Global plate model choice impacts reconstructions of the latitudinal biodiversity gradient

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Abstract

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# Keywords

Latitudinal biodiversity gradient, marine invertebrates, macroecology, global plate model, palaeogeographic uncertainty

# Introduction

Today, species richness decreases from the tropics to the poles. This phenomenon is known as the latitudinal biodiversity gradient (LBG), and is one of Earth’s longest recognised macroecological patterns [1–4]. While observed across numerous taxonomic groups in the terrestrial [2,3,5] and marine realm today [6,7,but see 8,9,10], the fossil record suggests that this broadly unimodal gradient was not always present, with flattened and bimodal gradients observed across a range of taxonomic groups at various points in Earth’s geological history [11–20]. Several studies have demonstrated that 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 persisted [4,20–24]. Conversely, during intervals of warmer climatic conditions (i.e. greenhouse and interglacial periods), various taxonomic groups have exhibited flattened LBGs, or even temperate peaks in biodiversity [12,13,15–17,25,26]. However, recent work suggests that our ability to recognise different types of LBG in deep time is hindered by incomplete and heterogeneous spatial sampling in the fossil record [27,28].

When examining the LBG in the present day, neontologists use the geographic coordinates where they collected their samples to infer the spatial distributions of taxa. However, palaeobiologists must contend with the movement of tectonic plates over geological timescales, which results in the geographic location of a fossil occurrence today 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 reconstructing the LBG in deep time. To do this, palaeobiologists routinely use Global Plate Models, or as sometimes referred to ‘palaeorotation models’ or ‘plate rotation models’ [18,19,24,26,29,30]. These models aim to reconstruct the tectonic evolution of the Earth by modelling the motion of continental–and sometimes marine–plates across its surface through geological time. Many of these Global Plate Models have been constructed [e.g. 31,32–34], varying in the way they define the geological boundaries of continents and how they rotate them through time, having consequence for how fossil occurrences might be palaeogeographically reconstructed [35,36]. However, to date, few palaeobiological studies (though see ref. [37,38]) have considered how different Global Plate Models might influence reconstructions of the latitudinal distributions of fossil occurrences.

Recent work has quantified the extent to which Global Plate Models can differ in their palaeogeographic reconstruction of fossil occurrences [36]. Here, we evaluate the sensitivity of reconstructions of the latitudinal biodiversity gradients to Global Plate Model choice. Specifically, we test the extent to which reconstructed latitudinal biodiversity gradients vary when using different Global Plate Models throughout the entire Phanerozoic (i.e. the last 540 million years). To do so, we reconstruct the palaeogeographic distribution of fossil occurrences for five major marine invertebrate groups, using data from the Paleobiology Database, and three commonly-applied Global Plate Models. We then describe the raw latitudinal distribution of occurrences before reconstructing the latitudinal biodiversity gradient using coverage-based rarefaction–a common sampling-standardisation approach–and quantify the variability of reconstructed gradients through time between Global Plate Models. We hypothesise that reconstructions of the latitudinal biodiversity gradient are more sensitive to Global Plate Model choice with increasing age of rotation. As such, we expect that reconstructions of the latitudinal biodiversity gradient are more constrained in Cenozoic intervals, becoming increasingly different between Global Plate Models in intervals of the Mesozoic and Palaeozoic.

# Materials and Methods

## Occurrence data

We downloaded Fortunian–Piacenzian (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 March 16 2023. Fossil occurrence data were downloaded using the PBDB API service and were restricted to marine environments and regular preservation (i.e. excluding form taxa and ichnotaxa). Occurrence data were subsequently binned into stratigraphic stage-level time bins following the Geological Timescale 2020 [39], 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. 1.2.1, with the ‘majority’ approach [40]. Subsequently, we removed all occurrences with less than 95% of their age range covered by their assigned temporal bin. After data preparation, the occurrence dataset contained 443,815 fossil occurrences from 78,730 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: PALEOMAP [33], GOLONKA [32], and MERDITH2021 [34]. Palaeogeographic reconstructions were generated using the GPlates Web Service (<https://gwsdoc.gplates.org>) via the palaeorotate() function in palaeoverse ver. 1.2.1 [40]. For each Global Plate Model, fossil occurrences were binned into one of six equal-area latitudinal bins, 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 palaeogeographic reconstructed due to model incompatibility was recorded for each Global Plate Model. This incompatibility can emerge for a variety of reasons including the spatiotemporal coverage of the Global Plate Model, as well as the timing of events, such as the origin or loss of a tectonic plate, or some segment of it.

## 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. 1.0.1 [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, in the R package iNEXT ver. 3.0.0 [43]. The rarefaction portion of this approach is equivalent to the method commonly known as shareholder quorum subsampling amongst palaeontologists [44,45]. Extrapolated values with an estimated sample size more than double that of the observed sample size were discarded, as recommended in ref. [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-low-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 reconstructed for–is dependent on the Global Plate Model used ([Figure 1](#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 ([Figure 1](#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: two bins for 10 geological stages (~11%), one bin for 41 stages (~44%), and zero bins for 42 bins (~45%).

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| Figure 1: Number of fossil collections within each Phanerozoic stage that could be palaeogeographically reconstructed using three Global Plate Models: GOLONKA [32], PALEOMAP [33], and MERDITH2021 [34]. (a) Raw counts of the number of fossil collections available for palaeolatitudinal binning per stage from each Global Plate Model. (b) The number of collections per million years available for palaeolatitudinal binning per stage from each Global Plate Model. Period abbreviations are as follows: Cambrian (Cm); Ordovician (O), Silurian (S), Devonian (D), Carboniferous (C), Permian (P), Triassic (Tr), Jurassic (J), Cretaceous (K), Paleogene (Pg) and Neogene (Ng). The Quaternary is not depicted. The geological time scale axis was added to the plot using the R package ‘deeptime’ ver. 1.0.1 [42]. |

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 ([Figure 2](#fig-spatial)). Specifically, average pairwise palaeolatitudinal differences between models is 2.54º for the Cenozoic, 4.51º for the Mesozoic, and 9.07º 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 ([Figure 2](#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 ([Figure 2](#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.

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| Figure 2: Phanerozoic trends in the spatial discrepancies between palaeogeographic reconstructions of fossil collections for three Global Plate Models: GOLONKA [32], PALEOMAP [33], and MERDITH2021 [34]. (a) Average (median; 5th and 95th percentiles) pairwise palaeolatitudinal distance between palaeogeographic reconstructions for fossil collections. (b) Average (median; 5th and 95th percentiles) pairwise geodesic distance between palaeogeographic reconstructions for fossil collections. In both panels, the ribbon depicts the 2.5th and 97.5th percentiles of the data. Period abbreviations are as follows: Cambrian (Cm); Ordovician (O), Silurian (S), Devonian (D), Carboniferous (C), Permian (P), Triassic (Tr), Jurassic (J), Cretaceous (K), Paleogene (Pg) and Neogene (Ng). The Quaternary is not depicted. The geological time scale axis was added to the plot using the R package ‘deeptime’ ver. 1.0.1 (Gearty, 2023). |

The shapes of the reconstructed latitudinal biodiversity gradients for each geological stage are mostly consistent between Global Plate Models (Fig. **?@fig-gradients-raw**; Fig. [Figure 3](#fig-gradients-sqs)). 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. **?@fig-heat-raw**; Fig. [Figure 4](#fig-heat-sqs)). Throughout the Phanerozoic, peak diversity tended to appear at mid-latitudes (Fig. **?@fig-heat-raw**; Fig. [Figure 4](#fig-heat-sqs)). 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. **?@fig-gradients-raw**; Fig. [Figure 3](#fig-gradients-sqs)). 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. **?@fig-gradients-raw**; Fig. [Figure 3](#fig-gradients-sqs)).

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| Figure 3: Phanerozoic stage-level reconstructions of the latitudinal biodiversity gradient for five major marine invertebrate groups (Bivalvia, Brachiopoda, Cephalopoda, Gastropoda, and Trilobita). Each individual plot depicts the estimated normalised genus richness within each palaeolatitudinal bin for three Global Plate Models (GPMs): GOLONKA [32], PALEOMAP [33], and MERDITH2021 [34]. Genus richness was estimated for each stage, palaeolatitudinal bin, and GPM using the iNEXT R package ver. 3.0.0 ([43]) with a coverage level (otherwise known as a quorum level) of 0.4. Genus richness was normalised for each stage and GPM by dividing the genus richness within each palaeolatitudinal bin by the maximum value across palaeolatitudinal bins. |

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| Figure 4: Phanerozoic heatmaps of normalised estimated genus richness for five major marine invertebrate groups (Bivalvia, Brachiopoda, Cephalopoda, Gastropoda, and Trilobita). Each individual panel depicts the normalised estimated genus richness (coverage-based rarefaction) for three Global Plate Models (GPMs): GOLONKA [32], PALEOMAP [33], and MERDITH2021 [34]. Heatmaps depict the normalised estimated genus richness within palaeolatitudinal bins (low, middle, and high) within the Northern and Southern Hemisphere. Genus richness was estimated for each stage, palaeolatitudinal bin, and GPM using the iNEXT R package ver. 3.0.0 [43] with a coverage level (otherwise known as a quorum level) of 0.4. Genus richness was normalised for each stage and GPM by dividing the genus richness within each palaeolatitudinal bin by the maximum value across palaeolatitudinal bins. Grey tiles indicate palaeolatitudinal bins without sufficient data to generate richness estimates. |

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| Figure 5: Phanerozoic heatmaps of the pairwise difference in normalised estimated genus richness for three Global Plate Models (GPMs): GOLONKA [32], PALEOMAP [33], and MERDITH2021 [34]. Difference between the normalised estimated genus richness within palaeolatitudinal bins for the GOLONKA and MERDITH2021 GPM (top panel). Difference between the normalised estimated genus richness within palaeolatitudinal bins for the PALEOMAP and GOLONKA GPM (middle panel). Difference between the normalised estimated genus richness within palaeolatitudinal bins for the PALEOMAP and MERDITH2021 GPM (bottom panel). Genus richness was estimated for each stage, palaeolatitudinal bin, and GPM using the iNEXT R package ver. 3.0.0 [43] with a coverage level (otherwise known as a quorum level) of 0.4. Genus richness was normalised for each stage and GPM by dividing the genus richness within each palaeolatitudinal bin by the maximum value across palaeolatitudinal bins. White tiles indicate palaeolatitudinal bins without sufficient data to generate richness estimates or where estimates are not available for both GPMs being compared. |

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 50% of stages in the Paleozoic, 68% in the Mesozoic, and 57% in the Cenozoic showing agreement between all three models (Fig. 5a). Notably, this also differed between the two hemispheres, with 65% in the Northern Hemisphere and 50% in the Southern Hemisphere in agreement throughout the Phanerozoic. 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. 5b). 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. XXX), likely due to the higher number of spatial bins containing enough data to be analysed.

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| Figure 6: Phanerozoic plot of the palaeolatitudinal bin (low, middle, high) with the greatest estimated genus richness within the Northern Hemisphere and Southern Hemisphere for each Global Plate Model (GPM): GOLONKA [32], PALEOMAP [33], and MERDITH2021 [34]. Grey shading highlights intervals in which the palaeolatitudinal bin with the greatest estimated genus richness is in agreement across the three GPMs. Genus richness was estimated for each stage, palaeolatitudinal bin, and GPM using the iNEXT R package ver. 3.0.0 (REF) with a coverage level (otherwise known as a quorum level) of 0.4. Period abbreviations are as follows: Cambrian (Cm); Ordovician (O), Silurian (S), Devonian (D), Carboniferous (C), Permian (P), Triassic (Tr), Jurassic (J), Cretaceous (K), Paleogene (Pg) and Neogene (Ng). The Quaternary is not depicted. The geological time scale axis was added to the plot using the R package ‘deeptime’ ver. 1.0.1 [42]. |

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| Figure 7: Phanerozoic plot of the normalised average rank order pairwise difference between latitudinal biodiversity gradients (estimated genus richness) for each Global Plate Models (GPMs): GOLONKA [32], PALEOMAP [33], and MERDITH2021 [34]. Genus richness was estimated for each stage, palaeolatitudinal bin, and GPM using the iNEXT R package ver. 3.0.0 (REF) with a coverage level (otherwise known as a quorum level) of 0.4. Average rank order differences are normalised by maximum possible average difference given the number of ranks available. Period abbreviations are as follows: Cambrian (Cm); Ordovician (O), Silurian (S), Devonian (D), Carboniferous (C), Permian (P), Triassic (Tr), Jurassic (J), Cretaceous (K), Paleogene (Pg) and Neogene (Ng). The Quaternary is not depicted. The geological time scale axis was added to the plot using the R package ‘deeptime’ ver. 1.0.1 [42]. |

# Discussion

Global Plate Models are regularly used in palaeobiology to reconstruct the palaeogeographic distribution of fossil occurrences [16,18,19,24,26,e.g. 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. [Figure 6](#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. 11,12–20]. 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. 4,19,20,22]. 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. 11,14–17,19]. 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 [27,28,e.g. 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. [Figure 3](#fig-gradients-sqs); [Figure 6](#fig-maxlat-sqs); [Figure 7](#fig-rank-sqs)), this can also impact reconstructions in more recent intervals such as the Tortonian in the Cenozoic (Fig. [Figure 3](#fig-gradients-sqs)).

Although during most geological stages there is broad agreement in the shape of the LBG between GPMs (Fig. [Figure 3](#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 ([Figure 3](#fig-gradients-sqs); [Figure 6](#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.

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. 20]. This is significant because 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 ([Figure 3](#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. **?@fig-gradients-raw**; [Figure 3](#fig-gradients-sqs)). 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. [47]; [48]; [18]), 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 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 ([18]). 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 alluding to the origin of the present-day latitudinal biodiversity gradient. This is due to: (1) differences in which fossil collections can be palaeogeographically reconstructed by any given Global Plate Models, and (2) differences in the palaeogeographic reconstruction themselves. 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.

In general, we find support for our hypothesis which states reconstructions of the latitudinal biodiversity gradient are more sensitive to GPM choice with increasing age of rotation ([Figure 2](#fig-spatial); [Figure 6](#fig-maxlat-sqs); [Figure 7](#fig-rank-sqs)). Specifically, we show that prior to the Mesozoic, differences between GPMs becomes 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. For example, in several intervals belonging to the Cenozoic (e.g. Aquitanian, Burdigalian, Langhian, Tortonian and Messinian) different latitudinal peaks in biodiversity could be estimated depending on Global Plate Model choice (e.g. [Figure 6](#fig-maxlat-sqs)).

# Unused text

Here, we test the sensitivity of deep-time Latitudinal Biodiversity Gradient reconstructions to the use of different Global Plate Models (GPMs). GPMs use the Euler Rotation Theorem to reconstruct the motion of tectonic plates on a sphere-like structure—the Earth. Based on a compilation of geological data (see [35] for an extensive review), a GPM divides tectonic plates into smaller sub-units that will move independently. It therefore takes two main inputs: (1) a set of tectonic elements and (2) a tree-like structured framework in which these elements moved throughout geological times relatively to a fixed anchor, called reference frame [35,49,50]. Two classes of GPMs exist. On the one hand, ‘Continental drift’ models aim at reconstructing the motion of present-day continental areas–discontinuous subset of rigid plates–as if they were ‘floating’ on the mantle [e.g. 32,33]. On the other hand ‘full-plate’ model describe in detail how plate borders have evolved through geological times [31,e.g. 51], therefore tackling the issue from a more mechanistic perspective. Latest models of the latter class also allow for plate deformation while moving [e.g. 52,53].

Many of the GPMs released so far are freely available via open-source platforms, such as GPlates [**boyden2011?**]. However, in the face of such an easy access, it becomes important for users to bear in mind that GPMs have been developed for a variety of purposes, and are not necessarily showing the same thing altogether. In particular, models using a mantle reference frame [e.g. 53,54] are constraining tectonic plate motion to the mantle. While perfectly suited to study the plate-mantle system, anchoring plate motion to the mantle removes additional factors responsible for plate motion (such as the rotation of the Earth) [35]. The palaeocoordinate estimates they produce are therefore naturally biased. Hence, models using a mantle reference frame should not be used to get palaeocoordinates, which is most of the time why these models are used in palaeobiology. Rather, people interested in actual palaeocoorinate estimates should favour the use of models using a palaeomagnetic reference frame, as palaeomagnetic data provide actual constraints for palaeolatitude [35]. This said, one should notice that this does not apply to palaeolongitude, which is harder to constrain, especially in deep time [35,49].

For our study, we therefore chose three GPMs using a palaeomagnetic reference frame, either among the most widely used in palaeobiology (PALEOMAP [33] and GOLONKA [32]) or among the cutting-edge of the field (MERDITH2021 [34]). The GOLONKA model comes from an earlier version of PALEOMAP. While the GOLONKA spans the entire Phanerozoic, the latest version of PALEOMAP (that we are using here) goes up to 750 Ma. As for it, the MERDITH2021 provides reconstructions for the last 1000 Ma. It comes from the combination of models spanning the Neoproterozoic [55], the beginning of the Phanerozoic until Early Devonian [56,57] and the last 410 Ma [54].

# Data accessibility

The data generated in this study have been included within the paper, its supplementary material, and dedicated GitHub repository .

# 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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