PALEONTOLOGY

The spatial structure of Phanerozoic marine animal diversity

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The global fossil record of marine animals has fueled long-standing debates about diversity change through time and the drivers of this change. However, the fossil record is not truly global. It varies considerably in geographic scope and in the sampling of environments among intervals of geological time. We account for this variability using a spatially explicit approach to quantify regional-scale diversity through the Phanerozoic. Among-region variation in diversity is comparable to variation through time, and much of this is explained by environmental factors, particularly the extent of reefs. By contrast, influential hypotheses of diversity change through time, including sustained long-term increases, have little explanatory power. Modeling the spatial structure of the fossil record transforms interpretations of Phanerozoic diversity patterns and their macroevolutionary explanations. This necessitates a refocus of deep-time diversification studies.

The fossil record of Phanerozoic marine biodiversity has long been a model system for understanding animal diversification through deep time (1–6). Numerous hypotheses have been proposed to explain these patterns. Some invoke long-term environmental change (7–9) or tectonic drivers (10), whereas others emphasize time-dependent processes, ranging from unconstrained, exponential diversification (3, 11) to diversity-dependent diversification constrained by biotic interactions (2, 5, 12). Inferred diversity patterns may also reflect the structure of the fossil record, including geological factors, such as rock amount (13) and lithification trends (4), or research practices, such as sampling variation resulting from worker interest or taxonomic culture (4, 5). However, there is little consensus about the relative importance of the many factors invoked by these hypotheses (3–5, 7, 10, 13, 14).

We argue that the spatial structure of the fossil record is one of the most influential factors affecting interpretations of diversity dynamics in deep time. Previous studies have acknowledged this problem but have not explicitly corrected for it (4, 6). The global fossil record, as currently documented, is not truly global (4, 15–17), and there is substantial variation through geological time in the numbers, sizes, and locations of spatial regions from which fossils have been reported. Therefore, nominally global diversity estimates among intervals of geological time derive from different points on their respective species-area curves, which introduces a confounding source of variation. Controlling for sampling intensity

alone does not address this (18); 50 to 60% of the changes in global sampling-standardized genus richness can be explained simply by changes in the geographic spread of fossil localities (Fig. 1, C and E). This correlation is unlikely to be driven by changes in habitable area because changes in shallow–marine sediment extent are not correlated with either global fossil taxon counts or the spatial extent of the global fossil record (Fig. 1, E and F, and fig. S1; data sources for environmental covariates are listed in table S1). Moreover, diversity levels are controlled by factors that have nonrandom spatial distributions [e.g., latitude and environment (19)], but most studies of diversity drivers through time have not explicitly accounted for the spatial distributions of important environmental factors, such as the development of reefs (20) or epeiric seaways (9).

We present a spatially explicit framework to estimate regional-scale diversity patterns through the Phanerozoic and their relationship to time and environment. We standardized the geographic scale of the analysis by drawing sets of fossil localities that represent regions of near-uniform spatial extent. This procedure was repeated at several different spatial scales. We then conducted spatiotemporally explicit tests of the influence on inferred diversity of time-dependent processes, local environmental factors, rock record and sampling variables, and research practices. We analyzed fossil occurrence data from the Paleobiology Database (21), consisting of 396,815 occurrences of 22,855 marine animal genera. Our spatial subsampling algorithm identifies all nested sets of adjacent fossil localities using their paleocoordinates (22). From this, we extracted regions with minimum-spanning tree (MST) lengths (6) of ~1500, 2000, 2500, 3000, and 3500 km. We estimated genus richness for each spatial region using shareholder quorum sub-

sampling (SQS) (5), alongside additional information such as spatial statistics (e.g., counts of occupied grid cells) and local environmental parameters (22).

Spatially standardized diversity estimates vary considerably across the globe within each time interval (Fig. 2), which is masked in global diversity curves. We find that diversity varies at least as much across spatial regions within intervals as it does through time (fig. S2). Our spatial-standardization procedure greatly diminishes a Permian peak in diversity that was present in global curves, which resulted from the broad spatial extent of Permian fossil localities in the Paleobiology Database (Fig. 1A and figs. S3 and S4). Furthermore, the sustained Mesozoic–Cenozoic global increase in diversity, a seminal feature of global diversity curves (2, 23–25), is transformed into a much more modest, stepwise increase across the Cretaceous–Paleogene (K/Pg) boundary (Fig. 2 and fig. S5). However, in agreement with existing sampling-standardized global curves (5, 6, 24), regional diversity is higher on average from the Ordovician to the early Devonian and in the Cenozoic, and it is lower on average in the late Paleozoic and early Mesozoic.

Low paleolatitudes (±0° to 30°) are best represented during the Paleozoic, whereas mid-paleolatitudes (±30° to 60°) are better represented during the Mesozoic to the Cenozoic, partly because of continental drift (fossil-record sampling is most intense in North America and Europe, and landmasses, on average, migrated northward over this interval). Low-paleolatitude diversity in the Paleozoic is similar to that of the Neogene (Fig. 2). Mid-paleolatitude diversity is lower than average in the Permian and higher than average in the Cenozoic. High paleolatitudes (±60° to 90°) are only informative for a handful of Paleozoic bins and consistently have low diversity. Results vary only slightly across different spatial-standardization criteria (22) (Fig. 2).

Major groups of marine invertebrates show pronounced variation in diversity through the Phanerozoic (Fig. 3), displaying patterns that generally mirror their respective global curves. Bivalves show a pattern of sustained increase through the Phanerozoic (5, 26) but with increasing variance among spatial regions through time. Brachiopods show a very different pattern than that of bivalves (5), with clear evidence of a marked decrease in average diversity across the Permian–Triassic (P/T) boundary. Cephalopods, by contrast, show evidence of higher diversity in the immediate aftermath of the P/T, which is consistent with global patterns observed in ammonoids (27). Gastropod diversity remained relatively stable across the Paleozoic-Mesozoic, but it experienced a sharp fourfold increase in diversity across the K/Pg [compared with a latest Cretaceous increase in global curves (5)];

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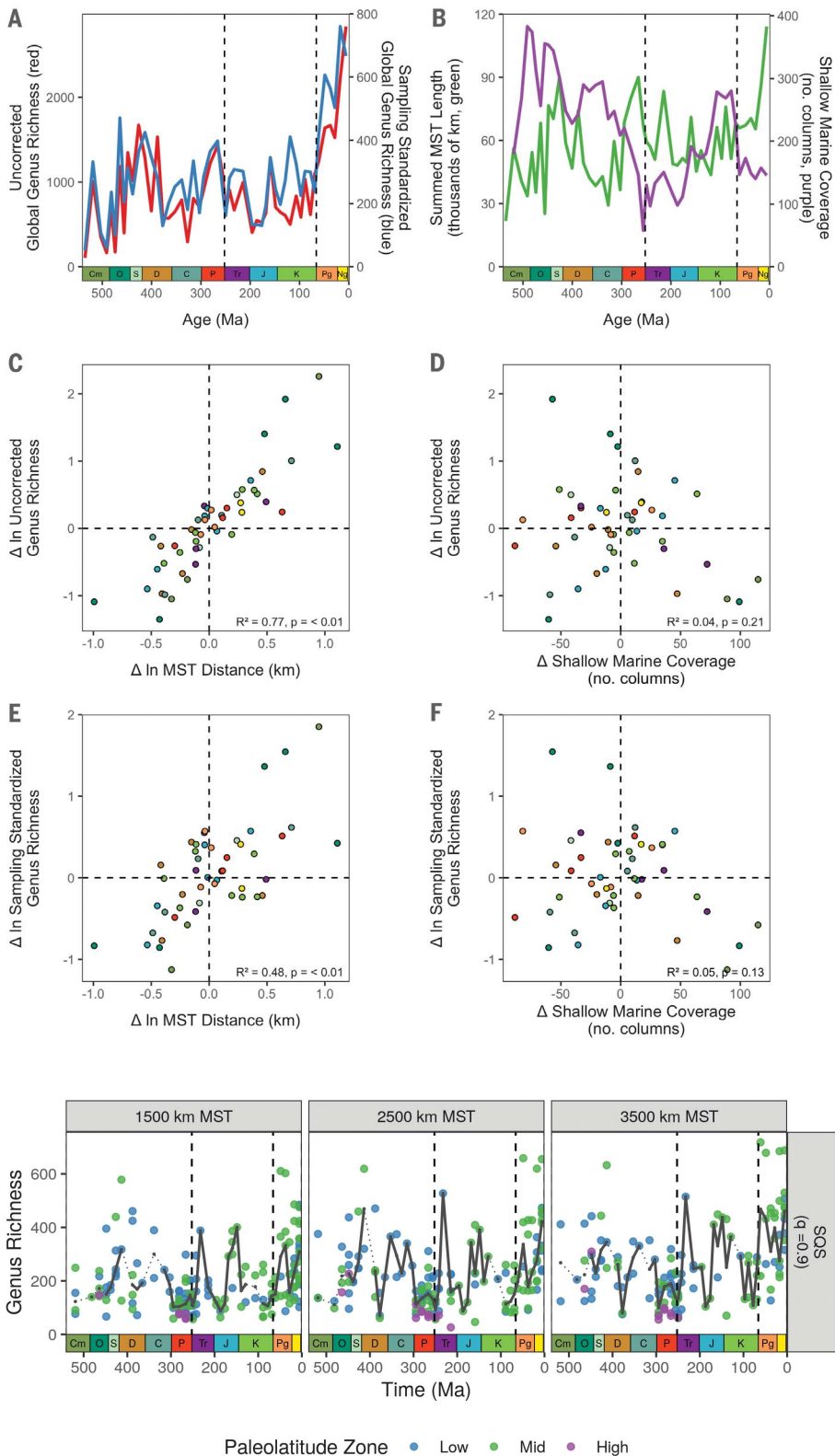
Fig. 1. Correlations between changes in Phanerozoic marine animal diversity (Eumetazoa excluding Tetrapoda) and changes in spatial sampling and habitable area. (**A**) Uncorrected and sampling standardized [SQS (5), quorum = 0.7] global genus richness per bin. Cm, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; Ng, Neogene. (**B**) Spatial sampling (summed MST length in kilometers) and habitable area [shallow marine coverage; number of (no.) columns]. (**C**) Relationship between spatial sampling and uncorrected genus richness per interval. R^2, coefficient of determination. (**D**) Relationship between habitable area (shallow marine coverage, no. columns) and uncorrected genus richness per interval. (**E**) Relationship between spatial sampling and sampling-standardized (SQS, quorum = 0.7) genus richness per interval. (**F**) Relationship between habitable area (shallow marine coverage, no. columns) and sampling-standardized (SQS, quorum = 0.7) genus richness per interval. All variables are first-differenced. R^2 and P values derive from linear model fits. For information about variables, see table S1. Colors of points in (C) to (F) match the colors of geological periods in (A) and (B).


Fig. 2. Spatially standardized diversity patterns for 1500, 2500, and 3500-km MST lengths. Genus richness estimated using SQS (5) [quorum (q) = 0.9]. Black lines and points indicate bin-level medians.

this appears to be the main driver of the modest stepwise increase across the K/Pg within marine animals as a whole.

We used linear mixed-effects models to assess the roles of selected environmental, sampling, and biotic variables as drivers of diversity change through time and space, evaluated with Akaike's information criterion and model averaging (22). We modeled temporal autocorrelation using a continuous-time first-order autoregressive cor-

relation structure (22). Exploratory analyses suggested that explanations for diversity change through time may differ between low and mid-paleolatitudes, which were therefore modeled separately. Insufficient data were available
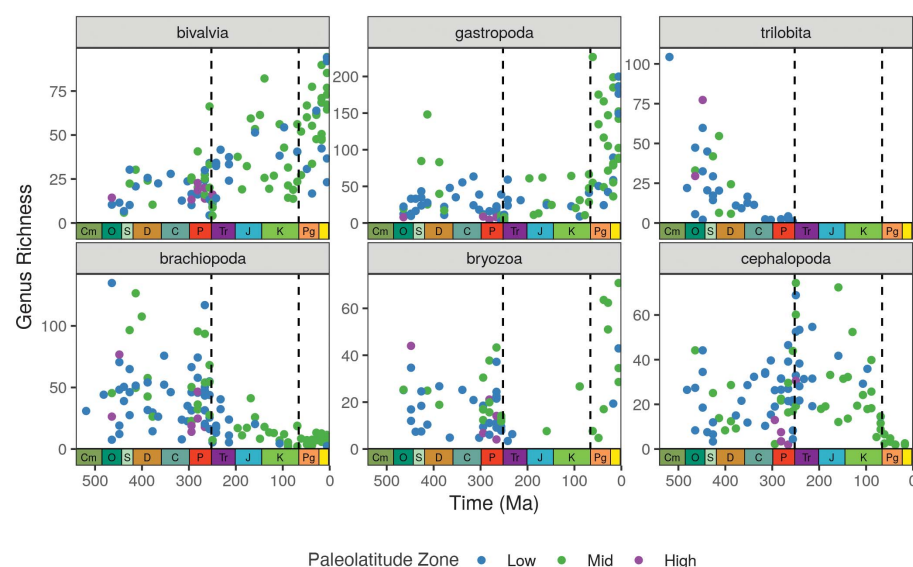
Fig. 3. Spatially standardized genus richness patterns for selected groups of marine invertebrates at 2000-km MST length. Richness estimated using SQS (*5*) (quorum = 0.8).

for high paleolatitudes. Our explanatory variables comprise several broad categories (table S1), including local environmental variables, shallow–marine sediment extent, temporal variables [including exponential diversification through time (*3*, *14*) and categorical variables describing equilibrial diversification phases (*2*) and short-term postextinction decreases], and variables related to research activity (including sampling variables and modern continental region identity). Modern continental region identity was specified as a random effect to control for geographic variation in research practices (e.g., taxonomic splitters versus lumpers) and to permit us to model time series autocorrelation (*22*).

The model selection procedure is relatively more decisive for mid- than for low paleolatitudes, with fewer models in the confidence set (models receiving an evidence ratio of ≤8; fig. S6 and tables S2 and S3) and higher average goodness of fit (table S4). Models incorporating a subset of our explanatory variables receive the strongest support for most spatial extents (table S3). Elevated mid-paleolatitude diversity is robustly associated with the proportion of reefal localities and with counts of references associated with spatial regions (reflecting either research or literature interest, high diversity driving high reference counts, or both; Fig. 4 and figs. S5, S7, and S8). There is also evidence that shallow–marine sediment extent is positively associated with diversity (Fig. 4). Marginal coefficients of modern continental regions show that Europe has higher diversity than other regions, perhaps because of variation in research or taxonomic practices (fig. S9). At low paleolatitudes, shal-

low–marine sediment extent, lithology counts, and reference counts are important at many spatial scales (Fig. 4 and fig. S8). Overall, however, at low latitudes, no single combination of explanatory variables is consistently important across all scales (table S2). An alternate set of model comparisons including continental fragmentation index (*10*) does not recover a prominent role for that variable (see "Sensitivity Analyses" in the supplementary materials).

Shallow–marine sediment extent, a proxy for global variation in shallow–marine habitat area (*28*), is positively related to the diversity of regional-scale assemblages (Fig. 4). This is consistent with the hypothesis that some changes in marine diversity were driven by factors associated with sea level, potentially via species-area effects (*7*, *9*). We also recover strong evidence that reefs are loci of high diversity (Fig. 4). This mirrors the present-day pattern in which reefs are biodiversity hotspots, hosting a disproportionate fraction of marine species (*29*). Therefore, both the flooding of continental interiors and the expansion and contraction of reefs are likely to drive changes in true global diversity.

Only one temporal variable is included consistently in the best-ranked models that explain marine animal diversity: a parameter differentiating pre-Cenozoic intervals from the Cenozoic (especially at mid-latitudes; Fig. 4, fig. S8, and tables S2 and S3). This indicates that there was, on average, approximately twofold greater diversity during the Cenozoic compared with earlier intervals (fig. S10).

No explanatory power can be attributed to the passage of continuous time [age in millions

of years (Ma)]. Model-averaged parameter estimates for the coefficient of time, which represents the net long-term diversification rate, are not significantly different from zero at either mid- (−0.000994 to 0.000891) or low (−0.000493 to 0.00246) paleolatitudes at any spatial scale (Fig. 4). This indicates a lack of support for the hypothesis of sustained exponential background diversification (*3*, *14*). Regressions of diversity solely as a function of time within individual pre-Cenozoic and Cenozoic diversification phases are also nonsignificant (fig. S11). Furthermore, we do not find evidence for low diversity immediately after mass extinction events at the time scale of our analysis (bin durations averaging 11 Ma), which suggests that the postextinction recovery of regional diversity has generally been rapid.

In contrast to the lack of secular temporal trends in Phanerozoic marine animals, individual groups show marked variation in diversity through time (Fig. 3). Ecological limits imposed by finite resources such as energy and space (*30*) provide one intuitive explanation for why highly dynamic patterns within individual groups sum to produce highly constrained net diversity in marine animals throughout the Phanerozoic (with the exception of a stepwise increase in the early Cenozoic). Zero-sum dynamics could result from direct biotic competition between specific groups or more diffuse competition among multiple clades (*26*) but could also arise via chance.

Patterns of global diversity through time have been the focus of seminal studies in paleobiology, and the implications of these patterns for macroevolutionary theory have long been debated (*2–5*, *11*, *14*, *24*, *25*). Our spatially explicit analysis provides a different conception, in which the variation in regional diversity is partitioned between time- and environment-dependent explanations. Diversity varies by several orders of magnitude among marine environments on Earth today (*19*), and we find that it has done so for much of the Phanerozoic. In contrast, we find little evidence for sustained increases in diversity through time. We also cast doubt on the prospect of directly estimating variation in true global diversity based on current knowledge of the fossil record. These observations urge scrutiny of the focus on time and time-varying climate or Earth system parameters in global fossil record studies (*2*, *7*, *8*, *10*). Nevertheless, the importance of local environment as a driver of regional diversity indicates that variation in summed global diversity might ultimately result from shifts in Earth's climate and tectonic state. By unmasking the spatial component of variation in diversity—hitherto obscured by global curves—our approach raises intriguing possibilities for the fossil record to shed light on the historic drivers of biological diversity on Earth.
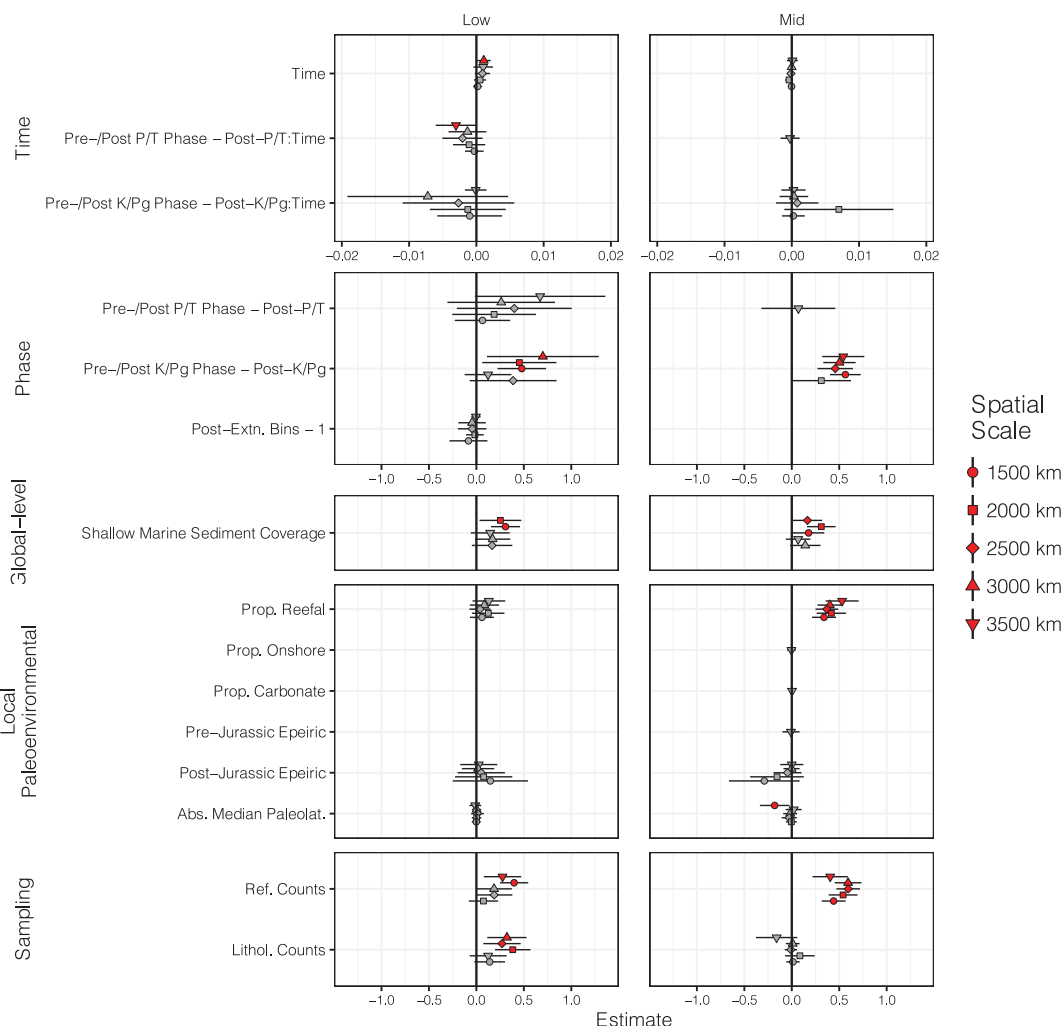
Fig. 4. Model-averaged parameter estimates for coefficients at low and mid-paleolatitudes. Models were fitted to spatially standardized diversity estimates using SQS (quorum = 0.9). See table S1 for descriptions of explanatory variables. Confidence intervals represent interquartile ranges. Red points signify estimates that do not overlap with zero; gray points indicate points that do. Extn., extinction; Prop., proportion; Abs., absolute; Paleolat., paleolatitude; Ref., reference; Lithol., lithology.

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Across time, but also across space

Fossils, especially those from marine systems, have long been used to estimate changes in patterns of diversity over time. However, fossils are patchy in their occurrence, so such temporal estimates generally have not included variations due to space. Such a singular examination has the potential to simplify, or even misrepresent, patterns. Close *et al.* used a spatially explicit approach to measure diversity changes in marine fossils across time and space. They found that, like modern systems, diversity varies considerably across space, with reefs increasing diversity levels. Accounting for this spatial-environmental variation will shed new light on the study of diversity over time.

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