

Plate tectonic regulation of global marine animal diversity

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Valentine and Moores [Valentine JW, Moores EM (1970) *Nature* 228:657–659] hypothesized that plate tectonics regulates global biodiversity by changing the geographic arrangement of continental crust, but the data required to fully test the hypothesis were not available. Here, we use a global database of marine animal fossil occurrences and a paleogeographic reconstruction model to test the hypothesis that temporal patterns of continental fragmentation have impacted global Phanerozoic biodiversity. We find a positive correlation between global marine invertebrate genus richness and an independently derived quantitative index describing the fragmentation of continental crust during supercontinental coalescence–breakup cycles. The observed positive correlation between global biodiversity and continental fragmentation is not readily attributable to commonly cited vagaries of the fossil record, including changing quantities of marine rock or time-variable sampling effort. Because many different environmental and biotic factors may covary with changes in the geographic arrangement of continental crust, it is difficult to identify a specific causal mechanism. However, cross-correlation indicates that the state of continental fragmentation at a given time is positively correlated with the state of global biodiversity for tens of millions of years afterward. There is also evidence to suggest that continental fragmentation promotes increasing marine richness, but that coalescence alone has only a small negative or stabilizing effect. Together, these results suggest that continental fragmentation, particularly during the Mesozoic breakup of the supercontinent Pangaea, has exerted a first-order control on the long-term trajectory of Phanerozoic marine animal diversity.

paleogeography | paleobiology | biodiversity | biogeography

Plate tectonics changed the way geoscientists view the dynamic Earth and its geological history. Among the first to articulate some of the fundamental biological expectations were Valentine and Moores (1), who hypothesized that the aggregation of continental crustal blocks into supercontinents may reduce biodiversity and that the breakup and separation of continental blocks may increase biodiversity. Many environmental factors have been cited as potential mechanisms relating biodiversity to global tectonics, including changing climate, sea level, nutrient flux, ocean–atmospheric circulation, total habitable area, and intercontinental connectivity (1–7). Hypothesized biotic drivers of biodiversity may also be tectonically influenced. For example, increased nutrient flux from oceanic rifting and continental denudation could affect global productivity and biodiversity (8), and coevolutionary interactions could be facilitated by changing geographic connectivity (9).

Despite the strong theoretical underpinnings of the supercontinent coalescence–breakup model of Phanerozoic biodiversity (1–7), there have been few quantitative tests of the hypothesis. Most attempts have used biogeographic patterns to test for evidence of secular trends in provinciality rather than directly testing for covariation between marine richness and plate tectonics (3, 10). This is, in part, because of concerns over the accuracy of fossil-based biodiversity reconstructions,

which may be complicated by spatial and temporal inequities in the quantity or quality of samples (11–18). Nevertheless, many major features in the fossil record of biodiversity are consistently reproducible, although not all have universally accepted explanations. In particular, the reasons for a long Paleozoic plateau in marine richness and a steady rise in biodiversity during the Late Mesozoic–Cenozoic remain contentious (11, 12, 14, 19–22).

Here, we explicitly test the plate tectonic regulation hypothesis articulated by Valentine and Moores (1) by measuring the extent to which the fragmentation of continental crust covaries with global genus-level richness among skeletonized marine invertebrates. To quantify paleogeographic state over time, we developed an index that is sensitive to the connectivity of continental crustal blocks, and we apply that index to reconstructed paleogeographies from an EarthByte (earthbyte.org) paleogeographic rotation model (23). The continental fragmentation index time series is then compared with estimates of global richness independently compiled from fossil occurrences in the Paleobiology Database (paleobiodb.org) (24).

Global tectonics is also predicted to exert a first-order control on regional patterns of sedimentation (25–28). Therefore, it is conceivable that an observed correlation between fossil diversity and tectonics could reflect a sampling bias in fossil data that is related to temporal variation in the abundance of preserved marine rock (15, 29–33). To assess this alternative hypothesis, we also compare our paleogeography and biodiversity time series with an independent time series describing the amount of North American marine rock (34). Other common data quality concerns in fossil biodiversity studies, such as incorrect taxonomic assignments (11), should be independent of paleogeography and are unlikely to drive observed patterns.

Significance

Understanding the processes that govern biodiversity is a central goal of biology. It has been hypothesized that global biodiversity is influenced by tectonically driven shifts in the arrangement of continental crust. We use globally distributed fossil data and quantitative analyses of shifting continental configurations in paleogeographic reconstructions to test this hypothesis. A significant component of the trajectory of marine animal diversity over the past 443 million years is attributable to the assembly and disassembly of the supercontinent Pangaea.

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Data deposition: The data reported in this paper have been deposited in a GitHub repository (<https://github.com/UW-Macrostrat/PNAS.201702297>).

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Results

Paleogeography. We developed an index to quantitatively describe the degree of continental fragmentation during the Phanerozoic (*Materials and Methods*). The index ranges between zero and 1, with 1 representing the state in which all continental blocks are completely separated, and zero representing the state in which all continental blocks are contiguous and arranged in a way that minimizes their ocean basin-facing perimeter. We calculate the index only for those continental blocks that are present throughout the entire duration of the Phanerozoic. Together, these persistent continental fragments comprise 88% of total present-day continental area in the EarthByte model (23).

The continental fragmentation index (Fig. 1) increases at the start of the Phanerozoic (541 Ma) in response to the breakup and dispersal of crustal blocks that previously formed the Proterozoic supercontinent of Rodinia (35). Peak Paleozoic continental disassembly occurs at ~470 Ma, near the Early/Middle Ordovician boundary. A series of alternating plateaus and declines follows the Late Ordovician peak in continental fragmentation, reflecting the progressive reaggregation of continental blocks, which ultimately culminated in the formation of the Phanerozoic supercontinent Pangaea.

The most notable feature of the Mesozoic portion of the fragmentation index is a steady rise that begins in the mid-Jurassic and culminates in a Phanerozoic maximum during the Late Cretaceous. This protracted increase in continental fragmentation reflects the breakup of Pangaea and, notably, the southern continent of Gondwana. Today, Gondwana is represented by the distinct continents of South America, Africa, Antarctica, and Australia, as well as the subcontinent of India (36). The marked decrease in the continental fragmentation index during the Late Cenozoic reflects the collision of dispersed Gondwanan continental blocks with Northern Hemisphere continents. This transition is most dramatically represented by the isolation of India during peak continental fragmentation and its mid-Cenozoic collision with Asia to form the Himalayas. If present-day plate

motions persist, the index will continue to decline as the last remnant of the ancient Tethys Sea, the Mediterranean, is eliminated by the collision of Africa with Eurasia. However, opening of the East African rift may partially offset this decrease.

Global Biodiversity. Global biodiversity estimates used here derive from the Paleobiology Database and are broadly comparable to other assessments of marine animal richness (12, 14). The specific Phanerozoic trajectory of marine animal genus richness remains contested (11, 13, 15–17, 21), but analyses consistently reproduce several long-term patterns. A quick rise to a volatile Paleozoic plateau (19), a drop during the end-Permian, a prolonged Early Mesozoic recovery, and a subsequent rise (9, 20–22) that eventually exceeded the Paleozoic maximum in the Late Mesozoic or Early Cenozoic (Fig. 2*A* and *B*) are all consistent features of the paleontological literature.

There are a number of qualitative similarities between the trajectory of Phanerozoic biodiversity (Fig. 2) and continental fragmentation (Fig. 1), which is consistent with the original formulations of the hypothesis (1). These similarities are quantitatively expressed by a positive rank-order correlation between continental fragmentation and global genus richness (range-through $\rho = 0.40$; in-bin $\rho = 0.51$). The correlation improves if the Cambrian–Ordovician, which witnessed the initial evolution and diversification of marine animal communities, is removed from the analysis (range-through $\rho = 0.64$; in-bin $\rho = 0.57$). The improvement in correlation is not because the Cambrian–Ordovician exhibits a pattern contrary to the hypothesis; it is an interval of rising biodiversity coincident with supercontinent breakup (20, 37, 38). However, the Cambrian–Ordovician deviates from the overall pattern in that the magnitude of fragmentation is relatively small (Fig. 1), but biodiversity accumulates at an unusually high rate relative to the rest of the Phanerozoic (Fig. 2*A*).

To explore the impact that individual time intervals have on the overall strength of the correlation between genus richness and continental fragmentation (Fig. 2*C* and *D*), we performed

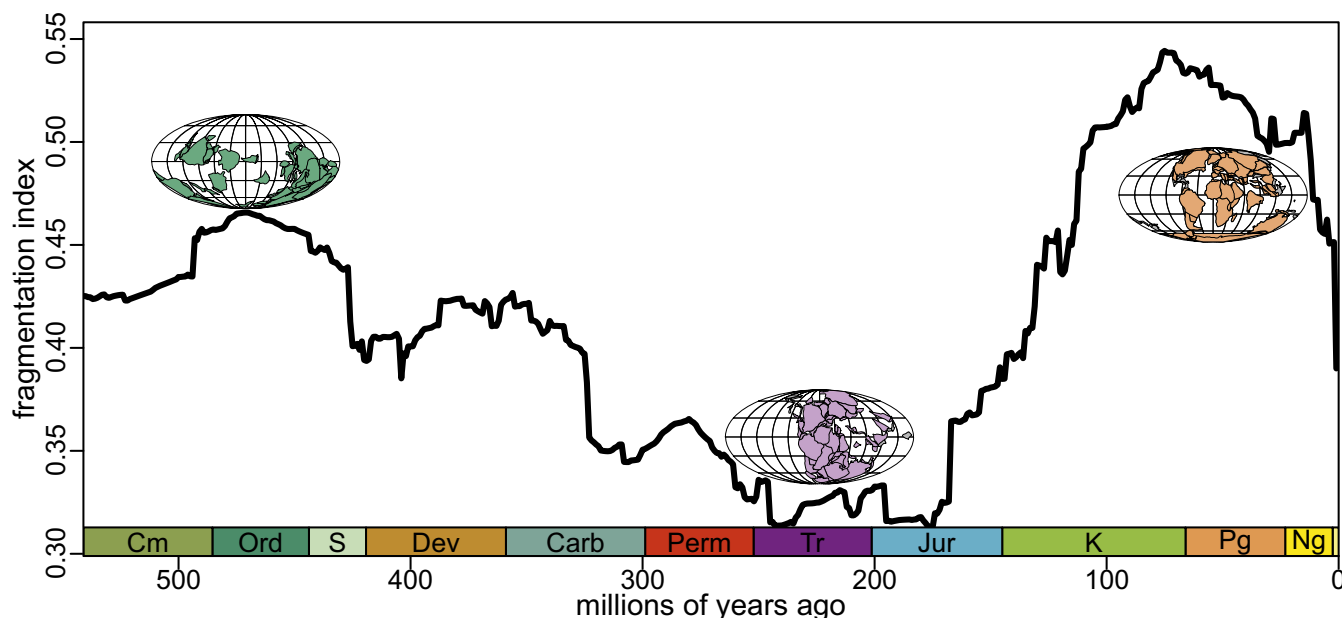


Fig. 1. An index of continental block fragmentation derived from the EarthByte paleogeographic reconstruction models calculated in million-year increments. An index value of unity indicates no plates are touching; an index value of zero corresponds to the state that would be achieved if all of continental blocks were contiguous and arranged in a single mass with a minimal ratio of perimeter to area. Example EarthByte-derived configurations (23) for the Early/Middle Ordovician (470 ma), the Middle/Late Triassic (237 ma), and Paleocene/Eocene (56 ma) are shown for visual reference. Smaller plates that do not persist throughout the entire Phanerozoic are not used in the index calculations and are grayed out in the inset maps. Carb, Carboniferous; Cm, Cambrian; Dev, Devonian; Jur, Jurassic; K, Cretaceous; Ng, Neogene; Ord, Ordovician; Perm, Permian; Pg, Paleogene; S, Silurian; Tr, Triassic.

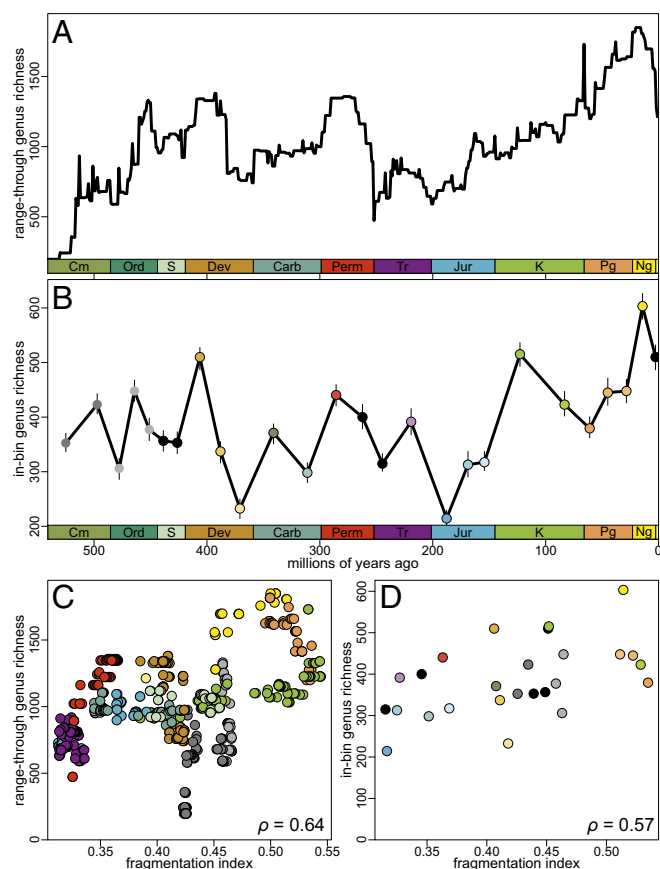


Fig. 2. Global time series of skeletonized marine genus richness and relationships with the continental fragmentation index (Fig. 1). (A) Range-through generic richness calculated in million-year increments. (B) Epoch-level, in-bin genus richness standardized using shareholder quorum subsampling (SQS) (18). Bars on points are 95% confidence intervals. Black circles identify custom epochs introduced to make interval duration more balanced. (C) Scatterplot of range-through generic richness vs. the continental fragmentation index. (D) Scatterplot of in-bin generic richness vs. the fragmentation index; the index value for the interval midpoint is shown. Spearman's ρ values in C and D do not include the Cambrian (dark gray points) and Ordovician (light gray points). Carb, Carboniferous; Cm, Cambrian; Dev, Devonian; Jur, Jurassic; K, Cretaceous; Ng, Neogene; Ord, Ordovician; Perm, Permian; Pq, Paleocene; S, Silurian; Tr, Triassic.

a jackknife analysis in which epochs were successively removed from the time series and the correlation recalculated without those data. This analysis attempts to specifically assess the contribution of each epoch to the overall correlation between biodiversity and continental fragmentation. For example, it has been hypothesized that the Pliocene–Pleistocene is fundamentally undersampled in fossil data compilations (39); this may be so, but we find that removing the Pliocene–Pleistocene from the analysis has little quantitative effect. Indeed, no single epoch drives the observed correlation (Fig. 3A). The Cisuralian (Early Permian) departs the most from the overall trend, with relatively high richness (Fig. 2A) during the last stages before final coalescence of Pangaea (Fig. 1). Conversely, the Triassic–Early Jurassic epochs are the most important drivers of the relationship, as they record a long interval of relatively low richness that is concurrent with the supercontinent Pangaea. However, even the removal of these data points does not strongly weaken the overall correlation between continental fragmentation and marine richness.

Last, we conducted basic time series analyses to examine the temporal dynamics of the relationship. First, we performed a

cross-correlation to assess the similarity of supercontinent fragmentation and global biodiversity when the biological response is lagged relative to tectonics and vice versa. The correlation between genus richness and fragmentation is high without a temporal lag, but it remains comparable even if the biodiversity time series is lagged relative to tectonics by several tens of millions of years (Fig. 3B). If the lag direction is reversed, such that the state of biodiversity precedes the state of continental fragmentation, then the correlation declines steadily toward zero as the lag increases. The same pattern of asymmetry and comparable lag-times is also apparent if subsampled biodiversity at the stage level is used (Fig. S1). Asymmetry is an indicator of statistical robustness because it is common for correlations to run in both lag directions when relationships are spurious. In this case, we only observe continued correlation in the direction consistent with general model expectations; there is no intuitive reason why changes in biodiversity should presage rearrangements of continental crust by tens of millions of years (1–7). Second, we observe no correlation between the continental fragmentation index and genus richness when the data are transformed by taking first differences ($\rho = 0.01$, $P = 0.79$). This finding indicates that the observed correlation in the raw time series is driven by the similarity of their long-term trends. In contrast, there is no observed relationship between continental fragmentation and marine richness on shorter, million-year timescales. This finding, too, is consistent with general model expectations, as continental configuration only changes over longer timescales.

Marine Rock Record. An independent time series describing the quantity of marine rocks on the continent (34) is also correlated with the continental fragmentation index ($\rho=0.33$; Fig. 3C). This result is consistent with the hypothesis that a principal mode

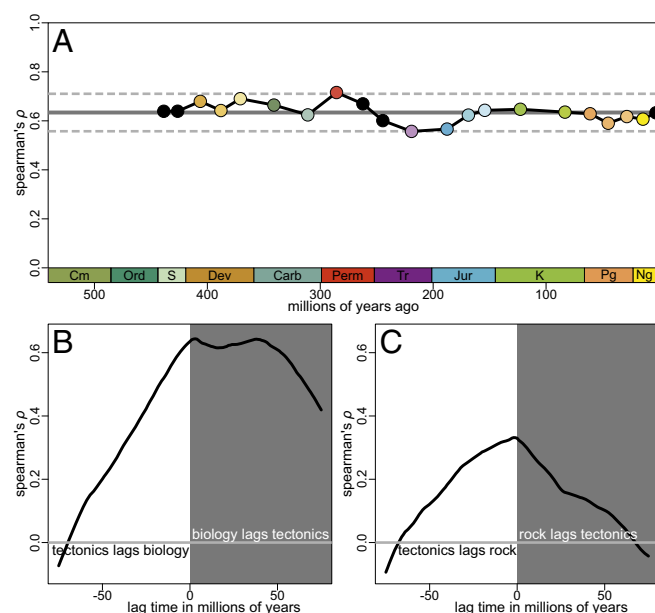


Fig. 3. Evidence for long- versus short-term covariation between tectonics and biodiversity. (A) Each point represents the correlation between the fragmentation index and marine richness if that geologic epoch is removed from the time series. Dotted lines represent 2σ from the mean. (B) Changing correlation between the fragmentation index and global richness when lagging the time series. (C) Changing correlation between the fragmentation index and marine rock when lagging the time series. Spearman's ρ values denote only post-Ordovician relationships. Carb, Carboniferous; Cm, Cambrian; Dev, Devonian; Jur, Jurassic; K, Cretaceous; Ng, Neogene; Ord, Ordovician; Perm, Permian; Pg, Paleogene; S, Silurian; Tr, Triassic.

of variability in the amount of shallow marine sedimentation occurring on the continents is attributable to the supercontinent coalescence–breakup cycle (28). However, this result also raises the possibility that there is a rock quantity-related sampling bias in the fossil data (15, 29–33), and the observed correlation between continental fragmentation and biodiversity instead reflects a confounded relationship with marine rock quantity. However, the raw time series describing the quantity of marine rock is uncorrelated with global marine richness ($\rho = 0.01$). Only when the marine richness and rock quantity time series are detrended by a first-differences transformation does any correlation emerge ($\rho = 0.22$, $P \ll 0.01$).

Together, these analyses indicate that there are fundamentally different temporal patterns of correlation among the three time series of continental fragmentation, marine sedimentation on the continents, and global biodiversity. Genus richness remains correlated with continental fragmentation when the biodiversity time series is lagged relative to the fragmentation index by tens of millions of years, but there is no comparable lagged relationship between marine rock and continental fragmentation (Fig. 3 *B* and *C*). Furthermore, marine richness and North American sedimentation are correlated when they are detrended by taking first differences, but there is no correlation between continental fragmentation and biodiversity when the data are detrended. The opposing nature of these results is not consistent with a confounded three-way relationship in which rock record-controlled sampling biases have driven a spurious correlation between marine richness and continental fragmentation. There is also no evidence to support the hypothesis that the long-term trajectory of Phanerozoic marine richness is an artifact of increasing rock quantities (11, 12, 14, 29, 30). Results instead suggest that only a small percentage of variance in biodiversity is explained by rock quantity, and only over short timescales (40, 41). Longer-term trends in biodiversity are instead well predicted by the supercontinent coalescence–breakup cycle.

Discussion

The history of marine biodiversity broadly mirrors patterns of supercontinent coalescence–breakup. This similarity is most dramatically expressed by a pronounced Late Mesozoic rise in both time series. This observation naturally raises a question (1–7): What aspects or correlates of continental crustal fragmentation are ultimately responsible for driving the trajectory of Phanerozoic marine richness?

The creation and destruction of intercontinental barriers to biological dispersal was originally envisioned as a primary causal connection between tectonically driven shifts in paleogeography and global biodiversity (1–7). Under this model, continental fragmentation results in the formation of geographic barriers that separate formerly well-mixed faunas. Vicariance then leads to evolution of new lineages and contributes to an overall increase in global taxonomic richness. However, eustatic sea level (3, 42–45) and ocean–atmospheric circulation (e.g., carbon cycling, global climate) (3, 38, 46, 47) can also be directly or indirectly affected by shifts in the geographic arrangement of continental crust. Because each of these tectonically linked processes has been invoked separately as a driver of global biodiversity, it is difficult to identify a single causal mechanism.

The correlations documented here are driven primarily by broad temporal alignment of Phanerozoic highs and lows in biodiversity and continental fragmentation. Similarities are particularly well expressed during intervals of increasing continental fragmentation and increasing biodiversity. Continental fragmentation–forced increases in biodiversity have been posited in one form or another for several different times in Earth history (20, 37, 38). The Cambrian–Ordovician is coincident with the final fragmentation of Rodinia, and the Late Mesozoic increase

in biodiversity is concurrent with peak-Phanerozoic fragmentation following the breakup of Pangaea.

Evidence that continental coalescence phases cause declines in biodiversity is less robust. The latter half of the Paleozoic records a prolonged period of plate collision to form Pangaea (Fig. 1), but this interval of supercontinent assembly is not matched by a corresponding decrease in marine richness (Fig. 2). Indeed, it has been argued that richness was on a slight upward trend during the Late Paleozoic (48). Continental fragmentation has decreased since reaching a peak during the Late Cretaceous. Although biodiversity also appears to be in a declining phase (Fig. 2), it is not clear to what extent this decline reflects an actual downturn in biodiversity (22, 49) versus idiosyncratic paleontological sampling of the tropics (39).

The suggestion that continental fragmentation and coalescence establish different biodiversity regimes has several implications for understanding the history of Phanerozoic marine richness. First, it implies that the Late Permian–mid-Jurassic biodiversity minimum was initiated by the end-Permian mass extinction (50), and the subsequent recovery was prolonged because the world was in a coalescence regime. Without the end-Permian mass extinction, the Paleozoic biodiversity plateau (51) would likely have persisted until the start of the next fragmentation regime. Second, if coalescence does serve to stabilize biodiversity, then the increase in genus richness observed during the Cenozoic will likely slow or cease sometime in the relatively near future (22, 49). A new interval of plate aggregation has been underway since the Late Cretaceous; this also suggests that any downturn in present-day taxonomic richness (52) may be followed by a protracted recovery phase that is more analogous to the Triassic than it is to the Paleogene, at least from the perspective of long-term plate tectonic boundary conditions. Finally, these results help to bridge long-debated, contrasting models for Phanerozoic fossil diversity, namely diversity-dependent logistic growth (12, 14, 51) versus nearly unbridled exponential increase (1, 21, 53, 54). Under our hybrid model, whether biodiversity is in an asymptotic or growth phase depends on the current paleogeographic continental fragmentation–coalescence regime.

The identification of paleogeographically mediated regimes that control biodiversity does not preclude most alternative hypotheses about long-term macroevolutionary mechanisms. For example, our results are consistent with models that emphasize the importance of mass extinctions and recovery intervals in governing the history of life (55). Indeed, we attribute the Late Permian–Middle Jurassic biodiversity low to a coupling of the end-Permian mass extinction and a continental coalescence regime. This view is also compatible with many hypotheses that are primarily biotic in nature. Changing productivity patterns (8), coevolutionary dynamics (9), latitudinal biodiversity gradients (48), incumbency and invasibility dynamics (56), and morphological/ecological character displacement (57) may all be facilitated or triggered by changing geographic connectivity. Even biotic hypotheses that do not have an obvious connection to the geographic arrangement of continental crust, such as the emergence of sexual characteristics (22), are, at worst, independent of the tectonic dynamics presented here and should not be considered mutually exclusive. Nevertheless, our results do provide compelling evidence that the shifting distribution and connectivity of continental landmass, either as the primary forcer or as a complement to other macroevolutionary processes, has been a fundamental driver of long-term global Phanerozoic biodiversity patterns.

Materials and Methods

Paleogeographic Reconstruction. Palecontinent geometries and positions were obtained from a curated version of an EarthByte (earthbyte.org) tectonic plate reconstruction model (23). Modifications involved the correction of basic geometry errors (e.g., crossing plate polygon vertices) and the

culling of continental plates that do not persist or that are not recognized throughout the entire Phanerozoic.

The paleogeographic reconstructions for each time interval were summarized by a new index of fragmentation. Our procedure creates two paleogeographic map variants for each 1-million-year increment. The first variant is a map of tectonic plates rotated to their inferred paleocoordinates under the rotation model. The second is identical to the first, but with all touching plate borders removed. The perimeter of all plates in the merged map is then divided by the total perimeter of all plates in the unmerged map; this creates an index equal to 1 when all plates are not touching (complete plate fragmentation). The circumference of a circle equal to the area of the continental plates is subtracted from this so that zero represents maximum aggregation. All geometry operations were conducted using the PostGIS (postgis.net) extension of PostgreSQL.

Fossil Biodiversity. Fossil data (downloaded January 16, 2017) comes from the Paleobiology Database (PBDB; paleobiodb.org) data service (24). Occurrences are limited to skeletonized marine invertebrates because of their abundant fossil records (58). Specifically, we include here Brachiopoda, Bivalvia, Anthozoa, Trilobita, Gastropoda, Crinoidea, Blastoidea, Edrioasteroidea, Ammonoidea, Nautiloidea, and Bryozoa. This constitutes the bulk of fossil occurrences in the PBDB. The dataset contains 20,712 unique genera, represented by a total of 691,495 fossil occurrences. A total of 17,725 unique genera and 569,808 occurrences remain after removing those that are not temporally constrained to two adjacent epochs in our timescale, that are not identified to the genus level, or that come from ephemeral continental plates that were not used in this analysis.

Here we use the number of unique genera, i.e., genus richness, as our measure of biodiversity. We present both uncorrected range-through genus richness and sampling standardized, SQS, in-bin genus richness (18). Range-through richness is calculated based on the ages of the first and last fossil occurrence of each genus in the Paleobiology Database. The maximum estimated age of the oldest occurrence and minimum estimated age of the youngest occurrence originate from the "max.ma" and "min.ma" fields, respectively. The pull-of-the-recent effect is subdued in this analysis because only fossil data are used. Standardized in-bin generic richness is calculated using S.M. Holland's R code for SQS (18), which subsamples a temporal bin based on the evenness of observed occurrences in that bin. We aggregated the Pliocene–Pleistocene and Guadalupian–Lopingian and divided the Triassic, Silurian, and Cambrian periods into halves to make the duration of time bins more balanced.

Analytic Accuracy. Most recent biodiversity analyses typically do not use range-through richness estimates (Fig. 2A), and instead rely on in-bin, sampling standardized biodiversity estimates (12, 14, 18) in some capacity (Fig. 2B). However, it has been noted that some sample size standardization methods can introduce other idiosyncrasies that distort biodiversity estimates (17), or possibly even remove real biological and environmental signals from the estimates (21, 40). Consequently, there is not a single definitive history of Phanerozoic fossil diversity.

Nevertheless, there are few a priori reasons to believe that taxonomic practice, geographically variable sampling, or other errors in our analysis should combine so as to yield systematic correlations with a completely independent time series. Moreover, other factors governing the nature of the fossil record that are linked to tectonics, such as changing sea level (3, 42–45) or the changing latitudinal distribution of continents (48), cannot be viewed only as potential sampling biases in this context. Instead, these types of long-term shifts in the character of the fossil record are precisely the type of process signals that have been hypothesized to couple shifting tectonic state to actual changes in the biosphere (4, 40, 59, 60). A strictly spurious correlation in the results documented here is only expected if global richness was used to generate paleogeographic reconstructions. Although patterns of regional faunal similarity and endemism are sometimes used to aid paleogeographic reconstructions, global richness, per se, has no direct bearing on how plate tectonic reconstructions are made.

Marine Rock. The Macrostrat database records the lithologic, environmental, spatial, and temporal attributes of geologic units derived from published stratigraphic columns (26, 61, 62). Although some data are global in scope, Macrostrat's coverage is complete only for North America. We therefore limit our rock record analysis to the North American portion of the database. Thus restricted, the data include 17,996 stratigraphic marine units, which are grouped into 4,585 unconformity-bound "sediment packages" that are comparable to third- or fourth-order stratigraphic sequences (10^5 - to 10^7 -y duration). All data are accessible via the Macrostrat data service.

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