Global plate model choice impacts reconstructions of the latitudinal biodiversity gradient

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Abstract

Here goes the abstract…

# Keywords

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

# Introduction (600 words)

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,**kinlock2017?**] and marine realm today [5,6,but see 7,8,9], the fossil record suggests 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 [e.g. 10,11–19]. 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 [4,19,e.g. 20,21–23]. 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 [e.g. 11,12,14–16,24,25]. 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 [26,27].

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 migration of tectonic plates over geological timescales; the geographic location of a fossil occurrence on the Earth’s surface today does not necessarily represent 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–sometimes also called ‘palaeorotation models’ or ‘plate rotation models’– [17,18,23,25,28,29]. These models aim to reconstruct the tectonic evolution of the Earth by modelling the motion of the continental– and sometimes marine–plates across its surface through geological time. Many Global Plate Models have been constructed [e.g. 30,31–33], 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 [34]. However, to date, few palaeobiological studies (though see ref. [35,36]) have considered how different Global Plate Models might influence reconstructions of the latitudinal distributions of fossil occurrences.

Here, we test how much Global Plate Model choice influences the recognition of ‘unimodal-type’ latitudinal biodiversity gradients throughout the Phanerozoic (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 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 strength of the gradient through time and the variability between Global Plate Models. We hypothesise that reconstructions of the latitudinal biodiversity gradient are more sensitive to plate rotation model choice with increasing age of rotation.

# Materials and Methods (600 words)

## 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 [37], 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, using the ‘majority’ approach [38]. 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 occurrences from 78,730 collections.

## Palaeogeographic reconstruction and 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 [32], GOLONKA [31], and MERDITH2021 [33]. Palaeogeographic reconstructions were generated using the GPlates Web Service (<https://gwsdoc.gplates.org>) via the palaeorotate() function in palaeoverse ver. 1.2.1 [38]. For each Global Plate Model, fossil occurrences were binned into one of six equal-area latitudinal bins, using the estimated palaeolatitudes ([Table 1](#tbl-bins)). These latitudinal bins broadly represent three climatic zones within each hemisphere: tropical, temperate, and polar. The number of fossil occurrences which were unable to be rotated due to model incompatibility was recorded for each Global Plate Model.

Table 1: Equal-area latitudinal bins used in this study. Bins are generated assumming a regular spheroid Earth model with a mean radius of ~6,371 km.

| Bin | Maximum | Midpoint | Minimum | Area (m2) | Proportion of Area |
| --- | --- | --- | --- | --- | --- |
| 1 | 90.00 | 65.915 | 41.83 | 8.49e+13 | 0.167 |
| 2 | 41.83 | 30.655 | 19.48 | 8.50e+13 | 0.167 |
| 3 | 19.48 | 9.740 | 0.00 | 8.50e+13 | 0.167 |
| 4 | 0.00 | -9.740 | -19.48 | 8.50e+13 | 0.167 |
| 5 | -19.48 | -30.655 | -41.83 | 8.50e+13 | 0.167 |
| 6 | -41.83 | -65.915 | -90.00 | 8.49e+13 | 0.167 |

## Quantifying the latitudinal biodiversity gradient

Subsequent data manipulation and visualisation were carried out using the Tidyverse suite of R packages [39]. 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 [40]. The rarefaction portion of this approach is equivalent to shareholder quorum subsampling [41,42]. Extrapolated values with an estimated sample size more than double that of the observed sample size were discarded [40].

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 tropical, temperate, and polar 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 latitudinal bins were put in rank order and the differences between models were computed and the mean calculated. 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. tropical-to-temperate-to-polar, temperate-tropical-polar, etc.).

As the estimated latitudinal distribution of biodiversity is closely tied to the distribution of fossil collections (REFs), we also computed the number of collections in each latitudinal bin and stratigraphic stage for each Global Plate Model. Furthermore, we calculated the mean geodesic distance between the reconstructed palaeocoordinates for each fossil collection to test whether reconstructions of the latitudinal biodiversity gradient are more sensitive to plate rotation model choice with increasing age of rotation.

# Results

## Palaeogeographic reconstructions

Palaeogeographic reconstruction of fossil collections using different Global Plate Models (GPMs) reveals that the number of collections available for allocation to palaeolatitudinal bins–collections which palaeocoordinates could be reconstructed for–is dependent on GPM choice (Fig. XXX). While in most geological stages, the number of collections available for allocation to palaeolatitudinal bins is similar, it varies considerably for others (Fig. XXX). 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%) of collections were reconstructed using PALEOMAP. This, along with spatial discrepancies in palaeogeographic reconstructions between GPMs, resulted in the number of samples allocated to each palaeolatitudinal bin (low, medium, high latitudes) varing with GPM (Fig. XXX). Of the 93 geological stages, the number of palaeolatitudinal bins containing enough samples (i.e. fossil collections) for estimating genus richness 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%) (Fig. XXX).

Analysis of the average pairwise geodesic distance and average pairwise palaeolatitudinal difference between palaeogeographically reconstructed fossil collections indicate, on average, an increasing difference between GPMs with age of reconstruction (Fig. XXX). Specifically, average latitudinal differences between models are XXX km and XXX for the Cenozoic, XXX km and XXX for the Mesozoic, and XXX km and XXX 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 palaeogeographic differences, for example in the Permian (Fig. XXX).

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| Figure 1: Phanerozoic trends in the spatial discrepancies between palaeogeographic reconstructions of fossil collections for three Global Plate Models: GOLONKA [31], PALEOMAP [32], and MERDITH2021 [33]. (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. 2; Fig. XXX). 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 (Figure 3). Throughout the Phanerozoic, peak diversity tended to appear at mid-latitudes (Fig. 3; Fig. XXX). 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. 2, Fig. 3)…. 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.

knitr::include\_graphics(path = "../figures/LBGs\_sqs.png")

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| Figure 2: 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 [31], PALEOMAP [32], and MERDITH2021 [33]. Genus richness was estimated for each stage, palaeolatitudinal bin, and GPM using the iNEXT R package ver. 3.0.0 ([40]) 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. |

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. The models were largely consistent in the number of stages for which estimated diversity was determined to be at high, mid or low latitudes (GOLONKA: XXX% high, XXX% mid, XXX% low; MERDITH2021: XXX% high, XXX% mid, XXX% low; PALEOMAP: XXX% high, XXX% mid, XXX% low). 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.

* Summary of reconstructions (could all points be reconstructed for each model?)
* Summary of results from metrics, do different gradients emerge?
* How much data did we lose for each model?

Figures Add eras to x-axes? (Will) - Figure 1 - Create figure of mean latitudinal pairwise distances, comparing in degrees and km, with a ‘ribbon’ showing 95% confidence intervals (Lucas) - Figure 2 - Normalised estimated SQS genus richness - change to “palaeolatitudinal bin” (Will) - Figure 3 - Most diverse bin and normalised rank order for SQS

* Supplement - Normalised estimated raw genus richness - spatial bins with 0 samples should be greyed out (Will)
* LBGs plotted as curves for each temporal bin
* Create number of collections plotted as curves for each temporal bin (Lucas)
* Additional heat maps for each pair of models with the difference in genera estimated

To write - Figure 2: The overall trend is the same, i.e. most diversity in southern hemisphere before the Permian, and in the northern hemisphere after the Permian, in all three models. Data absence is noticeable. Highest richness tends to be at mid latitudes, rather than low latitudes - but is this bias? Paleomap has weird high N latitudes peak in the Paleogene, why? - Figure 3a: Calculate number of bins for which we have matches and non-matches (currently greyed in the figure), comparison between the two hemispheres. More grey on the right - more agreement in more recent times. - Figure 3b: Reduced differences in the Mesozoic, why? Some of these differences reach 1, this represents the maximum amount of difference, i.e. completely opposite. =======

* Summary of reconstructions (could all points be reconstructed for each model?)
* Summary of results from metrics, do different gradients emerge?

# Discussion (700 words)

* Recap on importance of GPMs for deep time macroecology?
* What have we shown?
* Are some times or areas more problematic than others?
* Importance for other fields beyond palaeobiology?
* Consider importance of GPM choice in future work… or not?

# 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 the data analyses of the manuscript. W.G. produced the figures.

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