

1 **MIND THE UNCERTAINTY: GLOBAL PLATE MODEL CHOICE IMPACTS**

2 **DEEP-TIME PALAEOBIOLOGICAL STUDIES**

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24

## Abstract

- 25 1. Global Plate Models (GPMs) aim to reconstruct the tectonic evolution of the Earth by modelling  
26 the motion of the plates and continents through time. These models enable palaeobiologists to  
27 study the past distribution of extinct organisms. However, different GPMs exist that vary in  
28 their partitioning of the Earth's surface and the modelling of continental motions.  
29 Consequently, the preferred use of one GPM will influence palaeogeographic reconstruction of  
30 fossil occurrences and any inferred palaeobiological and palaeoclimatic conclusion.
- 31 2. Here, using five open-access GPMs, we reconstruct the palaeogeographic distribution of cell  
32 centroids from a global hexagonal grid and quantify palaeogeographic uncertainty across the  
33 entire Phanerozoic (540–0 Ma). We measure uncertainty between reconstructed coordinates  
34 using two metrics: (1) palaeolatitudinal standard deviation and (2) mean pairwise geodesic  
35 distance. Subsequently, we evaluate the impact of GPM choice on palaeoclimatic  
36 reconstructions when using fossil occurrence data. To do so, we use two climatically-sensitive  
37 entities (coral reefs and crocodylomorphs) to infer the palaeolatitudinal extent of subtropical  
38 climatic conditions for the last 240 million years.
- 39 3. Our results indicate that differences between GPMs increase with the age of reconstruction.  
40 Specifically, cell centroids rotated to older intervals show larger differences in palaeolatitude  
41 and geographic spread than those rotated to younger intervals. However, high palaeogeographic  
42 uncertainty is also observed in younger intervals within tectonically complex regions (i.e. in  
43 the vicinity of terrane and plate boundaries). We also show that when using fossil data to infer  
44 the distribution of subtropical climatic conditions across the last 240 Ma, estimates vary by 6–  
45 7° latitude on average, and up to 24° latitude in extreme cases.
- 46 4. Our findings confirm that GPM choice is an important consideration when studying past  
47 biogeographic patterns and palaeoclimatic trends. We recommend using GPMs that report true

48 palaeolatitudes (through palaeomagnetic data use) and incorporating palaeogeographic  
49 uncertainty into palaeobiological analyses.

## 50 **Introduction**

51 Akin to neontologists, palaeobiologists seek to understand the origin, distribution, and extinction of  
52 species across time and space (e.g. Alroy, 2014; Powell et al., 2015; Spano et al., 2016; Meseguer and  
53 Condamine, 2020; Boddy et al., 2022). However, while neontologists can study the present-day  
54 geographic distribution of taxa, palaeobiologists must contend with the shift of the continents over  
55 geological timescales. Specifically, the geographic location of fossil occurrences on the Earth's surface  
56 today does not necessarily represent their location *in vivo*; fossil remains found at tropical latitudes  
57 might have been deposited at temperate latitudes, and vice versa. Consequently, reconstructing the past  
58 geographic distribution—i.e. the palaeogeographic distribution—of fossil occurrences is fundamental to  
59 the study of macroecological patterns in deep time. To do so, palaeobiologists routinely use what are  
60 known as Global Plate Models (e.g. Brocklehurst et al., 2017; Allen et al., 2020; Dunne et al., 2020;  
61 Antell et al., 2020; Boddy et al., 2022; Jones et al., 2022; Zhang et al., 2022).

62 Global Plate Models (GPMs) aim to reconstruct the tectonic evolution of the Earth, modelling the  
63 motion of the continents across its surface through geological time. They do so using Euler's rotation  
64 theorem to describe the motion of geometries—such as tectonic plates or geological terranes—on a sphere  
65 (McKenzie and Parker, 1967; Morgan, 1968). Since the 1970s, numerous GPMs have been developed  
66 by both the scientific community (e.g. Scotese et al., 1988; Müller et al., 1993, 2019; Golonka et al.,  
67 1994; Golonka, 2007; Torsvik et al., 2008a; Seton et al., 2012; Domeier and Torsvik, 2014; Matthews  
68 et al., 2016; Torsvik and Cocks, 2017; Scotese and Wright, 2018; Vérard, 2019; Young et al., 2019;  
69 Merdith et al., 2021) and industry (e.g. Getech plc and Robertson Research) for purposes such as  
70 geological resource exploration (Markwick, 2019) and Earth System modelling (Lunt et al., 2016). A  
71 more recent shift to 'full-plate models' (e.g. Merdith et al., 2021) and deforming plate models (e.g.  
72 Gurnis et al., 2018; Müller et al., 2019) has increased the complexity of GPMs by describing—in detail—

73 how plate boundaries, deforming regions, and the plate-mantle system have evolved through time  
74 (Seton et al., 2023).

75 A GPM is made up of two key components. The first component is a set of ‘geometries’ dividing the  
76 surface of the Earth into individual tectonic elements that can be independently reconstructed. These  
77 elements include both ‘dynamic polygons’ (also known as ‘continuously closing plate polygons’),  
78 which change shape through time, and ‘static polygons’, whose shape and size are fixed. The former  
79 are used to model entire tectonic plates, whereas the latter are used to delineate continents, fault-bound  
80 tectonic blocks (‘terranes’), or any other arbitrary parcel of crust whose shape and size can be treated  
81 as fixed through the modelled time. Whether any given continent or crustal block can be appropriately  
82 treated as a static polygon depends on the spatial resolution and timescale being considered, and so the  
83 number and definition of static polygons can vary significantly between GPMs (with more recent and  
84 temporally more extensive GPMs tending to have more static polygons), resulting in differential  
85 partitioning of the Earth’s surface (Fig. S1). Differences in the polygonization of the Earth’s surface  
86 between GPMs also arise from different interpretations about the locations of ancient tectonic  
87 boundaries—which occurs more frequently in complicated geological areas and in deeper time.

88 The second key component of a GPM is a rotation file that describes the time-dependent motion of the  
89 tectonic elements as finite (or “total”) Euler rotations (Müller et al., 2018; Domeier and Torsvik, 2019).  
90 These ‘rotation files’ can be read and interpolated by software programs such as ‘GPlates’ (Müller et  
91 al., 2018) to reconstruct the motion of the tectonic elements through time, and enable the reconstruction  
92 of palaeocoordinates for fossil occurrence data (Boyden et al., 2011; Wright et al., 2013). It is important  
93 to note that rotation files can report the motion of tectonic elements with respect to one another  
94 (‘relative’ motion) and/or with respect to the Earth’s mantle *or* the planetary spin-axis (so-called  
95 ‘absolute’ motion) (Torsvik et al., 2008a). Only the latter reference frame (the motion of tectonic  
96 elements relative to Earth’s spin axis) is appropriate for the reconstruction of fossil occurrence data as  
97 it reports true palaeolatitudes (Seton et al. 2023). Recent work has demonstrated differences in the

98 palaeogeographic reconstruction of several fossil and geological datasets when using different GPMs  
99 (e.g. Cao et al., 2019; Boddy et al., 2022; Jones et al., 2022). Yet, the impact of model choice on  
100 palaeogeographic reconstructions at global Phanerozoic scale remains untested.

101 Quantifying this ‘palaeogeographic uncertainty’ is key to understanding the robustness of observed  
102 deep-time biodiversity patterns and their response to past climatic change (e.g. Mannion et al., 2014;  
103 Reddin et al., 2018). Here, we quantify spatial discrepancies in palaeogeographic reconstruction from  
104 five open-access GPMs. To do so, we reconstruct the palaeogeographic coordinates (i.e.  
105 palaeocoordinates) of centroids from a global hexagonal grid (~100 km spacing) across the last 540  
106 million years (Myr). By comparing these five reconstructions, we identify key spatial zones and  
107 timeframes of palaeogeographic uncertainty. Subsequently, we reconstruct the palaeogeographic  
108 distribution of two climatically-sensitive entities (fossil coral reefs and terrestrial crocodylomorphs) to  
109 evaluate the impact of GPM choice on estimations of the palaeolatitudinal extent of tropical climatic  
110 conditions over the last 240 Myr. We hypothesise that: (1) differences in palaeogeographic  
111 reconstruction increase with age, and (2) GPM choice can significantly influence reconstructions of  
112 palaeogeographic distributions of organisms and inferred palaeoclimatic conditions.

## 113 **Materials and Methods**

### 114 **Global Plate Models**

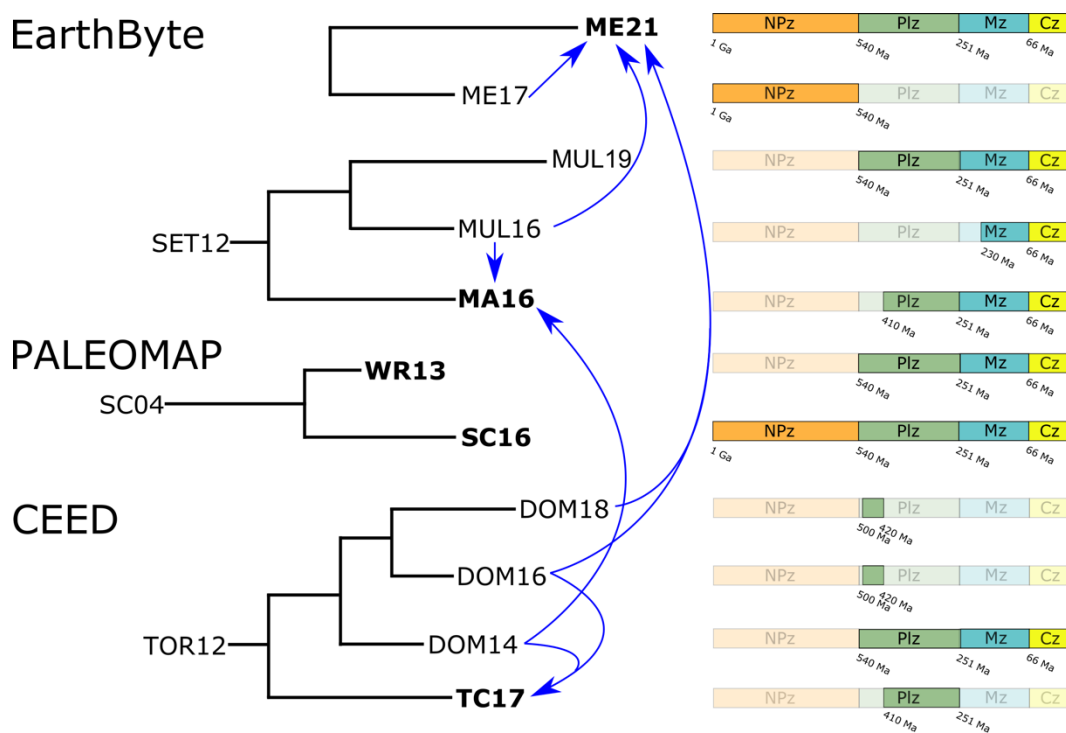
115 Five open-access Global Plate Models (GPMs) were used to evaluate spatiotemporal differences in  
116 palaeogeographic reconstructions: WR13 (Wright et al., 2013), MA16 (Matthews et al., 2016), TC17  
117 (Torsvik and Cocks, 2017), SC16 (Scotese, 2016; Scotese and Wright, 2018), and ME21 (Merdith et  
118 al., 2021). These GPMs have variable temporal coverage (see Table 1) with WR13, SC16, TC17, and  
119 ME21 covering the entirety of our Phanerozoic study period (540–0 Ma), while MA16 is limited to the  
120 Devonian–Recent (410–0 Ma).

121

122 **Table 1:** A summary table of the Global Plate Models used in this study. The table includes the  
 123 abbreviations used in this study, the names of models according to the GPlates Web Service  
 124 (<https://gwsdoc.gplates.org>), the temporal coverage of each model, and the relevant reference for each  
 125 model.

Abbreviation	GPlates ID	Temporal coverage	Reference
WR13	GOLONKA	0–550 Ma	(Wright et al., 2013)
MA16	MATTHEWS2016_pmag_ref	0–410 Ma	(Matthews et al., 2016)
TC17	TorsvikCocks2017	0–540 Ma	(Torsvik and Cocks, 2017)
SC16	PALEOMAP	0–1100 Ma	(Scotese, 2016; Scotese and Wright, 2018)
ME21	MERDITH2021	0–1000 Ma	(Merdith et al., 2021)

126



127

128 **Figure 1:** A ‘cladogram’-type representation of the relationship between Global Plate Models from the  
 129 three main model development groups (EarthByte, PALEOMAP project, and Centre for Earth  
 130 Evolution and Dynamics (CEED)) used in this study, and their respective temporal coverage. Blue  
 131 arrows indicate ‘horizontal transfers’ between models, i.e. amalgamations of models from different

132 groups. Global Plate Model abbreviations: TOR12 (Torsvik et al., 2012), DOM14 (Domeier and  
133 Torsvik, 2014), TC17 (Torsvik and Cocks, 2017), DOM16 (Domeier, 2016), DOM18 (Domeier, 2018),  
134 MA16 (Matthews et al., 2016), ME17 (Merdith et al., 2017), ME21 (Merdith et al., 2021), MUL16  
135 (Müller et al., 2016), MUL19 (Müller et al., 2019), SC04 (Scotese, 2004), SC16 (Scotese, 2016; Scotese  
136 and Wright, 2018), SET12 (Seton et al., 2012), WR13 (Wright et al., 2013). Models included in this  
137 study are represented in bold. Era abbreviations: Cenozoic (Cz), Mesozoic (Mz), Palaeozoic (Plz), and  
138 Neo-Proterozoic (NPz).

139 WR13 and SC16 both share a common lineage stemming from the plate model of Scotese (2004), but  
140 WR13 employed modifications to fit palaeomagnetic data summarised in (Torsvik and Van der Voo,  
141 2002), whereas SC16 was used to produce the widely-used set of Phanerozoic paleogeographic maps  
142 and digital elevation models (Scotese and Wright, 2018). The Scotese GPM has evolved slowly over  
143 the last three decades. Small, but significant, changes have occurred in the location of the core  
144 continents (e.g. North America, Europe, Gondwana), whereas major changes have occurred in the  
145 placement of N. China, S. China, Cimmeria, and the exotic terranes of western North America (Fig.  
146 S2). The time range of the Scotese GPM has also been extended further into the Precambrian (Scotese,  
147 2004, 2016; Scotese and Elling, 2017). TC16 primarily stems from the global paleomagnetic model of  
148 Torsvik et al. (2012), but it incorporates some changes made in the subsequent plate models of Domeier  
149 and Torsvik (2014) for the late Palaeozoic (410–250 Ma), and Domeier (2016) in the earlier Palaeozoic  
150 (500–410 Ma). Note that TC16 is presented in a mantle reference frame by default, but here we use the  
151 version which is available in the paleomagnetic reference frame. The model of MA16 is likewise built  
152 upon the model of Domeier and Torsvik (2014) for the late Paleozoic (410–250), and so MA16 and  
153 TC16 are very similar for that interval of time. For Mesozoic and Cenozoic time, MA16 is based on the  
154 model of Müller et al. (2016). Note that the model of Müller et al. (2016) exists in a mantle reference  
155 frame, and so too does the original model of MA16 for times between 250 and 0 Ma. However, a version  
156 cast into the paleomagnetic reference frame was subsequently made available, using the global apparent

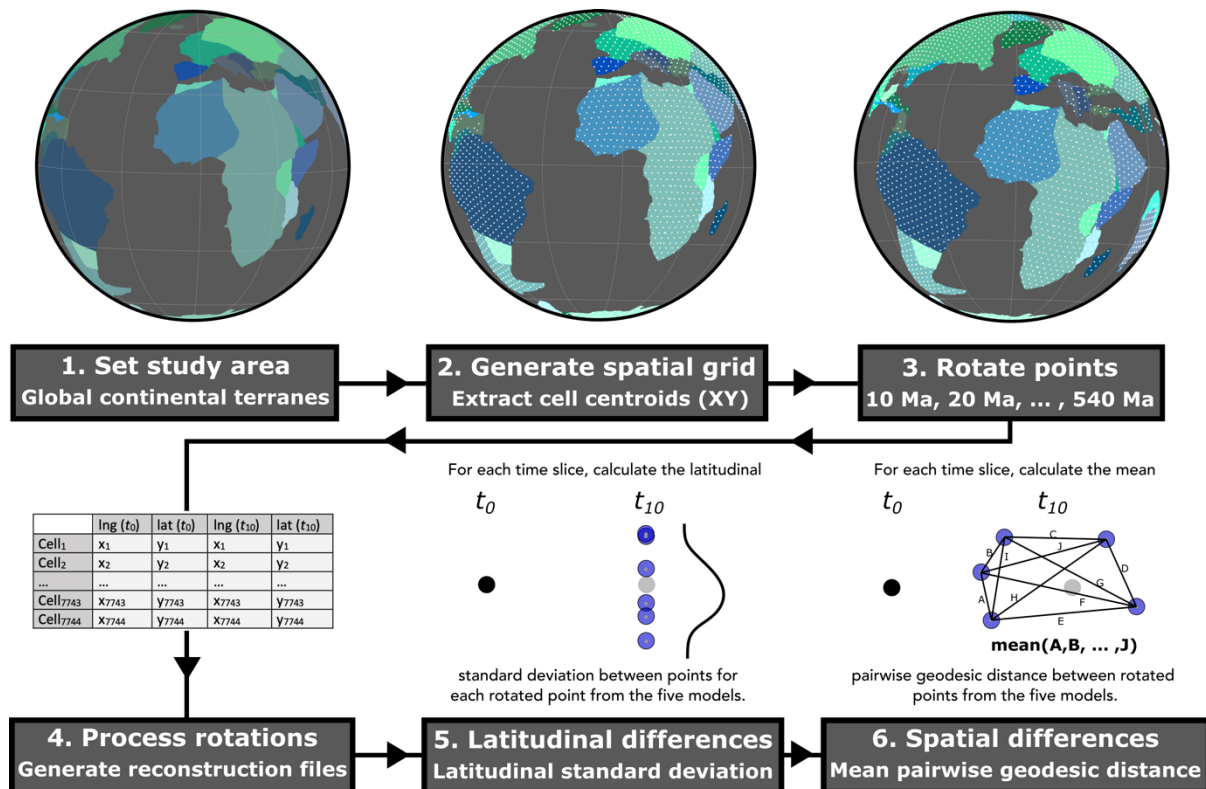
157 polar wander path from Torsvik et al. (2012), and here we utilize this later version. ME21 is largely a  
158 composition of several pre-existing models, namely the model of Merdith et al. (2017) from 1000–500  
159 Ma, the models of Domeier (2016; 2018) for the early Palaeozoic (500–410 Ma), and a modified version  
160 of Young et al. (2019) for the interval 410–0 Ma, and the entire 1000–0 Ma model interval is cast into  
161 a paleomagnetic reference frame. The model of Young et al. (2019) is modified from Matthews et al.  
162 (2016), which again was built from Domeier and Torsvik (2014) for the late Palaeozoic interval (410–  
163 250 Ma) and Müller et al. (2016) from 230–0 Ma. Thus, for the Palaeozoic interval (particularly the late  
164 Palaeozoic), there is some common ancestry between TC16, MA16 and ME21, and this extends into  
165 the Mesozoic and Cenozoic for MA16 and ME21. Nevertheless, the modifications made between these  
166 alternative models is a reflection of outstanding paleogeographic uncertainty. Figure 1 summarises the  
167 main interrelationships between these various GPMs.

## 168 **Quantifying spatiotemporal differences**

169 To quantify differences in palaeogeographic reconstruction (Fig. 1), we first generated a discrete global  
170 hexagonal grid (~100 km spacings) via the python library ‘h3’ v.3.7.6 (Uber, 2023). Most GPMs have  
171 a network of static polygons covering most of the Earth’s continental areas, and we retained only the  
172 grid cells that were included within a static polygon in each of the GPMs. Subsequently, we  
173 reconstructed palaeocoordinates for cell centroids across the last 540 Myr with a timestep of 10 Myr  
174 for each GPM, resulting in up to 54 time steps depending on GPM (Table 1). To do so, we used the  
175 python library ‘pygplates’ ver. 0.36.0 (Williams et al., 2017) to interact with the software GPlates  
176 (Boyden et al., 2011; Müller et al., 2018). Using the reconstructed palaeocoordinates for each cell—from  
177 each model—we calculated: (1) the standard deviation (SD) in palaeolatitude and (2) the mean pairwise  
178 geodesic distance (PGD) between reconstructed coordinates (up to five sets) for each cell. The former  
179 of these quantifies the potential uncertainty in palaeolatitude between models with significance for  
180 studies such as those focused on reconstructing the latitudinal biodiversity gradients in deep time (e.g.  
181 Allen et al., 2020; Song et al., 2020). The latter quantifies the uncertainty in palaeogeographic position



182 between models having significance for studies focused on themes such as reconstructing organisms'  
 183 geographic range sizes (e.g. Antell et al., 2020). Mean PGD was calculated using the R package  
 184 'geosphere' ver. 1.5-18 (Hijmans et al., 2021).



185 **Figure 2:** A graphical schematic of the simulation workflow used in this study. Using continental  
 186 tectonic elements, the study area is first established (1). Subsequently, a discrete global hexagonal grid  
 187 (~100 km spacings) is generated via the python library 'h3' v.3.7.6 (Uber, 2023) and cell centroids  
 188 extracted for cells intersecting with the continental tectonic elements (2). Cell centroids are then rotated  
 189 (3) at time intervals of 10 Myr throughout the Phanerozoic (540–0 Ma), for each model, using the  
 190 software GPlates via the 'pygplates' ver. 0.36.0 python library (Williams et al., 2017). Reconstruction  
 191 files are subsequently generated for each model (4), and the palaeolatitudinal standard deviation (5) and  
 192 the mean pairwise geodesic distance (6) calculated for each cell centroid between the five models for  
 193 each time step.

195

196 **Palaeoclimatic reconstruction**

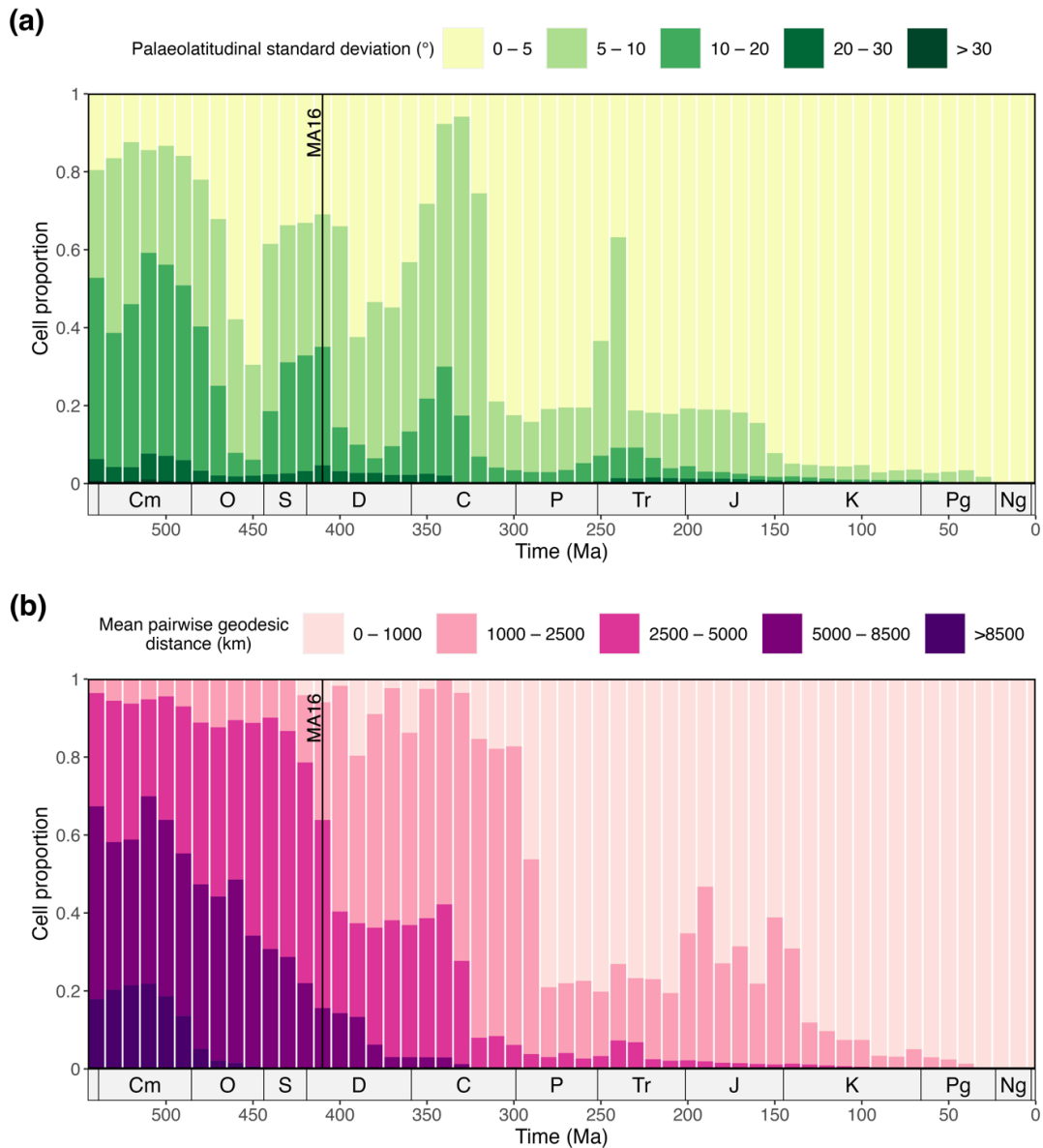
197 To test the influence of GPM choice on fossil-based palaeoclimatic reconstructions, we estimate the  
198 palaeolatitudinal extent of (sub-)tropical climatic conditions using two climatically sensitive entities:  
199 warm-water coral reefs and terrestrial crocodylomorphs. These entities are frequently used to infer the  
200 extent of (sub-)tropical palaeoclimatic conditions due to their limited thermal tolerance and geographic  
201 distribution today (e.g. Markwick, 2007; Burgener et al., 2023). Fossil crocodylomorph occurrences  
202 (=“Crocodylomorpha”) were downloaded from The Paleobiology Database (<https://paleobiodb.org/#/>)  
203 on the 9<sup>th</sup> of November 2022 and were restricted to terrestrial taxa and body fossils. Marine taxa were  
204 excluded as they appear to be less constrained by climatic factors than terrestrial taxa (Mannion et al.,  
205 2015). Fossil coral reef occurrences were downloaded from the PaleoReef Database (Kiessling and  
206 Krause, 2022) on the 10<sup>th</sup> of March 2022 and were restricted to scleractinian ‘true reefs’ with a tropical  
207 affinity. This led us to exclude pre-Anisian reef occurrences. At the end of the cleaning, the midpoint  
208 age of oldest crocodylomorph occurrence was 232.5 Ma, and the oldest reef occurrence was 231.5 Ma.  
209 Finally, fossil occurrences were split into 10 Myr time bins using the midpoint age of each occurrence’s  
210 age range. After data processing, 4638 terrestrial crocodylomorphs and 419 warm-water coral reef  
211 occurrences remained for analyses.

212 Using the five GPMs (Table 1), we reconstructed the palaeocoordinates for each occurrence based on  
213 the midpoint of its respective age range. Assuming hemispheric symmetry in climatic conditions, we  
214 subsequently identified the maximum absolute palaeolatitude within each time bin—for each model and  
215 entity—to infer the palaeolatitudinal extent of (sub-)tropical climatic conditions. Using this deduction,  
216 we quantified the potential uncertainty in the palaeolatitudinal extent of (sub-)tropical climatic  
217 conditions by calculating the palaeolatitudinal range between estimates for each time bin. Finally, for  
218 each fossil occurrence, we calculated the median, maximum and minimum reconstructed palaeolatitude  
219 from the five model estimates.

## 220 **Results**

### 221 **Spatiotemporal discrepancy trends**

222 Palaeolatitudinal SD and mean PGD demonstrate an increasing uncertainty in palaeogeographic  
223 reconstruction with age (Fig. 3–4; Fig. S3). Overall, GPMs are in good agreement for the last 100 Myr  
224 (mid-Cretaceous–Recent), with 97.4% of cells having a palaeolatitudinal SD less than 5° and a mean  
225 PGD less than 1000 km (Fig. 3). However, GPM reconstructions begin to substantially diverge at  
226 greater reconstruction ages with generally increasing uncertainty throughout the Mesozoic (251.9–66  
227 Ma) and Palaeozoic (538.8–251.9 Ma). For example, in the Cenozoic (66–0 Ma), 1.9% of cells have a  
228 palaeolatitudinal SD of more than 5°, going up to 14.8% of cells during the Mesozoic, and 53.8% during  
229 the Palaeozoic (Fig. 3a). This trend is further reflected by an increase in mean PGD with 1.2% of cells  
230 having a value of more than 1000 km in the Cenozoic, 20.2% during the Mesozoic, and 80% during the  
231 Palaeozoic (Fig. 3b). Differences in Cambrian (538.8–485.4 Ma) reconstructions are especially large,  
232 with a considerable proportion of cells having a palaeolatitudinal SD of more than 5° (~76.3%) and  
233 mean PGD of more than 1000 km (~90.1%) (Fig. 3; Fig. S3). Notably, despite this overall trend of  
234 increasing palaeogeographic uncertainty with age, uncertainty is relatively low during the latest  
235 Carboniferous and Permian in comparison to the rest of the Palaeozoic and early Mesozoic (Fig. 3).

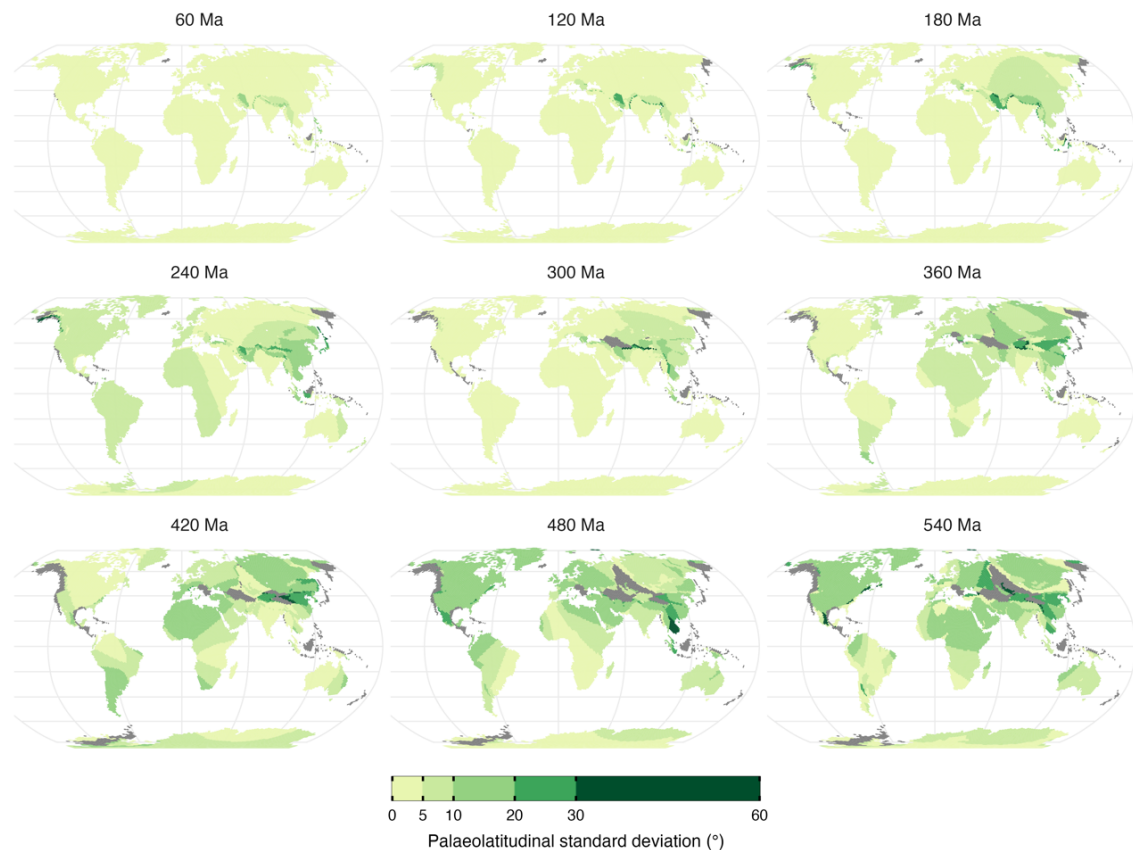


236

237 **Figure 3:** Phanerozoic trends in spatial discrepancies between Global Plate Models within 10 Myr time  
 238 steps. Values are categorised and depicted as proportions of cells. (a) Palaeolatitudinal standard  
 239 deviation between reconstructed palaeocoordinates for cell centroids. (b) Mean pairwise geodesic  
 240 distance between reconstructed palaeocoordinates for cell centroids. The black line depicts the temporal  
 241 limit (410 Ma) of the MA16 model (Matthews et al., 2016). The bar plots show increasing  
 242 palaeogeographic uncertainty between models with age of reconstruction. Period abbreviations are as  
 243 follows: Cambrian (Cm); Ordovician (O), Silurian (S), Devonian (D), Carboniferous (C), Permian (P),

244 Triassic (Tr), Jurassic (J), Cretaceous (K), Paleogene (Pg), and Neogene (Ng). The Quaternary is not  
245 depicted. The Geological Time Scale axis was added to the plot using the R package ‘deptime’ ver.  
246 1.0.1 (Gearty, 2023).

247 Our palaeolatitudinal SD and mean PGD results show palaeogeographic uncertainty is not evenly  
248 distributed in space (Fig. 4; Fig. S3). High palaeogeographic uncertainty is generally restricted to plate  
249 boundaries and active deformation zones during the Cenozoic and Mesozoic but extends to broader  
250 areas during the Palaeozoic (Fig. 4; Fig. S3; supplementary GIFs). For example, throughout the  
251 Cenozoic and Mesozoic, palaeogeographic reconstructions of South American cell centroids appear  
252 well constrained in comparison to those along the Eurasian-Indian and Eurasian-Arabian plate  
253 boundaries (Fig. 4; Fig. S3; supplementary GIFs).

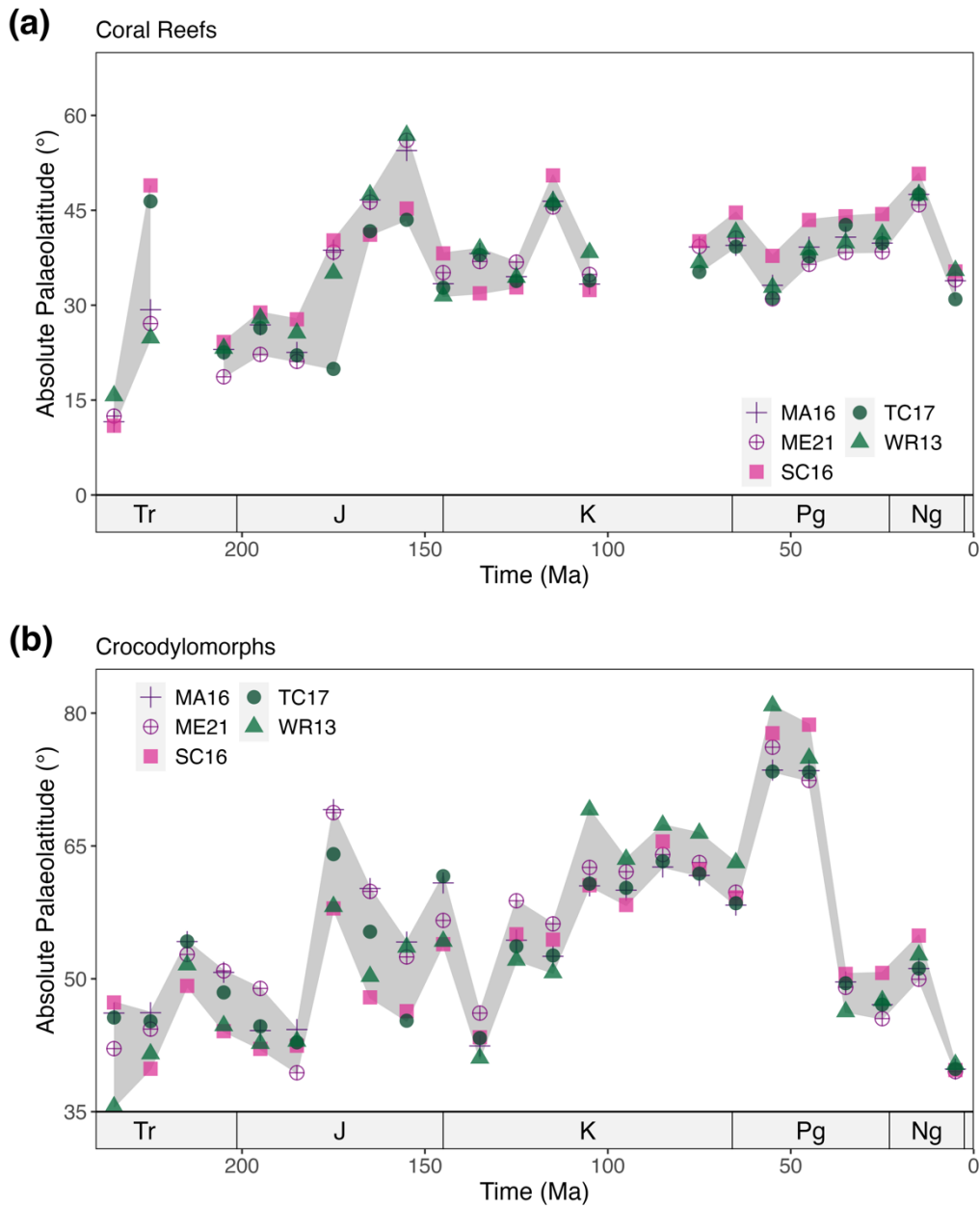


255 **Figure 4:** Categorized maps of the palaeolatitudinal standard deviation between reconstructed  
256 palaeocoordinates of cell centroids from Global Plate Models. Values are mapped onto a present-day

257 map with darker shades indicating greater palaeolatitudinal standard deviation between  
258 palaeocoordinates. Grey cells denote areas where palaeocoordinates could not be reconstructed at time  
259 of reconstruction for cell centroids by at least two models. Maps are presented in the Robinson  
260 projection (ESRI:54030).

## 261 **Palaeoclimatic reconstructions**

262 Our results suggest that reconstructions of the palaeolatitudinal extent of (sub-)tropical climatic  
263 conditions—based on terrestrial crocodylomorphs and coral reef occurrences—can vary by up to 12.3°  
264 latitude in crocodylomorphs and 24.1° in coral reefs, depending on GPM choice (Fig. 5). The average  
265 range between models along the 240 Myr time series is 7.7° for coral reefs and 6.5° for terrestrial  
266 crocodylomorphs (Fig. 5). However, despite these large observed differences, the direction of change  
267 (equatorward vs. poleward) in the extent of (sub-)tropical conditions is largely consistent between  
268 GPMs (Fig. 5). Both time series exhibit a significant positive correlation between age of reconstruction  
269 and the range in the extent of (sub-)tropical conditions from GPM estimates (Pearson's correlation test:  
270  $R = 0.43$ ;  $P = 0.05$  for coral reefs and  $R = 0.55$ ;  $P = 0.005$  for crocodylomorphs). Comparisons of  
271 reconstructed palaeocoordinates for all occurrences further support an increase in palaeolatitudinal  
272 uncertainty with age (Fig. S5). For example, the average palaeolatitudinal range between the five GPMs  
273 for each occurrence—within each time bin—increases significantly with age (Pearson's correlation test:  
274  $R = 0.49$ ;  $P < 0.001$  for coral reefs and  $R = 0.33$ ;  $P < 0.001$  for crocodylomorphs).



275

276 **Figure 5:** Palaeogeographic uncertainty in fossil-based reconstruction of the (sub-)tropics within 10  
 277 Myr time steps (0–240 Ma). For each time step, the maximum absolute reconstructed palaeolatitude of  
 278 coral reefs with a tropical affinity (a) and terrestrial crocodylomorphs (b) is depicted for each Global  
 279 Plate Model. The uncertainty of the palaeolatitude limit of subtropical reconstruction is depicted as  
 280 the range between the maximum absolute palaeolatitudes (grey ribbon), with an average uncertainty of  
 281 7.7° for coral reefs (a) and 6.5° for crocodylomorphs (b). Both time series exhibit a strong positive

282 correlation between age of reconstruction and palaeolatitudinal uncertainty ( $R = 0.43\text{--}0.55$ ;  $P \leq 0.05$ ).  
283 Global Plate Model abbreviations are the same as in Figure 1. The Geological Time Scale axis was  
284 added to the plot using the R package ‘deptime’ ver. 1.0.1(Gearty, 2023).

## 285 **Discussion**

### 286 **With age comes uncertainty**

287 In this study, we quantified palaeogeographic reconstruction differences between five Global Plate  
288 Models (GPMs). Our results demonstrate that palaeogeographic uncertainty increases with age (Fig. 3)  
289 suggesting caution is required when reconstructing deep-time macroecological trends such as  
290 geographic range sizes (e.g. Antell et al., 2020), latitudinal biodiversity gradients (e.g. Powell, 2009;  
291 Zhang et al., 2022), and organisms’ spatial response to global climatic change (e.g. Reddin et al., 2018).  
292 However, the issue of palaeogeographic uncertainty also has relevance for fields such as  
293 palaeoclimatology, where palaeotemperature proxies are used to reconstruct latitudinal temperature  
294 gradients (e.g. Zhang et al., 2019) and evaluate the performance of palaeoclimatic simulations (e.g. Lunt  
295 et al., 2021). Therefore, in the wake of additional methodological concerns that have been considered  
296 recently—e.g. spatial sampling bias in the geological record (e.g. Vilhena and Smith, 2013; Close et al.,  
297 2020; Jones and Eichenseer, 2021)—our work raises a new challenge for those working with fossil data  
298 in deep time. Following our results, we recommend that studies dealing with deep time  
299 palaeogeographic reconstructions should consider the robustness of their conclusions to GPM choice  
300 (e.g. Boddy et al., 2022), particularly for intervals older than  $\sim 300$  Ma. Moreover, akin to phylogenies,  
301 we advocate that reconstructed coordinates should be treated as the model-based estimates they are,  
302 rather than empirical data.

### 303 **Spatial clusters of palaeogeographic uncertainty**

304 Our results show that palaeogeographic reconstruction discrepancies are not only uneven in time, but  
305 also in space. During the Cenozoic and Mesozoic, high palaeogeographic uncertainty is clustered  
306 around active plate boundaries and tectonically complex regions such as along the Eurasian-Indian,



307 Eurasian-Arabian, and North American-Juan de Fuca plate boundaries (Fig. 4; Fig. S3). The high  
308 uncertainty values found in these areas is a direct result of differential partitioning in GPMs with cell  
309 centroids assigned to different geometries, each with their own unique reconstruction history (Fig. S1).  
310 This finding suggests that additional caution is warranted when reconstructing the palaeogeographic  
311 distribution of fossil occurrences originating from areas close to plate boundaries or within tectonically  
312 complex regions. Hence, reconstructions of fossil occurrences from cratonic areas—stable interior  
313 portions of continents—ought to be more consistent between GPMs than reconstructions of fossil  
314 occurrences from continental margins or the edges of tectonic blocks. However, our results also suggest  
315 that there is an overarching trend of increasing uncertainty among GPMs throughout the Palaeozoic,  
316 even in cratonic areas. Rather than differences in the delineation of static polygons, this reflects  
317 differences in the modelled rotation histories as prescribed by the rotation files.

### 318 **Pre-Jurassic palaeolongitudinal uncertainty**

319 The direct reconstruction of palaeolongitude is challenging for most of Earth's history. While  
320 palaeomagnetic data can be used to constrain the relative palaeolatitudinal position of plates and  
321 continents, they cannot directly constrain palaeolongitude (Vérard, 2019). Hotspot tracks, which record  
322 the motion of a tectonic plate over a mantle plume, enable the determination of palaeolongitude (with  
323 respect to the base of the mantle), but owing to the incessant recycling of oceanic crust, well-resolved  
324 hotspot tracks are limited to the last ~130 Ma (Seton et al. 2023). Marine magnetic anomalies enable  
325 the determination of relative palaeolongitude back to the time of Pangaea breakup (~200 Ma), but they  
326 cannot constrain absolute palaeolongitude. Other attempts to constrain palaeolongitude in deeper time  
327 remain controversial (Torsvik et al., 2008b; Mitchell et al., 2012). This has broad implications for  
328 palaeobiological studies such as those reconstructing organisms' geographic range sizes in deep time  
329 (e.g. Kiessling and Aberhan, 2007). However, this will only be an issue in cases where occurrences  
330 span a relatively wide number of terranes. Nevertheless, one should also bear in mind that the  
331 palaeolatitudinal distribution of the continents can also vary significantly between GPMs particularly

332 in the Palaeozoic (Fig. S4), likely resulting from increasing sparsity of palaeomagnetic data over that  
333 period, as shown by Torsvik et al. (2012).

### 334 **Reconstructing palaeoclimatic conditions**

335 Fossil occurrences of climatically-sensitive organisms are routinely used to estimate the distribution of  
336 past climatic conditions (e.g. Frakes et al., 1992; Scotese et al., 2021; Burgener et al., 2023). Here–  
337 using five different GPMs—we estimated the palaeolatitudinal extent of (sub-)tropical climatic  
338 conditions for the last 240 Myr using fossil terrestrial crocodylomorphs and warm-water coral reefs  
339 (Fig. 5). Our findings support previous work in demonstrating that GPM choice can strongly influence  
340 reconstructions of palaeoclimatic conditions when based on geological data (e.g. Cao et al., 2019).  
341 Moreover, our results suggest that previous conclusions based on the use of one GPM might be worth  
342 revisiting (e.g. Markwick, 1998; Kiessling, 2001). Nevertheless, while large differences ( $\sim 24.1^\circ$   
343 latitude) can be observed between GPMs in extreme cases, the direction of change (equatorward vs.  
344 poleward) is largely consistent between GPMs suggesting broad-scale relative patterns are constrained.  
345 Consequently—across temporal scales—the use of a single GPM can be useful for informing relative  
346 changes within a time series, but the magnitude of change relative to the present-day should be carefully  
347 considered.

### 348 **Study limitations**

349 We quantified Phanerozoic (540–0 Ma) palaeogeographic uncertainty between five GPMs using a  
350 global hexagonal grid ( $\sim 100$  km spacings). While the use of additional models such as the commonly  
351 applied Getech plate model would be desirable to further quantify palaeogeographic uncertainty (e.g.  
352 Chiarenza et al., 2019; Saupe et al., 2019), not all GPMs are open access and broadly available to the  
353 community. Despite this, the use of additional models is unlikely to change the general trends observed  
354 in this study which are primarily driven by limited data availability (e.g. palaeomagnetic data and  
355 constraints on palaeolongitude) and geological interpretation (e.g. tectonic boundaries). Furthermore,  
356 the spatial resolution of our study ( $\sim 100$  km spacings) may influence our results in the identification of

357 areas of high palaeogeographic uncertainty. For example, along geological boundaries, a finer-scale  
358 grid might further constrain the areal extent of these areas. Nevertheless, our results provide a first-  
359 order advisory note for those working with spatial data and advocates for the quantification of  
360 palaeogeographic uncertainty for individual datasets.

## 361 **Conclusion**

362 In conclusion, our study demonstrates that differences in palaeogeographic reconstruction increase with  
363 age. Consequently, an increasing level of caution is warranted when reconstructing fossil assemblages  
364 from older intervals, particularly for intervals older than ~300 Ma. Nevertheless, consideration is also  
365 required—even for younger intervals—for fossil occurrences originating from tectonically complex  
366 regions where the definition of tectonic boundaries lack consensus between Global Plate Models. Our  
367 study also demonstrates the impact Global Plate Model choice can have on broader conclusions such  
368 as reconstructions of palaeoclimatic conditions based on fossil occurrence data. Therefore, we endorse  
369 that studies dependent on deep-time palaeogeographic reconstructions should only use models based  
370 on a palaeomagnetic reference frame to reconstruct fossil palaeocoordinates, test the sensitivity of their  
371 conclusions to Global Plate Model choice, and quantify the palaeogeographic uncertainty associated  
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## 384 **Authors' contributions**

385 LAJ and SV conceived the project. All authors contributed to developing the project. LB, LAJ and MD  
386 wrote the code, conducted the analyses, and produced the figures. All authors contributed to writing the  
387 manuscript.

## 388 **Data availability**

389 The data generated in this study have been included within the paper, its supplementary material, and  
390 dedicated GitHub repository ([https://github.com/Bufan3369/rotation\\_sensitivity](https://github.com/Bufan3369/rotation_sensitivity)).

## 391 **Code availability**

392 Generation of the reconstruction grids and palaeocoordinates for fossil occurrence data were generated  
393 via pygplates run in python version 3.9.7. All data analyses were conducted in R version 4.2.2. The  
394 workflow is available both as R scripts and Jupyter notebooks on GitHub (accessible via:  
395 [https://github.com/Bufan3369/rotation\\_sensitivity](https://github.com/Bufan3369/rotation_sensitivity)).

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Supplementary information for  
**MIND THE UNCERTAINTY: GLOBAL PLATE MODEL CHOICE IMPACTS  
DEEP-TIME PALAEOBIOLOGICAL STUDIES**

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## SUPPLEMENTARY TEXT

### METHODOLOGICAL BASIS OF GLOBAL PLATE MODELS

Global Plate Models (or Global Plate Rotation Models, GPMs) use the Euler rotation theorem to describe the motion of geometries—such as tectonic plates or geological terranes—on a sphere. A variety of tools have been developed to build global plate tectonic models. However, the most widely used tool is the cross-platform and open-source GPlates ([www.gplates.org](http://www.gplates.org)) software (Boyden et al., 2011; Müller et al., 2018) which is frequently applied to reconstruct the past geographic distribution of fossil samples using various GPMs (e.g. Allen et al., 2020; Boddy et al., 2022; Jones & Eichenseer, 2021).

A GPM is primarily made up of two key components. The first component represents the geometries that define geological boundaries, such as terranes and/or parcels of oceanic crust. GPlates stores these geometries in their present-day positions. Each geometry requires an identity number (Plate ID) and the age at which it first appears. The second component of a GPM is the motion of these geometries through time. This information is stored in a user-editable hierarchical model of finite rotations (Ross & Scotese, 1988) which describes the motion of the geometries through time. GPlates reads and interpolates data from these ‘rotation files’ to reconstruct the motion of geometries. The most common geometries in GPMs are ‘static polygons’, otherwise known as ‘static plate polygons’ or simply ‘plate polygons’. Static polygon geometry files are typically made up of numerous polygons which represent individual tectonic plates. While these polygons can rotate across the globe, their shape does not change through time, hence the name static polygons. Each polygon within the geometry file carries a unique Plate ID and a time of appearance (and potentially disappearance) allowing tectonic plates to have an origin and ultimate demise. However, GPMs can have different static polygons (particularly between working groups) and therefore partitioning of the Earth may vary (Fig. S1). Consequently, plate IDs are unique to each static polygon file in GPMs, but they are not necessarily consistent between different GPMs. A specialised variant of plate polygons in plate tectonic modelling are known as continually-closing plate boundaries (Gurnis et al., 2012). These are time-evolving topologies of tectonic plate boundaries (rather than rotated ‘static’ present-day features), and they approximate the continuous evolution of plate boundaries using a set of dynamically changing plate polygons. This approach was developed to model the relationship between plate evolution and mantle dynamics. More recently, such evolving topological polygons have been expanded to capture deformation in Earth’s lithosphere (Gurnis et al., 2018; Müller et al., 2019), which can be used to ‘retro-deform’ geological sample location (e.g. fossil localities).

Global Plate Modelling requires a ‘reference frame’ in which the geometries like the plate polygons move. Several reference frames have been proposed, and the types of reference frames being used are extremely important to consider. Fundamentally, ‘mantle reference frames’ try to isolate the plate-mantle system by eliminating the effect of the centrifugal forces due to Earth rotation on the motion of

the ‘solid earth’ (lithosphere and mantle), namely true polar wander (TPW) (Steinberger & Torsvik, 2008). As both mantellic convection and TPW drive plates motion, removing TPW allows isolation of the plate-mantle system and in turn investigation of the motion of the Earth’s outer shell relative to the mantle. For that quality, they are mostly used by the geodynamics and tectonics community. However, removing TPW can have a negative impact upon the reconstruction of palaeocoordinates (i.e. for fossil occurrences or geological samples) (Seton et al., 2023). Therefore, the use of GPMs for palaeoclimatic or palaeobiological studies should carefully consider whether a mantle reference frame is appropriate. For palaeoclimatological and palaeobiological applications, a pure palaeomagnetic reference frame is likely to be more appropriate as it does not eliminate the effects of TPW and is therefore more likely to report true geographic palaeolatitudes.

To constrain the motion of tectonic plates, reference frames are compiling geological data. In particular, palaeolatitudes are robustly estimated using the palaeomagnetic record (i.e. from the inclination of magnetic minerals) (e.g. Beck, 1988; Merdith et al., 2021; Voo, 1993), but due to the radial symmetry of Earth’s magnetic field, palaeomagnetic data cannot be used to assess palaeolongitudes. Nevertheless, palaeolongitudinal positioning is possible in a mantle reference frame where a comprehensive set of hot spot tracks can be used to infer the absolute motion of tectonic plates with respect to the base of the mantle (assuming that mantle plumes do not have substantial movement or deflection). Two types of hotspot reference frames have been developed, ones that assume ‘fixed hotspots’ that do not move (e.g. Müller et al., 1993; Torsvik et al., 2008), and others that incorporate ‘moving hotspots’ to optimise the fits between hotspot tracks on plates and the source of the hotspots (e.g. O’Neill et al., 2005; Torsvik et al., 2008). The fixed-hotspot reference frame combines palaeomagnetic data with the positional information derived from volcanic hotspots tracks (Müller et al., 1993; Scotese, 2021). However, due the loss of oceanic crust, useful hotspot tracks only extend back until the Early Jurassic. Although (Torsvik et al., 2008) proposed a unifying reference frame constraining palaeolongitude over the last 320 Ma, it is not widely used (Boddy et al., 2022; Merdith et al., 2021).

Though there is currently no method to adequately constrain longitude for intervals prior to 200 Ma, several approaches have been taken to constrain longitudinal positions. A common solution is the ‘Africa-fixed’ reference frame (Scotese et al., 1988; Torsvik & Cocks, 2016). This approach affixes Africa to the prime meridian (Scotese, 2021) or to a set of active hotspots that surround Africa (Large Low Shear-wave Velocity Provinces) (Torsvik & Cocks, 2016). In these reference frames, Africa remains near the centre of the map, relative longitudinal motions between the plates are preserved and erratic shifts in longitude are eliminated. Another approach is to apply kinematic constraints to minimise trench advance and net rotation, and derive a mantle reference frame that also infers palaeolongitude (Müller et al., 2019, 2022; Tetley et al., 2019).

GPMs are often constructed to address specific applications, such as using mantle reference frames to model mantle convection and isolate the plate-mantle system. However, for the palaeoclimatic and

palaeobiological communities, it is crucial to understand what absolute reference frame is used as it may impact upon their reconstructions and subsequent conclusions. In addition to ‘rotation files’, which describe the relative and absolute plate motion paths, the subdivision of Earth’s crust into terranes (or blocks) can also introduce differences in the reconstruction of palaeocoordinates. In most cases, the source of this uncertainty is from varying interpretations of suture zones, where the geological boundaries are typically complex due to prolonged or multiple deformation events. As a result, one should evaluate the impact of GPM choice in relation to their data and understand that each variant carries spatially and temporally evolving uncertainties.

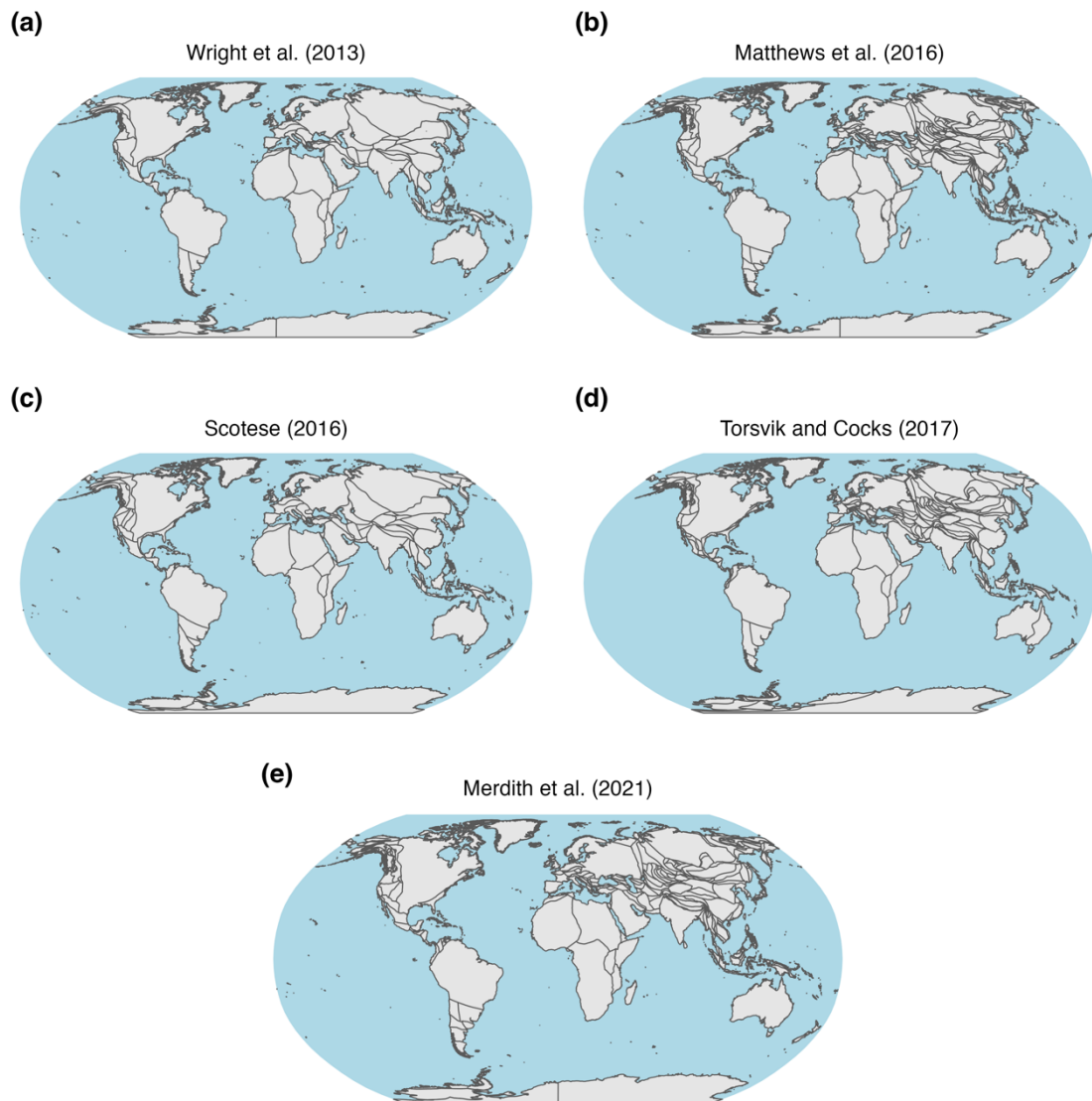
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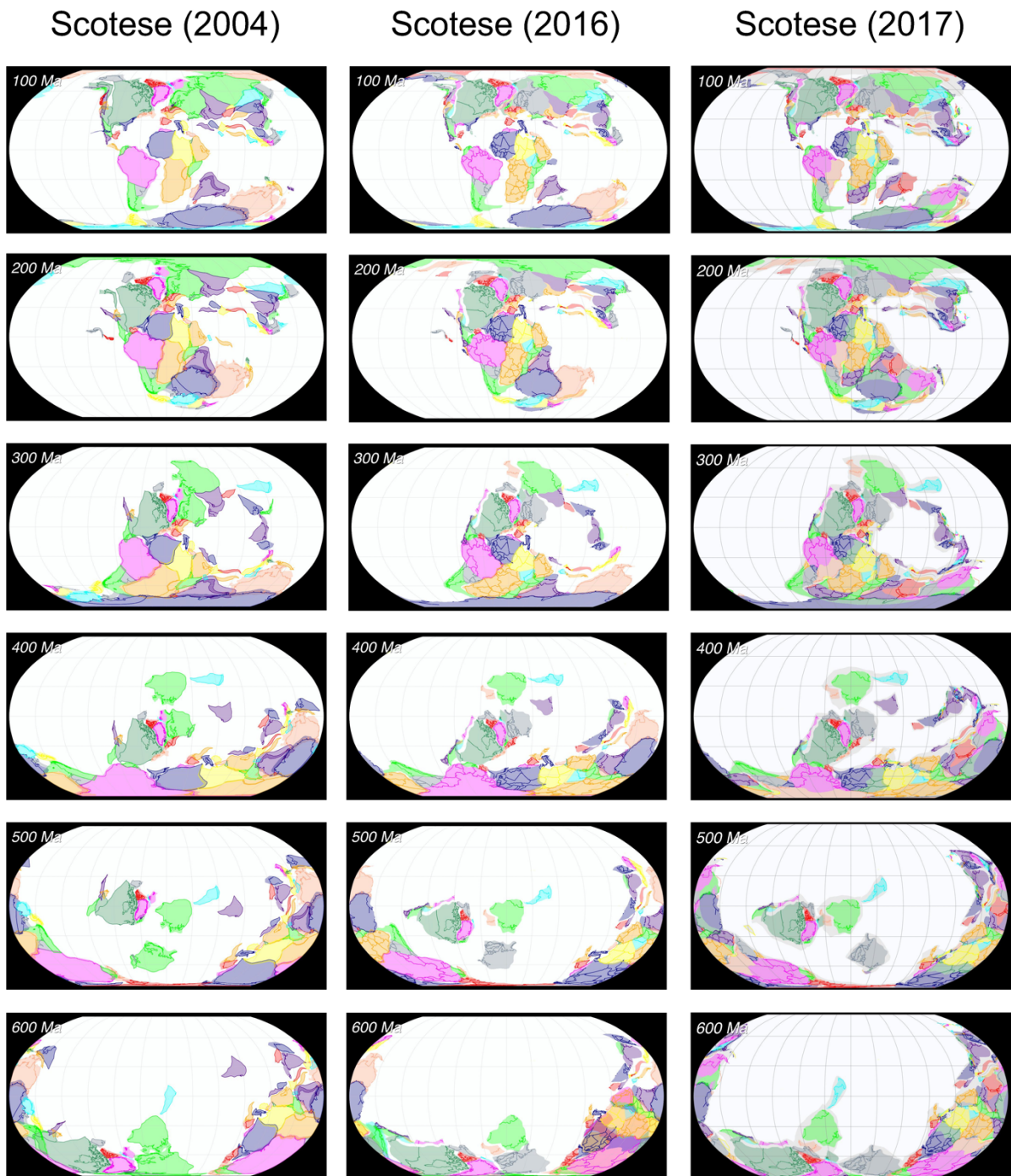
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## SUPPLEMENTARY FIGURES

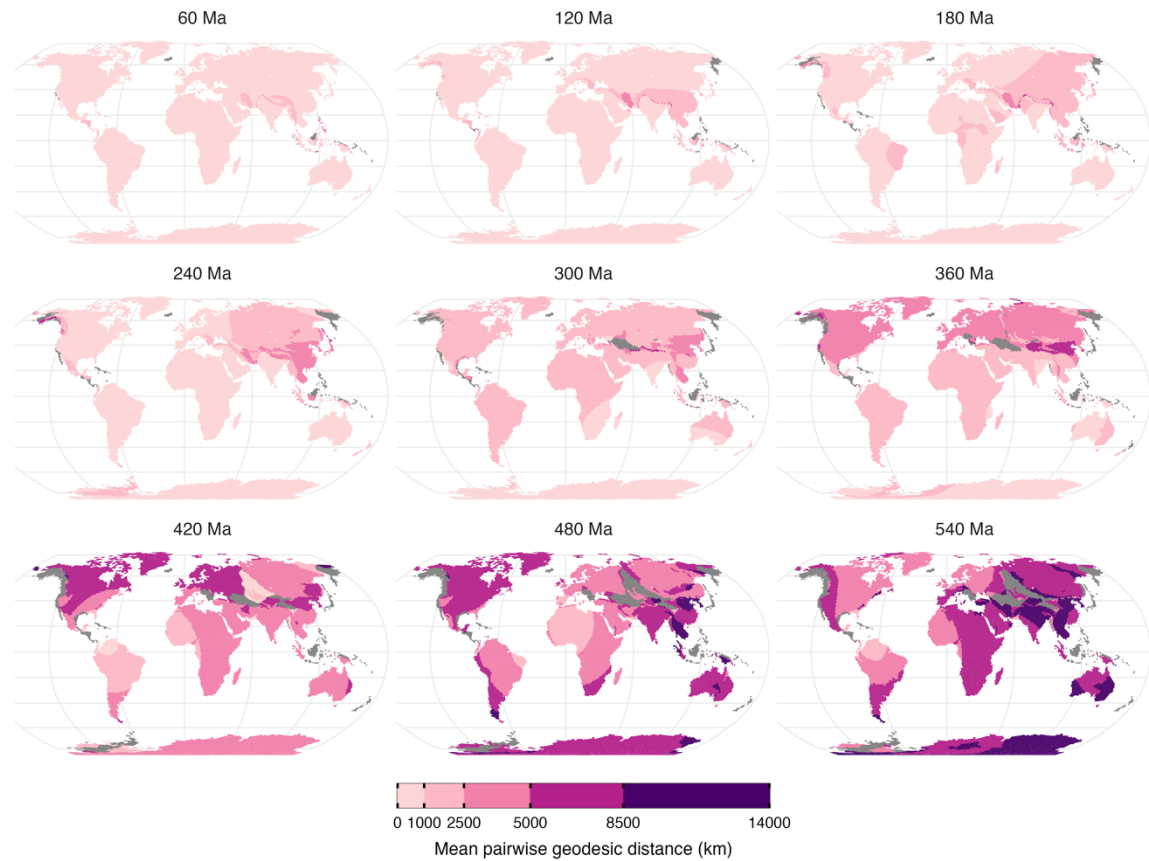


**Figure S1:** Continental plate polygons for Global Plate Models used in this study. Note: Global Plate Models partition continental plate polygons differently, including where polygons are partitioned, and how many partitions are present. Maps are presented in the Robinson projection (ESRI:54030).

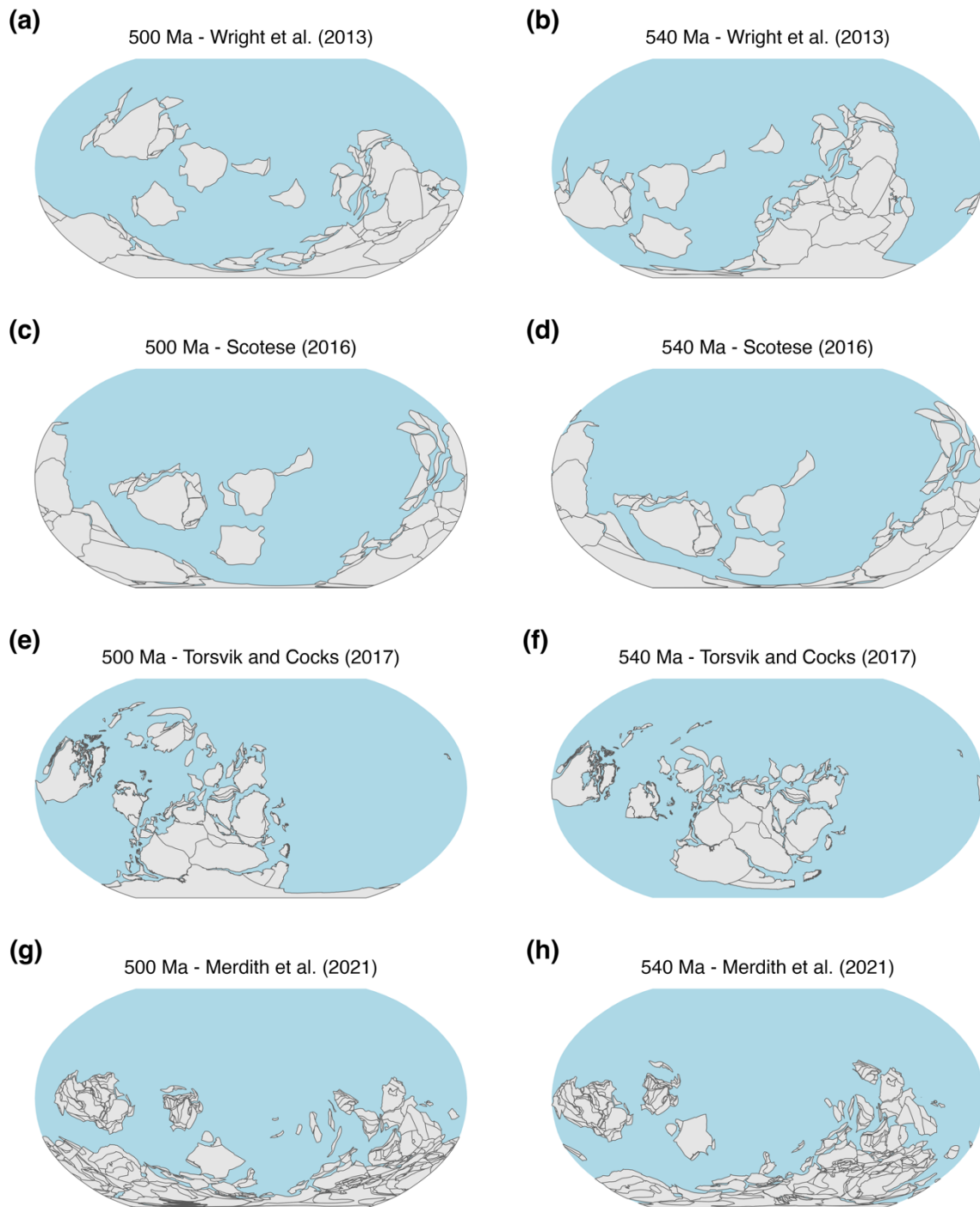




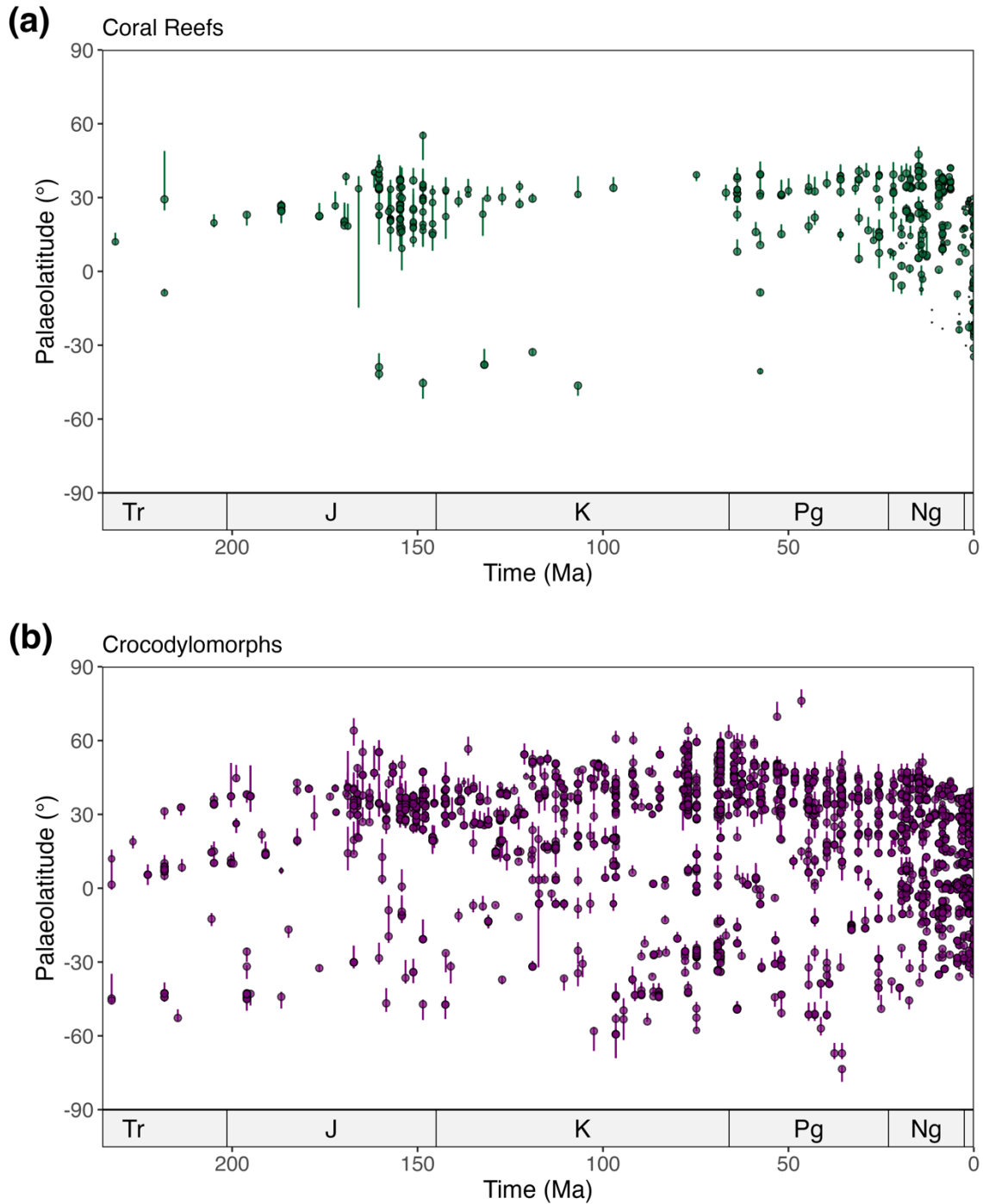
**Figure S2:** Evolution of the Scotese Global Plate Model (2004–2017). Small changes occur in the location of the ‘core’ continents. Major changes occur in the placement of N. China, S. China, Cimmeria, and the exotic terranes of western North America. The time range of the models has also evolved (though not fully depicted here), with Scotese (2004) ranging from 0–750 Ma, Scotese (2016) from 0–1100 Ma, and Scotese (2017) from 0–1500 Ma. Maps are presented in the Robinson projection (ESRI:54030).



**Figure S3.** Categorized maps of the mean pairwise geodesic distance between reconstructed palaeocoordinates of cell centroids from Global Plate Models. Values are mapped onto a present-day map with darker shades indicating greater geographic distance between palaeocoordinates. Grey cells denote areas where palaeocoordinates could not be reconstructed at time of reconstruction for cell centroids by at least two models. Maps are presented in the Robinson projection (ESRI:54030).



**Figure S4:** Reconstructed continental areas of the early and late Cambrian according to different Global Plate Models: WR13 (a, b), SC16 (c, d), TC17 (e, f) and ME21 (g, h). The left-hand side of the panel depicts palaeogeographic reconstructions of the Earth at 500 Ma (early Cambrian). The right-hand side of the panel depicts palaeogeographic reconstructions of the Earth at 540 Ma (late Cambrian). The MA16 Global Plate Model is not depicted here as the Cambrian is not within its temporal coverage. Maps are presented in the Robinson projection (ESRI:54030).



**Figure S5:** Palaeolatitudinal reconstruction of fossil coral reefs (a) and terrestrial crocodylomorphs (b) according to the five Global Plate Models used in this study. Each point represents the median of the palaeolatitude estimate for an occurrence. The size of the points is proportional to the logarithm of the number of models palaeocoordinates could be reconstructed from ( $n = 1$  to 5). Each bars depict the minimum and maximum palaeolatitudinal estimate for an occurrence. Pearson's correlation tests showed significant positive relations between the age of reconstruction and average range of palaeolatitudinal estimates per time interval ( $R = 0.33$ – $0.49$ ;  $P < 0.001$ ).