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Climate windows of opportunity for plant expansion during the Phanerozoic

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1 **Climate windows of opportunity for plant expansion during the**
2 **Phanerozoic**

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15

16 **Contributions**

17 KG, KJF, SAB and BJWM conceived and designed the investigation. KG wrote the model,
18 analysed the data and wrote the first draft of the manuscript with assistance from KJF and
19 BJWM. YG, YD, PP and LLT provided data and discussed results. All authors discussed
20 results and commented on the manuscript. KG agrees to serve as the author responsible for
21 correspondence.

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24

25

26

27 **Abstract**

28

29 Plants are likely to have had a profound influence on Earth's long-term climate through their
30 role in drawing down CO₂ and emitting O₂ into the atmosphere and their interactions with
31 soils and minerals. Local climatic factors, including water availability, light, and temperature,
32 play a key role in plant physiology and growth and have fluctuated substantially over
33 geological time. However, the impact of these key climate variables on global plant biomass
34 across the Phanerozoic have not yet been established.

35 **Introduction**

36

37 The rise of land plants during the Paleozoic Era is thought to have marked a turning
38 point in Earth history, with profound impacts on the planet's surface chemistry and climate ¹.
39 The earliest land plants (embryophytes) are first identified in the Ordovician period and are
40 morphologically simple compared to modern vascular plants, being rootless and non-
41 vascular, and bearing some similarities to bryophytes ². Throughout the Paleozoic, terrestrial
42 flora diversified with vascular plants (tracheophytes) first being recorded during the late
43 Silurian and radiating in the Devonian ³. Continuous adaptation to the local environment over
44 time drove the evolution of stems, leaves, wood and bark in the late Devonian and Early
45 Carboniferous ³. A later major step in plant evolution was the divergence of the angiosperms
46 (flowering plants), estimated to have occurred between 120-100 Ma based on the occurrence
47 of flowers in the fossil record ⁴. Angiosperms continued to diversify, eventually dominating
48 terrestrial plant assemblages throughout the remainder of the Cretaceous.

49 Plants likely had dramatic impacts on the composition of the atmosphere by drawing
50 down and photosynthetically fixing atmospheric CO₂ into organic biomolecules, and by
51 altering the continental weathering processes which are a key part of most major

52 biogeochemical cycles ^{5,6}. Through their influence on atmospheric composition and
53 biogeochemical cycles, it has been hypothesised that plants had a key role in driving both the
54 Hirnantian (~445 Ma) and Late Paleozoic (~300 Ma) ice ages ^{6,7} as well as mid-Paleozoic
55 oxygenation of the atmosphere ⁸ and the more recent Cenozoic cooling ^{9,10}. However, while
56 the general trajectory of plant evolution is relatively well understood, it remains difficult to
57 estimate a key factor for the magnitude of any climate or biogeochemical effects: global plant
58 biomass and productivity. The methods of quantification and modelling of the land biosphere
59 in the above cited work tend to rely on either box modelling, with no consideration of global
60 hydrology and the impact of water availability on key plant physiological processes ^{6,7,11}, or
61 on complex spatial vegetation models which are set up for specific time periods and are not
62 easily extended across Phanerozoic time ^{8,12}.

63 Earth's paleogeography is a key feature that regulates plant productivity and biomass
64 at the global scale as it modulates local hydrology and temperature ^{13,14}. Conditions dictated
65 by changes in paleogeography therefore can enhance or diminish plant growth and could
66 have been a key factor in the expansion of new plant groups and species ¹⁵. One of the
67 biggest changes in paleogeography during the Phanerozoic was the breakup of the
68 supercontinent Pangea (Figure S1) which saw the transition away from an Earth surface
69 where runoff was limited due to the reduction of inland rainfall ¹⁶. The breakup of the
70 supercontinent and the subsequent enhancement of the hydrological cycle via the formation
71 of a new ocean ¹⁷ may have led to the expansion of temperate zones and introduced new
72 niches which could have promoted angiosperm radiation during the Cretaceous ¹⁴. Despite
73 these important hypotheses, there has been relatively little exploration of emergent vegetation
74 dynamics under past climates. The most progress to date has been achieved through use of
75 the Sheffield Dynamic Global Vegetation Model (SDGVM) but this has been restricted to
76 post-Pangaea climates ^{12,18}.

77 Here, we developed a simplified deep-time dynamic global vegetation model which
78 can easily be run for a variety of past climates throughout the Phanerozoic to test the
79 hypothesis that paleogeography itself has influenced the spread of plants across Earth's
80 terrestrial land masses. We validate our model against present day distribution of vegetation
81 and the previous SDGVM work, and explore the effect of Phanerozoic continental dispersion,
82 temperature and runoff on the potential for the Earth to host plant biomass.

83 Our deep-time vegetation model is called FLORA: Fast Land Occupancy and
84 Reaction Algorithm. This acronym embodies the key considerations of the model;
85 computational speed, the ability to determine if each land grid cell in a climate model is
86 suitable for plant growth, providing an estimate of the total productivity and biomass for each
87 cell through modelling the photosynthesis and respiration reactions. Our model is largely
88 simplified from the Lund-Postdam-Jena DGVM (LPJ-DGVM)¹⁹ and captures the flow of
89 carbon from its atmospheric form (CO₂) to storage as biomass in plants (Figure 1). The
90 advantage of this simplification is that FLORA can be run very quickly and in-line with
91 larger biogeochemical frameworks while retaining very predictions of vegetation carbon
92 distribution to those of the LPJ-DGVM (Sitch et al., 2003).

93 We define Net Primary Productivity (NPP) as the net carbon stored after autotrophic
94 respiration²⁰. We assume that all plant carbon within the system is stored in the form of leaf
95 biomass for simplicity. Although root and sapwood biomass are present within the LPJ-
96 DGVM¹⁹, they are closely linked to the other biomass pools and are not required to
97 reproduce a reasonable fit to modern biomass (see validation below). Moreover, these
98 features were absent from early plants, thus we opt for the simplest approach. The methods
99 section outlines the equations that dictate the rate of photosynthesis and respiration, carbon
100 allocation and turnover as a response to local solar insolation, temperature and water
101 availability, as well as to the atmospheric CO₂ and O₂ levels.

102 Carbon flows and biomass are calculated over a grid of cells representing the
103 continental surface, and for three basic plant functional types: tropical, boreal and temperate.
104 The only distinction between each plant functional type is their performance at different
105 temperatures ²¹; each plant functional type has a different optimum temperature for
106 photosynthesis (Table S1). A simple competition model for each grid cell allows only the
107 contribution of the functional type for which the highest potential biomass is calculated, thus
108 dictating the ‘biome’ of the grid cell.

109 We ran FLORA subject to boundary conditions of the preindustrial CO₂ and O₂
110 levels, 0.5 degree gridded global runoff ²² and temperature ²³ measurements, and a
111 standardised insolation curve peaking at 400 W/m² at the equator ²⁴. Despite the simplicity of
112 the model, the predicted global pattern of biomass shows good agreement with the measured
113 global biomass (Figure 2) ²⁵. The largest errors occur in the tropics but vary from over-
114 prediction in South Asia and Indonesia, to under-prediction in tropical Africa. The maximum
115 error in a single grid cell is about 2×10^4 gC/m², but errors tend to be balanced when
116 considering larger areas (Figure 3). Our model also tends to slightly over-represent biomass in
117 the northern high mid-latitudes and under-represent biomass in the southern high mid-
118 latitudes.

119 Figure 3 shows the longitudinal and latitudinal biomass comparisons and the
120 relationship between the model and the global database ²⁵. These highlight that the model has
121 reasonable capabilities in capturing the key trends, and again show the slight over-prediction
122 of biomass in South-East Asia and under-prediction in tropical Africa. These differences may
123 be attributable to the yearly-averaged datasets that are used as forcings. For example,
124 seasonal changes in runoff and productivity are not captured which means monsoonal
125 climates are not well-represented. Overall, we consider the model to be appropriate to the

126 task it is designed for. It suitably reconstructs the major patterns of plant biomass on the
127 present-day Earth.

128

129 **Results & Discussion**

130 Potential plant biomass over the Phanerozoic

131 FLORA was run for the paleogeography, surface air temperature and runoff
132 calculated by Godderis et al. (2014) using the FOAM (Fast Ocean Atmosphere Model ²⁶)
133 climate model for 22 time points over the Phanerozoic. We set the CO₂ concentration for
134 each run based on proxy information, and box modelling where proxies are unavailable
135 (Table S2). For these runs we do not consider any evolutionary changes in the land biosphere,
136 thus our calculation is for ‘potential biomass’ under our generalised photosynthesis-
137 respiration model with modern plant functional types. The intention here is to understand the
138 biomass potential of past climates based on fundamental photosynthetic processes and
139 parameters. Our results are shown in Figure 4 and Figure 5 alongside model parameters: area,
140 runoff, CO₂ level and average temperature of each climate model run. These results indicate
141 two clear peaks in potential biomass; the first being during the Ordovician, and the second
142 being a broader peak from the Jurassic to the Paleogene (Figure 5A).

143 The peaks in potential biomass predicted by our model are consistent with times of
144 generally elevated global runoff (Figure 5A and D), which is understandable given the
145 absolute requirement for water for plant growth. Runoff also has the highest average r-
146 squared value across all time points (0.72; Figure S2) suggesting potential biomass is most
147 influenced by water availability. There is also some correlation between potential biomass
148 with temperature, where the expansion of ice caps during the late Paleozoic and the late
149 Cenozoic limited the habitable space, but very warm climates like the late Cretaceous also

150 limited productivity. Our findings compare well to those of Taylor et al. (2012), who coupled
151 the SDGVM to the Hadley Centre general circulation model (HadCM3L) for a more limited
152 set of paleoclimates. They also found high reconstructed global biomass across the
153 Cretaceous and Paleogene. The large disparity seen in the Cenomanian appears to be due to
154 differences in the exposed land area in the tropics between the climate model runs. The
155 modelling of Taylor et al. (2012) assumes a large exposed African continent in the tropics
156 whereas the reconstruction used in FOAM for this work has much of the continent flooded.
157 Nevertheless, both the previous work, and our new analysis agree that the breakup of Pangaea
158 (Figure S1) was accompanied by a substantial increase in the habitable space available for
159 plants.

160

161 Possible links between climate and plant evolution

162 Our results show an early peak in potential biomass at around 470 Ma (Figure 5A)
163 suggesting temperature and water availability were optimal for plant productivity at this time.
164 During this time period there was substantial low-latitude land mass which was sufficiently
165 dispersed to maintain a strong hydrological cycle, continental temperatures were also warm
166 and there were no permanent ice caps (e.g. Scotese et al., 2021). Embryophytes and other
167 morphologically simple plants present during the Ordovician lacked specialised vascular
168 tissues such as roots or stems ² that are typically associated with water conduction. These
169 early plants likely existed mostly in equilibrium with surrounding air ²⁸ and their distributions
170 were largely restricted to environments of high water availability. Despite many modern
171 bryophytes displaying poikilohydry, the water desiccation tolerance of early land plants
172 remains unknown, and colonisation of more arid, inland environments would require
173 morphological and physiological strategies to prevent plant water loss. According to the

174 FOAM climate model runs, global runoff was increasing between 540-470 Ma (Figure 5D).
175 This increase in water availability on land would allow for the increasing productivity on land
176 surface during the Ordovician, allowing early plants²⁸ to persist on land with minimal risk of
177 dehydration. As the optimal plant growth conditions became more widely distributed global
178 plant productivity is likely have increased in tandem.

179 In our model, the favourability of the land surface to plant growth decreases
180 throughout the post-Ordovician Paleozoic. Precipitation and runoff decrease markedly as the
181 amalgamation of Pangaea is completed, and the effects of the cooling in the late Paleozoic
182 also reduced the habitable space for plants. Silurian mesofossils indicate the presence of
183 lignified cell walls and tubular structures essential for water supply towards the peripheral
184 regions of plants which were further developed towards the Devonian²⁹. Tracheophytes
185 evolved between around 450–430 Ma³⁰ and the evolution of roots also fall between the
186 Silurian-Devonian period, beginning with rhizoid structures and ending with extensive
187 rooting systems^{31,32}. Thus, this period of increasing aridity is associated with the circular
188 evolution of morphological and physiological innovations in plants, focused towards water
189 acquisition, transport and retention.

190 The oldest angiosperm fossil is dated to 136 Ma³³, but molecular clocks suggest the
191 early history of angiosperms is cryptic³⁴, with diversification potentially as early as 195-246
192 Ma³⁰. In our model, potential biomass shows a significant increase around 200 Ma which is
193 sustained until the Neogene (Figure 5A). This increase in plant habitability is strongly linked
194 to a large rise in global precipitation and runoff following the breakup of Pangea. During this
195 time, equatorial Pangea transitioned from arid conditions to a ‘megamonsoonal’ circulation
196 which has previously been proposed to set the stage for the ecological expansion of flowering
197 plants¹⁴. The separation of land creates a water cycle in areas that previously were arid³⁵ and
198 the spread of land around the equator increases the land area experiencing high-moderate

199 temperatures for plant growth. Thus, our work supports the inference of a large expansion of
200 habitable space for plants being linked to the mid-late Mesozoic angiosperm radiation.

201

202 **Conclusion**

203

204 Global plant biomass is controlled by a combination of surface air temperature,
205 hydrology and photosynthetically-active radiation, and our simple model, FLORA, based on
206 these factors can reproduce a fair representation of present-day biomass distribution (Figure
207 3). In Earth's past, these factors have changed markedly due to the positioning of the
208 continents and changes in radiative forcing. When we run FLORA under the FOAM climate
209 model outputs, we find two clear peaks in the 'potential biomass' – a measure of the Earth
210 surface's ability to host plant life. This analysis shows a strong environmental incentive for
211 plant expansion during the Ordovician and a later window during the Jurassic-to-Paleogene,
212 which correspond with the initial land colonisation and the major radiation of Angiosperms
213 respectively. Moreover, the Silurian-Devonian saw increasing aridity, correlating with a
214 succession of plant adaptations in favour of water transport and retention. We propose that
215 these windows of opportunity played a key part in initiating these evolutionary expansions.

216

217

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222 **Methods**

223

224 **Model equations**

225 Most equations are directly taken or slightly altered from equations 1-25 in Sitch et al.
226 2003 and equations 4-26 from Haxeltine & Prentice, 1996. Photosynthesis rate, P (g
227 C/m²/year) is given by:

$$P = 3650ins \left(\frac{c_1}{c_2}\right) [c_2 - (2\theta - 1)s - 2(c_2 - \theta s)\sigma_c] \omega \quad (1)$$

228 where photosynthesis is scaled by water stress, ω and insolation, ins . ω is calculated as a
229 fraction of runoff that ranges from 0-1; 0 being no water available and 1 being maximum
230 water availability for plants. ins is assumed to be in a linear relationship with latitude, f_{lat} ²⁴.

$$ins = 150 + 250f_{lat} \quad (2)$$

231 Insolation increases as latitudes get closer to the equator and decrease as they go
232 towards the poles. The model substitutes PAR (Photosynthetically Active Radiation) for
233 insolation. σ_c, s, c_1, c_2 are taken from Sitch et al. (2003) and written as:

$$\sigma_c \left[1 - \frac{(c_2 - s)}{(c_2 - \theta s)} \right]^{0.5} \quad (3)$$

$$c_1 = \alpha f_{temp} \frac{(p_i - \Gamma_*)}{(p_i - 2\Gamma_*)} \quad (4)$$

$$c_2 = \frac{(p_i - \Gamma_*)}{\left(p_i - K_C \left(1 + \frac{pO_2}{K_O} \right) \right)} \quad (5)$$

$$s = \left(\frac{24}{h} \right) a \quad (6)$$

234 where α is the effective ecosystem-level quantum efficiency; θ is the shape parameter that
235 specifies the degree of co-limitation by light and Rubisco activity; h is the daylight hours

236 which for model simplicity is considered to be 24. f_{temp} is a plant-type specific temperature
 237 function that limits photosynthesis at high and low temperatures (Table S1). Γ_* is the CO₂
 238 compensation point given by:

$$\Gamma_* = \frac{pO_2}{2\tau} \quad (7)$$

239 where pO_2 is the ambient partial pressure of O₂ (Pa) taken from Krause et al., 2018 (Table
 240 S2), and p_i is the intracellular partial pressure of CO₂ (Pa) calculated using

$$p_i = \lambda p_a \quad (8)$$

241 p_a , is the ambient partial pressure of CO₂ and λ , a positive parameter that represents the
 242 stomata keeping a constant ratio of intracellular to ambient CO₂. The ratio ranges from 0.6-
 243 0.8 therefore a constant of 0.8 for C₃ plants is used (Haxeltine and Prentice 1996, Sitch et al.
 244 2003).

245 Temperature dependent kinetic parameters K_C , K_O and τ are modelled using

$$k = k_{25} Q_{10}^{0.1(T-25)} \quad (9)$$

246 taken from Haxeltine and Prentice (1996). K_C , K_O are the Michaelis constants for CO₂ and O₂
 247 inhibition in the Rubisco reaction. k_{25} is the parameter value at 25°C and Q_{10} is the relative
 248 change in parameter for every 10°C change in temperature.

249 Initial carbon allocation to leaves C_{leaf} (g C/m²/year) of the carbon acquired via
 250 photosynthesis is calculated using:

$$C_{leaf} = l_{max} P \quad (10)$$

251 using a leaf carbon allocation ratio, l_{max} . Under constant conditions, an allocation ratio of
 252 0.88 is given towards shoot growth³⁸. Within angiosperms and gymnosperms, allocation
 253 towards leaves has a maximum of approximately 0.75³⁹ which decreases with plant growth
 254 as more biomass is allocated towards the stems. The maximum value is used throughout

255 therefore assuming 75% of photosynthetic carbon is stored in the leaves. Carbon
 256 accumulation overtime is then calculated by:

$$C_{leaf(n+1)} = C_{leaf(n)}(1 - f_{leaf}) + l_{max}NPP \quad (11)$$

257 where f_{leaf} represents leaf turnover for each plant type (Table S1). Initial leaf carbon
 258 allocation is calculated using photosynthesis however to calculate leaf carbon accumulation
 259 for the global population of plants, NPP is used thereafter.

$$NPP = (1 - R_{growth})(P - R_{leaf}) \quad (12)$$

260 NPP is the net primary productivity (g C/m²/year). Carbon is acquired by
 261 photosynthesis and lost through growth respiration R_{growth} and maintenance
 262 respiration, R_{leaf} . 25% of total NPP goes towards R_{growth} (Sitch et al. 2003) whereas R_{leaf}
 263 is calculated using:

$$R_{leaf} = r \left(\frac{C_{leaf}}{cn_{leaf}} \right) g(T) \quad (13)$$

$$g(T) = \exp \left[308.56 \left(\frac{1}{52.02} - \frac{1}{T + 46.02} \right) \right] \quad (14)$$

264 R_{leaf} depends on a modified Arrhenius equation, $g(T)$, tissue respiration, r , and leaf specific
 265 C:N ratio, cn_{leaf} . r is the plant-type specific respiration rate (g C/g N/year) (Table S1).
 266 Values for the tropical and boreal plant types are taken from Sitch et al. (2003) and modified
 267 for the temperate plant-type. It follows the observation that plants of warmer environments
 268 have a lower respiration rate at any given temperature compared to plants from colder
 269 environments (Sitch et al., 2003).

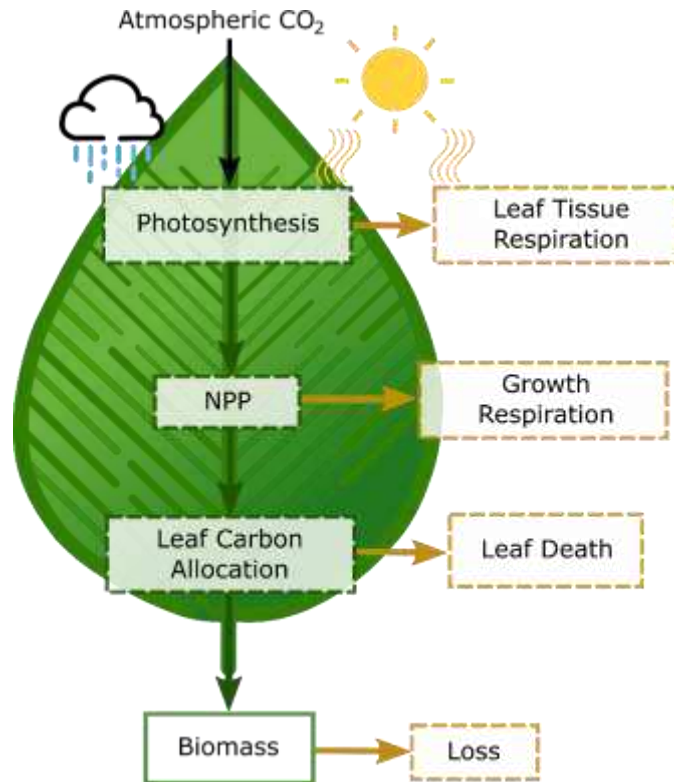
270 Biomass, B , (g C/m²/year) is the reservoir of carbon with inflow from leaf carbon
 271 accumulation and we assume a constant 10% outflow, representing combined biomass
 272 degradation processes, and chosen to reproduce overall modern biomass.

$$B_{(n+1)} = B_{(n)} + (C_{leaf(n)} - 0.1B_{(n)}) \quad (15)$$

273 Initial biomass $B_{(1)}$ is set at 250 kg C/m² which serves as the baseline for biomass
 274 growth/loss.

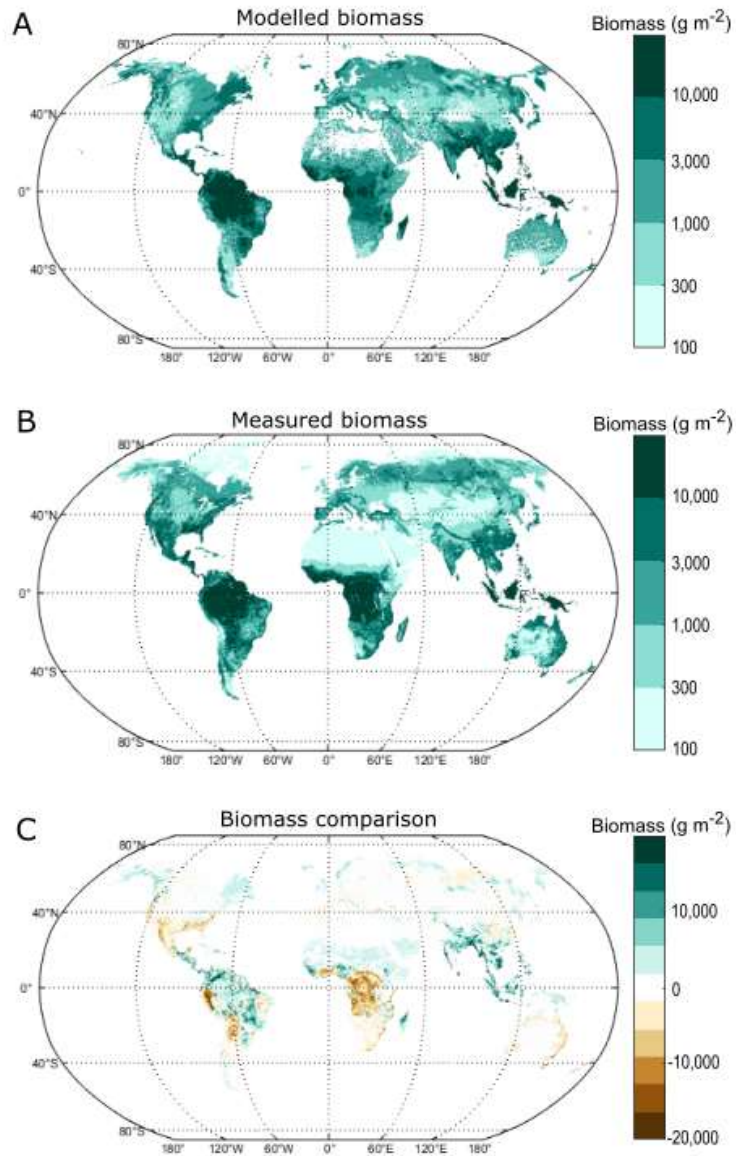
275 **Figures with caption**

276



277

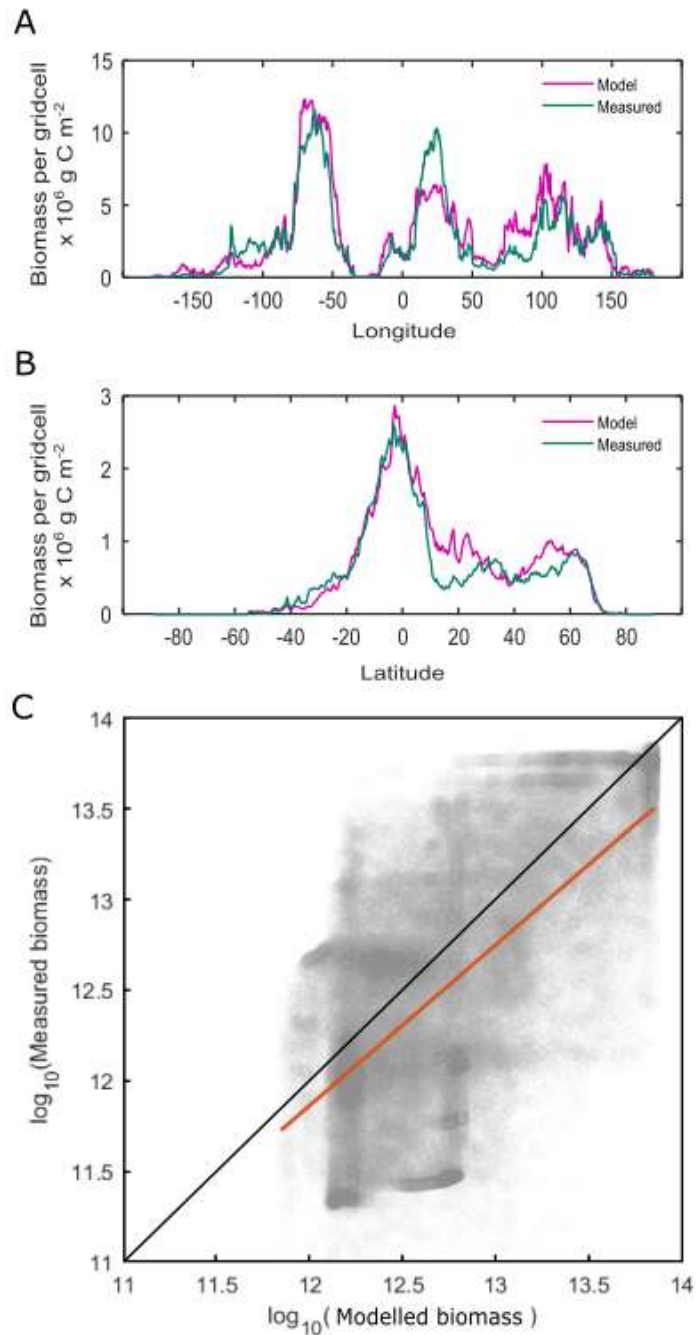
278 **Figure 1. Model flowchart.** Each arrow depicts the flow of carbon, green indicates carbon is
 279 preserved within the system while brown indicates its departure. Note: the model uses a single
 280 biomass pool and losses associated with respiration and leaf death affect the growth of the biomass
 281 pool. Processes are given in dashed boxes whereas reservoirs are presented in bold boxes. Processes
 282 that are affected by temperature (red lines), insolation (sun) and water stress (blue drops) are
 283 indicated. NPP: net primary productivity.



284

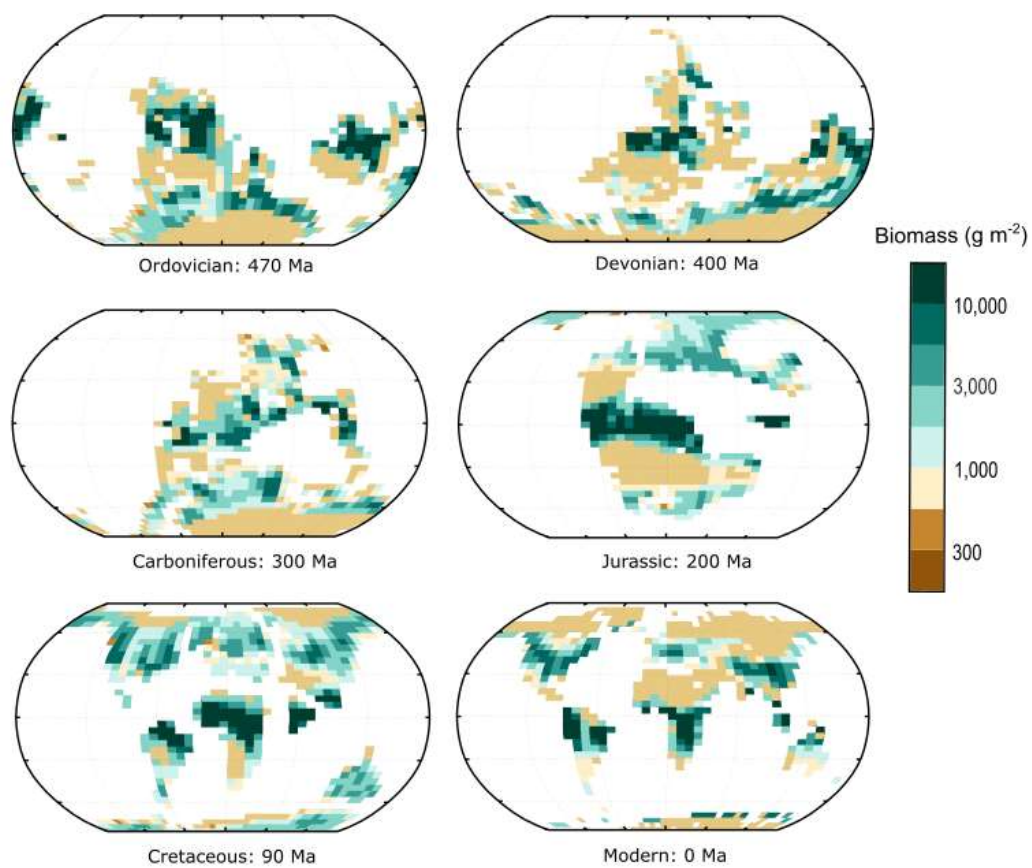
285 **Figure 2. Modelled and measured biomass comparison.** The model predicts a reasonable
 286 approximation of current biomass. **(A)** Actual above- and below-ground global biomass for the year
 287 2000 obtained from CDIAC ²⁵. **(B)** Model predicted biomass given average temperatures (between
 288 1900-1990) and ‘best estimation’ of yearly runoff from the year 2000. **(C)** Areas of over-prediction
 289 (green) and under-prediction (brown) of biomass.

290



291

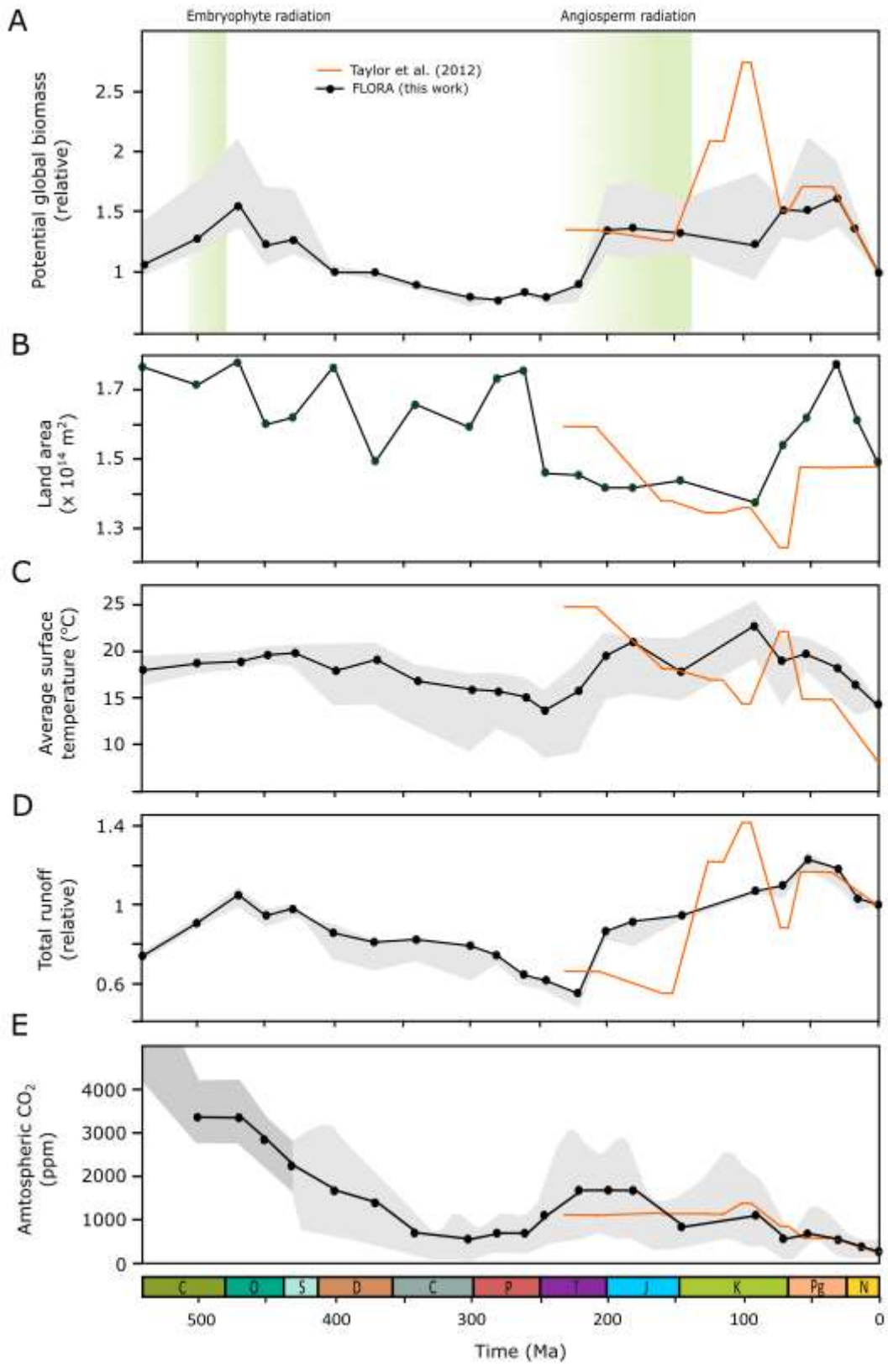
292 **Figure 3. Further modelled and measured biomass comparison.** (A) Sum of biomass between
 293 modelled (pink line) and measured (green line) data ²⁵ show overall longitude (-180°W to 180°E) and
 294 latitude (-90°S to 90°N) biomass patterns are preserved. Highest global plant biomass is present closer
 295 to the equator (0° Latitude). (B) Model predicted and measured biomass show a linear relationship
 296 (orange line) with an R-squared value of 0.408 in log space, or 0.606 in linear space. A 1:1 line is
 297 shown for comparison in black.



299

300 **Figure 4. Global potential biomass maps during the Phanerozoic.** Maps showing a selection of the
 301 potential biomass predictions from this model. Ma: millions of years.

302



303

304 **Figure 5. Global potential relative biomass, runoff, average temperature and CO_2 level during**

305 **the Phanerozoic (540-0 Ma). Proxies (temperature and runoff) depend on the predicted CO_2 level.**

306 Grey area represents the min/max values obtained at the min/max CO₂ level. Time periods are
307 highlighted at the bottom of the figure. Parameters and biomass used in Taylor et al. 2012 are shown
308 in orange; the length of the solid line represents time periods used. (A) Relative biomass over time (kg
309 C relative to present). Green highlights show predicted origin times: Em = embryophyte, Ang =
310 Angiosperm^{4,30}. (B) Total terrestrial land area (m²) present at each time point. (C, D) Predicted sum
311 of global runoff (mm/year) and average temperature (°C) overtime given specific CO₂ levels. Data
312 taken from Godderis et al. 2014. (E) Average CO₂ level (ppm, yellow line). An approximate CO₂
313 value (red dot) for each time period was chosen for the climate model. Dark grey area: predicted CO₂
314 level chosen from a combination of COPSE and GEOCARBSULF model. Data taken from Mills et al.
315 2019.

316

317 **Code Availability**

318 The FLORA model is written in MATLAB and is available from KG on request.

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421 **Ethics declarations**

422

423 No competing interests.

424

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