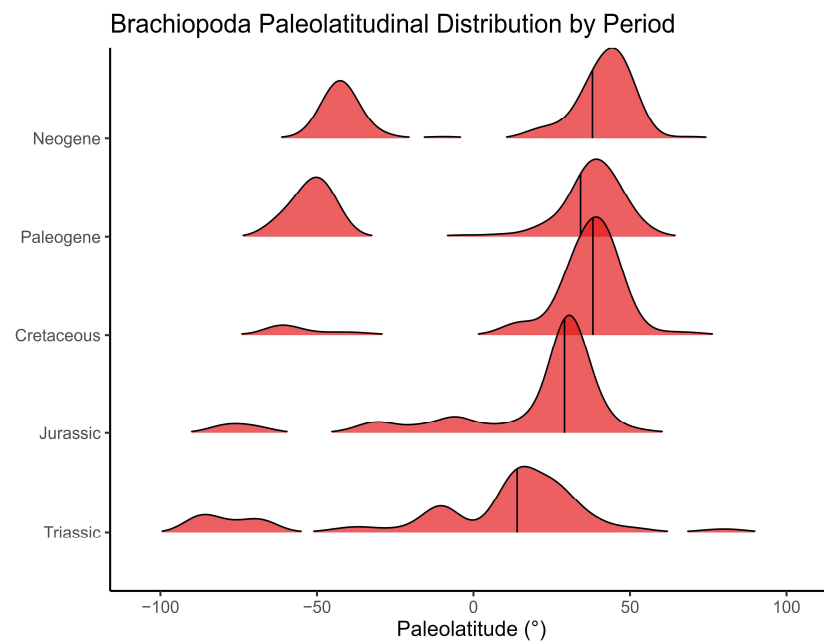


Figure 5. Spatiotemporal shifts in the paleolatitudinal distribution of brachiopods. The density ridge plots visualize the latitudinal reorganization of brachiopod occurrences from the Triassic to the Neogene. Paleolatitudes were reconstructed from modern coordinates utilizing the GPlates rotation model. Vertical black lines within the distributions indicate the primary density peaks for each interval, highlighting the Mesozoic poleward contraction within the Northern Hemisphere and the definitive emergence of a bimodal, anti-tropical distribution by the Cenozoic.

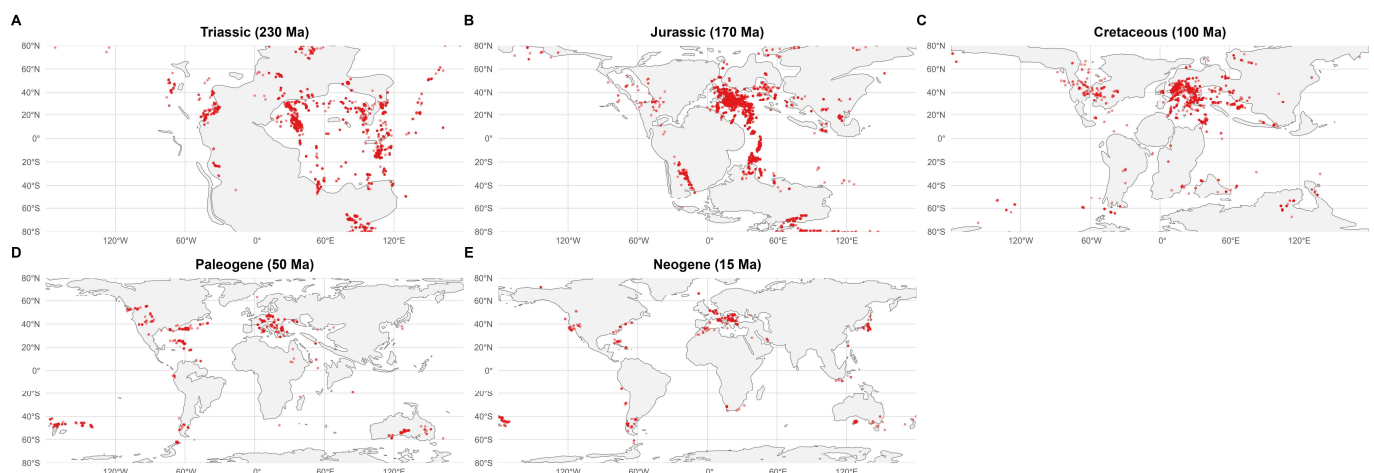


Figure 6. Paleogeographic distribution of brachiopod occurrences from the Triassic to the Neogene. Red points represent all brachiopod fossil occurrences assigned to each geological period, plotted on representative paleocoastline reconstructions for (A) Triassic (230 Ma), (B) Jurassic (170 Ma), (C) Cretaceous (100 Ma), (D) Paleogene (50 Ma), and (E) Neogene (15 Ma). Coastlines are from the PALEOMAP Paleocoastlines v7 dataset [44]. Darker shades result from overlapping points and indicate higher sampling density.

4. Discussion

The ecological transition from the Paleozoic to the Modern Evolutionary Fauna is frequently framed as a straightforward, competitive replacement of brachiopods by bivalves [46,47]. However, coverage-standardized and ecologically filtered estimates reveal a more complex trajectory. The post-Paleozoic history of Brachiopoda is characterized by dynamic macroevolutionary reorganization, spatial heterogeneity, hierarchical resilience, and a retreat into environmental refugia. This reframing aligns with evidence that macroevolu-

tionary patterns often diverge from simple competitive narratives and emphasize regional context and environmental drivers [14,48].

4.1. Spatial Decoupling: Regional Heterogeneity in Diversity Trajectories (H1)

A key finding of this study is the divergence between regional and global brachiopod diversity trajectories, supporting Hypothesis H1. Global aggregates suggest brachiopods maintained a diversification trajectory into the Late Cretaceous, with species-level radiations in the Jurassic, whereas the Chinese record shows a sustained diversity reduction after the Triassic. This spatial decoupling demonstrates that global diversity curves can mask substantial regional extirpations [49,50]. In China, post-Triassic brachiopod decline likely reflects regional habitat loss and tectonic reorganization. The Indosinian Orogeny uplifted the South China block, markedly reducing shallow carbonate platforms and habitats suitable for brachiopods [51,52]. This tectonic disruption was compounded by global Triassic–Jurassic boundary perturbations, including CAMP volcanism, oceanic anoxia, and carbonate platform stress [53–55]. These regional and global factors may have jointly suppressed brachiopod recovery, although disentangling their relative contributions requires additional stratigraphic and geochemical evidence.

The ecologically filtered bivalve data support this interpretation. Chinese bivalves did not decline synchronously with brachiopods at the Triassic–Jurassic boundary; instead, they reached a Late Jurassic peak before declining near the Jurassic–Cretaceous transition. This lagged response suggests that the ecological transition in China was not a single competitive displacement event, but a protracted, stepwise turnover. Once regional benthic communities were disrupted, ecological priority effects and persistent environmental barriers likely prevented brachiopod recolonization, even while the clade persisted globally [56,57]. Thus, what is often perceived as a global decline is better interpreted as a mosaic of asynchronous regional extirpations shaped by local drivers [58].

The mid-Cretaceous genus richness peak (Section 3.1) coincides with a major sea-level highstand that expanded epeiric habitats favorable for brachiopods [59,60] and fueled diversification within brachiopods (e.g., Sellithyrididae, Cancellothyrididae, Cyclothyrididae; Table S4). Although elevated sea level may have enhanced sampling, the peak persists after coverage-standardization, confirming a genuine macroevolutionary pulse. This Cretaceous diversification represents a key phase of reorganization, temporarily offsetting extinction pressures before the Cenozoic contraction.

4.2. Hierarchical Resilience and the Architecture of Survival (H2)

The hierarchical analysis provides insight into how brachiopods endured prolonged macroevolutionary crises (Hypothesis H2). Species richness fluctuated dramatically—from a peak of over 900 species in the Middle–Late Jurassic to a minimum of 62 species in the Eocene—while family richness remained constrained between 18 and 55 families across the entire 260-Myr interval. This decoupling between species-level volatility and family-level stability [61–63] indicates that the fundamental structural diversity of Brachiopoda was resilient. Extinction events and environmental perturbations acted primarily as filters that pruned diversity at the species level, rather than eliminating entire families.

The species-to-genus ratio illustrates this dynamic. During the Middle–Late Jurassic radiation, the ratio peaked at 4.5, reflecting speciose genera within thriving communities. During the Late Cretaceous, the ratio approached 1.6. This state of generic monotypy—where almost every surviving genus is represented by a single species—is a classic signature of a macroevolutionary bottleneck [27,63]. The persistence of the familial backbone despite repeated species-level pruning suggests a pattern of deep-lineage resilience rather than overall fragility [63]. This resilience likely has deep physiological and morphological

roots. Modern brachiopods retain a remarkable capacity to withstand environmental perturbations [64], and analogous endurance can be traced into deep time. During the Permian–Triassic mass extinction, for example, brachiopods reduced calcification costs through morphological simplification—such as fewer and less pronounced shell plicae—to persist under extreme environmental stress [65].

4.3. Macroecological Reorganization: Niche Displacement and Latitudinal Retreat (H3)

Beyond taxonomic diversity, the analysis of ecological niche occupation and paleolatitudinal distribution (Hypothesis H3) reveals that the Cenozoic transition was primarily a spatiotemporal restructuring. While brachiopods consistently maintained their primary occupancy within Shallow/Open Shelf environments across all intervals, the Cenozoic transition is marked by a severe proportional contraction from Carbonate/Reef settings—which had previously constituted a robust secondary niche during the Mesozoic. This ecological narrowing was accompanied by the emergence of a distinctly anti-tropical, bimodal latitudinal distribution with near-complete equatorial withdrawal.

This combined ecological and geographic retreat is consistent with escalating biological pressures during the Mesozoic Marine Revolution. The proliferation of durophagous predators and deep bioturbators reshaped shallow, warm-water benthic ecosystems [15,16,66,67]. As epifaunal, stationary suspension feeders, brachiopods were likely vulnerable to these pressures. Their Cenozoic displacement from tropical carbonate settings into temperate latitudes aligns with the broader marginward retreat documented in other declining benthic lineages [68]. Notably, this anti-tropical pattern departs from the “out of the tropics” model [69], in which tropical regions typically act as a source of global diversity: for brachiopods, the tropics appear to have become a zone of contraction rather than diversification. Unlike many bivalves that expanded ranges from tropical centers [70], brachiopods systematically withdrew toward temperate latitudes, where predation intensity is lower—a gradient with roots extending back to the Paleozoic [71,72].

This shift mirrors modern brachiopod biogeography, which exhibits a bimodal diversity peak in mid-latitude warm-temperate zones (~30–40° N/S) rather than at the equator [11,73]. Consistent with a long-term evasion strategy, most extant species possess smooth shells and occupy cryptic, low-metabolism habitats rather than investing in heavily reinforced defensive ornamentation [74]. These mid-latitude refugia may function both as holdouts for surviving lineages and as centers of ongoing speciation [73]. Moreover, the weak to moderate association between modern brachiopod ecomorphological traits and contemporary sea surface temperatures suggests that their current biogeographic and morphological landscape is primarily a legacy of deep-time macroevolutionary reorganizations rather than a direct response to modern climatic gradients [75]. The paleogeographic maps (Figure 6) provide direct visual evidence for this reorganization, tracing the gradual emptying of tropical regions and the coalescence of occurrences into two temperate bands by the Neogene.

Environmental tolerances likely reinforced this reorganization. As strictly marine organisms with limited tolerance for salinity fluctuations [76], brachiopods were largely prevented from colonizing the expanding brackish and estuarine niches of the Cenozoic. Furthermore, rather than being strictly relegated to polar cold-water or deep-sea environments, recent global analyses demonstrate that modern brachiopods reach their maximum diversity and distribution in mid-latitude temperate zones [11,73]. Their distinctively low baseline metabolic rates make them sensitive to elevated thermal stress and less competitive against energetically demanding bivalves in warm, tropical waters [77,78]. Consequently, Late Cretaceous–Paleogene global warming [79,80] likely rendered equatorial regions physiologically untenable. This climate-driven thermal stress, compounding with escalating

biotic pressures, effectively pushed brachiopod populations out of the tropics and restricted them to their modern mid-latitude optimum.

4.4. Limitations and Future Directions

Several limitations of this study should be acknowledged. First, although coverage-based standardization mitigates some sampling biases, the underlying fossil record remains uneven across regions and time intervals. The Chinese record, while well-documented for certain stages, may underrepresent specific environments or taxonomic groups. Second, the ecological filtering relied on genus-level imputation of functional traits; although justified for the relatively conserved epifaunal suspension-feeding guild, this approach may obscure finer intrageneric ecological variation. Third, the three-category environmental classification captures broad habitat shifts but does not resolve finer environmental gradients. Fourth, paleolatitudinal reconstructions depend on plate rotation models that carry inherent uncertainties, particularly for older intervals. Finally, the analyses focused on taxonomic richness and occurrence data; incorporating morphological disparity and body-size evolution in future work [61,81] could yield a more comprehensive understanding of brachiopod responses to environmental and biotic pressures.

5. Conclusions

The results indicate that the post-Paleozoic trajectory of Brachiopoda is not adequately captured by a narrative of simple decline. While the clade underwent a reduction in taxonomic richness and ecological dominance relative to its Paleozoic zenith, it also experienced a complex, multi-dimensional reorganization. Regional trajectories decoupled from global aggregates (H1), deep-lineage familial stability persisted through severe species-level bottlenecks (H2), and ecological niche occupation and geographic distribution shifted toward temperate, open-shelf settings (H3). The spatial heterogeneity of these patterns further indicates that this transition was not globally uniform. Rather than merely representing the declining remnants of a previously dominant fauna, modern brachiopods reflect the outcomes of prolonged ecological filtering, geographic redistribution, and hierarchical resilience.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d18080476/s1>. Figure S1. Global 10-Myr bin genus richness of the unfiltered brachiopod dataset from the Triassic to the Quaternary. This figure provides a refined macroevolutionary diversity trajectory of Brachiopoda at 10-Myr bin intervals based on unified occurrence data from the Paleobiology Database (PBDB) and Geobiodiversity Database (GBDB). Coverage-standardized genus richness ($q = 0$, $C = 0.95$) is denoted by the solid green line with circular markers, while raw genus richness is represented by the dashed green line with triangular markers. Figure S2. Stage-level genus richness of ecologically filtered Brachiopoda at minimum threshold coverage. This figure illustrates the macroevolutionary diversity trajectory of Brachiopoda restricted to an ecologically equivalent guild (epifaunal, stationary suspension feeders), based on occurrence data from the Paleobiology Database (PBDB) and Geobiodiversity Database (GBDB). Unlike the primary analysis at a fixed coverage of $C = 0.95$, this figure presents results standardized to the minimum sample coverage ($C = 0.633$) observed across all valid geological stages. Red curves represent the regional Chinese dataset, while blue curves denote the global dataset excluding China. Coverage-standardized genus richness ($q = 0$) is shown as solid lines with circular markers, plotted alongside raw genus richness (dashed lines with triangular markers). Dotted lines bridge temporal gaps where intervening stages were excluded due to insufficient sampling ($SC < 0.6$). Background shading corresponds to major geological periods. Figure S3. Stage-level genus richness of ecologically filtered Bivalvia at minimum threshold coverage. This figure illustrates the macroevolutionary diversity trajectory of Bivalvia restricted to an ecologically equivalent guild (epifaunal, stationary suspension feeders), based on occurrence data from the Paleobiology Database

(PBDB) and Geobiodiversity Database (GBDB). Unlike the primary analysis at a fixed coverage of $C = 0.95$, this figure presents results standardized to the minimum sample coverage ($C = 0.648$) observed across all valid geological stages. Red curves represent the regional Chinese dataset, while blue curves denote the global dataset excluding China. Coverage-standardized genus richness ($q = 0$) is shown as solid lines with circular markers, plotted alongside raw genus richness (dashed lines with triangular markers). Dotted lines bridge temporal gaps where intervening stages were excluded due to insufficient sampling ($SC < 0.6$). Background shading corresponds to major geological periods. Figure S4. 10-Myr bin genus richness trajectories for ecologically filtered Brachiopoda and Bivalvia. This figure provides a complementary high-resolution temporal analysis to Figure 2, contrasting the macroevolutionary dynamics of Brachiopoda (left panel) and Bivalvia (right panel) restricted to an ecologically equivalent guild (epifaunal, stationary suspension feeders). Red curves represent the regional Chinese dataset, while blue curves denote the global dataset excluding China. Coverage-standardized genus richness (Hill number order $q = 0$, extrapolated to a fixed coverage of $C = 0.95$) is shown as solid lines with circular markers, plotted alongside raw genus richness (dashed lines with triangular markers). Dotted lines bridge temporal gaps where intervening bins were excluded from the analysis due to insufficient sample coverage ($SC < 0.6$). Figure S5. Stage-level genus richness trajectories for ecologically filtered Echinodermata. This figure illustrates the genus richness of echinoderms based on ecologically filtered occurrence data from the Paleobiology Database (PBDB) and Geobiodiversity Database (GBDB). Due to the high prevalence of sampling gaps and insufficient data coverage ($SC < 0.6$) across most geological stages, the reliable analytical window is restricted to the Triassic and early Jurassic periods. Red curves represent the regional Chinese dataset, while blue curves denote the global dataset excluding China. Coverage-standardized genus richness (Hill number order $q = 0$, extrapolated to a fixed coverage of $C = 0.95$) is shown as solid lines with circular markers, plotted alongside raw genus richness (dashed lines with triangular markers). Background shading corresponds to major geological periods. Table S1. Summary of brachiopod occurrence data through successive processing steps. Table S2. Stage-level taxonomic richness of the global unfiltered brachiopod dataset. The table presents the raw and coverage-standardized (Hill number order $q = 0$, extrapolated to a fixed coverage of $C = 0.95$) richness estimates for brachiopod species, genera, and families. Data are aggregated by standard international geological stages based on the midpoint ages of their stratigraphic ranges. Intervals with insufficient sample coverage ($SC < 0.6$) were excluded from the analysis and are denoted by “NA”. Table S3. 10-Myr bin-level taxonomic richness of the global unfiltered brachiopod dataset. The table presents the raw and coverage-standardized (Hill number order $q = 0$, extrapolated to a fixed coverage of $C = 0.95$) richness estimates for brachiopod species, genera, and families. Data are aggregated into equal-duration 10-Myr intervals spanning from the Triassic to the Quaternary (260 Ma to the present). Table S4. Most abundant brachiopod families per period and representative Neogene genera. Table S5. Occurrence frequency and proportion of the five most abundant post-Paleozoic brachiopod families across three environmental categories.

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Data Availability Statement: The raw fossil occurrence data underlying this research are publicly accessible from the Paleobiology Database (PBDB; <https://paleobiodb.org>) and the Geobiodiversity Database (GBDB; <https://geobiodiversity.com>). The complete analytical pipeline, including all R scripts used for data cleaning, ecological filtering, diversity standardization, and visualization, is openly available in the GitHub repository: <https://github.com/fachengsg/Brachiopod-Diversity-Dynamics-Mesozoic-Cenozoic> (accessed on 28 July 2026).

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Abbreviations

The following abbreviations are used in this manuscript:

CR/E	Coverage-based Rarefaction and Extrapolation
SC	Sample Coverage
PBDB	Paleobiology Database
GBDB	Geobiodiversity Database

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