

1 **Title:** Spatiotemporal patterns in the woodiness of flowering plants

2 **Running Title :** Global woodiness patterns

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38

39 **Biosketch**

40 **Ao Luo** is a PhD candidate at Peking University and is mainly interested in macroecology and  
41 macroevolutionary in angiosperms. His work focuses on investigating large-scale species  
42 diversity patterns and the macroevolutionary mechanisms underlying them.

43

1 **Title:** Spatiotemporal patterns in the woodiness of flowering plants

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3

4 **Abstract**

5 **Aim**

6 Woody and herbaceous habits represent one of the most distinct contrasts among  
7 angiosperms, and the proportion of woody species in floras (i.e. “woodiness” hereafter)  
8 represents a fundamental structural element of plant diversity. Despite its core influence  
9 on ecosystem processes, spatiotemporal patterns in woodiness remain poorly  
10 understood. Here, we aim to demonstrate the global spatiotemporal patterns in  
11 angiosperm woodiness and their relationship with environmental factors.

12 **Location**

13 Global

14 **Time period**

15 Cenozoic, 66 Ma to present.

16 **Major taxa studied**

17 Angiosperms

18 **Methods**

19 Using newly-compiled data on the growth forms and distributions of  
20 approximately 300,000 angiosperm species and an angiosperm phylogeny, we mapped  
21 the current global geographical patterns in angiosperm woodiness, reconstructed  
22 ancestral states of growth forms through the angiosperm phylogeny, and demonstrated  
23 the Cenozoic evolutionary dynamics of woodiness. We evaluated the relationships  
24 between woodiness and current and paleo climate.

25 **Results**

26 We found that ca. 42.7% of angiosperms are woody. Woodiness decreased spatially  
27 from the equator towards latitudes, temporally since the early Cenozoic. Temperature  
28 was the best predictor of the spatiotemporal decline in woodiness and positively  
29 correlates with woodiness. Despite the temporal decline in woodiness,  
30 macroevolutionary herbaceous-to-woody transitions increased through time and  
31 contributed to the evolution of woody floras in temperate drylands, while the opposite  
32 transitions decreased through time and contributed to herbaceous floras in tropical and  
33 subtropical drylands.

34 **Main conclusions**

35 Our study improves understanding of the spatiotemporal dynamics of angiosperm  
36 woodiness. Our findings suggest that temperature is likely a determinant of  
37 spatiotemporal woodiness variations, highlighting the role of temperature in maintain  
38 growth form composition of ecosystems. Our study also calls for attention to growth  
39 form transitions (e.g. secondary woodiness) in temperate drylands that were neglected  
40 before.

41

42 **Keywords:** angiosperms, growth forms, woody plants, herbaceous plants,  
43 environmental temperature, secondary woodiness, ancestral state reconstruction,  
44 macroevolution

45

## 46 **1 INTRODUCTION**

47 Spatial variation in the proportion of woody and herbaceous growth forms has  
48 generated one of the largest contrasts among terrestrial ecosystems, with forests  
49 displaying widely contrasting functional properties compared with grasslands  
50 (Kerkhoff, Moriarty, & Weiser, 2014; Šímová et al., 2018; Zanne et al., 2014). Woody  
51 and herbaceous species do not only show distinct global distributions associated with  
52 contemporary environmental conditions, but also reveal distinct evolutionary histories  
53 and responses to paleo-environmental changes (Carlquist, 2013; Klimešová,  
54 Tackenberg, & Herben, 2016; Rice et al., 2019; Šímová et al., 2018), which might prime  
55 them to respond very differently to climate change (Engemann et al., 2016; Hawkins,  
56 Rodríguez, & Weller, 2011; Zanne et al., 2018). Understanding spatiotemporal  
57 variation in the proportion of woody species and the underlying ecological and  
58 evolutionary drivers could enhance our ability to predict potential changes in terrestrial  
59 ecosystems in response to future climate change (Myers-Smith et al., 2011; Ordonez &  
60 Svenning, 2019).

61 Biologists have long noted changes in the proportion of woody species  
62 (“woodiness” hereafter) with latitude (Sinnott & Bailey, 1915) and suggested that  
63 woodiness is higher in the tropics (Engemann et al., 2016; Moles et al., 2014; Moles et  
64 al., 2009). Although woodiness patterns have been mapped previously at local to  
65 regional scales (Droissart et al., 2018; Engemann et al., 2016), the geographical pattern  
66 of angiosperm woodiness at the global scale remains unmapped, likely due to a lack of  
67 data on the growth forms and distributions across hundreds of thousands of plant  
68 species. Studies have demonstrated strong associations of geographical patterns in  
69 woody and herbaceous species richness with contemporary climate, especially water  
70 availability (Francis & Currie, 2003; O'Brien, 1998) and environmental temperature  
71 (Latham & Ricklefs, 1993; Z. Wang, Fang, Tang, & Lin, 2011). However, the drivers  
72 of woody and herbaceous species richness may differ (Hawkins et al., 2011). The  
73 sensitivity of the woody growth form to winter coldness was recognized already as the  
74 basis of Raunkiaer’s classification of plant life forms (Raunkiaer, 1934), because  
75 woody species generally carry their stems and renewal buds higher above ground than  
76 do herbaceous species, exposing them to colder temperatures in seasonal climates.  
77 Compared with woody species, herbaceous species tend to have a higher rate of niche  
78 evolution and weaker niche conservatism due to their shorter lifespan, and hence tend

79 to be less sensitive to freezing (Smith & Beaulieu, 2009; Zanne et al., 2018). These  
80 findings suggest that environmental temperature may dominate the spatial variations in  
81 woodiness. In addition to temperature, woody and herbaceous plants also have different  
82 hydraulic conductance and drought tolerance abilities (Lens et al., 2016), and thus that  
83 precipitation may also influence woodiness variations. Yet the drivers underlying  
84 global geographical patterns in the woodiness of angiosperms remain elusive  
85 (Engemann et al., 2016; Moles et al., 2014; Zanne et al., 2018).

86 Woodiness is an evolutionarily dynamic trait and macroevolutionary transitions  
87 both from woody to herbaceous states (“WtoH” hereafter) and vice versa (“HtoW”  
88 hereafter) may have occurred frequently in different clades during the evolutionary  
89 history of flowering plants (Cronquist, 1968; Zanne et al., 2014). Although debated, the  
90 woody growth form is generally thought to be ancestral in angiosperms, suggesting that  
91 the herbaceous state, representing an adaptation to a fast life cycle in cold and arid  
92 climates (Klimešová et al., 2016), may have evolved from woody ancestors (i.e., WtoH  
93 transition) (Neupane et al., 2017; Zanne et al., 2018). Evolutionary transitions from  
94 herbaceous to woody state (i.e., HtoW transitions), also known as “secondary  
95 woodiness”, have also been demonstrated in at least eight orders (Spicer & Groover,  
96 2010), and are often found on tropical islands or tropical mountain peaks (Carlquist,  
97 2013; Lens, Davin, Smets, & del Arco, 2013; Neupane et al., 2017; Nürk, Atchison, &  
98 Hughes, 2019). The climatic moderation hypotheses proposed to explain the patterns in  
99 secondary woodiness suggests that low temperature seasonality enhances HtoW  
100 transitions (Sherwin Carlquist, 1974). As herbaceous growth form represents an  
101 adaptation to cold climate (Zanne et al., 2014), the WtoH transitions are expected to be  
102 more frequent in temperate regions. However, the temporal and geographical patterns  
103 of WtoH and HtoW transitions at the global scale remain even more elusive than the  
104 global spatiotemporal patterns of woodiness. Assessing them in more detail will shed  
105 light on the response of this trait to paleoenvironmental changes.

106 Here, we study the global geographical patterns of angiosperm woodiness and  
107 explore the relationships between these patterns and climatic factors, using a large  
108 dataset on the growth forms and distributions of ca. 300,000 angiosperm species on the  
109 global scale. By integrating these data with a recently developed mega-phylogeny  
110 (Smith & Brown, 2018), we explore the evolutionary transitions of WtoH and HtoW  
111 over space and through evolutionary time. Specifically, we address the following two

112 questions: 1) Do climate factors, especially temperature, well predict spatiotemporal  
113 patterns in the woodiness of angiosperms? 2) When and where did evolutionary HtoW  
114 and WtoH transitions occur and why? We expect that: 1) Environmental temperature,  
115 especially winter coldness, is the best predictor of spatiotemporal patterns in  
116 angiosperm woodiness. 2) HtoW transitions are more frequent in the tropics and warm  
117 periods, while WtoH transitions are more frequent in temperate regions and cool  
118 periods.

119

## 120 **2 Materials and Methods**

### 121 **2.1 Growth forms and distributions of global angiosperms**

122 We compiled data on growth forms of angiosperm species from published floras  
123 (e.g. *Flora of North America*, *Flora of China*, etc.), online databases and peer-reviewed  
124 journal articles (see appendix 1 for the list of data sources). Species names from  
125 different sources were standardized following the *Catalogue of Life*  
126 (<http://www.catalogueoflife.org>) which provides an updated list of accepted Latin  
127 names and synonyms of angiosperm species. We compiled the records of growth form  
128 of each species and supplemented these data with the information of the corresponding  
129 genera and families of species if clearly recorded as being exclusively woody or  
130 herbaceous from available data sources (appendix 1). In total, our database contained  
131 growth forms of 300,112 angiosperm species, belonging to 11,638 genera and 425  
132 families. Following previous studies (Engemann et al., 2016; FitzJohn et al., 2014;  
133 Šímová et al., 2018), species were classified into two categories: woody and herbaceous.  
134 Woody species was defined following (Zanne et al., 2014) (i.e. species having a  
135 prominent aboveground stem that is persistent under changing environmental  
136 conditions), and included trees, shrubs, and lianas. Herbaceous species included herbs  
137 and herbaceous vines. Following previous studies (Fang, Tang, & Wang, 2011; Zanne  
138 et al., 2014), most bamboo (Bambusoideae), cacti (Cactaceae), and palm (Arecaceae)  
139 species were classified as woody species and only a few were classified as herbaceous.  
140 When different data sources reported different growth forms for a species, we  
141 determined its growth form as the one reported in more than two-thirds of the data  
142 sources. If none of the growth forms was supported by more than two-thirds of the data  
143 sources, we marked its growth form as ‘unclear’ and excluded it from the following  
144 analyses.

145 The database of global distributions of angiosperm species  
146 (<https://en.geodata.pku.edu.cn/index.php?c=content&a=list&catid=198>) was compiled  
147 from published continental and regional floras, checklists, peer-reviewed articles,  
148 herbarium specimens, and online databases (see appendix 1 for the list of data sources).  
149 Some data sources contain coordinates of species occurrences, while most of them  
150 recorded species distributions using either administrative units at different scales (e.g.  
151 villages, towns, cities, provinces/states, and countries) or geographical units (e.g.  
152 mountains and nature reserves). We georeferenced these records using the GeoNames  
153 geographical database (containing over 25 million geographical names,  
154 <http://www.geonames.org>), Global Administrative Areas Database (containing  
155 boundaries of global geopolitical units at different levels, <https://gadm.org/>) and the  
156 World Geographical Scheme for Recording Plant Distributions (containing names and  
157 boundaries of geographical units commonly used in specimen collections,  
158 <https://www.tdwg.org/standards/wgsrpd/>). To reduce the potential effect of area on  
159 diversity estimates, adjacent smaller geopolitical units were merged together to create  
160 units of similar size (ca. 270,000 km<sup>2</sup>). The final map divided the world land area into  
161 480 geographical units. This scheme of geopolitical units have been used for the  
162 compilation of species distributions in several previous studies (Shrestha et al., 2018;  
163 Xu et al., 2019; Xu, Wang, Rahbek, Lessard, & Fang, 2013). To improve the quality of  
164 species distribution data, we screened the distribution maps of most species and  
165 removed records of introduced and cultivated species following *Plants of the World*  
166 *Online* (<http://www.plantsoftheworldonline.org/>).

167

## 168 **2.2 Data on climate and global biomes**

169 To evaluate the effects of contemporary climate on geographical patterns in  
170 angiosperm woodiness (i.e. the proportion of woody species in local floras), we used  
171 climatic variables representing the mean and extreme values of temperature and  
172 precipitation, including mean annual temperature (MAT), mean temperature of  
173 warmest quarter (MTWQ), minimum temperature of the coldest month (Tmin), mean  
174 annual precipitation (MAP), precipitation of the warmest quarter (PWQ), and  
175 precipitation of the coldest quarter (PCQ). We obtained these variables from the  
176 WorldClim database (v2.1, <https://www.worldclim.org>) with a spatial resolution of 30



177  $\times 30$  arc seconds (ca.  $1 \times 1 \text{ km}^2$  at the equator). We then estimated the mean values of  
178 each climate variable within each geopolitical unit. As the geographical units are  
179 relatively large and may contain large climate heterogeneity, we also estimated the  
180 minimum, maximum and ranges of each variable within each geographical unit for  
181 comparison. Moreover, we estimated the mean, minimum and maximum values of each  
182 climate variable within the distribution range of each species. To explore the  
183 relationship between temporal variations in angiosperm woodiness and paleoclimate,  
184 we used the global mean paleotemperature reconstructed by the deep-sea benthic  
185 foraminifer oxygen isotope ( $\delta^{18}\text{O}$ ) from ocean drilling cores, which has been widely  
186 used as a proxy of paleotemperature in previous studies (Westerhold et al., 2020; Zachos,  
187 Pagani, Sloan, Thomas, & Billups, 2001). To evaluate the potential influence of biomes on  
188 growth form transitions, we obtained data on the global biome boundaries from Olson  
189 et al. (2001), and then estimated the area proportion of each biome within each  
190 geopolitical unit.

191

### 192 **2.3 Phylogenies of global angiosperms and ancestral growth form** 193 **reconstruction**

194 Recent advances in large-scale phylogenies of angiosperms provide opportunities  
195 to explore the evolution of angiosperm growth forms. Here, we used the dated  
196 phylogeny containing 353,185 seed plant species generated by Smith & Brown (i.e.  
197 ALLOTB) (Smith & Brown, 2018), which has recently been used in macroecological  
198 and biogeographic studies (Sandel et al., 2019; Weigelt, König, & Kreft, 2019). This  
199 phylogeny was constructed by placing the molecular phylogenies (containing 79,855  
200 species in total) constructed for major clades (i.e. orders) in a backbone provided by the  
201 Open Tree of Life (Hinchliff et al., 2015; Smith & Brown, 2018). Species without DNA  
202 data were added into the molecular backbone phylogeny following the resolution  
203 provided by the Open Tree of Life. The relationships between many species in this  
204 phylogeny are not resolved, which may influence the reconstruction of ancestral states  
205 and hence the estimation of angiosperm woodiness. Hence, we used the Yule  
206 bifurcation process (Roquet, Thuiller, & Lavergne, 2013; Thuiller et al., 2011) to  
207 resolve the polytomies within genera. Specifically, for each genus containing  
208 unresolved species as polytomies, we randomly resolved the polytomies using the Yule

209 bifurcation process, which leads to random relationships between species within genera.  
210 We generated 100 resolved phylogenies by repeating this process 100 times.

211 We reconstructed the ancestral states of growth forms using the maximum  
212 parsimony method in the R package “*castor*” (Louca & Doebeli, 2017). In the  
213 reconstruction analysis, growth form was used as a two-state trait (i.e., woody vs.  
214 herbaceous). The growth form of each branch was identified as the state with a higher  
215 probability. If the probability of a branch being woody was equal to that being  
216 herbaceous, its growth form was assigned as the growth form of its ancestor branch. To  
217 assess the uncertainties induced by random topologies due to the polytomy resolving  
218 procedure, we repeated the ancestral state reconstruction using the 100 randomly-  
219 resolved phylogenies separately.

220 Previous studies indicate that woody and herbaceous growth forms tend to have  
221 different evolutionary rates (Smith & Donoghue, 2008), which may bias the ancestral  
222 state reconstruction (Höhna et al., 2016). To confirm the reconstruction results based  
223 on the maximum parsimony method, we repeated the ancestral reconstruction analyses  
224 using the Hidden State Speciation and Extinction (HiSSE) model in RevBayes (Höhna  
225 et al., 2016). The HiSSE model is a state-dependent Markov model which could account  
226 for the impact of possible state-dependent evolution on ancestral-state reconstructions  
227 (Höhna et al., 2016). We use HiSSE instead of other alternatives, namely BiSSE,  
228 because issues with BiSSE leading to type I error have been identified (Maddison &  
229 FitzJohn, 2014). We used HiSSE models with two and three hidden states (see Table  
230 S1 for the details on the priors), and 2000 stochastic maps were generated for each  
231 model. The first 100 generations were used to tune parameters. The convergence and  
232 effective sample size was evaluated after discarding 25% of posterior samples as burn-  
233 in. Both models converged well and the effective sample sizes (ESS) for key parameters  
234 were all higher than 200.

235

## 236 **2.4 Temporal dynamics in the woodiness of angiosperms**

237 To evaluate the temporal dynamics in the woodiness of angiosperms, we estimated  
238 the proportion of woody branches in each 1 Ma time interval as the ratio of the number  
239 of woody branches and the total number of branches within that time interval using the  
240 ancestral reconstructions of growth forms based on the maximum parsimony method  
241 and the HiSSE models separately. The estimation based on the maximum parsimony

242 method was repeated for each of the 100 randomly-resolved phylogenies. We estimated  
243 the mean woodiness in each 1 Ma time interval across the 100 phylogenies to show the  
244 temporal dynamics in angiosperm woodiness and the 2.5<sup>th</sup> and 97.5<sup>th</sup> quantiles to show  
245 the 95% confidence intervals. Despite differences in the age estimates for the deep splits  
246 in the angiosperm crown groups, most studies agree on consistent patterns of the  
247 evolutionary chronicle of angiosperms during the Cenozoic (starting from 66 million  
248 years ago (Ma)) (Sauquet & Magallon, 2018; Smith & Brown, 2018; Zanne et al., 2014).  
249 Thus, we only focused on the evolutionary dynamics of woodiness during the youngest  
250 era, the Cenozoic, to avoid uncertainty in the estimation of woodiness during older eras.  
251

## 252 **2.5 Spatiotemporal patterns in growth form transitions**

253 We estimated the transitions between woody and herbaceous growth forms (see  
254 Fig. 3d for an illustrative diagram) using the ancestral growth form reconstructions  
255 estimated by the maximum parsimony method and the HiSSE models separately. A  
256 growth form transition event was identified when the reconstructed growth form of a  
257 branch differed from that of its parent branch. We recorded two directions of growth  
258 form transitions, i.e., from woody to herbaceous growth form and vice versa. To  
259 evaluate the temporal variation in growth form transitions, we estimated the proportion  
260 of transitions for each direction within each 1 Ma time interval.

261 To explore the contribution of growth form transitions to local floras, we divided  
262 the Cenozoic into three time periods (i.e., 60 – 40 Ma, 40 - 20 Ma, 20 - present). We  
263 then estimated the proportion of extant species experiencing growth form transitions  
264 during these time periods in local floras. Specifically, we estimated the proportions of  
265 species experiencing woody-to-herbaceous (WtoH) and herbaceous-to-woody (HtoW)  
266 transitions in local herbaceous and woody floras, respectively.  
267

## 268 **2.6 Statistical analyses**

269 As woodiness was estimated as a percentage, the relationships between the  
270 geographical patterns of woodiness and climate variables were evaluated using  
271 binomial generalized linear models (GLMs) with a logit link following previous studies  
272 (Dobson & Barnett, 2008; McCullagh & Nelder, 1989). Considering that the  
273 relationship between woodiness and climate may not be linear, we fitted GLM models

274 both with and without a quadratic term of climate variables. Model performance was  
275 evaluated using pseudo- $R^2$ , which was estimated as (McCullagh & Nelder, 1989):

276 
$$pseudo-R^2 = 1 - (residual\ deviance/null\ deviance)$$

277 To evaluate whether the climate heterogeneity within geographical units may influence  
278 the relationships between woodiness and climate, we conducted the following two  
279 analyses. First, we repeated all GLM models using the mean, minimum and maximum  
280 of climate variables within geographical units. Second, we conducted partial  
281 regressions with both the range and the mean of each climatic variable as the predictors  
282 of woodiness. Then the independent  $R^2$  of the mean climatic variables was extracted  
283 and considered as the explanatory power of climate after the climatic heterogeneity  
284 within geographical units was controlled for. Similarly, we also evaluated the  
285 relationships between growth form and climate at species level using the growth forms  
286 of species and the climate variables within their distribution ranges.

287 Furthermore, to select the best multiple models explaining the geographical  
288 patterns in woodiness in local floras, we fitted all possible combinations of the six  
289 explanatory variables considered, and then selected the model with the lowest Akaike  
290 information criterion (AIC) as the best model. Models with  $\Delta AIC < 2$  were considered  
291 equally good (Burnham & Anderson, 2002). Preliminary analyses indicated that mean  
292 annual temperature (MAT) and mean annual precipitation (MAP) were included in all  
293 of the best models (Table S2). Then partial regressions were used to compare the  
294 independent and joint effects of MAT and MAP on geographical patterns in angiosperm  
295 woodiness. All these analyses were conducted at the global scale, both hemispheres and  
296 across different longitudinal regions, including the Asia-Oceania region, the Europe-  
297 Africa region, and the New World. To test whether the latitudinal gradient in  
298 angiosperm woodiness varies across these longitudinal regions and southern/northern  
299 hemispheres, we conducted ANOVA analysis on the following binomial GLM model:

300 
$$Woodiness \sim Latitude + Region + Latitude:Region$$

301 Chi-squared test was used to test the significance of the regression coefficients. All  
302 statistical analyses were conducted in R version 3.6.1 (<http://www.r-project.org>).

303

## 304 **3 RESULTS**

### 305 **3.1 Spatial patterns in woodiness**

306 Among extant angiosperms, 42.7% were woody species (Table S3). This  
307 proportion was slightly lower than a previous estimation for vascular plants (45–  
308 48%). Woody species accounted for 6.6% of monocotyledonous and 55.8% of  
309 dicotyledonous species. Woodiness at genus and family levels shows bimodal  
310 distributions (Fig. S1). At the genus level, 89.0% of genera exclusively consisted of  
311 either woody or herbaceous species, while 72.0% and 42.6% were exclusively woody  
312 or herbaceous at the family and order level, respectively.

313 The woodiness of angiosperm floras significantly decreased from ca. 56% on  
314 average at the equator to ca. 10% at high latitudes (Fig. 1a, Fig. S2). On the global scale,  
315 tropical rainforests had the highest woodiness (ca. 70%), while arctic ecosystems had  
316 the lowest woodiness (below 15%). This latitudinal gradient in angiosperm woodiness  
317 was similar across different longitudinal regions, i.e., the New World, Europe-Africa,  
318 and Asia-Oceania, and between the southern and northern hemispheres (Fig. S2, Table.  
319 S4).

320 GLM regressions for geographical woodiness and species-level growth forms  
321 indicated that the minimum temperature of the coldest month ( $T_{min}$ ) was the strongest  
322 predictor of the current spatial pattern in woodiness at the global scale, across different  
323 longitudinal regions and in both hemispheres (Table 1), and woodiness increased with  
324  $T_{min}$  (Fig. 1; Fig. S3). The results were consistent when mean, minimum and maximum  
325 values of climatic variables were used and whether or not the quadratic terms of these  
326 variables were included (Tables S5-8). The range of climate variables within  
327 geographical units had much weaker relationships with woodiness than the mean,  
328 maximum and minimum values of the corresponding variables, especially temperature  
329 (Table S6). Moreover, the independent  $R^2$  of mean climatic variables also indicated that  
330  $T_{min}$  was the strongest predictor of spatial woodiness variations (Table S7). These  
331 results suggested that climate heterogeneity within geographical units did not bias our  
332 findings.

333 Stepwise regression analyses indicated that the best model with multiple  
334 explanatory variables includes not only  $T_{min}$  but also mean annual precipitation (MAP,  
335 Table S2), suggesting a combined effect of energy and humidity.  $T_{min}$  had consistently  
336 higher independent explanatory power on the spatial pattern of woodiness than MAP  
337 as shown by variance partitioning analyses (independent explained variance of  $T_{min}$ :  
338 17.2 – 51.7%; independent effects of MAP: 2.2–7.5%)(Fig. S4).

339

### 340 **3.2 Temporal patterns in woodiness**

341 The temporal patterns in global woodiness reconstructed by the maximum  
342 parsimony and HiSSE models were highly consistent with each other (Fig. 1b, Figs.  
343 S5-S7). Specifically, during the evolutionary history of angiosperms, woodiness  
344 fluctuated considerably through time (Fig. S5). During the Cenozoic when most extant  
345 species had diversified, the woodiness was highest during the Paleocene and the early  
346 Eocene (66–55 Ma), ca. 52–53%, and continuously declined thereafter to the  
347 contemporary level (i.e., 42.7%) (Fig. 1b; Figs. S6-S7). Two dramatic declines can be  
348 identified: from early to mid-Eocene (55–38 Ma) and from early Miocene (23 Ma) to  
349 the present. This temporal trend in angiosperm woodiness was consistent across  
350 different continents (Fig. S8). These results suggested that the proportion of woody  
351 lineages at the global scale was lower than that of herbaceous lineages during most time  
352 of the Cenozoic, and the current proportion of woody lineages was much lower than  
353 that at any previous time during the Cenozoic. Similar to the positive association  
354 between spatial woodiness variation and temperature, the temporal woodiness variation  
355 was significantly positively correlated with paleotemperature during the Cenozoic  
356 (Pseudo- $R^2=0.795$ ,  $p<0.001$ , Fig. 1d). Moreover, our results indicated that herbaceous  
357 lineages had significantly higher speciation rates than woody lineages, while the  
358 extinction rates of the two growth forms were similar (Figs. S6-7).

359

### 360 **3.3 Growth form transitions**

361 During the period between 60–20 Ma, HtoW transitions were less frequent than  
362 WtoH transitions (Fig. 2), coinciding with the declining woodiness during this period.  
363 In contrast, during the last 20 Ma, HtoW transitions were dominant (Fig. 2). During this  
364 period, HtoW transitions occurred mainly in large families such as Asteraceae and  
365 Fabaceae (Table S9), probably because of the accelerated speciation in these families  
366 due to gaining woody growth form and the advantage of xylem in managing the  
367 hydraulic supply to foliage (Carlquist, 2013). It's noteworthy that HtoW transitions  
368 contribute to the woodiness through time by no more than 0.3% (Fig. S9). After  
369 removing the clades experiencing any evolutionary transitions between woody and  
370 herbaceous growth forms, the temporal changes in woodiness remained the same (Fig.  
371 S9). Hence, growth form transitions did not dominated woodiness changes through time.

372 During the Cenozoic, HtoW transitions were more frequent in temperate drylands  
373 than in other ecosystems (Fig. 3). Moreover, the difference in HtoW transitions between  
374 temperate drylands and other ecosystems was especially pronounced during the last 20  
375 Ma. Hence, woody species arising from secondary woodiness were an important part  
376 of the woody floras in temperate drylands, especially in deserts and xeric shrublands  
377 (Table S10). For example, in the drylands in Central Asia and the southern  
378 Mediterranean, HtoW transitions contribute more than half of the woody species in  
379 local woody floras (Fig. 3).

380 In contrast, WtoH transitions in the Cenozoic, especially during the last 20 Ma,  
381 were more frequent in savannas and tropical and subtropical grasslands compared to  
382 other ecosystems (Fig. 3; Table S10). Specifically, WtoH transitions during the last 20  
383 Ma accounted for >15% of herbaceous species in many regions in sub-Saharan Africa  
384 and Mesoamerica, where climate is warm and dry.

## 385 **4 DISCUSSION**

### 386 **4.1 The global geographical pattern in angiosperm woodiness and its** 387 **drivers**

388 We demonstrated a clear latitudinal gradient in angiosperm woodiness, supporting  
389 a long-standing hypothesis based on data of a small fraction of angiosperms (Sinnott &  
390 Bailey, 1915). The spatial resolution of the present study is relatively coarse and.  
391 Previous studies indicated that spatial resolution may influence species diversity  
392 patterns (Rahbek & Graves, 2001; Z. Wang et al., 2009) and hence patterns in  
393 woodiness. However, studies based on regional data found a similar latitudinal  
394 gradients in woodiness at a finer resolution (e.g. 100 km \* 100 km) supporting our  
395 results (Engemann et al., 2016). Moreover, the woodiness estimated here did not reflect  
396 the forest coverage. Some biomes at high latitudes of the northern hemisphere (e.g. the  
397 boreal forests) have high forest coverage were dominated by only a few woody species.

398 Our results indicated that annual minimum temperature had the strongest  
399 association with spatial woodiness variation. Other than annual minimum temperature,  
400 precipitation had a significant but relatively weaker association with spatial woodiness  
401 variation (Table 1). These results supported our first hypothesis that winter coldness

402 dominates the spatial variations in woodiness. Previous studies indicate that differences  
403 in physiological constraints tend to lead to differences in temperature demands between  
404 woody and herbaceous plants (Engemann et al., 2016; Hawkins et al., 2011). For  
405 example, the aboveground parts of herbaceous plants can die back in winter with buds  
406 positioned on or below ground to avoid coldness stress while woody plants with buds  
407 and branches high above the ground cannot (Engemann et al., 2016; Zanne et al., 2018;  
408 Zanne et al., 2014). Moreover, woody and herbaceous plants have been found to differ  
409 in their evolutionary niche conservatism, which may have also contributed to the  
410 dominant role of winter coldness on the woodiness pattern (Smith & Beaulieu, 2009;  
411 Zanne et al., 2018; Zanne et al., 2014). Woody lineages have longer generation times  
412 and slower rates of molecular and niche evolution hence stronger niche conservatism  
413 than herbaceous lineages (Smith & Beaulieu, 2009; Smith & Donoghue, 2008). These  
414 previous findings suggest that woody lineages may have stronger constraints on the  
415 evolution of new adaptations outside their ancestral habitats than herbaceous lineages  
416 (Smith & Beaulieu, 2009; Zanne et al., 2014). As a consequence, with the retraction of  
417 tropical-like climates and the emergence of seasonal and cold climates at high latitudes  
418 since the Oligocene (Zachos et al., 2001), high latitudes may have experienced more  
419 local extinctions of woody species as shown by fossil records (Shiono, Kusumoto,  
420 Yasuhara, & Kubota, 2018) and have lower woodiness compared with low latitudes  
421 (Kerkhoff et al., 2014). Therefore, we propose that differential niche conservatism and  
422 freezing tolerance between woody and herbaceous angiosperms might be a reason why  
423 winter coldness dominated the latitudinal decrease in woodiness.

424

## 425 **4.2 Evolution of angiosperm woodiness and its association with global** 426 **temperature changes**

427 Our findings on the decrease in woodiness were in line with pollen records in East  
428 Asia (Barbolini et al., 2020) and the New World (Graham, 2011), which indicated that  
429 the proportion of pollens of woody plants has decreased since the early Eocene while  
430 that of herbaceous plants increased. We showed that indicated that herbaceous lineages  
431 had significantly higher speciation rates than woody lineages, while the extinction rates



432 of the two growth forms are similar (Figs. S6-7). The difference in speciation rate  
433 between the two growth forms rather than extinction difference may have played a role  
434 in the temporal trends of woodiness.

435 The positive association between temporal woodiness variation and  
436 paleotemperature during the Cenozoic (Fig. 1d) suggested that the evolutionary decline  
437 in woodiness might have similarly been affected by decreasing paleotemperature. The  
438 paleoclimate of the Cenozoic is characterized by an almost continuous temperature  
439 declined since the late Paleocene and the early Eocene (Zachos et al., 2001). The late  
440 Paleocene and the early Eocene represent the warmest period during the Cenozoic (i.e.,  
441 a “greenhouse”), i.e. the Paleocene-Eocene Thermal Maximum (55 Ma) (Beerling &  
442 Royer, 2011). The “greenhouse” climate in this period led to dramatic expansions of  
443 tropical and subtropical habitats. Typically, fossil records and vegetation reconstruction  
444 based on pollen profiles suggest that the rainforests in the New World (Graham, 2011)  
445 extended to the Arctic Circle during the Paleocene. This dramatic expansion of tropical  
446 and subtropical habitats may have favored the coexistence of a large number of woody  
447 angiosperm species and hence increased woodiness on the global scale. Indeed, our  
448 results suggest that the woodiness of angiosperms peaked (52.7%, Fig. 1b) during the  
449 Paleocene-Eocene Thermal Maximum.

450 After the Paleocene-Eocene Thermal Maximum, the global climate cooled down,  
451 which eventually led to the transition from a “greenhouse” to an “icehouse” climate at  
452 the Eocene-Oligocene transition (34 Ma) (Zachos et al., 2001). Fossil and pollen  
453 records suggest that with the decline in global temperature tropical and subtropical  
454 evergreen broadleaf forests retreated, while grasslands and tundra expanded (Graham,  
455 2011). Open tropical habitats (i.e., savannas), temperate grasslands, and arctic and  
456 alpine ecosystems including tundra slowly developed and eventually became dominant  
457 over vast areas on different continents from mid-Miocene (since 15 Ma) onwards  
458 (Graham, 2011). The retreat of “closed ecosystems” (forests) and the expansion of  
459 “open ecosystems” (non-forested) may have allowed more herbaceous species to  
460 coexist, which may have led to the high diversification of herbaceous species (see Figs.  
461 S6-S7). For example, the diversification of major herbaceous lineages, including  
462 Poaceae (Strömberg, 2011), Gnaphalieae within Asteraceae (Nie et al., 2016),  
463 Ranunculaceae (W. Wang et al., 2016), and Valerianaceae (Bell & Donoghue, 2005),  
464 considerably accelerated since the Miocene, and these groups became dominant in the

465 new open habitats in both tropical and temperature regions. At the same time, the retreat  
466 of closed ecosystems may have reduced the habitats where many woody angiosperm  
467 species could coexist and the decrease in woodiness. Together, these findings suggest  
468 that global cooling since the early Eocene may have played a major role in the decline  
469 in angiosperm woodiness.

470

### 471 **4.3 Spatiotemporal patterns in growth form transitions**

472 Frequent macroevolutionary transitions between woody and herbaceous growth  
473 forms have been considered to be associated with the rapid radiation of species in new  
474 environments (Nürk et al., 2019). We found HtoW transitions contributed substantially  
475 to the woody flora of temperate drylands including Central Asia and the southern  
476 Mediterranean. Similarly, recent studies at local scales also find that many woody  
477 species in temperate drylands are from secondary woodiness. For example, Neupane *et*  
478 *al.* (2017) identified much secondary woodiness in the Mediterranean drylands. Our  
479 results together with previous findings suggest that temperate drylands may represent a  
480 hotspot of secondary woodiness, which is in contrast to our hypothesis and the  
481 expectation of the climatic moderation hypotheses (Sherwin Carlquist, 1974; Lens et  
482 al., 2013; Nürk et al., 2019). Moreover, these results also suggest that secondary  
483 woodiness species distribute more widely than previously known.

484 The “climatic moderation hypothesis” (Sherwin Carlquist, 1974; S. Carlquist, 1974;  
485 Nürk et al., 2019) suggests that warm and unseasonal climates lead to secondary  
486 woodiness (i.e. HtoW transitions), while cool climates lead to woodiness loss (i.e.  
487 WtoH transitions). However, this hypothesis could not explain the more frequent  
488 secondary woodiness in drylands presumably exerting strong drought stress on both  
489 woody and herbaceous species than in other ecosystems. Instead, the secondary  
490 woodiness in drylands, especially in deserts and xeric shrublands, may be associated  
491 with the rapid expansion of these ecosystems on the global scale since the mid-late  
492 Cenozoic (Guo et al., 2002; Hsü, Ryan, & Cita, 1973) and the rapid diversification of  
493 woody (especially shrub) species in these new habitats. Woody species from secondary  
494 woodiness tend to have larger phenotypic trait space (Nürk et al., 2019) and better  
495 drought-induced embolism resistance than their herbaceous relatives (Dória et al.,  
496 2018), which may be one of the reasons for the higher contribution of secondary  
497 woodiness to dryland floras. Indeed, the high proportions of secondary woody species

498 in central Asian deserts, the Sahara Desert, and the deserts in southwest North America  
499 coincide with the onset of desertification processes in these regions (Guo et al., 2002;  
500 Hsü et al., 1973).

501 We also found that WtoH transitions in the Cenozoic, especially during the last 20  
502 Ma, revealed the highest contribution to the herbaceous floras of savannas and tropical  
503 and subtropical grasslands compared to other ecosystems. This result is consistent with  
504 a previous study on angiosperm functional trait evolution (Zanne et al., 2014).  
505 Specifically, based on a large phylogeny, Zanne *et al.* (2014) showed that the transition  
506 rate from freezing-unexposed woody state to freezing-unexposed herbaceous state was  
507 almost four times of the vice versa transition. One of the possible reasons for the  
508 frequent WtoH transitions and their high contribution to the herbaceous floras in  
509 savannas and tropical and subtropical grasslands is the strong fire disturbance (Keeley  
510 & Rundel, 2005; van der Werf et al., 2010) which strongly affects savanna vegetation  
511 structures and lowers the height of trees and the proportion of woody plants (Furley,  
512 Rees, Ryan, & Saiz, 2008). Recent paleontological studies in Africa and the New World  
513 suggest that savannas and tropical and subtropical grasslands dramatically expanded  
514 with the decline of rainforests since the late Miocene in association with the increasing  
515 importance of fire disturbance (Dupont, Rommerskirchen, Mollenhauer, & Schefuss,  
516 2013; Hoetzel, Dupont, Schefuß, Rommerskirchen, & Wefer, 2013; Kissling et al.,  
517 2012; Linder & Verboom, 2015), which has likely enhanced WtoH transitions and  
518 hence improved the contribution of WtoH transitions to the herbaceous floras in these  
519 regions.

520

## 521 **5 CONCLUSION**

522 Woody and herbaceous habits are among the most ecologically distinct contrasts  
523 within angiosperms, and their proportion in floras represents a fundamental structural  
524 element of species diversity within ecosystems (Kerkhoff et al., 2014; Šímová et al.,  
525 2018; Zanne et al., 2014). Based on a unique database containing the growth forms and  
526 distributions of over 300,000 angiosperm species, our study provided a comprehensive  
527 description of the spatiotemporal patterns in angiosperm woodiness at the global scale,  
528 and identified annual minimum temperature among climatic variables as the best  
529 predictor of woodiness variations. Moreover, our study also calls for attention on the  
530 contribution of growth form transitions to floras in tropical and temperate drylands.

531 Future studies could evaluate whether on-going climate change may influence species  
532 composition of ecosystems via changes in woodiness.  
533

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731 **Data Accessibility Statement:**

732 All data and R codes used in the analyses of the paper are uploaded to Figshare  
733 website (<https://doi.org/10.6084/m9.figshare.13727815>).

734

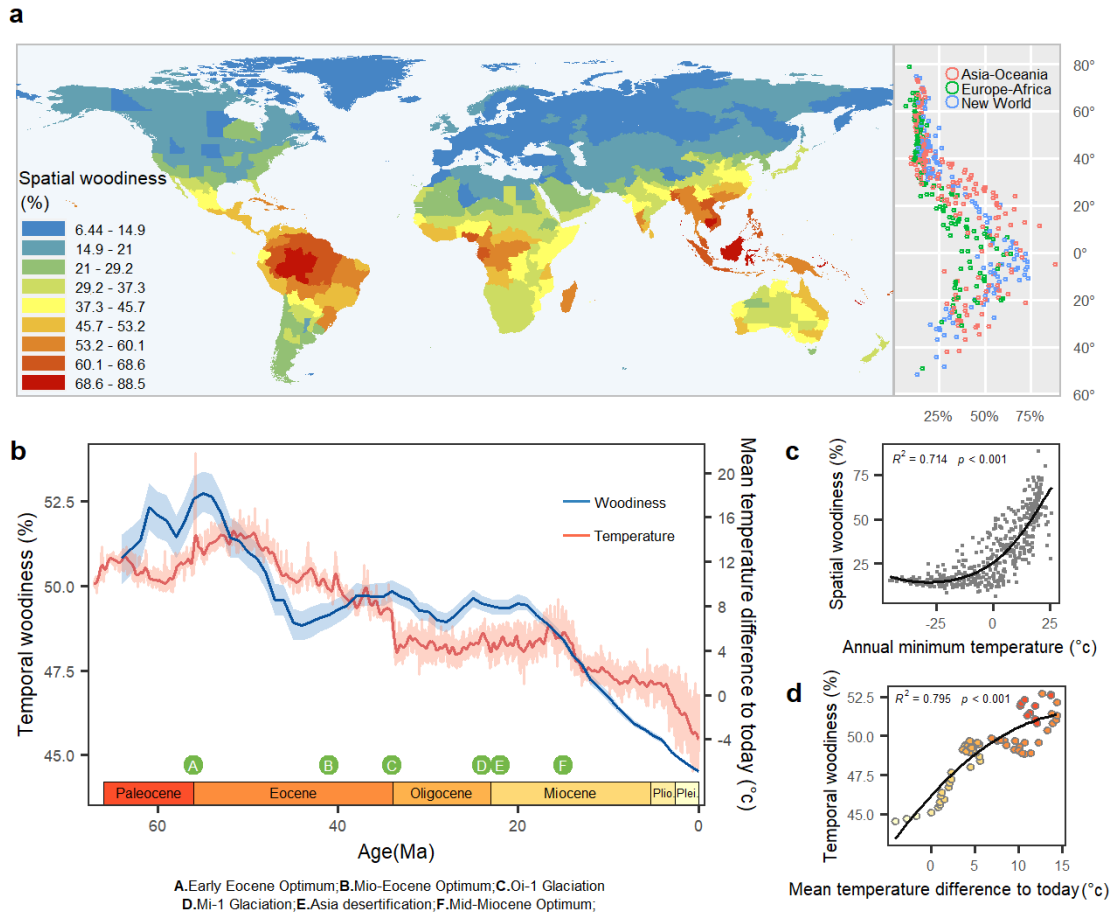
735 **Figures and Tables**

736 **Table 1.** The relationships between spatial variation in the woodiness of angiosperms and climate  
 737 variables. The pseudo- $R^2$  and significance were evaluated by binomial generalized linear models (GLMs)  
 738 with a quadratic term. MAT, mean annual temperature; Tmin, annual minimum temperature; MTWQ,  
 739 mean temperature of the warmest quarter; MAP, mean annual precipitation; PWQ, precipitation of the  
 740 warmest quarter; PCQ, precipitation of the coldest quarter. \*,  $p < 0.05$ ; \*\*,  $p < 0.01$ ; \*\*\*,  $p < 0.001$ .

741

Climate	Pseudo- $R^2$					
	Globe	New World	Asia-Oceania	Europe-Africa	North hemisphere	South hemisphere
<b>MAT (C°)</b>	0.579***	0.831***	0.57***	0.586***	0.559***	0.412***
<b>Tmin (C°)</b>	0.714***	0.883***	0.703***	0.792***	0.690***	0.547***
<b>MTWQ (C°)</b>	0.315***	0.452***	0.34***	0.366***	0.319***	0.227***
<b>MAP (mm)</b>	0.519***	0.566***	0.629***	0.251***	0.496***	0.451***
<b>PWQ (mm)</b>	0.369***	0.324***	0.496***	0.225***	0.316***	0.288***
<b>PCQ (mm)</b>	0.226***	0.264***	0.322***	0.620*	0.229***	0.259***

742



743

744 **Fig 1 Global spatial and temporal patterns in the proportion of woody species of**

745 **angiosperms a**, Spatial pattern in angiosperm woodiness (ie the proportion of woody species

746 in local floras) **b**, Temporal changes in angiosperm woodiness (blue line) and paleotemperature

747 (red line) in the Cenozoic, light red line is smoothed by 20 kyr, deep red line is smoothed by 1

748 myr (Westerhold et al., 2020; Zachos et al., 2001) The shaded light blue area represents the 95%

749 confidence interval of angiosperm woodiness (see Methods for details) Plei, Pleistocene; Plio,

750 Pliocene **c, d**, Relationships between woodiness and temperature over space (**c**) and through

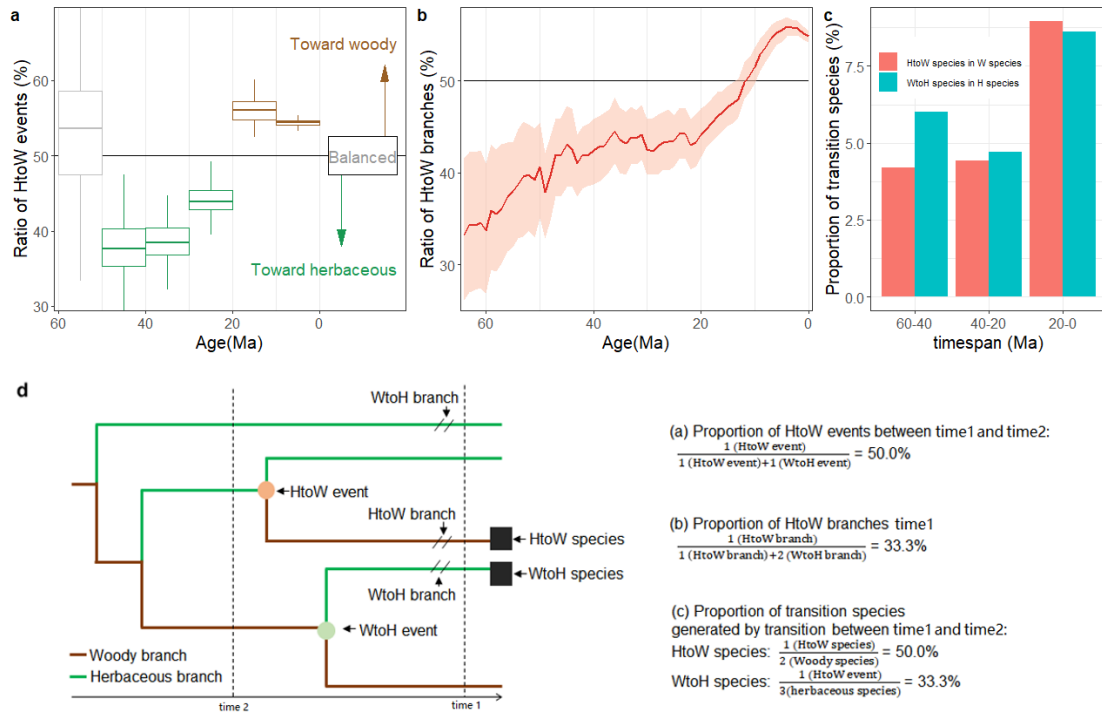
751 time (**d**) The solid lines were fitted by binomial generalized linear models with a quadratic term,

752 and the pseudo- $R^2$  and  $p$  values of these models were shown on the top left The colors of the

753 points in (**d**) represent different geological periods as shown in (**b**), with darker colors denoting

754 older ages

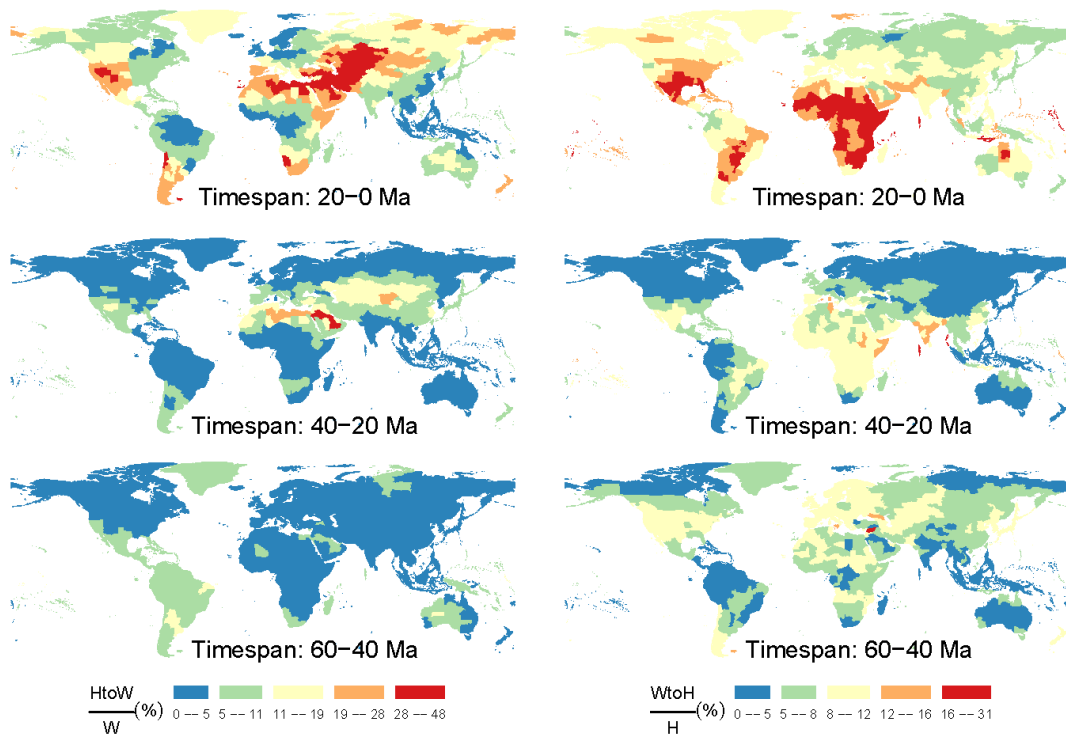
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757 **Fig 2 Changes in growth form transitions over time a**, Temporal changes in the proportion  
 758 of herbaceous-to-woody (HtoW) transition events to the total number of transition events  
 759 (HtoW and woody-to-herbaceous (WtoH) transitions) A value >50% means that HtoW  
 760 transitions are more frequent than WtoH transitions **b**, Temporal changes in the proportion of  
 761 branches generated by HtoW transitions to the total number of transition branches in both  
 762 directions (HtoW and WtoH transitions) The shaded area represents the 95% confidence  
 763 interval of the estimations **c**, The proportion of species generated by growth form transitions  
 764 during each timespan **d**, An illustrative diagram showing growth form transitions.

765



766

767 **Fig 3 The contribution of transition species to contemporary local floras** The contribution

768 of species generated by growth form transitions during each timespan to the local floras of the

769 corresponding growth forms H and W, number of herbaceous and woody species respectively;

770 WtoH and HtoW, number of species generated by woody-to-herbaceous and herbaceous-to-

771 woody transitions during a timespan, respectively

772