Global plate model choice impacts reconstructions of the latitudinal biodiversity gradient

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# Abstract

The latitudinal biodiversity gradient of declining species richness from the Equator towards the poles is one of the most pervasive macroecological patterns on Earth today. However, the ubiquity of this trend over geological timescales remains unclear. One reason for this uncertainty is that palaeobiologists need Global Plate Models to estimate the latitudinal position of organisms’ remains at time of deposition. However, Global Plate Models only constitute hypotheses for how tectonic plates have moved over Earth’s history, and so reconstructions of the latitudinal biodiversity gradient might also vary based on the Global Plate Model used. Here, using the fossil record of five major marine invertebrate groups, we evaluate the impact of Global Plate Model choice on reconstructions of the latitudinal biodiversity gradient over the Phanerozoic. Our results show that Global Plate Model choice can lead to different conclusions about the shape and strength of latitudinal biodiversity gradients in deep time, even at a coarse spatial scale. These findings suggest additional caution is needed when reconstructing deep-time macroecological patterns and macroevolutionary events, such as the origin of the present-day latitudinal biodiversity gradient. We therefore advocate for future palaeobiogeographic studies to conduct sensitivity analyses testing the impact of Global Plate Model choice on their conclusions, and for greater interdisciplinary collaboration between palaeobiologists and palaeogeographic modellers to avoid common issues in the use of Global Plate Models.

# Keywords

Latitudinal diversity gradient, palaeobiogeography, palaeobiology, tectonics, palaeogeographic uncertainty

# Introduction

Today, species richness decreases from the tropics to the poles. This phenomenon, known as ‘The Latitudinal Biodiversity Gradient’, is one of Earth’s longest recognised and most prevalent macroecological patterns [1–4]. It has historically been observed across numerous taxonomic groups in the terrestrial [2,3,5] and marine realm [6,7], and is potentially currently experiencing a major transition [8–10]. The fossil record suggests that such changes in the shape and strength of latitudinal biodiversity gradients (LBGs) is not unique, with flattened and bimodal gradients observed across a range of taxonomic groups at various points in Earth’s geological history [11–21]. Several studies have demonstrated that the broadly unimodal gradient–tropical peaks and poleward declines in taxonomic richness–have been restricted to the last 30 million years (Myr), and intervals of the Palaeozoic when cool icehouse climatic regimes dominated [4,16,21–24]. Conversely, during intervals of warmer climatic conditions (i.e. greenhouse and interglacial periods), some taxonomic groups have exhibited flattened latitudinal biodiversity gradients, or even temperate peaks in biodiversity [12,13,15,17,18,25,26]. However, recent work suggests that our ability to recognise different types of latitudinal biodiversity gradient in deep time is hindered by incomplete and heterogeneous spatial sampling in the fossil record, casting doubt on the reliability of these findings [27,28].

When examining macroecological patterns–such as the latitudinal biodiversity gradient–in the present day, neontologists use the geographic coordinates where they collected their samples to infer the spatial distributions of their taxa. However, palaeobiologists must contend with the movement of tectonic plates over geological timescales, which results in the geographic coordinates for where a fossil was found not necessarily representing its location *in* *vivo*. Being able to accurately translate modern-day locality coordinates into the geographic distributions of fossil taxa is therefore a fundamental step in estimating the latitudinal biodiversity gradient in deep time. To do this, palaeobiologists routinely use Global Plate Models (GPMs), sometimes also referred to as ‘palaeorotation models’ or ‘plate rotation models’ [16,19,20,26,29,30]. These models constitute hypotheses for the tectonic evolution of the Earth, developed by modelling the motion of continental–and sometimes marine–plates across its surface through geological time. Many of these GPMs have been constructed [e.g. 31,32–34], varying in the how they define the geological boundaries of continents and how they rotate them through time, having consequences for how fossil occurrences might be palaeogeographically reconstructed [35,36]. However, to date, few palaeobiological studies (though see refs. [37,38]) have considered how different GPMs might influence reconstructions of the latitudinal distributions of fossil occurrences.

Recent work has quantified the extent to which GPMs can differ in their estimation of the palaeogeographic distribution of fossil occurrences [36]. Here, we evaluate how sensitive reconstructions of the latitudinal biodiversity gradient in deep can be to GPM choice. Specifically, we test the extent to which the shape and strength of latitudinal biodiversity gradients vary when using different GPMs, throughout the entire Phanerozoic (i.e. the last 540 million years). To do so, we estimate the palaeogeographic distribution of fossil occurrences for five major marine invertebrate groups, using data from The Paleobiology Database, and four commonly applied GPMs. We then describe the raw latitudinal distribution of occurrences generated by each GPM before reconstructing the latitudinal biodiversity gradient using coverage-based rarefaction, and quantifying the variability of reconstructed gradients through time between GPMs.

# Materials and Methods

## Occurrence data

We downloaded Fortunian–Holocene (541–0 Ma) fossil occurrence data from the Paleobiology Database (PBDB; <https://paleobiodb.org/>) for five major marine invertebrate groups (Bivalvia, Brachiopoda, Cephalopoda, Gastropoda, Trilobita) on December 16 2024. Fossil occurrence data were downloaded using the PBDB Application Programming Interface (API) service and were restricted to marine environments and regular preservation (i.e. excluding form taxa and ichnotaxa). Occurrence data were subsequently binned into chrostratigraphic stage-level time bins following the International Geological Time Scale ver. 2023/09, with the exception of Holocene and Pleistocene stages which were collapsed into their equivalent Epoch-level bins (i.e. Holocene and Pleistocene). Temporal binning was carried out using the bin\_time() function from the palaeoverse R package ver. 1.4.0, with the ‘majority’ approach [39]. Subsequently, all occurrences with less than 50% of their age range covered by their assigned temporal bin were removed. To minimise differences in how individuals enter data into the PBDB, such as geographically lumping or splitting of collections, we rounded the geographic coordinates of all fossil collections to two decimal places and collapsed collections from the same time and place with the same occurrences. After data preparation, the occurrence dataset contained 281,243 fossil occurrences from 67,198 fossil collections.

## Palaeogeographic reconstruction and palaeolatitudinal binning

To reconstruct the palaeogeographic distributions of fossil occurrences, we used localities’ present-day coordinates and midpoint age from their assigned temporal bins with three Global Plate Models: GOLONKA [32], TorsvikCocks2017 [40], PALEOMAP [33], and MERDITH2021 [34]. Palaeogeographic reconstructions were generated using the GPlates Web Service (<https://gwsdoc.gplates.org>) via the palaeorotate() function in palaeoverse ver. 1.4.0 [39]. For each Global Plate Model, fossil occurrences were binned into one of six equal-area latitudinal bins via the lat\_bins\_area() function in palaeoverse ver. 1.4.0 [39], using the estimated palaeolatitudes from palaeogeographic reconstruction (Table S1). These latitudinal bins broadly represent three climatic zones within each hemisphere today: tropical, temperate, and polar. The number of fossil occurrences which were unable to be palaeogeographically reconstructed due to model incompatibility was recorded for each Global Plate Model.

## Quantifying the latitudinal biodiversity gradient

Subsequent data manipulation and visualisation were carried out using the Tidyverse suite of R packages [41] and the deeptime R package ver. 2.1.0 [42]. The raw number of genera were counted per stage per palaeolatitudinal bin for each Global Plate Model. We also estimated the latitudinal biodiversity gradient using coverage-based interpolation and extrapolation of Hill numbers with a coverage level of 0.4, using the R package iNEXT ver. 3.0.1 [43]. The rarefaction portion of this approach is equivalent to the method commonly known as Shareholder Quorum Subsampling (SQS) amongst palaeontologists [44,45]. Extrapolated values with an estimated sample size more than double that of the observed sample size were discarded, as recommended by [43].

We compared estimated latitudinal biodiversity gradients using two approaches. Firstly, for each stage, we computed the palaeolatitudinal bin with maximum estimated richness for each Global Plate Model. Subsequently, we calculated the number of stages in which estimated gradients agree, as well as the number of bins with a low, mid-, and high palaeolatitudinal peak in diversity. Secondly, we calculated the mean pairwise rank order difference between Global Plate Models. That is, for each stage and Global Plate Model, the palaeolatitudinal bins were put in rank order and the differences between models were computed and the mean calculated. To enable fair comparison between stages with a heterogeneous number of bins, average rank order differences were normalised by maximum possible average difference given the number of ranks available. The former of these metrics tests whether models agree on where peak diversity is concentrated in each Global Plate Model. The latter, tests for differences in the estimated ordered distribution of diversity (e.g. low-to-mid-to-high, mid-to-low-to-high, etc.).

As the estimated latitudinal distribution of biodiversity is closely tied to the distribution of fossil collections, we also computed the number of collections in each palaeolatitudinal bin and stratigraphic stage for each Global Plate Model. Furthermore, to test whether reconstructions of the latitudinal biodiversity gradient are more sensitive to Global Plate Model choice with increasing age of rotation, we calculated the median pair-wise palaeolatitudinal difference and great-circle distance (otherwise known as the Haversine distance) between Global Plate Models for each palaeogeographically reconstructed fossil collection. As we were only interested in palaeolatitudinal differences between models, we set palaeolongitudinal coordinates to 0 during calculations of great-circle distance. We include this metric in addition to palaeolatitudinal differences–measured in degrees of latitude–to account for the decreasing geographic distance between degrees of latitude with increasing latitude.

# Results

## Palaeogeographic reconstructions

Palaeogeographic reconstruction of fossil collections reveals that the number of collections available for allocation to palaeolatitudinal bins–collections which palaeocoordinates could be generated for–is dependent on the Global Plate Model used (**?@fig-coll-time**). While in most geological stages, the number of collections available for allocation to palaeolatitudinal bins is similar, it varies considerably for others (**?@fig-coll-time**). For example, of the 464 fossil collections in the Tortonian (Cenozoic), palaeocoordinates could be generated for 463 (~100%) fossil collections when using the PALEOMAP GPM, but only 250 (~54%) when using the GOLONKA and MERDITH2021 models. Conversely, of the 2503 fossil collections available for the Anisian (Triassic), palaeocoordinates were generated for 2442 (~98%) and 2376 (~95%) fossil collections using GOLONKA and MERDITH2021, yet only 2030 (~81%) when using PALEOMAP. This, along with spatial discrepancies in palaeogeographic reconstructions between Global Plate Models, resulted in the number of samples allocated to each palaeolatitudinal bin (low, medium, high palaeolatitudes) varing with Global Plate Model (Figure S2). Of the 93 geological stages, the number of palaeolatitudinal bins containing enough samples (i.e. fossil collections) for estimating genus richness also varies between Global Plate Models by two bins for 10 geological stages (~11%), one bin for 41 stages (~44%), and zero bins for 42 bins (~45%).

Analysis of the average pairwise palaeolatitudinal difference and pairwise great-circle distance between palaeogeographically reconstructed fossil collections indicate, on average, an increasing difference between Global Plate Models with age of reconstruction (**?@fig-spatial**). Specifically, average pairwise palaeolatitudinal differences between models is 2.54º latitude for the Cenozoic, 4.51º latitude for the Mesozoic, and 9.07º latitude for the Palaeozoic. Similarly, average pairwise great-circle distance between models is 263.12 km for the Cenozoic, 482.92 km for the Mesozoic, and 952.13 km for the Palaeozoic. However, while there is a general increasing difference between the palaeogeographic reconstruction of fossil collections with age of reconstruction, there are intervals of low palaeolatitudinal differences, for example in the Permian (**?@fig-spatial**). Nevertheless, prior to the Late Jurassic, there is generally a larger variability (spread) in palaeolatitudinal difference and great-circle distance than during the Late Jurassic, Cretaceous and Cenozoic (**?@fig-spatial**). For example, for some reconstructed fossil collections of the Jurassic (*n* = 846), Triassic (*n* = 197), Permian (*n* = 296), Carboniferous (*n* = 96), Devonian (*n* = 175), Silurian (*n* = 35), Ordovician (*n* = 512), and Cambrian (*n* = 258), palaeolatitudinal differences can be larger than 25º latitude.

The shapes of the reconstructed latitudinal biodiversity gradients for each geological stage are mostly consistent between Global Plate Models (**?@fig-gradients-sqs**; Fig. S2). For all three Global Plate Models, we observe the same overall trend in LBGs over geological time, namely that the peak in diversity tended to lie in the Southern Hemisphere prior to the Permian, but shifted to the Northern Hemisphere after the Permian, in all three models (**?@fig-heat-sqs**; Fig. S3). Throughout the Phanerozoic, peak diversity tended to appear at mid-latitudes (**?@fig-heat-sqs**; Fig. S3). However, during some intervals, we see considerable variation in the shape of the LBG between Global Plate Models. For example, during the Guzhangian, Tremadocian, Sakmarian, Artinskian, Ladinian, and Lutetian (**?@fig-gradients-sqs**; Fig. S2). Notably, this is not restricted to older intervals, with PALEOMAP reconstructions suggesting biodiversity peaked at high northern latitudes during several stages of the Paleogene (Aquitanian, Burdigalian, Langhian, Tortonian and Messinian), while GOLONKA and MERDITH2021 suggest a tropical peak in biodiversity (**?@fig-gradients-sqs**; Fig. S2).

We quantified the differences between diversity estimates obtained using the three Global Plate Models by evaluating the extent to which the models agreed on which palaeolatitudinal bin contained the most diversity in each hemisphere. Our results show that the extent to which peaks in reconstructed palaeolatitudinal diversity were consistent between models was variable through time, with only 64% of stages in the Palaeozoic, 76% in the Mesozoic, and 68% in the Cenozoic showing agreement between all three models. Notably, this differed between the two hemispheres, with 65% in the Northern Hemisphere and 50% in the Southern Hemisphere in agreement throughout the Phanerozoic (**?@fig-maxlat-sqs**). We also compared the shape of the LBGs by calculating the normalised average rank order difference of palaeolatitudinal bins between each pair of models. Overall, during the Mesozoic, there was more agreement between the models on the rank order of richness in palaeolatitudinal bins; no pair of models disagreed by more than 0.6 (**?@fig-rank-sqs**). However, during the Palaeozoic and Cenozoic, in some cases, pairs of models wholly disagreed on the rank order of diversity in palaeolatitudinal bins (normalised rank order difference of 1). This was less common when calculated using the raw data rather than the iNEXT diversity estimates (Fig. S6), likely due to the higher number of spatial bins containing enough data to be analysed.

# Discussion

Global Plate Models are regularly used in palaeobiology to reconstruct the palaeogeographic distribution of fossil occurrences [16,17,19,20,26,29,30,37]. In this study, we evaluated whether Global Plate Model (GPM) choice impacts the reconstruction of the latitudinal biodiversity gradient over the Phanerozoic. This gradient is one of the most universal patterns in macroecology today [2,3], and its accurate characterisation is dependent on the latitude at which occurrences are believed to have been observed. Our results demonstrate that choice of GPM when estimating the palaeolatitude of fossil occurrences (latitudinal position at time of deposition) can have a strong influence on the reconstructed latitudinal biodiversity gradient, including simple metrics such as the palaeolatitudinal bin with peak biodiversity (**?@fig-maxlat-sqs**).

The fossil record suggests that the latitudinal biodiversity gradient has varied in shape and strength through time, with previous analyses demonstrating unimodal, flattened, and bimodal gradients at various points in Earth’s geological history [e.g. 11,12–15,17–21]. Our results broadly agree with these findings, suggesting that the strength and shape of the latitudinal biodiversity gradient has varied through time, regardless of which GPM is used to reconstruct the palaeogeographic distribution of fossil occurrences. Previous work has also shown that apparent tropical peaks and poleward declines in taxonomic richness appear to be restricted to the last 30 million years, and intervals of the Palaeozoic when cool icehouse climatic regimes persisted [e.g. 4,20,21,23]. Conversely, during intervals of warmer climatic conditions (i.e. greenhouse and interglacial periods), various taxonomic groups have exhibited flattened latitudinal biodiversity gradients, or even temperate peaks in biodiversity [e.g. 11,14,15,17,18,20]. These studies suggest that climate is a major driver of the latitudinal biodiversity gradient over evolutionary timescales. However, the extent to which these observed latitudinal patterns are the result of inherent biases (e.g. variable fossil preservation, stratigraphic completeness), as opposed to biological processes, remains uncertain [e.g. 27,28,46]. Although our results support the notion of a dynamic gradient through time, we demonstrate that the strength and the shape of the latitudinal biodiversity gradient can vary depending on the GPM selected for palaeogeographic reconstruction. While this is most apparent in older geological stages, such as those of the Palaeozoic (Fig. **?@fig-gradients-sqs**; **?@fig-maxlat-sqs**; **?@fig-rank-sqs**), this can also impact reconstructions in more recent intervals such as the Tortonian, Cenozoic (**?@fig-gradients-sqs**).

Although during most geological stages there is broad agreement in the shape of the LBG between GPMs (**?@fig-gradients-sqs**), there are some for which this is not the case. For example, in 16 stage-hemisphere combinations (2 Northern Hemisphere, 14 Southern Hemisphere), disagreement between models can be as extreme as concluding that a latitudinal biodiversity gradient has a tropical peak in biodiversity under one model, and a polar peak in biodiversity under another, such as in the Southern Hemisphere of the Pridoli (**?@fig-gradients-sqs**; **?@fig-maxlat-sqs**). As such, the magnitude of palaeolatitudinal uncertainty represented across different GPMs can lead to markedly different LBG reconstructions and subsequent interpretations, even at a coarse spatial scale. This is most extreme in the Southern Hemisphere, likely a consequence of the lower number of occurrences and sampling coverage available for this hemisphere resulting in a higher sensitivity to small regional differences. Nevertheless, in less extreme examples, 43 stage-hemisphere combinations (19 Northern Hemisphere, 24 Southern Hemisphere) still demonstrate that the latitudinal biodiversity gradient would be reconstructed as having a tropical peak in diversity under one GPM, and a temperate peak in diversity under another. Consequently, in order to robustly test whether certain types of gradients are limited to specific climate states (e.g. unimodal gradients in icehouse periods), consideration of a range of Global Plate Models is required. Across temporal scales, differences in the reconstruction of latitudinal biodiveristy gradients between GPMs could also impact conclusions about the timing of events such as the origin of the present-day latitudinal biodiversity gradient [e.g. 21]. This is significant as to be able to test the evolutionary drivers of such events, their timing must be robustly constrained.

Using extrapolation as a means to address sampling bias may also be contributing to the strength of contrasts: our approach uses relative abundance data to determine how much extrapolation is required, meaning that estimates of richness can be highly sensitive to the shifting of a handful of collections between palaeolatitudinal bins. The LBGs reconstructed using the raw data are more consistent with each other than those produced using extrapolation and rarefaction (**?@fig-gradients-sqs**; Fig. S2); this could support the notion that our extrapolation approach is overly sensitive, but may also be due to a stronger signal of sampling bias pushing the raw LBGs closer to each other.

## Study limitations

The reconstruction of regional palaeobiodiversity is complicated. Despite the abundance of data within the Paleobiology Database, there remain numerous gaps in our dataset, illustrated by the absence of data in many individual palaeolatitudinal bins and even in a small number of entire temporal stages (**?@fig-gradients-sqs**; Fig. S2). While some of these gaps are attributable to a lack of shallow marine shelf area within certain spatio-temporal bins, many might be filled through additional fossil data collection in the future. Ideally, we would have preferred to subdivide data into more than six latitudinal bins for analyses. However, unfortunately, higher spatial resolution in this case results in noisier and patchier latitudinal gradients which are governed more strongly by sampling bias than by true diversity trends. Furthermore, while many recent spatial palaeobiodiversity studies have relied on using equal-area rectangular or hexagonal cells (e.g. refs [19,47,48]), further subdivision of our latitudinal bins would likewise introduce more noise into our analyses.

Another source of potential limitation lies in how we quantified the latitudinal biodiversity gradients. We decided to quantify the most diverse bin for each model and calculate the average rank order difference between pairwise models. Both of these metrics have the benefit of utilising relative diversity rather than raw differences, which should be less susceptible to sampling biases, especially when SQS is used. We found the rank order difference to be particularly promising as a way to quantify the relative differences between two gradients. However, the maximum average rank order difference is highly dependent on the number of bins that are sampled. We normalised for this dependence; however, it is important to note that with fewer bins it takes fewer rank order changes to achieve a higher normalised score.

There exist many other ways to quantify latitudinal biodiversity gradients. For example, the sum of squares could be used to calculate the raw deviation of one gradient from another. However, such a calculation could be heavily biased by sampling intensity. Another option would be to compare the fit of various regression models to assess the modality and shape of the gradients [19]. However, the sensitivity and success of this type of approach are heavily dependent on the number of latitudinal bins available for fitting. Finally, a variety of null models, such as the modern unimodal gradient or the bimodal gradient of past greenhouse periods [4], could be established. The deviation of an observed gradient from these null models could be used to assess how well the gradient is explained by a particular hypothesis. However, this approach has its own set of limitations, including how the set of null models/hypotheses is selected and where the null gradients are centred latitudinally. The assessment of these various alternative approaches is outside of the scope of this study. However, we believe that any of these other methods would echo our findings that Global Plate Model choice can be critical in reconstructing latitudinal biodiveristy gradients in deep time.

## Perspectives

Determining the palaeocoordinates at which organisms’ remains were deposited is a fundamental step in many macroecological and macroevolutionary analyses, and although our results indicate that caution is necessary in doing this, we have additional, specific recommendations. Firstly, we recommend that researchers carefully consider which GPM is most suitable for their work. The spatiotemporal coverage of different GPMs, the proportion of occurrence data palaeogeographic coordinates can be generated for, the data types taken into account when producing the models, and which models were previously used for similar analyses, might all be relevant to making an informed decision. Secondly, we strongly advise consideration of palaeogeographic uncertainty between different GPMs, along with the evaluation of the potential impact of model choice on conclusions. For example, workflows could be implemented using multiple different Global Plate Models, with palaeogeographic uncertainty included in figures through error bars, or results generated with different GPMs included in supplementary material. Finally, we recommend greater collaboration between palaeobiologists and palaeogeographic modellers in future palaeobiogeographic studies [e.g. 36]. Common issues such as the use of Global Plate Models in the mantle reference frame, and confusion over nomenclature, may be reduced through greater exchange between those building Global Plate Models and those using them in secondary research [35].

# Conclusion

Our study demonstrates that the reconstruction of latitudinal biodiversity gradients in deep time is not a trivial task. The use of one Global Plate Model over another can lead to different reconstructions of the palaeolatitudinal distribution of biodiversity, influencing conclusions about the shape and strength of latitudinal biodiversity gradients in deep time, as well as constraining macroevolutionary events such as the origin of the present-day latitudinal biodiversity gradient. In general, we find support for our hypothesis which states reconstructions of the latitudinal biodiversity gradient are more sensitive to Global Plate Model choice with increasing age of rotation. Specifically, our findings show that prior to the Mesozoic, differences between Global Plate Models become increasingly larger with age of rotation. However, we also find that even small differences in the palaeogeographic reconstruction of fossil occurrences between models can have a large impact on reconstructions of the latitudinal biodiversity gradient in younger intervals (e.g. Aquitanian, Burdigalian, Langhian, Tortonian and Messinian). For future palaeobiogeographic studies, we recommend greater interdisciplinary collaboration between palaeobiologists and palaeogeographic modellers to avoid common issues in the use of Global Plate Models. We also endorse that future studies test the sensitivity of their conclusions to Global Plate Model choice, and quantify the palaeogeographic uncertainty associated with their data.

# Data accessibility

The data and code generated in this study have been included within the paper, its supplementary material, and dedicated GitHub repository: <https://github.com/LewisAJones/LBG-GPM-choice>. In addition, they have been uploaded to a dedicated to Zenodo repository: <XXX>.

# Authors’ contributions

L.A.J conceived the project. All authors contributed to the development of the project. All authors contributed to the writing of the manuscript. All authors contributed to data analyses. W.G. and L.B. produced the figures.

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