Global plate model choice impacts reconstructions of the latitudinal biodiversity gradient

—

Lewis A. Jones1, Bethany J. Allen2,3, William Gearty4, and Lucas Buffan4

—

1Grupo de Ecoloxía Animal, Departamento de Ecoloxía e Bioloxía Animal, Universidade de Vigo, 36310 Vigo, Spain.

2Department of Biosystems Science and Engineering, ETH Zürich, 4058 Basel, Switzerland.

3Computational Evolution Group, Swiss Institute of Bioinformatics, 1015 Lausanne, Switzerland.

4Smithsonian National Museum of Natural History, Department of Paleobiology, Washington, DC, 20560, USA

5Département de Biologie, École Normale Supérieure de Lyon, Université Claude Bernard Lyon 1, 69342 Lyon Cedex 07, France.

—

**All authors contributed equally to this work**

**Corresponding author:** LewisAlan.Jones@uvigo.es

¶ 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] and marine realm today [5,6], 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. 7,8–15]. Several studies have demonstrated that tropical peaks and poleward declines in taxonomic richness are restricted to the last 30 million years (Myr), and intervals of the Palaeozoic, when cool icehouse climatic regimes persisted [e.g. 4,15–18]. 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. 8,9,11–13,19,20]. However, recent work suggests that the recognition of different types of LBG in deep time is limited by incomplete and heterogeneous spatial sampling [21].

When examining the LBG in the present day, neontologists use the direct geographic distribution of organisms. However, palaeobiologists must contend with the shift of the continents over geological timescales; the geographic location of a fossil occurrence on the Earth’s surface today does not necessarily represent its location *in vivo*. Consequently, reconstructing the past geographic distribution of fossil occurrences is fundamental to reconstructing the LBG in deep time. To do so, palaeobiologists routinely use what is known as Global Plate Models [14,18,20,22–24]. These models aim to reconstruct the tectonic evolution of the Earth by modelling the motion of the continents across its surface through geological time. Many of these Global Plate Models exist [e.g. 25,26–28], 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 [29]. However–to date–few palaeobiological studies (though see ref. [30,31]) have considered how different Global Plate Models might influence reconstructions of the latitudinal distribution of fossil occurrence.

Here, we test whether 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 Palaeobiology Database and three Global Plate Models. Subsequently, we reconstruct 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 hypothesis that reconstructions of the latitudinal biodiversity gradient are more sensitive to plate rotation model choice with 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 02 2023. Fossil occurrence data were downloaded using the PBDB API service and were restricted to marine environments, valid taxa and regular preservation (i.e. excluding form taxa and ichnotaxa). Occurrence data were subsequently binned into stratigraphic time bins following the Geological Timescale 2020 [32]. To do so, we used the bin\_time() function from the palaeoverse R package ver. 1.1.1.900 using the ‘majority’ approach [33]. 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 347,193 occurrences from 56,283 collections.

## Palaeogeographic reconstruction and binning

To reconstruct the palaeogeographic distribution of fossil occurrences, we used occurrences’ present-day coordinates and midpoint age from assigned temporal bins with three Global Plate Models: PALEOMAP [27], GOLONKA [26], and MERDITH2021 [28]. Palaeogeographic reconstructions were generated using the GPlates Web Service (<https://gwsdoc.gplates.org>) via the palaeorotate() function in palaeoverse ver. 1.1.1.900 [33]. Subsequently, for each Global Plate Model, fossil occurrences were binned into one of twelve equal-area latitudinal bins (assuming a regular spheroid Earth model with a radius of ~6,371 km), using the estimated palaeolatitudes ([Table 1](#tbl-bins)).

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 | 73.235 | 56.47 | 4.24e+13 | 0.083 |
| 2 | 56.47 | 49.150 | 41.83 | 4.25e+13 | 0.083 |
| 3 | 41.83 | 35.920 | 30.01 | 4.25e+13 | 0.083 |
| 4 | 30.01 | 24.745 | 19.48 | 4.25e+13 | 0.083 |
| 5 | 19.48 | 14.540 | 9.60 | 4.25e+13 | 0.083 |
| 6 | 9.60 | 4.800 | 0.00 | 4.25e+13 | 0.083 |
| 7 | 0.00 | -4.800 | -9.60 | 4.25e+13 | 0.083 |
| 8 | -9.60 | -14.540 | -19.48 | 4.25e+13 | 0.083 |
| 9 | -19.48 | -24.745 | -30.01 | 4.25e+13 | 0.083 |
| 10 | -30.01 | -35.920 | -41.83 | 4.25e+13 | 0.083 |
| 11 | -41.83 | -49.150 | -56.47 | 4.25e+13 | 0.083 |
| 12 | -56.47 | -73.235 | -90.00 | 4.24e+13 | 0.083 |

## Quantifying the latitudinal biodiveristy gradient

* Metrics used to quantify the gradient

# Results (600 words)

* 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

# Authors’ contributions

# Funding

# Acknowledgements

# References

1. Humboldt A von, Bonpland A. 1807 *Essai sur la géographie des plantes; accompagne d’un tableau physique des régions équinoxiales*. Paris: Fr. Schoell.

2. Willig MR, Kaufman DM, Stevens RD. 2003 Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. *Annual review of ecology, evolution, and systematics* **34**, 273309.

3. Hillebrand H. 2004 On the generality of the latitudinal diversity gradient. *The American Naturalist* **163**, 192211.

4. Mannion PD, Upchurch P, Benson RBJ, Goswami A. 2014 The latitudinal biodiversity gradient through deep time. *Trends in Ecology & Evolution* **29**, 42–50. (doi:[10.1016/j.tree.2013.09.012](https://doi.org/10.1016/j.tree.2013.09.012))

5. Roy K, Jablonski D, Valentine JW. 2000 [Dissecting latitudinal diversity gradients: Functional groups and clades of marine bivalves.](https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1690525/) *Proceedings of the Royal Society B: Biological Sciences* **267**, 293–299.

6. Valentine JW, Jablonski D. 2015 A twofold role for global energy gradients in marine biodiversity trends. *Journal of Biogeography* **42**, 997–1005. (doi:[10.1111/jbi.12515](https://doi.org/10.1111/jbi.12515))

7. Rose PJ, Fox DL, Marcot J, Badgley C. 2011 Flat latitudinal gradient in Paleocene mammal richness suggests decoupling of climate and biodiversity. *Geology* **39**, 163–166. (doi:[10.1130/G31099.1](https://doi.org/10.1130/G31099.1))

8. Mannion PD, Benson RB, Upchurch P, Butler RJ, Carrano MT, Barrett PM. 2012 A temperate palaeodiversity peak in mesozoic dinosaurs and evidence for late cretaceous geographical partitioning. *Global Ecology and Biogeography* **21**, 898908.

9. Yasuhara M, Hunt G, Dowsett HJ, Robinson MM, Stoll DK. 2012 Latitudinal species diversity gradient of marine zooplankton for the last three million years. *Ecology Letters* **15**, 1174–1179. (doi:[10.1111/j.1461-0248.2012.01828.x](https://doi.org/10.1111/j.1461-0248.2012.01828.x))

10. Powell MG, Moore BR, Smith TJ. 2015 Origination, extinction, invasion, and extirpation components of the brachiopod latitudinal biodiversity gradient through the phanerozoic eon. *Paleobiology* **41**, 330341.

11. Nicholson DB, Holroyd PA, Valdes P, Barrett PM. 2016 Latitudinal diversity gradients in mesozoic non-marine turtles. *Royal Society open science* **3**, 1–8.

12. Allen BJ, Wignall PB, Hill DJ, Saupe EE, Dunhill AM. 2020 The latitudinal diversity gradient of tetrapods across the permo-triassic mass extinction and recovery interval. *Proceedings of the Royal Society B: Biological Sciences* **287**. (doi:[10.1098/rspb.2020.1125](https://doi.org/10.1098/rspb.2020.1125))

13. Song H, Huang S, Jia E, Dai X, Wignall PB, Dunhill AM. 2020 Flat latitudinal diversity gradient caused by the PermianTriassic mass extinction. *Proceedings of the National Academy of Sciences*, 1–6. (doi:[10.1073/pnas.1918953117](https://doi.org/10.1073/pnas.1918953117))

14. Zhang S-H, Shen S-Z, Erwin DH. 2022 Latitudinal diversity gradient dynamics during carboniferous to triassic icehouse and greenhouse climates. *Geology* **50**, 1166–1171. (doi:[10.1130/G50110.1](https://doi.org/10.1130/G50110.1))

15. Fenton IS, Aze T, Farnsworth A, Valdes P, Saupe EE. 2023 Origination of the modern-style diversity gradient 15 million years ago. *Nature* **614**, 708–712. (doi:[10.1038/s41586-023-05712-6](https://doi.org/10.1038/s41586-023-05712-6))

16. Fenton IS, Pearson PN, Dunkley Jones T, Farnsworth A, Lunt DJ, Markwick P, Purvis A. 2016 The impact of Cenozoic cooling on assemblage diversity in planktonic foraminifera. *Philosophical Transactions of the Royal Society B: Biological Sciences* **371**, 1–12. (doi:[10.1098/rstb.2015.0224](https://doi.org/10.1098/rstb.2015.0224))

17. Marcot JD, Fox DL, Niebuhr SR. 2016 Late cenozoic onset of the latitudinal diversity gradient of north american mammals. *Proceedings of the National Academy of Sciences* **113**, 71897194.

18. Kröger B. 2018 Changes in the latitudinal diversity gradient during the great ordovician biodiversification event. *Geology* **46**, 127130.

19. Kiessling W, Simpson C, Beck B, Mewis H, Pandolfi JM. 2012 Equatorial decline of reef corals during the last Pleistocene interglacial. *Proceedings of the National Academy of Sciences* **109**, 21378–21383. (doi:[10.1073/pnas.1214037110](https://doi.org/10.1073/pnas.1214037110))

20. Dunne EM, Farnsworth A, Greene SE, Lunt DJ, Butler RJ. 2020 Climatic drivers of latitudinal variation in Late Triassic tetrapod diversity. *Palaeontology* **64**, 101–117. (doi:<https://doi.org/10.1111/pala.12514>)

21. Jones LA, Dean CD, Mannion PD, Farnsworth A, Allison PA. 2021 Spatial sampling heterogeneity limits the detectability of deep time latitudinal biodiversity gradients. *Proceedings of the Royal Society B: Biological Sciences* **288**, 20202762. (doi:[10.1098/rspb.2020.2762](https://doi.org/10.1098/rspb.2020.2762))

22. Brocklehurst N, Day MO, Rubidge BS, Fröbisch J. 2017 Olson’s extinction and the latitudinal biodiversity gradient of tetrapods in the permian. *Proceedings of the Royal Society B: Biological Sciences* **284**, 18.

23. Antell GS, Kiessling W, Aberhan M, Saupe EE. 2020 Marine Biodiversity and Geographic Distributions Are Independent on Large Scales. *Current Biology* **30**, 115–121.e5. (doi:[10.1016/j.cub.2019.10.065](https://doi.org/10.1016/j.cub.2019.10.065))

24. Boag TH, Gearty W, Stockey RG. 2021 Metabolic tradeoffs control biodiversity gradients through geological time. *Current Biology* **31**, 2906–2913.e3. (doi:[10.1016/j.cub.2021.04.021](https://doi.org/10.1016/j.cub.2021.04.021))

25. Seton M *et al.* 2012 Global continental and ocean basin reconstructions since 200 Ma. *Earth-Science Reviews* **113**, 212–270. (doi:[10.1016/j.earscirev.2012.03.002](https://doi.org/10.1016/j.earscirev.2012.03.002))

26. Wright N, Zahirovic S, Müller RD, Seton M. 2013 Towards community-driven paleogeographic reconstructions: integrating open-access paleogeographic and paleobiology data with plate tectonics. *Biogeosciences* **10**, 1529–1541. (doi:[10.5194/bg-10-1529-2013](https://doi.org/10.5194/bg-10-1529-2013))

27. Scotese C, Wright NM. 2018 [PALEOMAP paleodigital elevation models (PaleoDEMs) for the phanerozoic PALEOMAP project](https://www.earthbyte.org/paleodem-resource-scotese-and-wright-2018/).

28. Merdith AS *et al.* 2021 Extending full-plate tectonic models into deep time: Linking the neoproterozoic and the phanerozoic. *Earth-Science Reviews* **214**, 103477.

29. Seton M, Williams SE, Domeier M, Collins AS, Sigloch K. 2023 Deconstructing plate tectonic reconstructions. *Nature Reviews Earth & Environment*, 1–20. (doi:[10.1038/s43017-022-00384-8](https://doi.org/10.1038/s43017-022-00384-8))

30. Boddy CE, Mitchell EG, Merdith A, Liu AG. 2022 Palaeolatitudinal distribution of the Ediacaran macrobiota. *Journal of the Geological Society* **179**, jgs2021–030. (doi:[10.1144/jgs2021-030](https://doi.org/10.1144/jgs2021-030))

31. Jones LA, Mannion PD, Farnsworth A, Bragg F, Lunt DJ. 2022 Climatic and tectonic drivers shaped the tropical distribution of coral reefs. *Nature Communications* **13**, 3120. (doi:[10.1038/s41467-022-30793-8](https://doi.org/10.1038/s41467-022-30793-8))

32. Gradstein FM, Ogg JG, Schmitz MD, Ogg GM. 2020 *Geologic time scale 2020*. Elsevier.

33. Jones LA *et al.* 2023 palaeoverse: a community-driven R package to support palaeobiological analysis. (doi:[10.31223/X5Z94Q](https://doi.org/10.31223/X5Z94Q))