

# 1 **Paleoclimate and current climate collectively shape the phylogenetic and** 2 **functional diversity of trees worldwide**

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142 **Abstract**

143 Trees are of vital importance for ecosystem functioning and services at local to global scales, yet we  
144 still lack a detailed overview of the global patterns of tree diversity and the underlying drivers,  
145 particularly the imprint of paleoclimate. Here, we present the high-resolution (110 km) worldwide  
146 mapping of tree species richness, functional and phylogenetic diversities based on ~7 million  
147 quality-assessed occurrences for 46,752 tree species (80.5% of the estimated total number of tree  
148 species), and subsequent assessments of the influence of paleo-climate legacies on these patterns.  
149 All three tree diversity dimensions exhibited the expected latitudinal decline. Contemporary  
150 climate emerged as the strongest driver of all diversity patterns, with Pleistocene and deeper-time  
151 ( $>10^7$  years) paleoclimate as important co-determinants, and, notably, with past cold and drought  
152 stress being linked to reduced current diversity. These findings demonstrate that tree diversity is  
153 affected by paleoclimate millions of years back in time and highlight the potential for tree diversity  
154 losses from future climate change.

155 Understanding the global distribution of tree diversity and its underlying drivers has been an  
156 enduring pursuit of scientists, at least as far back as Alexander von Humboldt. Achieving this aim is  
157 becoming ever more urgent due to forest degradation and land use change <sup>1-4</sup>, and also for aiding  
158 forest restoration efforts <sup>5</sup>. Although our understanding of the global extent of tree cover has been  
159 greatly improved via remote sensing <sup>6</sup> and large networks of forest tree plots <sup>7,8</sup>, there are still gaps  
160 in our knowledge of the global patterns and drivers of tree diversity. Previous studies have often  
161 focused on tree species richness (SR) (e.g., <sup>9</sup>). However, SR does not directly represent species'  
162 evolutionary history and does not provide trait-based insight into their functioning and role in  
163 ecosystems. Phylogenetic diversity (PD; <sup>10,11</sup>) and functional diversity (FD; <sup>12</sup>) have been  
164 introduced as promising, more informative biodiversity variables than SR and have been  
165 successfully used in a wide variety of ecological applications, including conservation prioritization  
166 <sup>13-15</sup>. Indeed, FD is better coupled than SR to ecosystem functioning, e.g., productivity responses to  
167 climate change and forest multi-functionality <sup>16-18</sup>. In addition, PD and FD are more informative  
168 than SR in describing mechanisms of species coexistence and ecosystem functioning <sup>19,20</sup>, and thus  
169 shed light on species extinction and conservation <sup>13,14,21-23</sup>.

170 Many studies have emphasized the importance of current climate and edaphic conditions as key  
171 determinants of species diversity (e.g., <sup>24,25</sup>). However, paleoclimate could leave an influential  
172 legacy, e.g. via speciation, extinction or dispersal, on contemporary SR, and on phylogenetic and  
173 functional structures of forest ecosystems <sup>8,26-32</sup>. Earth climate has experienced continuous changes  
174 during geological time <sup>33</sup>, such as cooling or warming trends and events, and major climatic  
175 transitional periods have coincided with global ecosystem shifts <sup>34-37</sup>. Climatically-stable regions  
176 tend to have high speciation and low extinction rates, resulting in higher SR, FD, and PD <sup>38,39</sup>.  
177 Contrastingly, wide climate oscillations (like glacial-interglacial cycles) can dramatically truncate  
178 species' ranges and the chances of local diversification and adaptation, increasing the likelihood of

179 extinction and the removal of species with suboptimal traits, thereby decreasing all three facets of  
180 diversity<sup>40–43</sup>. However, rapid climate change may alternatively cause range fragmentation and  
181 further allopatric speciation as the result of isolation, potentially increasing net diversification rates  
182 <sup>27</sup>.

183 Due to the non-equivalency between the facets of diversity<sup>44–47</sup>, the responses of SR, PD and FD to  
184 different climatic conditions may vary. For example, warm and humid climates are hypothesized to  
185 increase diversification rates<sup>48,49</sup>, dispersal and establishment<sup>50</sup>, and decrease extinction<sup>27,51</sup>, thus  
186 increasing SR and PD, but not necessarily FD, as comparable climates more likely predispose  
187 species towards similar functional traits<sup>25,52–55</sup>. Thus, contemporary species diversity patterns can  
188 be the result of historical climate legacies and present-day environment, although the relative  
189 importance of these factors for FD and PD could be different.

190 Variable geological climates, i.e., warm and humid, or cold and dry in different paleo-time periods,  
191 had remarkably divergent influences on tree diversities. However, previous studies have  
192 concentrated mostly on assessing the effect of the cold and dry Last Glacial Maximum (LGM)  
193 imprints that occurred ~27 – 19 thousand years ago (kya), but deeper-time perspectives may also be  
194 important. For instance, ref.<sup>26</sup> found that palm tree diversity in Africa was affected by deep-time  
195 climate during the late Pliocene (3.3 – 3.0 million years ago [mya]) and the late Miocene (11.6 – 7.3  
196 mya), respectively. Similarly, ref.<sup>27</sup> found that the late Miocene climate influenced global patterns  
197 of conifer phylogenetic structure. Recently, ref.<sup>31</sup> reported opposite effects of LGM and Miocene  
198 tree cover on tree phylogenetic endemism. Hence, considering paleoclimate jointly across a range  
199 of time frames could be helpful in better understanding the factors shaping tree diversities. However,  
200 only a few SR studies have explicitly considered this<sup>26</sup>, and even fewer in FD and PD research<sup>42</sup>.



201 Here, we go beyond global mapping of tree species richness<sup>9</sup> by estimating species composition  
202 and, based thereon, functional and phylogenetic diversity. We subsequently analyze the relative  
203 roles of past and present climates in shaping global patterns of tree SR, FD, and PD. We first  
204 compiled the most updated dataset of tree species including occurrence records, functional traits,  
205 and tree phylogeny, covering 46,752 tree species or 80.5% of the species in the GlobalTreeSearch  
206 list<sup>47,56,57</sup>. We subsequently mapped global tree SR, FD, and PD. To understand the potential  
207 effects of paleoclimatic change on tree diversities completely, we examined the relative importance  
208 of three paleoclimatic states in determining current SR, FD and PD patterns, with consideration of  
209 other potential contemporary covariates, such as current climate, elevation, and human activities  
210 (Table S1). Specifically, we explored the influence of paleoclimate related to important climate  
211 states of the late Cenozoic, the time frame where current species diversity to a large extent have  
212 evolved: i) the warm and humid late Miocene, *ca.* 11.63 – 7.25 mya; the mid-Pliocene Warm period,  
213 *ca.* 3.264 – 3.025 mya; the cold and dry Pleistocene glaciations (represented by the LGM, ~ 21 kya);  
214 and Pleistocene warm interglacials (IG, ~ 787 kya and ~ 130 kya) (Figs. S1 & S2). In doing so, our  
215 study addressed three main goals: (1) mapping global contemporary tree SR, FD and PD; (2)  
216 assessing the relative importance of present-day environment, Quaternary glacial-interglacial  
217 oscillations, and deeper-time effects on today's SR, FD and PD patterns, to help understand the  
218 fundamental processes determining accumulation and maintenance of tree diversity; and (3)  
219 investigating spatial divergence between FD and PD, and identifying the underlying driving factors.

## 220 **Results**

### 221 **Global patterns of tree diversities**

222 The global tree SR, FD, and PD distributions show classic latitudinal gradients<sup>58–60</sup>, with low  
223 diversities at high latitudes and the highest diversities in the tropics (grid cell maximum value of

224 3261 spp. for SR and cumulative branch lengths of 641 and 61,183 Myrs for FD and PD,  
225 respectively at 110 km resolution, Fig. S3), particularly in the Neotropical lowlands (Amazonia)  
226 (Fig. 1). The latitudinal pattern is stronger in America and Asia-Australasia than in Africa-Europe,  
227 due to the interruption of the diversity gradients by deserts in northern Africa, where the diversity  
228 indices (SR, FD, and PD) are as low as at latitudes harboring the boreal climate. The similarity of  
229 the spatial patterns among the three diversity measures reflects the monotonic relationships  
230 observed between them (Fig. S4).

### 231 **Drivers of global tree diversity**

232 Due to the high associations between SR, FD, and PD, their individual relationships with the tested  
233 predictors are mostly consistent (Figs. 2 & Table S2). After controlling for spatial autocorrelation,  
234 simultaneous autoregressive models (SARs) explain more than 94% (global models) and 78%  
235 (regional models) of the variance (Table S2) in the response variables (SR, PD, and FD). Present-  
236 day annual precipitation (AP) and mean annual temperature (MAT) are the overall strongest drivers  
237 with positive effects on SR, FD, and PD globally, and for AP also regionally except for two regions  
238 where other drivers are stronger (Australasia, Nearctic). The effect of MAT varies in strength and  
239 sign among regions, showing both positive and negative effects on diversity (Fig. 2, Table S2).  
240 Elevation range and human modification index (HMc) have consistent positive effects on SR, FD  
241 and PD globally as well as regionally. Four out of the six paleoclimatic variables show significant  
242 relations to all three diversity dimensions (Fig. 2). Globally, the Miocene MAT anomaly (i.e.,  
243 Miocene MAT minus present MAT), the Miocene AP anomaly, and the LGM AP anomaly have  
244 positive relations to all diversity indices, while the LGM MAT anomaly have a weak negative  
245 relation to SR ( $p < 0.05$ , Table S2) and no relation to FD and PD (Fig. 2). Hence, SR, PD and FD  
246 consistently increase with increasing high precipitation in the Miocene and LGM relative to the

247 present, while SR, but not FD or PD, is generally reduced by increasing warm during LGM at a  
248 global scale. However, although some of these global relationships are mirrored regionally, not all  
249 paleoclimatic predictors are significant nor show consistent relationships across the biogeographic  
250 regions, e.g., with LGM AP anomaly showing negative associations in Australasia and Miocene  
251 MAT anomaly in Afrotropic for all three indices (Table S2).

252 Taken all together, precipitation-related effects were stronger and more consistent (among regions)  
253 climatic drivers of diversity (SR, FD, PD) than were temperature-related effects, with this true both  
254 for current climate (AP) and for paleoclimates (Miocene AP anomaly; IG AP anomaly).

#### 255 **Spatial divergence between functional and phylogenetic diversities and its drivers**

256 FD and PD are tightly and positively related (Fig. S4c). Deviations (FD residuals) from this linear  
257 relationship show marked spatial patterning (Fig. 3). Across North America, western and southern  
258 Europe, central Africa, eastern Asia, and eastern Australia, FD is generally higher than predicted by  
259 PD (i.e., overdispersion), whilst the opposite (i.e., FD deficit) is revealed in western Australia, much  
260 of southern and eastern Africa, west of the Andes (Peru), and central parts of northern Eurasia.

261 The relative importance of the factors explaining variation in FD residuals are different from those  
262 explaining their variations (Fig. 4 vs. Fig. 2b & 2c). Overall, current AP is correlated negatively  
263 with the FD residuals both globally and regionally, but is only the strongest driver at global scale  
264 (Figs. 4 & 5, Table S3). MAT and non-climatic factors show weak or no relations, except for MAT  
265 for Indo-Malay and the Neotropics. The effects of the paleoclimate are variable. At global scale, the  
266 Miocene AP anomaly and the LGM MAT anomaly are negatively related to the FD residuals, while  
267 the LGM AP anomaly is positively related (Figs. 4 & 5). However, these relationships are  
268 inconsistent across biogeographic regions (Figs. 4 & 5).

## 269 **Discussion**

270 Based on an unprecedented tree occurrence database, our study maps strong latitudinal patterns in  
271 all three diversity dimensions (SR, PD, and FD) at global scale. The SR-linked global latitudinal  
272 patterns of Faith's PD and FD matches previous empirical and modeled studies of tree species  
273 richness (e.g.,<sup>9,61</sup>), tree functional diversity in the New World<sup>62</sup>, and tree phylogenetic diversity at  
274 a regional scale<sup>31</sup>. It has been reported that speciation in rainforest environments has taken place at  
275 least since the Paleocene (~58 mya)<sup>63,64</sup>, probably coupled to jointly high temperatures and  
276 precipitation<sup>38,49,51,65</sup>. Moreover, the relatively stable environment, compared to high latitudes, may  
277 also resulted in low extinction rates, making the tropics both “cradles (species diversifying)” and  
278 “museums (species persistence)” of species diversity<sup>49,66</sup>. In addition, long speciation history and  
279 lower extinction rates in the tropics could result in both higher phylogenetic diversity and functional  
280 diversity<sup>38,48,49,51</sup>, but see<sup>35</sup>.

281 Our results provide evidence that paleoclimate complements current climate in shaping tree  
282 diversity globally and regionally, and that these effects are not only related to the recent prehistory  
283 – such as the Last Glacial period, represented by the LGM 21,000 years ago – but also much deeper  
284 time scales. These results extend previous findings for other organism groups notably for species  
285 richness and endemics<sup>39,42</sup> and for trees or plant clades including trees in specific regions and  
286 biomes<sup>26,27,29,67–70</sup>, to trees globally. Importantly, they go beyond species richness to the more  
287 ecologically meaningful indices, functional and phylogenetic diversity.

288 Notably, we found that precipitation effects were stronger and more consistent (across regions)  
289 drivers than temperature effects, especially in relation to the wet and warm middle Miocene (11.6 –  
290 7.5 mya), and the dry, cold LGM. The middle Miocene, the warmest and wettest interval in the late

291 Cenozoic, was a period of forest expansion<sup>34,71</sup>, due to warming coupled with elevated atmospheric  
292 CO<sub>2</sub> (>500 ppm)<sup>72–74</sup>. This likely promoted high species diversity globally due to a higher  
293 diversification rate and lower extinction rate<sup>38,48,51</sup>. The Myrtaceae family<sup>75</sup> and the genus *Quercus*  
294<sup>76</sup> are examples that follow this pattern. As a legacy of forest expansion, the generally warmer and  
295 wetter climate in the late Miocene compared to the contemporary climate have a positive  
296 associations to tree SR, FD, and PD<sup>37</sup>. We also see this in our results at the global scale and for  
297 most regions with positive effects of both Miocene AP and MAT (Fig. 2). The weak negative  
298 association between the LGM MAT anomaly and SR, but not with FD and PD, could indicate that  
299 global cold climate in LGM (Fig. S1) caused range retractions or even extinctions of certain species.  
300 Likely, the intensity of these processes were not strong enough to significantly decrease the  
301 communities' FD and PD, probably due to the high tree diversity accumulated in previous warm  
302 and humid periods<sup>36,75</sup>. Indeed, both tree FD and PD showed the tendency to level-off with SR  
303 increase (Fig. S6), a similar pattern reported by<sup>54</sup>, indicating that closely related tree species have  
304 more similar traits, i.e., the functional space tightly packed<sup>30,70</sup>. The LGM precipitation anomaly  
305 was positively related to tree SR, PD and FD, likely reflecting widespread forest contractions during  
306 the generally dry LGM and tree survival in moist refugia<sup>77,78</sup>. Furthermore, the diversity of drier  
307 forests itself is generally lower due to a limited number of niches and the physiological limits of  
308 species drought tolerance<sup>79</sup>. Our results suggest that paleoclimate affects not just forest biodiversity,  
309 but also forest ecosystem functioning given the effects found here, which corroborates other studies  
310 on FD<sup>16,17</sup> and PD<sup>20,27,67</sup>. Notably, a recent study has found that paleoclimatic legacies in tree FD  
311 negatively affect stand productivity in Northern Hemisphere temperate forests<sup>80</sup>.

312 The relationships between paleoclimate and SR, FD, and PD were partially repeated within  
313 biogeographic regions, there was also substantial inter-region variation in these relations (Fig. 2).  
314 For example, not all of the four significant relationships found globally were retained regionally,

315 and new relations emerged in some cases. These variable regional relations may reflect differing  
316 regional paleoclimatic histories, differences in the overall climatic and geographic setting, as well  
317 as methodological effects, e.g., different covariation among explanatory variables. For example, in  
318 Australasia, only the LGM AP anomaly showed significant, negative relationships with FD and PD,  
319 possibly because the temperature there was rather stably high during the last millions of years, with  
320 precipitation being more variable and lower (Fig. S2).

321 The regions representing FD surplus relative to PD, i.e., where species were found to be more  
322 functionally diverse (high FD) than expected from PD, largely coincided with high SR regions (Figs.  
323 3 & 1a), represented by warm and humid climate today. This suggests that communities in warm  
324 and humid conditions have accumulated more FD than expected compared to dry or cold regions.  
325 This FD surplus could be caused by high competition, high heterogeneous environments, or  
326 otherwise diversifying trait evolution<sup>19,62,81–83</sup>. We found that all precipitation variables were  
327 important for explaining the FD deviation from PD, even though their effects differed (Figs. 4 & 5).  
328 Surprisingly, high current precipitation tended to correspond to FD deficits, i.e., areas where species  
329 were more functionally similar than predicted by PD, both globally and in several biogeographic  
330 regions. Even though the observed FD in many wet and warm areas were higher than expected from  
331 PD, an explanation for the observed relationship could be that moist tropical forests harbor large  
332 numbers of shade-tolerant species, which have evolved along a similar evolutionary path (i.e.,  
333 stabilizing selection) to adapt to the shady environment, thus showing high levels of ecological  
334 equivalence<sup>83,84</sup>.

335 Building on recent progress in the harmonization of several databases on tree species distributions,  
336 functional traits, phylogenetic relatedness, and global paleoclimate, we have found that the tropics  
337 harbor the highest diversity across not only taxonomic, but also functional and phylogenetic

338 dimensions, while high latitudes have lower diversity values for all diversity measures.  
339 Nevertheless, there are important and informative deviations between the patterns in FD and PD,  
340 including a signature consistent with less ecological filtering in moist, shady tropical forest  
341 environments<sup>84</sup>. Importantly, we found evidence that current tree phylogenetic and functional  
342 diversities are likely shaped not only by the contemporary environment, but also by past climate as  
343 far back as the Miocene (~10 Mya). Notably, we see long-term reductions in FD and PD in relation  
344 to past climatic cold or drought stress, likely affecting current forest ecosystem functioning<sup>80</sup>.  
345 These findings highlight the importance of climate for tree diversity and forest ecosystems, and that  
346 losses from future climate change could have strong and very long-lasting effects.

## 347 **Methods**

### 348 ***Tree species and their range maps***

349 In this study, we used the world tree species list<sup>56</sup> and species range maps compiled by<sup>47,57</sup>. Briefly,  
350 the world tree species checklist (GlobalTreeSearch, GTS<sup>56</sup>) was used to extract the global tree  
351 species list for the current study. Tree species included in the GTS is based on the definition by the  
352 IUCN's Global Tree Specialist Group (GTSG), i.e., "a woody plant with usually a single stem  
353 growing to a height of at least two meters, or if multi-stemmed, then at least one vertical stem five  
354 centimeters in diameter at breast height"<sup>56</sup>. This list was subsequently standardized via the  
355 Taxonomic Name Resolution Service (TNRS) online tool<sup>85</sup> to remove synonyms. The occurrence  
356 records of the selected species were collated from five widely used and publicly accessible  
357 databases, namely: the Global Biodiversity Information Facility (GBIF; <http://www.gbif.org>), the  
358 public domain Botanical Information and Ecological Network v.3 (BIEN;  
359 <http://bien.nceas.ucsb.edu/bien/>;<sup>86,87</sup>), the Latin American Seasonally Dry Tropical Forest Floristic  
360 Network (DRYFLOR; <http://www.dryflor.info/>;<sup>88</sup>), the RAINBIO database  
361 (<http://rainbio.cesab.org/>;<sup>89</sup>), and the Atlas of Living Australia (ALA; <http://www.ala.org.au/>). The  
362 compiled occurrence data was accessed<sup>57</sup> and the high-quality records were then used to generate  
363 range maps based on the alpha hull algorithm via the *Alphahull* package<sup>90,91</sup> in R (ver. 3.5.1; <sup>92</sup>).  
364 We further validated the range maps using an external independent dataset<sup>9</sup>. The estimated range  
365 maps of the 46,752 tree species were rasterized to 110 km equal-area grid cells (~1 degree at the  
366 Equator), a resolution commonly used in global diversity studies (e.g.,<sup>45</sup>), using the *letsR* package<sup>93</sup>.  
367 For detailed information on the range map estimations and external validation, see<sup>47</sup>.

### 368 ***Phylogeny***



369 We constructed a phylogenetic tree for the tree species using the largest seed-plant phylogeny  
370 presently available (the ALLMB tree <sup>94</sup>). This dated phylogeny combines a backbone tree <sup>95</sup>, which  
371 was built using sequence data from public repositories (GenBank) to reflect deep relationships, with  
372 previous knowledge of phylogenetic relationships and species names from the Open Tree of Life  
373 (Open Tree of Life synthetic tree release 9.1 and taxonomy version 3,  
374 <https://tree.opentreeoflife.org/about/synthesis-release/v9.1>). This phylogeny was matched to our  
375 tree species dataset, and any species that were not in our dataset were removed from the tree.  
376 Subsequently, some species missing from the phylogeny were manually added, using the same  
377 approach as ref. <sup>94</sup>.

### 378 ***Functional trait data***

379 Eight ecologically relevant and commonly used traits <sup>96</sup> were selected for functional diversity  
380 analyses, i.e., leaf nitrogen content, wood density, leaf phosphorus content, leaf dry matter content,  
381 plant max height, seed dry mass, specific leaf area, and leaf area. Originally, we compiled 21  
382 functional traits from the TRY (<https://try-db.org/TryWeb/Home.php>; <sup>97,98</sup>, TOPIC <sup>99-105</sup>, and BIEN  
383 (<http://bien.nceas.ucsb.edu/bien/>; <sup>86,87</sup>) databases. As many of the species' trait were missing, we  
384 imputed missing values via an gap-filling algorithm with Bayesian Hierarchical Probabilistic Matrix  
385 Factorization (BHPMF, <sup>106-108</sup>), which is mostly based on both trait-trait correlation matrix and the  
386 phylogentic signal of traits (Refer to ref. <sup>47</sup> for the detailed gap-filling procedure). In this process,  
387 all the 21 traits were used to maximally benefit from the correlations among them.

### 388 ***Environmental variables***

389 We compiled 17 environmental variables, including current climate, paleo-climate, human effects,  
390 topographic heterogeneity and evolutionary history (Supplementary Table S1). Climate, both  
391 present-day and paleoclimate, is generally assumed to be a vital predictor of species distribution and

392 diversity patterns (e.g.,<sup>26,27,29,39,109,110</sup>). Due to the data availability of the paleoclimates, we  
393 included two bioclimatic predictors commonly used in relevant studies: annual mean temperature  
394 (MAT) and annual precipitation (AP). Current climate variables were extracted from WorldClim  
395 (v.2, [www.worldclim.org](http://www.worldclim.org)) at a resolution of 30 arc-seconds (~1 km at the equator), averaging global  
396 climate data from the period 1970 - 2000<sup>111</sup>. We selected six paleo-time periods spanning from *ca.*  
397 11.6 – 7.2 mya to *ca.* 21 kya, representing climatic conditions either warmer, cooler, or similar  
398 compared to the present-day climate. Specifically, each bioclimatic layer of the late Miocene  
399 climate (11.61 – 7.25 mya<sup>37</sup>) and mid-Pliocene Warm period (~ 3.264 – 3.025 mya;<sup>112,113</sup>) were  
400 averaged to represent the warmer climate compared to present day (hereafter Miocene). Pliocene  
401 Marine Isotope Stage M2, a glacial interval in the late Pliocene (~ 3.3 mya;<sup>113,114</sup>), was used to  
402 represent the Pliocene global cooling period, while the Last Glacial Maximum (LGM, ~ 21 kya)  
403 was used to present the more recent global cooling event compared to M2<sup>113,115</sup>. We further  
404 constructed a current climate (hereafter Interglacial, IG) analog using the mean value per  
405 bioclimatic layer between the Pleistocene Marine Isotope Stage 19 (MIS 19), the oldest Pleistocene  
406 interglacial (~ 787 kya<sup>113</sup>), and the Last Interglacial (LIG; ~ 130 kya<sup>116</sup>). The mid-Pliocene Warm  
407 Period, Pliocene M2, Pleistocene MIS19, and the LIG data were extracted from Paleoclim  
408 ([www.paleoclim.org](http://www.paleoclim.org)), at a resolution of 2.5 arc-minutes (~ 4.5 km at the equator)<sup>113</sup>, and the LGM  
409 data was extracted from the CHELSA database ([www.chelsa-climate.org](http://www.chelsa-climate.org)) at a resolution of 30 secs  
410<sup>115</sup>.

411 In addition to climate, other factors, such as human activities, topographic heterogeneity, and  
412 evolutionary history, can also affect plant distributions<sup>9,26,117,118</sup>. The Human Modification map  
413 (HMc<sup>119</sup>)<sup>119</sup> was used as a proxy of human activities. Compared to the commonly used human  
414 footprint index and human influence index maps<sup>120</sup>, HMc has been modelled with the incorporation  
415 of 13 most recent global-scale anthropogenic layers (with the median year of 2016) to account for

416 the spatial extent, intensity, and co-occurrence of human activities, many of which showing high  
417 direct or indirect impact on biodiversity<sup>121</sup>. HMc was extracted at a resolution of 1 km<sup>2</sup><sup>119</sup>. The  
418 elevation range is the absolute difference between the maximum and minimum elevation value  
419 within a specific area. We computed the elevation/topographic range within each 110 ×110 km grid  
420 cell based on the digital elevation model at 90 m resolution (<http://srtm.csi.cgiar.org/>). Elevation  
421 range is a proxy of environmental heterogeneity, which is considered as a universal driver of  
422 biological diversity<sup>122,123</sup>. To analyze the potential effects of evolutionary and biogeographic  
423 history, we also included the biogeographic regions as an additional variable. We applied the  
424 definition of biogeographic regions from ref.<sup>124</sup>, which defines 12 regions globally using cladistic  
425 and phylogenetic analyses of plant species, and plate tectonics. However, due to the varying data  
426 size in each of the 12 regions, we combined them into six regions, i.e., Afrotropic, Australasia,  
427 Indo-Malay, Nearctic, Neotropic, Palearctic, largely similar to the biogeographic realms proposed  
428 by ref.<sup>125</sup>. All predictors were extracted from various databases, which we describe in further detail  
429 in the supplement (Supplementary Table S1).

430 Except for the biogeographic regions and elevation range, mean values for all predictors were  
431 extracted at a 110 ×110 km resolution. The variable extractions and averaging were carried out in  
432 the *letsR* package. Due to the low reliability and/or missing environmental variables for many  
433 islands<sup>126</sup>, we removed insular grid cells from small islands, and 11,950 grid cells with records  
434 were kept (Fig. S5).

### 435 ***Phylogenetic and functional diversity***

436 Phylogenetic diversity (PD) was calculated for each 110 ×110 km grid cell as the sum of the branch  
437 lengths of all co-occurring species as defined by ref.<sup>10</sup>. Among the many existing, somewhat

438 overlapping matrices of PD, the one we selected is the most widely used due to its easy calculation  
439 and interpretation and a more robust basis for conservation <sup>10,13,14</sup>.

440 Functional diversity (FD) was calculated in an analogous manner to PD <sup>127</sup>. A Principal Component  
441 Analysis (PCA) was applied to the eight traits to eliminate trait redundancy. Values of all traits  
442 were log transformed to improve normality and were standardized before analysis. Then a  
443 dendrogram based on the first three PCs (explaining 84% of the total variation) was constructed  
444 using Gower's distance via the *vegan* <sup>128</sup> and *fastcluster* <sup>129</sup> packages. This dendrogram was used to  
445 calculate FD as the sum of the total branch lengths connecting a set of species in the 110 × 110 km  
446 grid cell. Both PD and FD were calculated using the *letsR* and *picante* <sup>130</sup> packages.

447 To investigate the bivariate relationships between FD and PD, an ordinary least squares model was  
448 implemented. We further plotted the residuals of model to show any deviation between FD and PD.

#### 449 ***Statistical analyses***

450 To test the long-term climate stability hypothesis, we calculated the anomaly for MAT and AP  
451 between the four paleo-time periods and the present-day, i.e., past minus present, to represent the  
452 amplitude of the climate changes within each time-scale (Fig. S1) <sup>26,27,29,39,118</sup>. On average,  
453 compared to the present, mean annual temperature (MAT) was much higher in the Miocene, slightly  
454 higher in the Pliocene M2 period, much lower in the LGM, and similar in the IG (Fig. S2a). During  
455 Pliocene M2 and IG, annual precipitation (AP) was similar to the present-day, while the Miocene  
456 and LGM had slightly higher or lower precipitation, respectively than the contemporary  
457 precipitation (Fig. S2b). The paleo-time periods selected, thus, represent (on average) cold, warm,  
458 and similar paleo-climates compared to present-day conditions.

459 Pearson correlation coefficients showed a low level of correlations between MAT, AP, and their  
460 respective anomaly variables (Fig. S6). However, MAT and AP of Pliocene M2 and Pleistocene IG

461 anomaly showed relatively high correlations (Fig. S7) with or without accounting for the spatial  
462 autocorrelation (using the *SpatialPack* package<sup>131</sup>). Consequently, we removed the two Pliocene  
463 M2 variables from further analyses.

464 We used ordinary least squares models (OLSs) and simultaneous autoregressive models (SARs), if  
465 the OLS model residuals exhibited spatial autocorrelation (SAC), to evaluate the relative  
466 importance of the predictor variables in determining the variation in each of the three diversity  
467 indices and the residuals of bivariate relationships between FD and PD. We used the SAR error  
468 model because of its superior performance compared to other SAR model types<sup>132</sup>. The SAR error  
469 model adds a spatial weights matrix to an OLS regression to accounts for SAC in the model  
470 residuals. A series of spatial weights, i.e., *k*-means neighbor of each site, were tested and *k* = 1.5  
471 was used for all SARs models as it can successfully account for the SAC (see Supplementary results  
472 of statistical analyses). Residual SAC was examined in all models (both OLS and SAR) using  
473 Moran's *I* test, and Moran's *I* correlograms were also used to visualize the spatial residuals of the  
474 models. Model explanatory power was represented by adjusted  $R^2$  (OLSs) and Nagelkerke pseudo-  
475  $R^2$  (SARs)<sup>133</sup>, while the Akaike Information Criterion (AIC) and Bayesian information criterion  
476 (BIC) were used to compare the models for each diversity index<sup>134</sup>. SARs and Moran's *I* tests were  
477 carried out using the *spdep* package<sup>135</sup>. Both OLS and SAR models were run by including current  
478 MAT and AP, the six anomaly variables, and the other non-climate predictors (elevation range and  
479 HMc) to investigate their relative contributions to each diversity index. In addition to the global  
480 models, we ran the same models for each biogeographic region to test whether the global  
481 relationships varied among regions. Moreover, we ran three additional global models for the FD and  
482 PD indices, selecting only one paleoclimate (both MAT and AP) from the three paleo-time periods  
483 at the time, and keeping other variables the same in each model to investigate whether the effects of  
484 the different paleoclimate predictors changed compared to the full models (including all paleo

485 climatic predictors). Before running the models, we inspected the normality of all predictors and  
486  $\log_{10}$ -transformed variables if needed. All response variables (three diversity indices) were  $\log_{10}$ -  
487 transformed. Thereafter, we standardized all predictor variables by transforming all variables to a  
488 mean of zero and a standard deviation of one to derive more comparable estimates<sup>136</sup>.

#### 489 *Supplementary results of statistical analyses*

490 We found that for all models (both global and regional), SAR models performed better than the  
491 corresponding OLS models, regarding to AIC, BIC, and  $R^2$  (Tables S2-S3), and all SAR models  
492 successfully accounted for SAC in model residuals ( $p \gg 0.05$ , Figs. S8-S11). Thus, we only  
493 represented the results from SARs models in the text, even though the significance of some  
494 predictors varied between OLS and SAR models (Fig. S12). In addition, we found that the effects of  
495 paleoclimate variables showed no change between the full models, including all paleoclimate  
496 variables and models using paleoclimate of each paleo-period (Fig. S13-S14). This clearly shows  
497 the robustness of their relationships with the tree diversity indices.

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## 785 **Acknowledgments**

786 We thank Brad Boyle for valuable database and informatics assistance and advice, and TRY  
787 contributors for sharing their data. This work was conducted as a part of the BIEN Working Group,  
788 2008–2012. We thank all the data contributors and numerous herbaria who have contributed their  
789 data to various data compiling organizations (see the herbarium list below) for the invaluable data  
790 and support provided to BIEN. We thank the New York Botanical Garden; Missouri Botanical  
791 Garden; Utrecht Herbarium; the UNC Herbarium; and GBIF, REMIB, and SpeciesLink. The staff at  
792 CyVerse provided critical computational assistance.

793 We acknowledge the herbaria that contributed data to this work: A, AAH, AAS, AAU, ABH,  
794 ACAD, ACOR, AD, AFS, AK, AKPM, ALCB, ALTA, ALU, AMD, AMES, AMNH, AMO,  
795 ANGU, ANSM, ANSP, AQP, ARAN, ARIZ, AS, ASDM, ASU, AUT, AV, AWH, B, BA, BAA,  
796 BAB, BABY, BACP, BAF, BAFC, BAI, BAJ, BAL, BARC, BAS, BBB, BBS, BC, BCMEX, BCN,  
797 BCRU, BERE, BESA, BG, BH, BHCB, BIO, BISH, BLA, BM, BOCH, BOL, BOLV, BONN,  
798 BOON, BOTU, BOUM, BPI, BR, BREM, BRI, BRIT, BRLU, BRM, BSB, BUT, C, CALI, CAN,  
799 CANB, CANU, CAS, CATA, CATIE, CAY, CBM, CDA, CDBI, CEN, CEPEC, CESJ, CGE,  
800 CGMS, CHAM, CHAPA, CHAS, CHR, CHSC, CIB, CICY, CIIDIR, CIMI, CINC, CLEMS, CLF,  
801 CMM, CMMEX, CNPO, CNS, COA, COAH, COCA, CODAGEM, COFC, COL, COLO, CONC,  
802 CORD, CP, CPAP, CPUN, CR, CRAI, CRP, CS, CSU, CSUSB, CTES, CTESN, CU, CUVC, CUZ,  
803 CVRD, DAO, DAV, DBG, DBN, DES, DLF, DNA, DPU, DR, DS, DSM, DUKE, DUSS, E, EA,  
804 EAC, EAN, EBUM, ECON, EIF, EIU, EMMA, ENCB, ER, ERA, ESA, ETH, F, FAA, FAU,  
805 FAUC, FB, FCME, FCO, FCQ, FEN, FHO, FI, FLAS, FLOR, FM, FR, FRU, FSU, FTG, FUEL,  
806 FULD, FURB, G, GAT, GB, GDA, GENT, GES, GH, GI, GLM, GMDRC, GMNHJ, GOET, GRA,  
807 GUA, GZU, H, HA, HAC, HAL, HAM, HAMAB, HAO, HAS, HASU, HB, HBG, HBR, HCIB,  
808 HEID, HGM, HIB, HIP, HNT, HO, HPL, HRCB, HRP, HSC, HSS, HU, HUA, HUAA, HUAL,  
809 HUAZ, HUCP, HUEFS, HUEM, HUFU, HUJ, HUSA, HUT, HXBH, HYO, IAA, IAC, IAN, IB,  
810 IBGE, IBK, IBSC, IBUG, ICEL, ICESI, ICN, IEA, IEB, ILL, ILLS, IMSSM, INB, INEGI, INIF,  
811 INM, INPA, IPA, IPRN, IRVC, ISC, ISKW, ISL, ISTC, ISU, IZAC, IZTA, JACA, JBAG, JBGP,  
812 JCT, JE, JEPS, JOTR, JROH, JUA, JYV, K, KIEL, KMN, KMNH, KOELN, KOR, KPM, KSC,  
813 KSTC, KSU, KTU, KU, KUN, KYO, L, LA, LAGU, LBG, LD, LE, LEB, LIL, LINC, LINN, LISE,  
814 LISI, LISU, LL, LMS, LOJA, LOMA, LP, LPAG, LPB, LPD, LPS, LSU, LSUM, LTB, LTR, LW,  
815 LYJB, LZ, M, MA, MACF, MAF, MAK, MARS, MARY, MASS, MB, MBK, MBM, MBML,

816 MCNS, MEL, MELU, MEN, MERL, MEXU, MFA, MFU, MG, MGC, MICH, MIL, MIN, MISSA,  
817 MJG, MMMN, MNHM, MNHN, MO, MOL, MOR, MPN, MPU, MPUC, MSB, MSC, MSUN, MT,  
818 MTMG, MU, MUB, MUR, MVFA, MVFQ, MVJB, MVM, MW, MY, N, NA, NAC, NAS, NCU,  
819 NE, NH, NHM, NHMC, NHT, NLH, NM, NMB, NMNL, NMR, NMSU, NSPM, NSW, NT, NU,  
820 NUM, NY, NZFRI, O, OBI, ODU, OS, OSA, OSC, OSH, OULU, OWU, OXF, P, PACA, PAMP,  
821 PAR, PASA, PDD, PE, PEL, PERTH, PEUFR, PFC, PGM, PH, PKDC, PLAT, PMA, POM, PORT,  
822 PR, PRC, PRE, PSU, PY, QCA, QCNE, QFA, QM, QRS, QUE, R, RAS, RB, RBR, REG, RELC,  
823 RFA, RIOG, RM, RNG, RSA, RYU, S, SACT, SALA, SAM, SAN, SANT, SAPS, SASK, SAV,  
824 SBBG, SBT, SCFS, SD, SDSU, SEL, SEV, SF, SFV, SGO, SI, SIU, SJRP, SJSU, SLPM, SMDB,  
825 SMF, SNM, SOM, SP, SPF, SPSF, SQF, SRFA, STL, STU, SUU, SVG, TAES, TAI, TAIF, TALL,  
826 TAM, TAMU, TAN, TASH, TEF, TENN, TEPB, TEX, TFC, TI, TKPM, TNS, TO, TOYA, TRA,  
827 TRH, TROM, TRT, TRTE, TU, TUB, U, UADY, UAM, UAMIZ, UB, UBC, UC, UCMM, UCR,  
828 UCS, UCSB, UCSC, UEC, UESC, UFG, UFMA, UFMT, UFP, UFRJ, UFRN, UFS, UGDA, UH,  
829 UI, UJAT, ULM, ULS, UME, UMO, UNA, UNB, UNCC, UNEX, UNITEC, UNL, UNM, UNR,  
830 UNSL, UPGB, UPEI, UPNA, UPS, US, USAS, USF, USJ, USM, USNC, USP, USZ, UT, UTC,  
831 UTEP, UU, UVIC, UWO, V, VAL, VALD, VDB, VEN, VIT, VMSL, VT, W, WAG, WAT,  
832 WELT, WFU, WII, WIN, WIS, WMNH, WOLL, WS, WTU, WU, XAL, YAMA, Z, ZMT, ZSS,  
833 and ZT.

834 W.-Y.G., J.M.S.-D., and J.-C.S. acknowledge support from the Danish Council for Independent  
835 Research | Natural Sciences (Grant 6108-00078B) to the TREECHANGE project. J.-C.S. also  
836 considers this work a contribution to his VILLUM Investigator project “Biodiversity Dynamics in a  
837 Changing World” funded by VILLUM FONDEN. C.B. was supported by the National Research  
838 Foundation of Korea (NRF) grant funded by the Korean government (MSIT)  
839 (2018R1C1B6005351). A.S.M. was supported by the Environment Research and Technology  
840 Development Fund (S-14) of the Ministry of the Environment, Japan. J.P. (Jan Pisek) was  
841 supported by the Estonian Research Council grant PUT1355. J.P. (Josep Peñuelas) was funded by  
842 the European Research Council Synergy grant ERC-2013-SyG-610028 IMBALANCE-P. A.G.G.  
843 (Alvaro G. Gutiérrez) was funded by FONDECYT 11150835 and 1200468. The BIEN working  
844 group was supported by the National Center for Ecological Analysis and Synthesis, a center funded  
845 by NSF EF-0553768 at the University of California, Santa Barbara and the State of California.  
846 Additional support for the BIEN working group was provided by iPlant/CyVerse via NSF DBI-  
847 0735191. B.J.E. and C.M. were supported by NSF ABI-1565118 and NSF HDR-1934790. B.J.E.



848 was also supported by the Global Environment Facility SPARC project grant (GEF-5810). B.J.E.,  
849 C.V., and B.S.M. acknowledge the FREE group funded by the synthesis center CESAB of the  
850 French Foundation for Research on Biodiversity (FRB) and EDF. J.-C.S. and B.J.E. acknowledge  
851 support from the Center for Informatics Research on Complexity in Ecology (CIRCE), funded by  
852 the Aarhus University Research Foundation under the AU Ideas program.

### 853 **Author contributions**

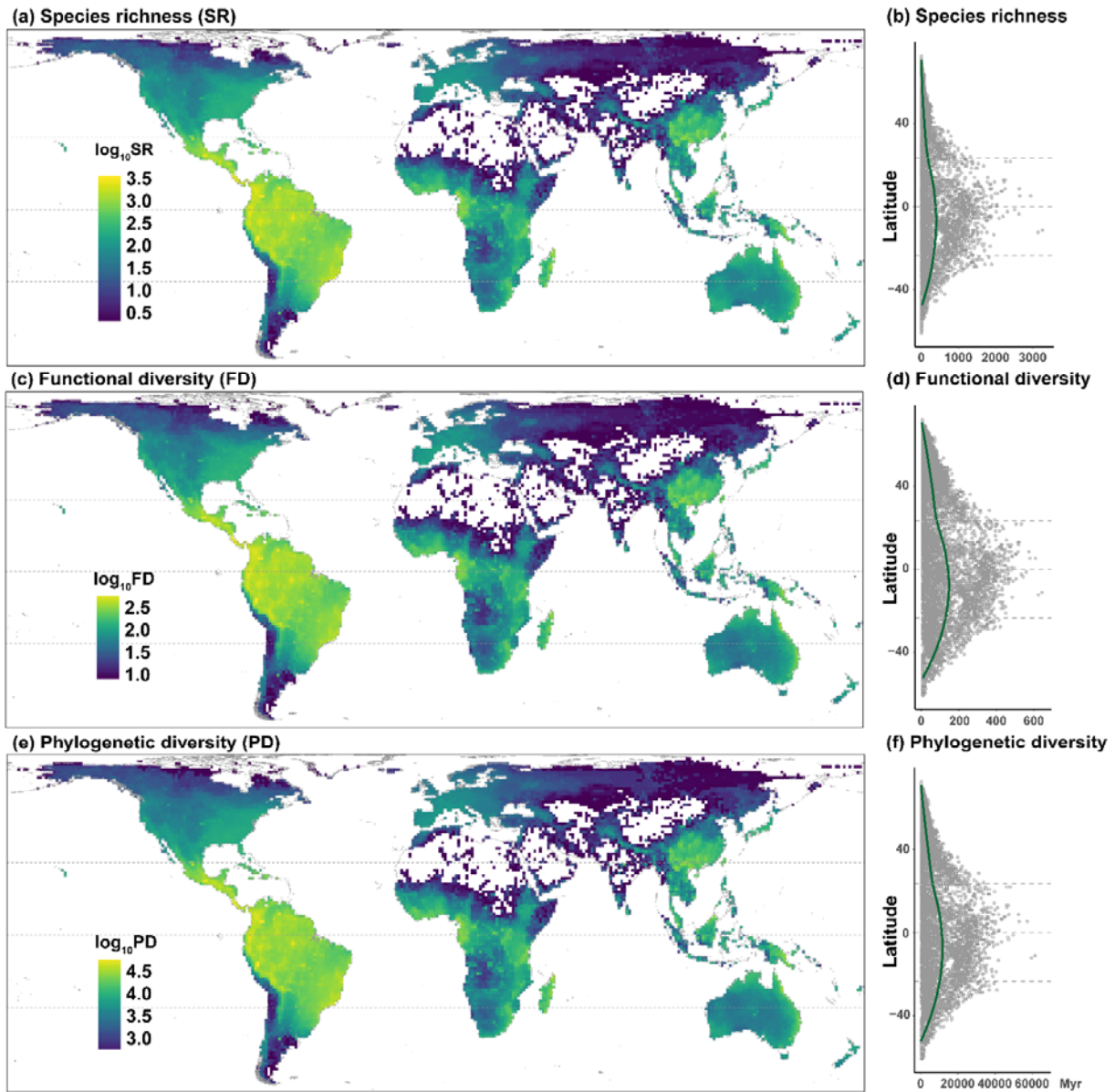
854 W.-Y.G., J.M.S.-D., and J.-C.S. conceived the project; J.M.S.-D., W.-Y.G., and all others collected  
855 the data; W.-Y.G. analyzed the data; W.-Y.G. interpreted the data; W.-Y.G., J.M.S.-D., and J.-C.S.  
856 wrote the manuscript. All authors contributed data, discussed the results, revised manuscript drafts,  
857 and contributed to writing and approved the final manuscript.

### 858 **Competing interests**

859 The authors declare no competing interests.

### 860 **Data and materials availability:**

861 All the occurrences are deposited in BIEN (<https://bien.nceas.ucsb.edu/bien/>), and the phylogeny  
862 and imputed functional trait data are available via ref. <sup>47</sup>.



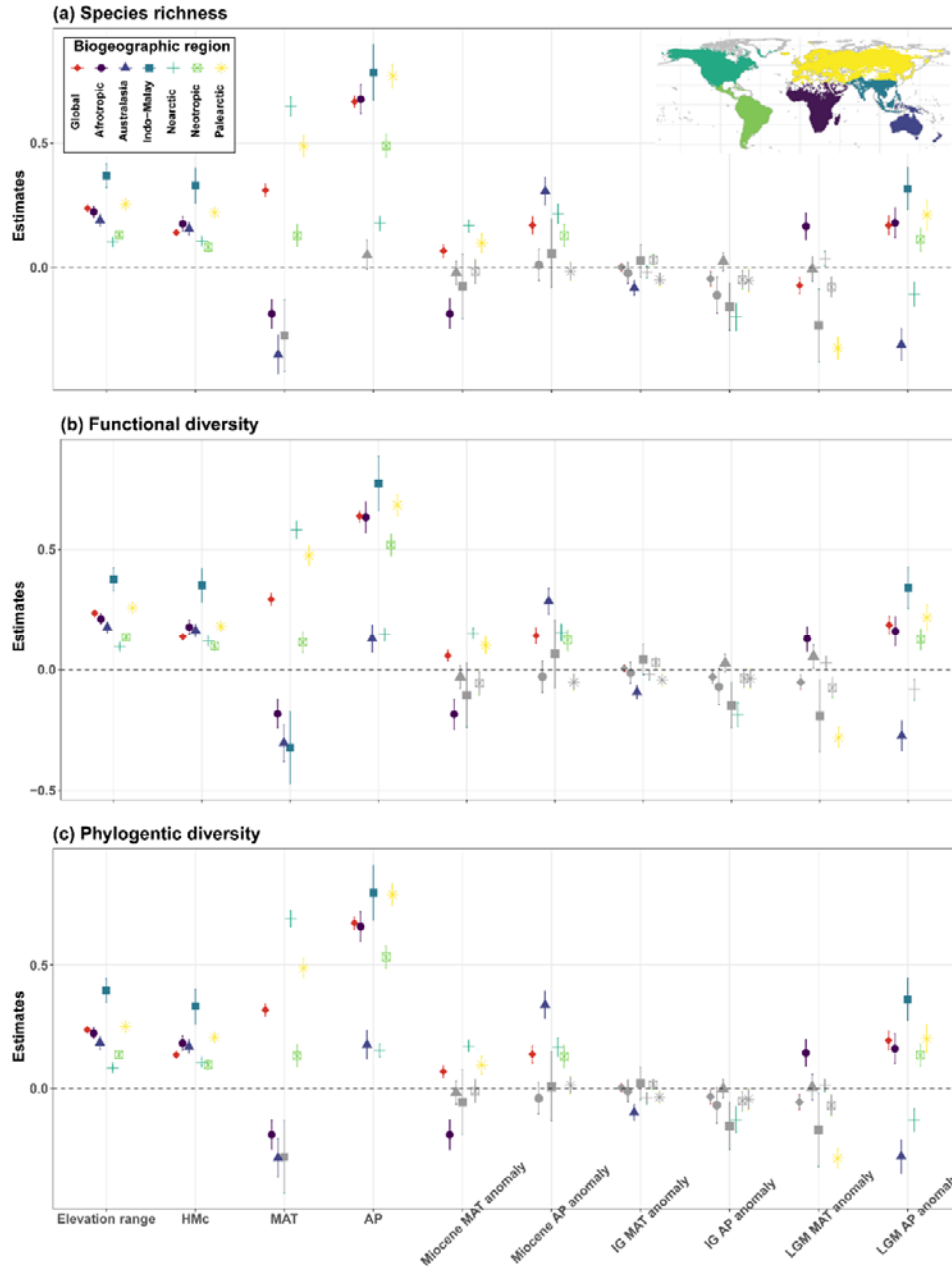
863 **Figures**

864

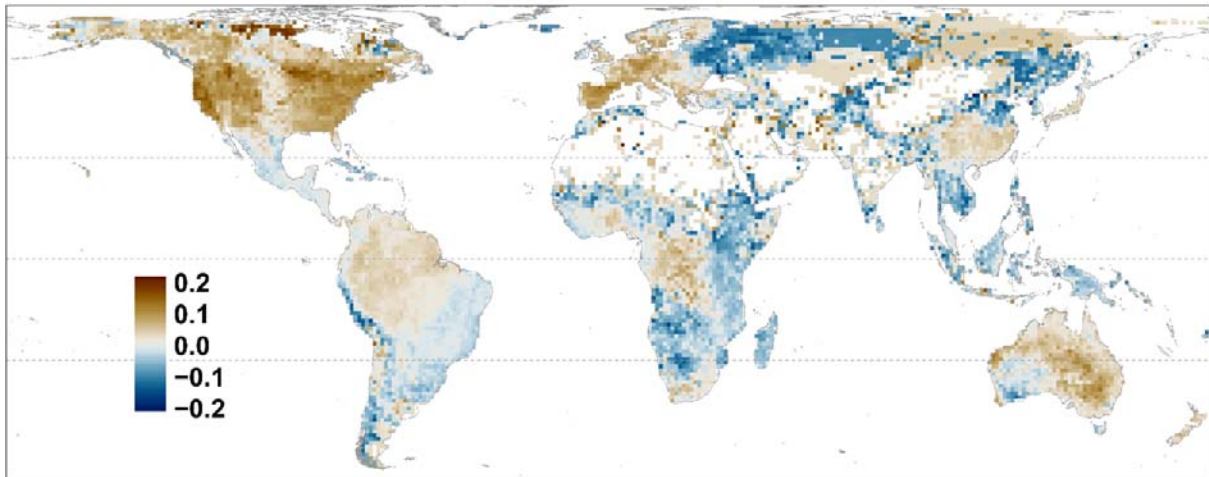
865 **Fig. 1** Global patterns of tree (a) species richness, (c) functional diversity, and (e) phylogenetic diversity. In

866 (b), (d) and (f), the fitted line is the lowess regression. Maps use the Behrmann projection at 110 km × 110

867 km spatial resolution. Myr: Million years.

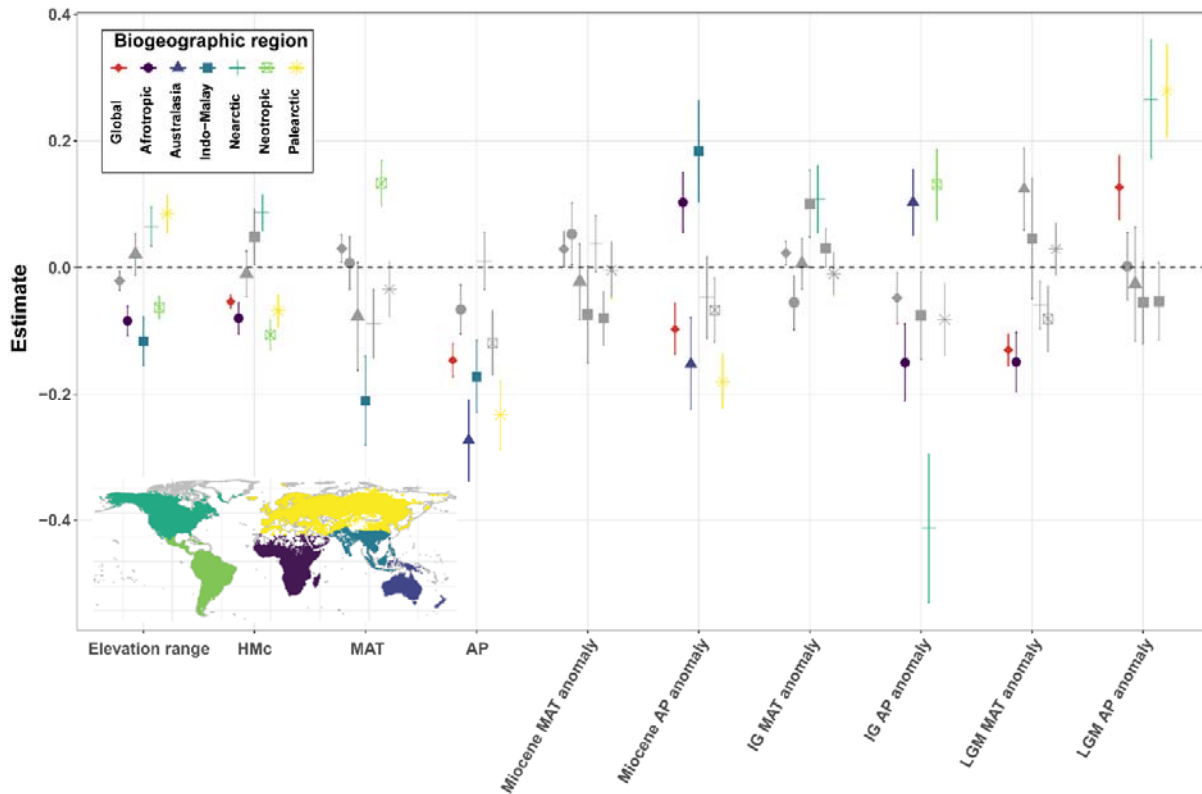


868 **Fig. 2** Effects of the tested environmental variables on tree (a) specie richness (SR), (b) functional diversity  
 869 (FD) and (c) phylogenetic diversity (PD). Estimates ( $\pm 1$  standard error) of effects were obtained from  
 870 simultaneous autoregressive (SAR) models. Different colors and shapes indicate biogeographic regions.  
 871 Non-significant variables ( $p > 0.05$ ) are indicated in grey. Results from OLS models are shown in Table S2.  
 872 HMc: human modification index; MAT: mean annual temperature; AP: Annual precipitation; IG: Pleistocene  
 873 Interglacial; LGM: Last Glacial Maximum. Anomaly was calculated as the past minus the present state.



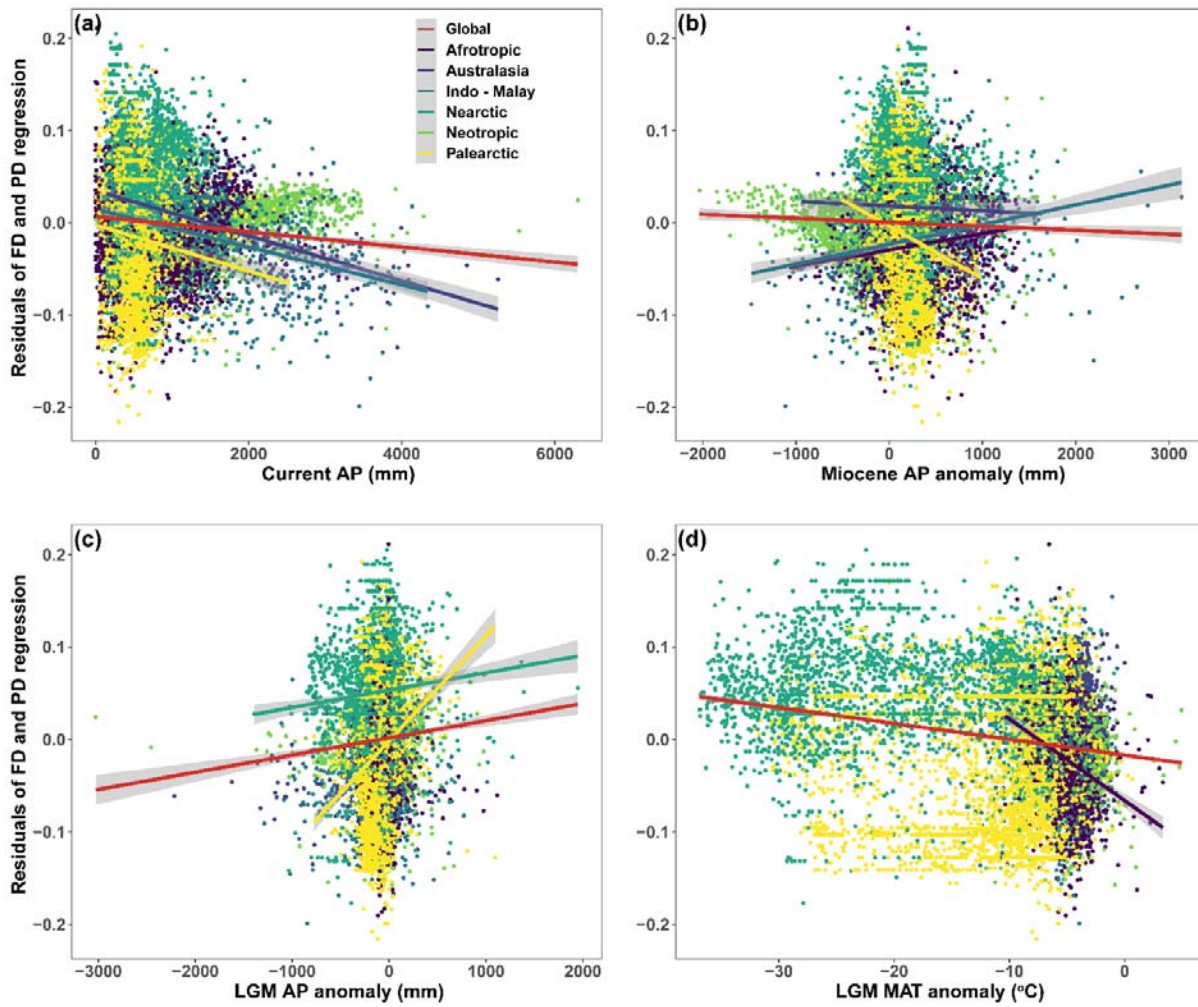
874

875 **Fig. 3** Global patterns of the residuals (deviation) from the ordinary least regression between functional  
876 diversity (FD) and phylogenetic diversity (PD) ( $FD = 0.90PD$ ,  $R^2 = 0.987$ ,  $p < 0.0001$ ). Brown (positive)  
877 areas are areas of higher FD than expected based on PD, whereas blue (negative) areas depict areas with  
878 lower FD than expected from the observed PD. Map uses the Behrmann projection at  $110 \text{ km} \times 110 \text{ km}$   
879 spatial resolution.



880

881 **Fig. 4** Effects of the tested environmental variables on the residuals from the regression between functional  
882 diversity (FD) and phylogenetic diversity (PD) (Fig. 3). Estimate ( $\pm 1$  standard error) of effects were obtained  
883 from simultaneous autoregressive (SAR) models. Different colors and shapes indicate biogeographic regions.  
884 Non-significant variables ( $p > 0.05$ ) are indicated in grey. Results from OLS models are shown in Table S3.  
885 HMc: human modification index; MAT: mean annual temperature; AP: Annual precipitation; IG: Pleistocene  
886 Interglacial; LGM: Last Glacial Maximum. Anomaly was calculated as the past minus the present state.



887

888 **Fig. 5** Bivariate regressions between the residuals from the regression of functional diversity (FD) on  
889 phylogenetic diversity (PD) and significant explanatory climate variables. Anomaly was calculated as the  
890 past minus the present state. For each subplot, only significant relationships are shown (Fig. 4,  $p < 0.05$ ).