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EVOLUTION

Preservation bias obscures gradual Ordovician reef evolution

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The fossil record often creates an illusion of sudden evolutionary bursts, which may reflect preservation biases rather than actual biological events. The Great Ordovician Biodiversification Event (GOBE) appears to mark the abrupt rise of diverse reef-building metazoans during the late Darriwilian (~460 Ma), seemingly contradicting gradual evolutionary models. Here, we demonstrate this apparent burst is largely an artifact of a global sea-level fall (~475 to 460 Ma) that produced widespread unconformities. Integrated stratigraphic and fossil occurrence data reveal early reef-builders likely appeared earlier than the late Middle Ordovician, but their record was erased by sea-level-driven erosion. During the peak of this sea-level fall (Dapingian Stage, 471 to 469 Ma), both carbonate deposition and fossil occurrences were minimal, with significant correlation between carbonate preservation and reef-builder occurrences. The subsequent transgression enabled these already-diversified organisms to recolonize shallow-water environments simultaneously across multiple regions, generating a misleading impression of sudden diversification. This "Sppil–Rongis effect" biased our understanding of the GOBE in reef ecosystems, illustrating how stratigraphic incompleteness can distort evolutionary patterns. Rather than a discrete evolutionary event, the GOBE reflects a continuous trajectory, interrupted and reshaped by sea-level fluctuations.

Great Ordovician Biodiversification Event | reef | sea-level change | unconformity

Reconstructing evolutionary history requires addressing preservation gaps that distort our understanding of the development of life. This challenge becomes particularly pronounced when interpreting major biodiversification events, such as the Great Ordovician Biodiversification Event (GOBE), where apparent rapid diversification may reflect preservation biases rather than true evolutionary dynamics (1–6). The reef ecosystem transformation during the GOBE offers an exceptional case for disentangling genuine evolutionary signals from preservational artifacts. The late Middle Ordovician transition in reef communities has long appeared revolutionary—diverse skeletal metazoans seemingly appeared without evolutionary precursors and simultaneously colonized several paleocontinents (7, 8). Traditional interpretations attribute this pattern to environmental triggers, including increased ocean oxygenation (9), global cooling (10), and shifts in ocean chemistry (11). However, recent discoveries challenge traditional narratives about GOBE reef evolution, as early reef-building stromatoporoids (12) and bryozoans (13, 14) from the late Tremadocian demonstrate that key reef-builders had evolved well before their presumed Middle Ordovician "origin."

This apparent discontinuity warrants closer examination in light of the "Sppil–Rongis effect" (15)—the inverse of the Signor–Lipps effect (16). While the Signor–Lipps effect renders catastrophic extinctions gradual in the fossil record, the Sppil–Rongis effect can make gradual diversification seem abrupt when preservation conditions improve. Meanwhile, stratigraphic analysis reveals a global sea-level fall spanning the late Floian to early–middle Darriwilian (~475 to 460 Ma) that created widespread unconformities across multiple paleocontinents (17), precisely coinciding with the gap in reef-builder fossil record (7). Although many studies have discussed the possibility that erosional unconformities—driven by sea-level fall—might delay the first fossil occurrences, these ideas have remained largely theoretical (18), as unconformity formation is controlled by local tectonic processes in addition to fluctuations in eustatic sea level, making global correlation difficult.

By integrating stratigraphic sequences from major paleocontinents with fossil occurrence data, we demonstrate that global regression eliminated shallow-water carbonate environments necessary for both reef development and fossil preservation, producing the illusion of sudden diversification across continents when sea levels subsequently rose in the middle–late Darriwilian. This rapid recolonization of newly available habitats generated a false signal of explosive diversification. This reinterpretation reframes our understanding of GOBE reef ecosystem evolution—not as a revolutionary event

Significance

Understanding major evolutionary transitions requires distinguishing true biological signals from preservation artifacts. Our research challenges conventional interpretations of the Great Ordovician Biodiversification Event in reef ecosystems by revealing how sea-level fluctuations created a misleading pattern. By correlating global sea-level changes with fossil occurrences across paleocontinents, we demonstrate that the apparent sudden emergence of diverse reef communities reflects improved preservation conditions rather than an evolutionary burst. Early reef-builders likely evolved gradually, but their record was masked by extensive erosion during a major regression. This result transforms our understanding of early reef ecology and demonstrates how taphonomic biases can generate illusory evolutionary patterns, thereby reframing the Cambrian Explosion and Ordovician Biodiversification as components of one extended diversification process.

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but as a preservation artifact—highlighting how sea-level-driven preservation biases can fundamentally distort evolutionary narratives.

Stratigraphic and Paleogeographic Distribution of Early Skeletal Reefs and Reef Builders. Reef-building metazoans were traditionally thought to have originated abruptly and simultaneously across various paleocontinents during the late Darriwilian, resulting in the first skeletal-dominant reef ecosystem (7, 8). This conventional view framed their appearances as a revolutionary event, with diverse stromatoporoids (19) and corals (20) appearing with scant evidence of evolutionary precursors (Fig. 1). However, recent discoveries have challenged this view, revealing a more complex and extended evolutionary history for these key reef-builders and reefs formed by them.

Stromatoporoids are documented from the late Tremadocian–early Floian of South China, where *Lophiostroma* formed the earliest known stromatoporoid reefs (12). Previously assigned upper Darriwilian stromatoporoid reefs in the Sino-Korean Block (21, 22) have been reassigned to the middle Darriwilian based on conodont biostratigraphy (23). The earliest known occurrence of stromatoporoids in Laurentia is represented by several genera (*Cystostroma*, *Labechia*, *Pachystylostroma*, and *Pseudostylodictyon*) in the late Darriwilian (19, 24). In Siberia, *Priscastroma* and *Cystostroma* first occurred during the middle to late Darriwilian (19, 25, 26), while in Baltica, the first stromatoporoid record is the early Katian, likely influenced by its latitudinal shift during the Ordovician (27).

Early tabulate coral taxonomy has recently undergone revision. The Tremadocian "*Lichenaria*" has been reinterpreted as a possible alga *Amsassia* (28), with confirmed tabulate corals first appearing in the late Darriwilian of Laurentia (*Billingsaria*, *Lamottia*, and *Eofletcheria*) (20) and Siberia (*Billingsaria* and *Lyopora*) (29). While Laurentian tabulate corals constructed reefs as early as the late Darriwilian (20), Siberian tabulate coral reef development was delayed until the Late Ordovician (29). Rugose corals appeared in the late Darriwilian in South China (*Calostylis*) (30) and Iran (*Lambelasma*?) (31), but they did not form reefs until the Late Ordovician (7).

For bryozoans, while early Cambrian *Protomelission* has been reported (32), it lacks the calcified skeleton required for reef building, and its identification remains debated (33). The late Cambrian *Pywackia* (34) has been reinterpreted as a cnidarian (35), while another early Cambrian bryomorph (36) is more likely a rivulariacean cyanobacterium. The earliest unquestionable bryozoan, *Prophyllodictya*, is found in the lower Tremadocian of South China (37), with the late Tremadocian *Nekhorosheviella* representing the earliest known reef-building bryozoan (13, 14). *Profistulipora*, reported from the Tremadocian of Siberia (38), remains uncertain as a reef-builder. Larger bryozoan reefs appeared in the late Darriwilian and beyond across multiple paleocontinents (7, 8).

This systematic review confirms that key reef-building organisms, including stromatoporoids and bryozoans, had evolved by the Early Ordovician, forming reefs, and persisted into the Middle Ordovician. The late Darriwilian, however, marks the first appearance of a "diversified fauna" of corals and stromatoporoids represented by multiple genera across several paleocontinents. The apparent gap in skeletal reefs and reef-builder occurrences during the Dapingian–early Darriwilian, followed by a sudden expansion in the late Darriwilian, suggests either a genuine disappearance and re-evolution event, or more likely, a preservation bias that obscured their continuous existence.

Sea-level Changes and Stratigraphic Records. The Middle Ordovician sea-level fall (17) led to widespread unconformities across multiple paleocontinents, with varying durations and reflooding timelines documented in northern Gondwana (39), Laurentia (40), and Baltica (41) (Fig. 2). This regression is recognized as the Sauk–Tippecanoe sequence boundary in Laurentia (40) and the Huaiyuan Epeirogeny Event 1 in Sino-Korean Block (23, 42), the two paleocontinents with the most diverse Darriwilian metazoan-dominated reef records.

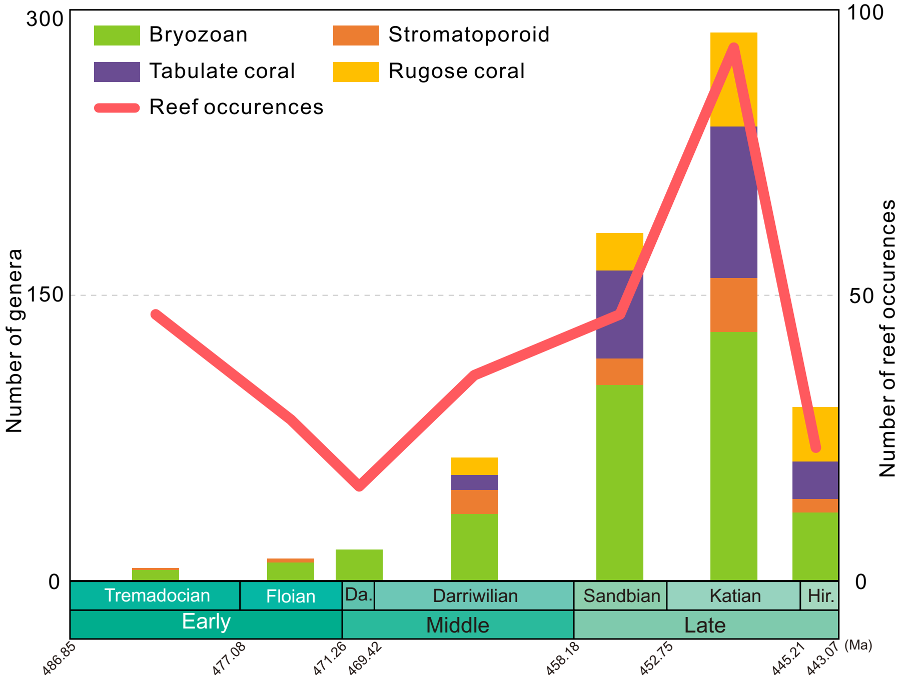

Fig. 1. Diversity (number of genera) of reef-building metazoans (stromatoporoids, tabulate and rugose corals, and bryozoans) and reef occurrences through time. An apparent abrupt increase occurs in the late Darriwilian.

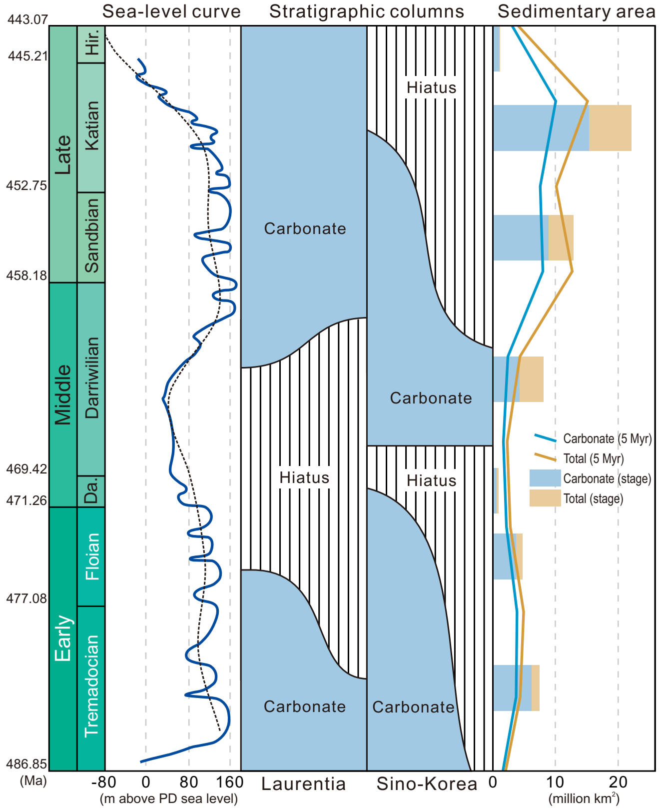

Fig. 2. Global sea-level curve during the Ordovician (43), schematic stratigraphic columns for Laurentia (40) and Sino-Korean Block (42), and carbonate and siliciclastic sedimentary rock area. Note the correlation between the sea-level lowstand and reduced sedimentary rock area during the Dapingian–early Darriwilian interval. Da., Dapingian; Hir., Hirnantian.

In Laurentia, the unconformity spans much of the Whiterockian (latest Floian–earliest Sandbian), reaching its peak during the Dapingian (40). Notably, the Chazy Group, which hosts the earliest diverse stromatoporoid-coral-bryozoan reef assemblage in Laurentia (24), directly overlies this unconformity (40, 44). In Sino-Korean Block, the Huaiyuan Epeirogeny Event 1 persisted from the Furongian–earliest Dapingian to early Darriwilian (Dw1) (42). The earliest transgressive deposits represent supra- to intertidal successions unsuitable for reef-builders (45), and stromatoporoids and bryozoans only began to thrive once the platform was fully submerged in the middle Darriwilian (Dw2) (21–23, 46).

Similar gaps in Dapingian–early Darriwilian strata are observed across Gondwana, including Australia (47) and the Middle East (48). While continuous Dapingian–early Darriwilian successions exist in South China (49), Baltica (41), and Siberia (50), these regions, nevertheless, still record sea-level fall during this time interval. However, instead of reef-bearing carbonates, they are dominated by facies typically unfavorable for reef-builders.

Carbonate Preservation and Fossil Occurrences. Analysis of Macrostrat stratigraphic data reveals a dramatic decline in carbonate preservation during the Dapingian stage (Fig. 2). Carbonate area decreases from 3.69 million km^2 in the Floian to only 0.64 million km^2 in the Dapingian—an 83% reduction—before rebounding to 4.30 million km^2 in the Darriwilian. The observed reduction may even be underestimated due to misclassification (e.g., late Tremadocian–Floian Filmore Formation in Utah (51) misclassified as Dapingian in Macrostrat) or due to grouping (e.g., Beekmantown Group in Ontario–Quebec (52) spanning late Tremadocian to early Darriwilian). This pattern represents a global signature of the sea-level fall and creates a severe reduction in preservation potential for reef-building organisms (7).

Fossil occurrence data for reef-building metazoans mirror this pattern (Figs. 1 and 3). Bryozoans, while present throughout the Tremadocian–Dapingian, increase dramatically in the Darriwilian (53). Stromatoporoids are entirely absent during the Dapingian, despite their presence in earlier stages (12, 21). Similarly, tabulate and rugose corals do not appear in the Dapingian or earlier intervals, but exhibit multiple genera in the Darriwilian across various paleocontinents. Independently compiled reef occurrence data from PaleoReefDatabase (PARED) further corroborate this trend, showing a minimum during the Dapingian (17 reefs compared to 29 to 48 in adjacent stages) (Fig. 1).

Statistical analysis confirms significant correlations between carbonate preservation area and fossil occurrences. Strong positive correlations exist between carbonate area and total diversity (r = 0.84) and between carbonate area and PARED reef occurrences (r = 0.98). Even stronger correlations are observed between carbonate area and total samples (r = 0.91). Individual taxonomic groups also show strong correlations with carbonate area, with most diversity measures and all sample counts being statistically significant (Table 1).

To test the robustness of these correlations across different temporal scales, we additionally analyzed the data using standardized 5-My time bins. This approach maintains slightly lower, but still statistically significant correlations between carbonate area and most fossil occurrences (Table 1), although the relationship with reef occurrences becomes nonsignificant (r = 0.60, P = 0.117). This discrepancy most likely reflects the common practice of recording fossil and reef occurrences according to stratigraphic stages rather than precise numerical ages, making the stage-level correlation more reliable for interpreting preservation patterns.

Overall, these strong correlations highlight the critical role of preservation biases in shaping observed diversity patterns. The consistent pattern across different taxonomic groups and temporal scales reinforces our interpretation that the apparent diversification reflects preservation artifacts rather than true evolutionary signals. The significant loss of carbonate environments and the corresponding drop in fossil occurrences during the Dapingian, followed by their simultaneous increase in the Darriwilian, provide compelling evidence that the apparent sudden diversification is largely a preservation artifact, rather than a genuine evolutionary event.

Discussion and Conclusions

As demonstrated by the taxonomic and stratigraphic evidence presented above, reef-building metazoans show a pattern consistent with our preservation bias hypothesis (Fig. 4). The compiled records clearly indicate the earliest known reef-building stromatoporoids (12) and bryozoans (37) during the Early Ordovician, followed by an apparent gap, and then simultaneous reappearance across multiple paleocontinents during the Middle Ordovician transgression. Most significantly, the emergence of diverse reef assemblages in Laurentia (44) and the Sino-Korean Block (23) aligns precisely with the termination of regional unconformities, strongly supporting preservation biases rather than evolutionary processes as the primary factor shaping observed diversity patterns. The development of diverse metazoan-dominated reefs above unconformities has been interpreted as first major expansion on a regional scale (44), but these patterns likely reflect preservation biases masking a continuous evolutionary history rather than a true evolutionary origin.

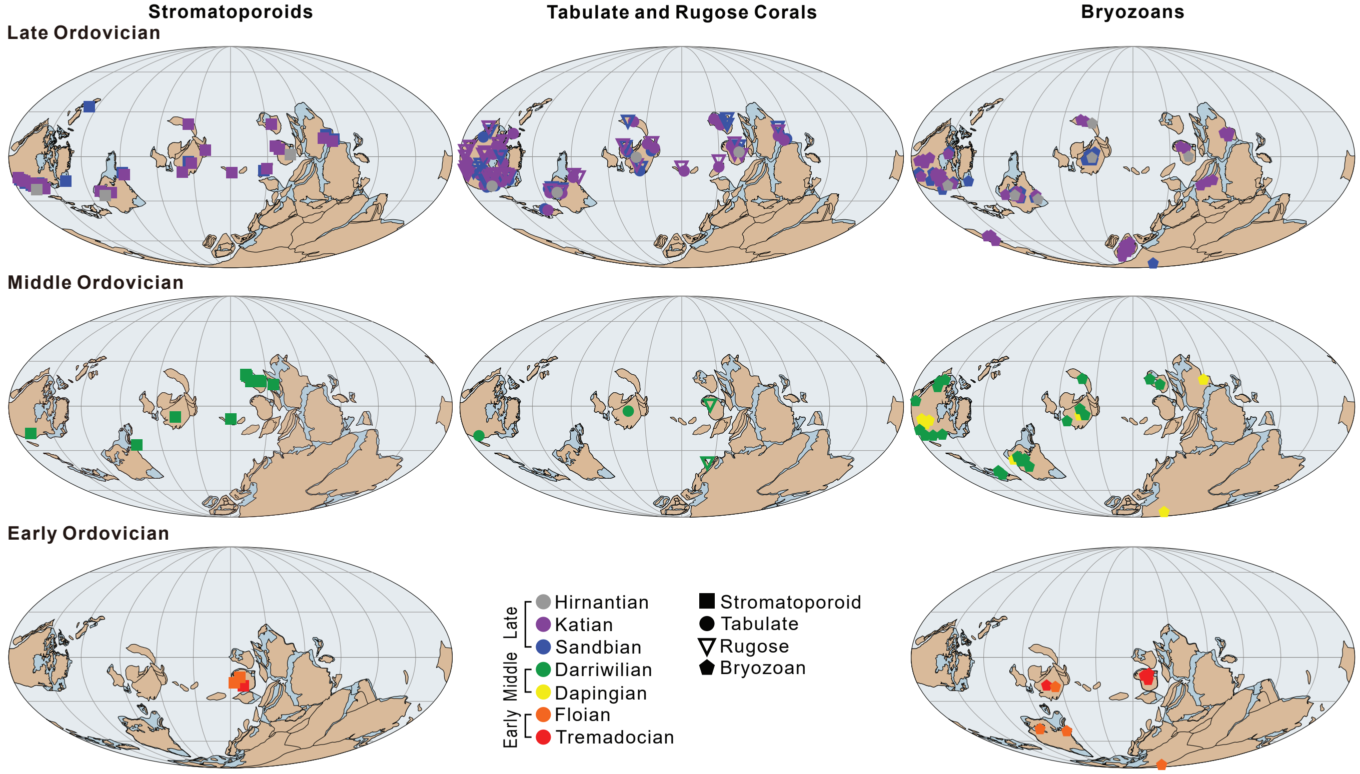

Fig. 3. Global paleogeographic maps of the Early, Middle and Late Ordovician, showing the distribution of reef-building metazoans (stromatoporoids, tabulate and rugose corals, and bryozoans). Data acquired from PBDB.

South China provides an informative contrast to this pattern. Despite the absence of significant hiatuses (49), stromatoporoids appear only in the late Tremadocian–early Floian (12, 21) and later in the Katian (55). This absence reflects the dominance of deeper water facies unsuitable for reef-builders during the Middle Ordovician (49). Similarly, Baltica preserves an almost complete Ordovician succession where corals and stromatoporoids do not appear until the Late Ordovician, due to its higher paleolatitude position (27, 56). Despite these absences, both regions experienced significant increases in other shelly faunas during the Middle Ordovician, highlighting the importance of facies control in shaping the fossil record (3, 4).

The Sppil–Rongis effect (15) explains the apparent sudden appearance and diversification of reef-building organisms during the Middle Ordovician (Fig. 4). During the global sea-level fall (17), shallow marine environments—the preferred habitat for reef-building metazoans—were significantly reduced, and resulting erosion removed much of their sedimentary record. When sea levels rose again, previously diverse reef-builders reappeared abruptly with considerable diversity in the fossil record, producing the illusion of rapid diversification. The preservation bias disproportionately affects carbonate-producing benthic organisms, amplifying the apparent suddenness of their diversification compared to other components of the GOBE (1, 8).

Traditional interpretations of reef evolution in the GOBE have framed it as a rapid and unprecedented diversification event (7, 8). In contrast, our analysis suggests that it represents part of a longer evolutionary trajectory, largely obscured by preservation biases. This is further supported by the significant correlation between preservation area and fossil occurrences. Our findings align with recent proposals to view the Cambrian Explosion and GOBE as one extended diversification rather than distinct evolutionary events (1–4, 6, 57, 58). The gradual evolution of reef-building metazoans from the late Cambrian through the Ordovician (8, 59), though partially obscured by preservation biases, supports the hypothesis that these traditionally separated "events" as a continuous evolutionary trajectory extending

Table 1. Correlations between carbonate preservation area and fossil occurrence metrics

	Diversity correlation		Sample count correlation		Sample count correlation (5 My bin)	
	r value	*P* value	r value	*P* value	r value	*P* value
Stromatoporoid	0.85	0.012	0.86	0.012	0.89	0.003
Tabulate coral	0.87	0.016	0.88	0.008	0.90	0.002
Rugose coral	0.68	0.090*	0.87	0.010	0.86	0.006
Bryozoan	0.84	0.019	0.87	0.011	0.68	0.006
Total	0.84	0.017	0.91	0.004	0.78	0.021
Reef	–	–	0.98	0.000	0.60	0.117*

"Diversity Correlation" shows the relationship between carbonate area and the number of genera for each group (stromatoporoid, tabulate/rugose coral, and bryozoan), while "Sample Count Correlation" represents the relationship and the number of samples collected. "Sample Count Correlation (5 My bin)" shows the same relationship analyzed using standardized 5-My time bins. The "Total" row reflects the combined data from the four taxonomic groups, and the "Reef" row represents correlations with reef occurrences from PARED.

*Not statistically significant ($P > 0.05$).

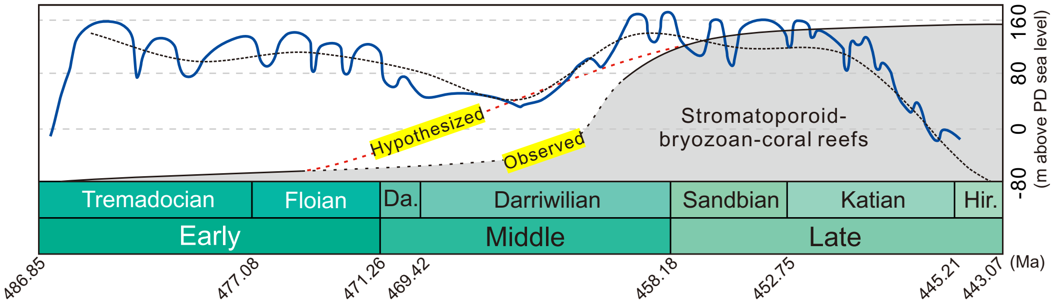

Fig. 4. Schematic illustration of the Sppil–Rongis effect in reef evolution, coupled with sea-level changes (43). In this model, the Middle Ordovician stratigraphic gap created the illusion of abrupt appearance and diversification of reef-building organisms. The hypothesized true diversity pattern (dotted line) shows a gradual increase beginning before the late Darriwilian. Relative diversity of stromatoporoid-bryozoan-coral reefs is modified after ref. 54. Da., Dapingian; Hir., Hirnantian.

through the early Paleozoic, with preservation artifacts creating the illusion of sudden diversification pulses (4).

Methods

We compiled data on Ordovician reef-building metazoans (rugose and tabulate corals, stromatoporoids, and bryozoans) from the Paleobiology Database (PBDB; accessed on 18 March 2025). However, for stromatoporoids (19), supplemented by recent publications (60, 61), and for bryozoans (38), we relied on specialized sources rather than PBDB data for diversity counts. Questionable occurrences [e.g., Early Ordovician corals (28) and pulchrilaminids (62)] were systematically excluded from analyses. Additional information on reef occurrences was extracted from PARED (accessed on 27 September 2024) (63), and lithostratigraphic data (mostly for North American and the Caribbean successions) were retrieved from Macrostrat (accessed on 1 March 2025) (64).

To evaluate how preservation biases affect fossil occurrences and diversity, we calculated carbonate area and percentage for each Ordovician stage based on Macrostrat and analyzed their correlation with fossil occurrences (and diversity) using Pearson correlation coefficients. Correlation analyses, conducted using Python's sciPy package, determined the strength and statistical significance of these relationships ($\alpha = 0.05$). All code used for these analyses is available at: 10.5281/zenodo.15117466.

Data, Materials, and Software Availability. Code data have been deposited in Zenodo (10.5281/zenodo.15117466) (65).

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