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. 1.2.0, 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. 1.2.0 [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 (600 words)

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| Figure 1: Graphic |

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| Figure 2: Graphic |

* 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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