

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 change¹⁻⁴, and also for aiding
158 forest restoration efforts⁵. Although our understanding of the global extent of tree cover has been
159 greatly improved via remote sensing⁶ and large networks of forest tree plots^{7,8}, 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.,⁹). 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;^{10,11}) and functional diversity (FD;¹²) 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
166¹³⁻¹⁵. Indeed, FD is better coupled than SR to ecosystem functioning, e.g., productivity responses to
167 climate change and forest multi-functionality¹⁶⁻¹⁸. In addition, PD and FD are more informative
168 than SR in describing mechanisms of species coexistence and ecosystem functioning^{19,20}, and thus
169 shed light on species extinction and conservation^{13,14,21-23}.

170 Many studies have emphasized the importance of current climate and edaphic conditions as key
171 determinants of species diversity (e.g.,^{24,25}). 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^{8,26-32}. Earth climate has experienced continuous changes
174 during geological time³³, such as cooling or warming trends and events, and major climatic
175 transitional periods have coincided with global ecosystem shifts³⁴⁻³⁷. Climatically-stable regions
176 tend to have high speciation and low extinction rates, resulting in higher SR, FD, and PD^{38,39}.
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^{40–43}. 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 ²⁷.

183 Due to the non-equivalency between the facets of diversity^{44–47}, 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^{48,49}, dispersal and establishment⁵⁰, and decrease extinction^{27,51}, thus
186 increasing SR and PD, but not necessarily FD, as comparable climates more likely predispose
187 species towards similar functional traits^{25,52–55}. 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.²⁶ 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.²⁷ found that the late Miocene climate influenced global patterns
197 of conifer phylogenetic structure. Recently, ref.³¹ 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 this²⁶, and even fewer in FD and PD research⁴².

201 Here, we go beyond global mapping of tree species richness⁹ 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^{47,56,57}. 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^{58–60}, 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 (HM_c) 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.,^{9,61}), tree functional diversity in the New World⁶², and tree phylogenetic diversity at
274 a regional scale³¹. It has been reported that speciation in rainforest environments has taken place at
275 least since the Paleocene (~58 mya)^{63,64}, probably coupled to jointly high temperatures and
276 precipitation^{38,49,51,65}. 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^{49,66}. In addition, long speciation history and
279 lower extinction rates in the tropics could result in both higher phylogenetic diversity and functional
280 diversity^{38,48,49,51}, but see³⁵.

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^{39,42} and for trees or plant clades including trees in specific regions and
286 biomes^{26,27,29,67–70}, 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^{34,71}, due to warming coupled with elevated atmospheric
292 CO₂ (>500 ppm)^{72–74}. This likely promoted high species diversity globally due to a higher
293 diversification rate and lower extinction rate^{38,48,51}. The Myrtaceae family⁷⁵ and the genus *Quercus*
294⁷⁶ 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 PD³⁷. 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^{36,75}. Indeed, both tree FD and PD showed the tendency to level-off with SR
303 increase (Fig. S6), a similar pattern reported by⁵⁴, indicating that closely related tree species have
304 more similar traits, i.e., the functional space tightly packed^{30,70}. 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^{77,78}. 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 tolerance⁷⁹. 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^{16,17} and PD^{20,27,67}. Notably, a recent study has found that paleoclimatic legacies in tree FD
311 negatively affect stand productivity in Northern Hemisphere temperate forests⁸⁰.

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^{19,62,81–83}. 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^{83,84}.

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 environments⁸⁴. 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 functioning⁸⁰.
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 list⁵⁶ and species range maps compiled by^{47,57}. Briefly,
350 the world tree species checklist (GlobalTreeSearch, GTS⁵⁶) 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"⁵⁶. This list was subsequently standardized via the
355 Taxonomic Name Resolution Service (TNRS) online tool⁸⁵ 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/>;^{86,87}), the Latin American Seasonally Dry Tropical Forest Floristic
360 Network (DRYFLOR; <http://www.dryflor.info/>;⁸⁸), the RAINBIO database
361 (<http://rainbio.cesab.org/>;⁸⁹), and the Atlas of Living Australia (ALA; <http://www.ala.org.au/>). The
362 compiled occurrence data was accessed⁵⁷ and the high-quality records were then used to generate
363 range maps based on the alpha hull algorithm via the *Alphahull* package^{90,91} in R (ver. 3.5.1;⁹²).
364 We further validated the range maps using an external independent dataset⁹. 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.,⁴⁵), using the *letsR* package⁹³.
367 For detailed information on the range map estimations and external validation, see⁴⁷.

368 ***Phylogeny***

369 We constructed a phylogenetic tree for the tree species using the largest seed-plant phylogeny
370 presently available (the ALLMB tree ⁹⁴). This dated phylogeny combines a backbone tree ⁹⁵, 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. ⁹⁴.

378 ***Functional trait data***

379 Eight ecologically relevant and commonly used traits ⁹⁶ 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>; ^{97,98}, TOPIC ⁹⁹⁻¹⁰⁵, and BIEN
383 (<http://bien.nceas.ucsb.edu/bien/>; ^{86,87}) 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, ¹⁰⁶⁻¹⁰⁸), which is mostly based on both trait-trait correlation matrix and the
386 phylogentic signal of traits (Refer to ref. ⁴⁷ 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.,^{26,27,29,39,109,110}). 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) at a resolution of 30 arc-seconds (~1 km at the equator), averaging global
396 climate data from the period 1970 - 2000¹¹¹. 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 mya³⁷) and mid-Pliocene Warm period (~ 3.264 – 3.025 mya;^{112,113}) 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;^{113,114}), 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^{113,115}. 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 kya¹¹³), and the Last Interglacial (LIG; ~ 130 kya¹¹⁶). The mid-Pliocene Warm
407 Period, Pliocene M2, Pleistocene MIS19, and the LIG data were extracted from Paleoclim
408 (www.paleoclim.org), at a resolution of 2.5 arc-minutes (~ 4.5 km at the equator)¹¹³, and the LGM
409 data was extracted from the CHELSA database (www.chelsa-climate.org) at a resolution of 30 secs
410¹¹⁵.

411 In addition to climate, other factors, such as human activities, topographic heterogeneity, and
412 evolutionary history, can also affect plant distributions^{9,26,117,118}. The Human Modification map
413 (HMc¹¹⁹)¹¹⁹ was used as a proxy of human activities. Compared to the commonly used human
414 footprint index and human influence index maps¹²⁰, 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 biodiversity¹²¹. HMc was extracted at a resolution of 1 km²¹¹⁹. 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^{122,123}. 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.¹²⁴, 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.¹²⁵. 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 islands¹²⁶, 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.¹⁰. 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 ^{10,13,14}.

440 Functional diversity (FD) was calculated in an analogous manner to PD ¹²⁷. 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* ¹²⁸ and *fastcluster* ¹²⁹ 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* ¹³⁰ 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) ^{26,27,29,39,118}. 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* package¹³¹). 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 types¹³². 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)¹³³, while the Akaike Information Criterion (AIC) and Bayesian information criterion
476 (BIC) were used to compare the models for each diversity index¹³⁴. SARs and Moran's I tests were
477 carried out using the *spdep* package¹³⁵. 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 estimates¹³⁶.

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.

498 **References**

- 499 1. Chazdon, R. L. Beyond deforestation: Restoring forests and ecosystem services on degraded lands.
500 *Science* **320**, 1458–1460 (2008).
- 501 2. Potapov, P. *et al.* The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000
502 to 2013. *Sci. Adv.* **3**, e1600821 (2017).
- 503 3. Watson, J. E. M. *et al.* The exceptional value of intact forest ecosystems. *Nature Ecology and*
504 *Evolution* **2**, 599–610 (2018).
- 505 4. Hansen, M. C., Stehman, S. V & Potapov, P. V. Quantification of global gross forest cover loss. *Proc.*
506 *Natl. Acad. Sci. U. S. A.* **107**, 8650–8655 (2010).
- 507 5. Bastin, J. F. *et al.* The global tree restoration potential. *Science (80-.).* **364**, 76–79 (2019).
- 508 6. Hansen, M. C. *et al.* High-resolution global maps of 21st-century forest cover change. *Science (80-.).*
509 **342**, 850–853 (2013).
- 510 7. Crowther, T. W. *et al.* Mapping tree density at a global scale. *Nature* **525**, 201–205 (2015).
- 511 8. Bruelheide, H. *et al.* Global trait–environment relationships of plant communities. *Nat. Ecol. Evol.* **2**,
512 1906–1917 (2018).
- 513 9. Keil, P. & Chase, J. M. Global patterns and drivers of tree diversity integrated across a continuum of
514 spatial grains. *Nat. Ecol. Evol.* **3**, 390–399 (2019).
- 515 10. Faith, D. P. Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* **61**, 1–10 (1992).
- 516 11. Faith, D. P. The PD Phylogenetic Diversity Framework: Linking Evolutionary History to Feature
517 Diversity for Biodiversity Conservation. in 39–56 (2016). doi:10.1007/978-3-319-22461-9_3
- 518 12. Petchey, O. L. & Gaston, K. J. Functional diversity: Back to basics and looking forward. *Ecology*
519 *Letters* **9**, 741–758 (2006).
- 520 13. Mazel, F. *et al.* Prioritizing phylogenetic diversity captures functional diversity unreliably. *Nat.*
521 *Commun.* **9**, 2888 (2018).
- 522 14. Tucker, C. M. *et al.* A guide to phylogenetic metrics for conservation, community ecology and
523 macroecology. *Biol. Rev.* **92**, 698–715 (2017).
- 524 15. Jarzyna, M. A. & Jetz, W. Detecting the Multiple Facets of Biodiversity. *Trends in Ecology and*
525 *Evolution* **31**, 527–538 (2016).
- 526 16. Huang, X., Su, J., Li, S., Liu, W. & Lang, X. Functional diversity drives ecosystem multifunctionality in a
527 *Pinus yunnanensis* natural secondary forest. *Sci. Rep.* **9**, 1–8 (2019).
- 528 17. Díaz, S. *et al.* Functional Diversity — at the Crossroads between Ecosystem Functioning and
529 Environmental Filters. in *Terrestrial Ecosystems in a Changing World* 81–91 (Springer, Berlin,
530 Heidelberg, 2007). doi:10.1007/978-3-540-32730-1_7
- 531 18. Díaz, S. & Cabido, M. Vive la différence: Plant functional diversity matters to ecosystem processes.
532 *Trends in Ecology and Evolution* **16**, 646–655 (2001).
- 533 19. Safi, K. *et al.* Understanding global patterns of mammalian functional and phylogenetic diversity.
534 *Philos. Trans. R. Soc. B Biol. Sci.* **366**, 2536–2544 (2011).

- 535 20. Donoghue, M. J. A phylogenetic perspective on the distribution of plant diversity. *Proc. Natl. Acad. Sci. U. S. A.* **105**, 11549–11555 (2008).
536
- 537 21. Oliveira, B. F., Sheffers, B. R. & Costa, G. C. Decoupled erosion of amphibians' phylogenetic and
538 functional diversity due to extinction. *Glob. Ecol. Biogeogr.* **29**, 309–319 (2020).
- 539 22. Faith, D. P. Phylogenetic diversity, functional trait diversity and extinction: Avoiding tipping points
540 and worst-case losses. *Philos. Trans. R. Soc. B Biol. Sci.* **370**, 1–10 (2015).
- 541 23. Park, D. S., Feng, X. & Maitner, B. S. Darwin's naturalization conundrum can be explained by spatial
542 scale. *Proceedings of the National Academy of Sciences* 201918100 (2020).
543 doi:10.5281/zenodo.3710499
- 544 24. Whittaker, R. J. & Field, R. Tree Species Richness Modelling: An Approach of Global Applicability?
545 *Oikos* **89**, 399–402 (2000).
- 546 25. Wright, I. J. *et al.* Modulation of leaf economic traits and trait relationships by climate. *Glob. Ecol. Biogeogr.* **14**, 411–421 (2005).
547
- 548 26. Blach-Overgaard, A., Kissling, W. D., Dransfield, J., Balslev, H. & Svenning, J. C. Multimillion-year
549 climatic effects on palm species diversity in Africa. *Ecology* **94**, 2426–2435 (2013).
- 550 27. Eiserhardt, W. L., Borchsenius, F., Sandel, B., Kissling, W. D. & Svenning, J. C. Late Cenozoic climate
551 and the phylogenetic structure of regional conifer floras world-wide. *Glob. Ecol. Biogeogr.* **24**, 1136–
552 1148 (2015).
- 553 28. Ordonez, A. & Svenning, J.-C. Consistent role of Quaternary climate change in shaping current plant
554 functional diversity patterns across European plant orders. *Sci. Rep.* **7**, 42988 (2017).
- 555 29. Svenning, J. C. & Skov, F. Could the tree diversity pattern in Europe be generated by postglacial
556 dispersal limitation? *Ecology Letters* **10**, 453–460 (2007).
- 557 30. Ordonez, A. & Svenning, J. C. Geographic patterns in functional diversity deficits are linked to glacial-
558 interglacial climate stability and accessibility. *Glob. Ecol. Biogeogr.* **24**, 826–837 (2015).
- 559 31. Sandel, B. *et al.* Current climate, isolation and history drive global patterns of tree phylogenetic
560 endemism. *Glob. Ecol. Biogeogr.* **29**, 4–15 (2020).
- 561 32. Blonder, B. *et al.* Late Quaternary climate legacies in contemporary plant functional composition.
562 *Glob. Chang. Biol.* **24**, 4827–4840 (2018).
- 563 33. Zachos, J., Pagani, H., Sloan, L., Thomas, E. & Billups, K. Trends, rhythms, and aberrations in global
564 climate 65 Ma to present. *Science* **292**, 686–693 (2001).
- 565 34. Dunn, R. E., Strömberg, C. A. E., Madden, R. H., Kohn, M. J. & Carlini, A. A. Linked canopy, climate,
566 and faunal change in the Cenozoic of Patagonia. *Science (80-.)*. **347**, 258–261 (2015).
- 567 35. Meseguer, A. S. & Condamine, F. L. Ancient tropical extinctions at high latitudes contributed to the
568 latitudinal diversity gradient. *Evolution (N. Y.)*. evo.13967 (2020). doi:10.1111/evo.13967
- 569 36. Herbert, T. D. *et al.* Late Miocene global cooling and the rise of modern ecosystems. *Nat. Geosci.* **9**,
570 843–847 (2016).
- 571 37. Pound, M. J. *et al.* A Tortonian (Late Miocene, 11.61–7.25Ma) global vegetation reconstruction.
572 *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **300**, 29–45 (2011).
- 573 38. Svenning, J. C., Borchsenius, F., Bjorholm, S. & Balslev, H. High tropical net diversification drives the

- 574 New World latitudinal gradient in palm (Arecaceae) species richness. in *Journal of Biogeography* **35**,
575 394–406 (John Wiley & Sons, Ltd (10.1111), 2008).
- 576 39. Sandel, B. *et al.* The influence of late quaternary climate-change velocity on species endemism.
577 *Science (80-.)*. **334**, 660–664 (2011).
- 578 40. McGlone, M. S., Buitenwerf, R. & Richardson, S. J. The formation of the oceanic temperate forests of
579 New Zealand. *New Zealand Journal of Botany* **54**, 128–155 (2016).
- 580 41. Liebergesell, M. *et al.* Functional resilience against climate-driven extinctions - Comparing the
581 functional diversity of European and north American tree floras. *PLoS One* **11**, e0148607 (2016).
- 582 42. Svenning, J.-C., Eiserhardt, W. L., Normand, S., Ordonez, A. & Sandel, B. The Influence of
583 Paleoclimate on Present-Day Patterns in Biodiversity and Ecosystems. *Annu. Rev. Ecol. Evol. Syst.* **46**,
584 551–572 (2015).
- 585 43. Dynesius, M. & Jansson, R. Evolutionary consequences of changes in species' geographical
586 distributions driven by Milankovitch climate oscillations. *Proc. Natl. Acad. Sci. U. S. A.* **97**, 9115–9120
587 (2000).
- 588 44. Devictor, V. *et al.* Spatial mismatch and congruence between taxonomic, phylogenetic and
589 functional diversity: the need for integrative conservation strategies in a changing world. *Ecol. Lett.*
590 **13**, no-no (2010).
- 591 45. Pollock, L. J., Thuiller, W. & Jetz, W. Large conservation gains possible for global biodiversity facets.
592 *Nature* **546**, 141–144 (2017).
- 593 46. Mazel, F., Mooers, A. O., Riva, G. V. D. & Pennell, M. W. Conserving Phylogenetic Diversity Can Be a
594 Poor Strategy for Conserving Functional Diversity. *Syst. Biol.* **66**, 1019–1027 (2017).
- 595 47. Guo, W.-Y. *et al.* Half of the world's tree biodiversity is unprotected and is increasingly threatened
596 by human activities. *bioRxiv* 2020.04.21.052464 (2020). doi:10.1101/2020.04.21.052464
- 597 48. Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M. & West, G. B. Toward a metabolic theory of
598 ecology. in *Ecology* **85**, 1771–1789 (2004).
- 599 49. Brown, J. H. Why are there so many species in the tropics? *J. Biogeogr.* **41**, 8–22 (2014).
- 600 50. Steinbauer, M. J. *et al.* Accelerated increase in plant species richness on mountain summits is linked
601 to warming. *Nature* **556**, 231–234 (2018).
- 602 51. Gillooly, J. F. & Allen, A. P. Linking global patterns in biodiversity to evolutionary dynamics using
603 metabolic theory. *Ecology* **88**, 1890–4 (2007).
- 604 52. Wright, I. J. *et al.* The worldwide leaf economics spectrum. *Nature* **428**, 821–827 (2004).
- 605 53. Wright, I. J. *et al.* Global climatic drivers of leaf size. *Science (80-.)*. **357**, 917–921 (2017).
- 606 54. Swenson, N. G. *et al.* Constancy in functional space across a species richness anomaly. *Am. Nat.* **187**,
607 E83–E92 (2016).
- 608 55. Ordonez, A. & Svenning, J. C. Greater tree species richness in eastern North America compared to
609 Europe is coupled to denser, more clustered functional trait space filling, not to trait space
610 expansion. *Glob. Ecol. Biogeogr.* **27**, 1288–1299 (2018).
- 611 56. Beech, E., Rivers, M., Oldfield, S. & Smith, P. P. GlobalTreeSearch: The first complete global database
612 of tree species and country distributions. *J. Sustain. For.* **36**, 454–489 (2017).

- 613 57. Serra-Diaz, J. M., Enquist, B. J., Maitner, B., Merow, C. & Svenning, J. C. Big data of tree species
614 distributions: how big and how good? *For. Ecosyst.* **4**, 30 (2017).
- 615 58. Hillebrand, H. On the Generality of the Latitudinal Diversity Gradient. *Am. Nat.* **163**, 192–211 (2004).
- 616 59. Gaston, K. J. Global patterns in biodiversity. *Nature* **405**, 220–227 (2000).
- 617 60. Pianka, E. R. Latitudinal Gradients in Species Diversity: A Review of Concepts. *Am. Nat.* **100**, 33–46
618 (2002).
- 619 61. Barthlott, W. *et al.* Geographic Patterns of Vascular Plant Diversity at Continental to Global Scales
620 (Geographische Muster der Gefäßpflanzenvielfalt im kontinentalen und globalen Maßstab).
621 *Erdkunde* **61**, 305–315 (2007).
- 622 62. Lamanna, C. *et al.* Functional trait space and the latitudinal diversity gradient. *Proc. Natl. Acad. Sci. U.*
623 *S. A.* **111**, 13745–13750 (2014).
- 624 63. Wing, S. L. *et al.* Late Paleocene fossils from the Cerrejon Formation, Colombia, are the earliest
625 record of Neotropical rainforest. *Proc. Natl. Acad. Sci.* **106**, 18627–18632 (2009).
- 626 64. Antonelli, A. *et al.* Amazonia is the primary source of Neotropical biodiversity. *Proc. Natl. Acad. Sci.*
627 **115**, 6034–6039 (2018).
- 628 65. Chu, C. *et al.* Direct and indirect effects of climate on richness drive the latitudinal diversity gradient
629 in forest trees. *Ecology Letters* **22**, 245–255 (2019).
- 630 66. Fine, P. V. A. Ecological and Evolutionary Drivers of Geographic Variation in Species Diversity. *Annu.*
631 *Rev. Ecol. Evol. Syst.* **46**, 369–392 (2015).
- 632 67. Feng, G. *et al.* Species and phylogenetic endemism in angiosperm trees across the Northern
633 Hemisphere are jointly shaped by modern climate and glacial–interglacial climate change. *Glob. Ecol.*
634 *Biogeogr.* **28**, 1393–1402 (2019).
- 635 68. Kissling, W. D. *et al.* Quaternary and pre-Quaternary historical legacies in the global distribution of a
636 major tropical plant lineage. *Glob. Ecol. Biogeogr.* **21**, 909–921 (2012).
- 637 69. Blonder, B. *et al.* Linking environmental filtering and disequilibrium to biogeography with a
638 community climate framework. *Ecology* **96**, 972–985 (2015).
- 639 70. Ordonez, A. & Svenning, J. C. Functional diversity of North American broad-leaved trees is
640 codetermined by past and current environmental factors. *Ecosphere* **7**, (2016).
- 641 71. Pound, M. J., Haywood, A. M., Salzmann, U. & Riding, J. B. Global vegetation dynamics and
642 latitudinal temperature gradients during the Mid to Late Miocene (15.97–5.33Ma). *Earth-Science*
643 *Rev.* **112**, 1–22 (2012).
- 644 72. Osborne, C. P. Atmosphere, ecology and evolution: What drove the Miocene expansion of C4
645 grasslands? *Journal of Ecology* **96**, 35–45 (2008).
- 646 73. Greenop, R., Foster, G. L., Wilson, P. A. & Lear, C. H. Middle Miocene climate instability associated
647 with high-amplitude CO₂ variability. *Paleoceanography* **29**, 845–853 (2014).
- 648 74. Steinhorsdottir, M., Jardine, P. E. & Rember, W. C. Near-Future p CO₂ during the hot Mid Miocene
649 Climatic Optimum. *Paleoceanogr. Paleoclimatology* (2020). doi:10.1029/2020PA003900
- 650 75. Lucas, E. J. & Bünge, M. O. Myrtaceae in the Atlantic forest: their role as a ‘model’ group. *Biodivers.*
651 *Conserv.* **24**, 2165–2180 (2015).

- 652 76. Deng, M., Jiang, X. L., Hipp, A. L., Manos, P. S. & Hahn, M. Phylogeny and biogeography of East Asian
653 evergreen oaks (*Quercus* section *Cyclobalanopsis*; Fagaceae): Insights into the Cenozoic history of
654 evergreen broad-leaved forests in subtropical Asia. *Mol. Phylogenet. Evol.* **119**, 170–181 (2018).
- 655 77. Piñeiro, R., Dauby, G., Kaymak, E. & Hardy, O. J. Pleistocene population expansions of shade-tolerant
656 trees indicate fragmentation of the African rainforest during the ice ages. *Proc. R. Soc. B Biol. Sci.*
657 **284**, 20171800 (2017).
- 658 78. Zozomová-Lihová, J., Melichárková, A., Svitok, M. & Španiel, S. Pleistocene range disruption and
659 postglacial expansion with secondary contacts explain the genetic and cytotype structure in the
660 western Balkan endemic *Alyssum austrodalmaticum* (Brassicaceae). *Plant Syst. Evol.* **306**, 1–25
661 (2020).
- 662 79. Niinemets, Ü. & Valladares, F. Tolerance to shade, drought, and waterlogging of temperate northern
663 hemisphere trees and shrubs. *Ecol. Monogr.* **76**, 521–547 (2006).
- 664 80. Conradi, T., Van Meerbeek, K., Ordonez, A. & Svenning, J. Biogeographic historical legacies in the net
665 primary productivity of Northern Hemisphere forests. *Ecol. Lett.* **23**, 800–810 (2020).
- 666 81. Muscarella, R. *et al.* Functional convergence and phylogenetic divergence during secondary
667 succession of subtropical wet forests in Puerto Rico. *J. Veg. Sci.* **27**, 283–294 (2016).
- 668 82. Swenson, N. G. & Enquist, B. J. Opposing assembly mechanisms in a Neotropical dry forest:
669 implications for phylogenetic and functional community ecology. *Ecology* **90**, 2161–2170 (2009).
- 670 83. Kraft, N. J. B., Valencia, R. & Ackerly, D. D. Functional traits and niche-based tree community
671 assembly in an Amazonian forest. *Science (80-.)*. **322**, 580–582 (2008).
- 672 84. Hubbell, S. P. Neutral theory and the evolution of ecological equivalence. *Ecology* **87**, 1387–1398
673 (2006).
- 674 85. Boyle, B. *et al.* The taxonomic name resolution service: An online tool for automated standardization
675 of plant names. *BMC Bioinformatics* **14**, 16 (2013).
- 676 86. Enquist, B. J., Condit, R. R., Peet, R. K., Schildhauer, M. & Thiers, B. M. The Botanical Information and
677 Ecology Network (BIEN): Cyberinfrastructure for an integrated botanical information network to
678 investigate the ecological impacts of global climate change on plant biodiversity. *PeerJ* **4**, e2615v2
679 (2016).
- 680 87. Enquist, B. J. *et al.* The commonness of rarity: Global and future distribution of rarity across land
681 plants. *Sci. Adv.* **5**, eaaz0414 (2019).
- 682 88. Banda, K. R. *et al.* Plant diversity patterns in neotropical dry forests and their conservation
683 implications. *Science (80-.)*. **353**, 1383–1387 (2016).
- 684 89. Dauby, G. *et al.* RAINBIO: a mega-database of tropical African vascular plants distributions.
685 *PhytoKeys* **74**, 1–18 (2016).
- 686 90. Pateiro-López, B. & Rodríguez-Casal, A. Generalizing the Convex Hull of a Sample: The R Package
687 *alphahull*. *J. Stat. Softw.* **34**, (2015).
- 688 91. Kirkpatrick, D. G. & Seidel, R. On the Shape of a Set of Points in the Plane. *IEEE Trans. Inf. Theory* **29**,
689 551–559 (1983).
- 690 92. R Core Team. R: A Language and Environment for Statistical Computing. (2019).

- 691 93. Vilela, B. & Villalobos, F. LetsR: A new R package for data handling and analysis in macroecology.
692 *Methods Ecol. Evol.* **6**, 1229–1234 (2015).
- 693 94. Smith, S. A. & Brown, J. W. Constructing a broadly inclusive seed plant phylogeny. *Am. J. Bot.* **105**,
694 302–314 (2018).
- 695 95. Magallón, S., Gómez-Acevedo, S., Sánchez-Reyes, L. L. & Hernández-Hernández, T. A metacalibrated
696 time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytol.* **207**, 437–
697 453 (2015).
- 698 96. Díaz, S. *et al.* The global spectrum of plant form and function. *Nature* **529**, 167–171 (2016).
- 699 97. Kattge, J. *et al.* TRY - a global database of plant traits. *Glob. Chang. Biol.* **17**, 2905–2935 (2011).
- 700 98. Kattge, J. *et al.* TRY plant trait database – enhanced coverage and open access. *Glob. Chang. Biol.* **26**,
701 119–188 (2020).
- 702 99. Aubin, I., Beaudet, M. & Messier, C. Light extinction coefficients specific to the understory
703 vegetation of the southern boreal forest, Quebec. *Can. J. For. Res.* **30**, 168–177 (2000).
- 704 100. Aubin, I., Messier, C. & Kneeshaw, D. Population structure and growth acclimation of mountain
705 maple along a successional gradient in the southern boreal forest. *Écoscience* **12**, 540–548 (2005).
- 706 101. Aubin, I. *et al.* Traits to stay, traits to move: A review of functional traits to assess sensitivity and
707 adaptive capacity of temperate and boreal trees to climate change. *Environmental Reviews* **24**, 164–
708 186 (2016).
- 709 102. Thiffault, N., Titus, B. D. & Munson, A. D. Silvicultural options to promote seedling establishment on
710 *Kalmia-Vaccinium*-dominated sites. *Scand. J. For. Res.* **20**, 110–121 (2005).
- 711 103. Titus, B. D. *et al.* Post-harvest nitrogen cycling in clearcut and alternative silvicultural systems in a
712 montane forest in coastal British Columbia. *For. Chron.* **82**, 844–859 (2006).
- 713 104. Wiebe, S., Morris, D., Luckai, N. & Reid, D. Coarse Woody Debris Dynamics Following Biomass
714 Harvesting: Tracking Carbon and Nitrogen Patterns During Early Stand Development in Upland Black
715 Spruce Ecosystems. *Int. J. For. Eng.* **23**, 25–32 (2012).
- 716 105. Masse, J., Prescott, C. E., Müller, C. & Grayston, S. J. Gross nitrogen transformation rates differ in
717 reconstructed oil-sand soils from natural boreal-forest soils as revealed using a ¹⁵N tracing method.
718 *Geoderma* **282**, 37–48 (2016).
- 719 106. Shan, H. *et al.* Gap Filling in the Plant Kingdom---Trait Prediction Using Hierarchical Probabilistic
720 Matrix Factorization. in *Proceedings of the 29th International Conference on Machine Learning*
721 1303–1310 (2012).
- 722 107. Fazayeli, F., Banerjee, A., Kattge, J., Schrod, F. & Reich, P. B. Uncertainty quantified matrix
723 completion using bayesian hierarchical matrix factorization. in *Proceedings - 2014 13th International*
724 *Conference on Machine Learning and Applications, ICMLA 2014* 312–317 (IEEE, 2014).
725 doi:10.1109/ICMLA.2014.56
- 726 108. Schrod, F. *et al.* BHPMF - a hierarchical Bayesian approach to gap-filling and trait prediction for
727 macroecology and functional biogeography. *Glob. Ecol. Biogeogr.* **24**, 1510–1521 (2015).
- 728 109. Dynesius, M. & Jansson, R. Evolutionary consequences of changes in species' geographical
729 distributions driven by Milankovitch climate oscillations. *Proc. Natl. Acad. Sci.* **97**, 9115–9120 (2000).

- 730 110. Jetz, W. & Rahbek, C. Geographic range size and determinants of avian species richness. *Science* (80-
731 .). **297**, 1548–1551 (2002).
- 732 111. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land
733 areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).
- 734 112. Hill, D. J. The non-analogue nature of Pliocene temperature gradients. *Earth Planet. Sci. Lett.* **425**,
735 232–241 (2015).
- 736 113. Brown, J. L., Hill, D. J., Dolan, A. M., Carnaval, A. C. & Haywood, A. M. Paleoclim, high spatial
737 resolution paleoclimate surfaces for global land areas. *Sci. Data* **5**, 180254 (2018).
- 738 114. Dolan, A. M. *et al.* Modelling the enigmatic Late Pliocene Glacial Event - Marine Isotope Stage M2.
739 *Glob. Planet. Change* **128**, 47–60 (2015).
- 740 115. Karger, D. N. *et al.* Climatologies at high resolution for the earth's land surface areas. *Sci. Data* **4**,
741 170122 (2017).
- 742 116. Otto-Bliesner, B. L., Marshall, S. J., Overpeck, J. T., Miller, G. H. & Hu, A. Simulating arctic climate
743 warmth and icefield retreat in the last interglaciation. *Science* (80-.). **311**, 1751–1753 (2006).
- 744 117. Kreft, H. & Jetz, W. Global patterns and determinants of vascular plant diversity. *Proc. Natl. Acad. Sci.*
745 **104**, 5925–5930 (2007).
- 746 118. Zhang, J., Nielsen, S. E., Mao, L., Chen, S. & Svenning, J. C. Regional and historical factors supplement
747 current climate in shaping global forest canopy height. *J. Ecol.* **104**, 469–478 (2016).
- 748 119. Kennedy, C. M., Oakleaf, J. R., Theobald, D. M., Baruch-Mordo, S. & Kiesecker, J. Managing the
749 middle: A shift in conservation priorities based on the global human modification gradient. *Glob.*
750 *Chang. Biol.* **25**, 811–826 (2019).
- 751 120. Sanderson, E. W. *et al.* The Human Footprint and the Last of the Wild. *Bioscience* **52**, 891–904 (2002).
- 752 121. Schulze, K. *et al.* An assessment of threats to terrestrial protected areas. *Conservation Letters* **11**,
753 e12435 (2018).
- 754 122. Slavich, E., Warton, D. I., Ashcroft, M. B., Gollan, J. R. & Ramp, D. Topoclimate versus macroclimate:
755 How does climate mapping methodology affect species distribution models and climate change
756 projections? *Divers. Distrib.* **20**, 952–963 (2014).
- 757 123. Stein, A., Gerstner, K. & Kreft, H. Environmental heterogeneity as a universal driver of species
758 richness across taxa, biomes and spatial scales. *Ecology Letters* **17**, 866–880 (2014).
- 759 124. Morrone, J. J. Biogeographical regions under track and cladistic scrutiny. *Journal of Biogeography* **29**,
760 149–152 (2002).
- 761 125. Olson, D. M. *et al.* Terrestrial Ecoregions of the World: A New Map of Life on Earth. *Bioscience* **51**,
762 933 (2001).
- 763 126. Harter, D. E. V. *et al.* Impacts of global climate change on the floras of oceanic islands - Projections,
764 implications and current knowledge. *Perspectives in Plant Ecology, Evolution and Systematics* **17**,
765 160–183 (2015).
- 766 127. Mouchet, M. *et al.* Towards a consensus for calculating dendrogram-based functional diversity
767 indices. *Oikos* **117**, 794–800 (2008).
- 768 128. Oksanen, J. *et al.* vegan: Community Ecology Package. (2019).

- 769 129. Müllner, D. fastcluster[®]: Fast Hierarchical, Agglomerative Clustering Routines for R and Python. *J.*
770 *Stat. Softw.* **53**, 1–18 (2015).
- 771 130. Kembel, S. W. *et al.* Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* **26**,
772 1463–1464 (2010).
- 773 131. Osorio, F., Vallejos, R. & Cuevas, F. SpatialPack: Computing the Association Between Two Spatial
774 Processes. (2016).
- 775 132. Kissling, W. D. & Carl, G. Spatial autocorrelation and the selection of simultaneous autoregressive
776 models. *Glob. Ecol. Biogeogr.* **17**, 59–71 (2008).
- 777 133. Nagelkerke, N. J. D. A note on a general definition of the coefficient of determination. *Biometrika* **78**,
778 691–692 (1991).
- 779 134. Burnham, K. P. & Anderson, D. R. Multimodel inference: Understanding AIC and BIC in model
780 selection. *Sociological Methods and Research* **33**, 261–304 (2004).
- 781 135. Bivand, R. S. & Wong, D. W. S. Comparing implementations of global and local indicators of spatial
782 association. *Test* **27**, 716–748 (2018).
- 783 136. Schielzeth, H. Simple means to improve the interpretability of regression coefficients. *Methods Ecol.*
784 *Evol.* **1**, 103–113 (2010).

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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,
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823 RFA, RIOC, RM, RNG, RSA, RYU, S, SACT, SALA, SAM, SAN, SANT, SAPS, SASK, SAV,
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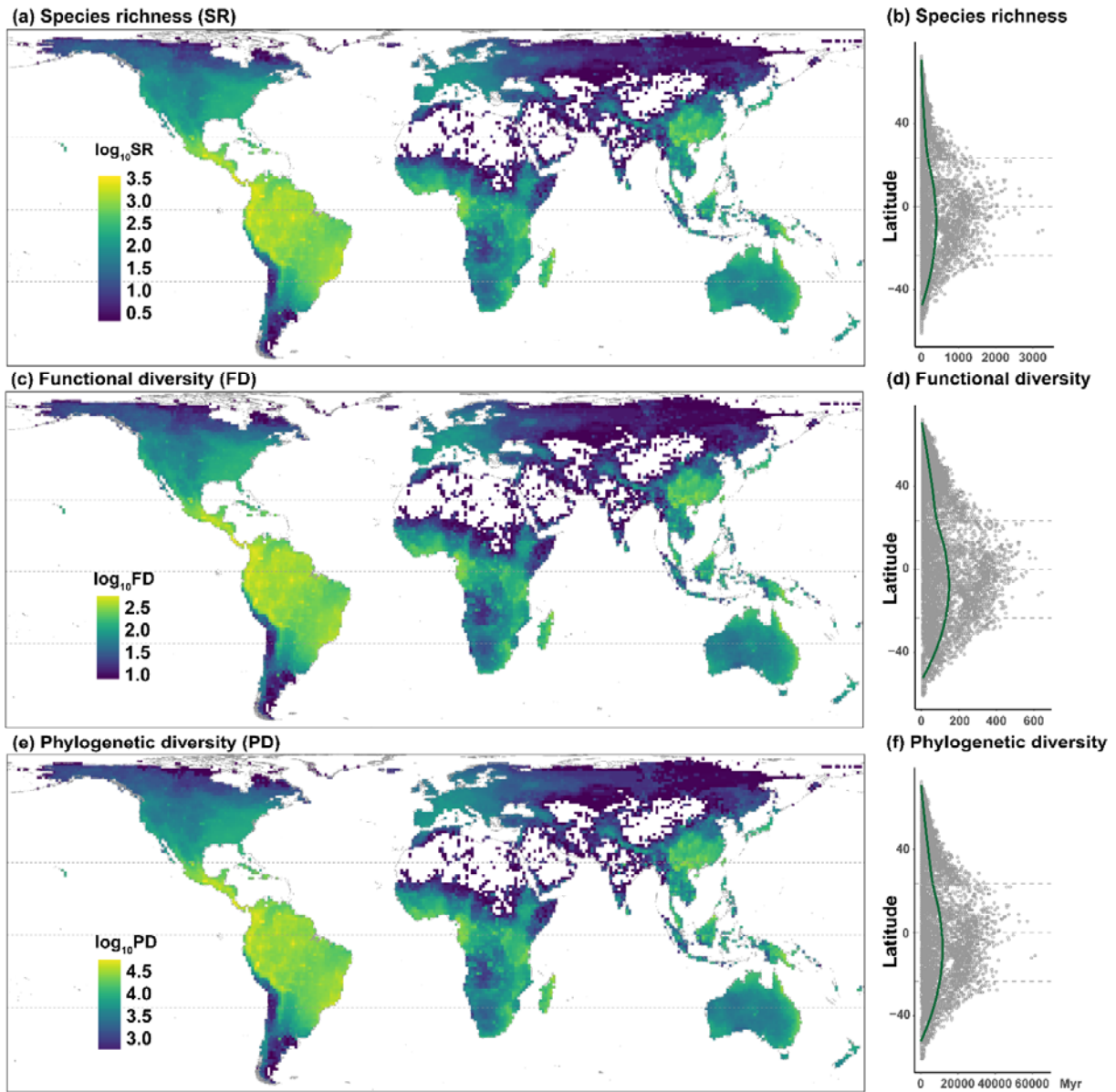
854 W.-Y.G., J.M.S.-D., and J.-C.S. conceived the project; J.M.S.-D., W.-Y.G., and all others collected
855 the data; W.-Y.G. analyzed the data; W.-Y.G. interpreted the data; W.-Y.G., J.M.S.-D., and J.-C.S.
856 wrote the manuscript. All authors contributed data, discussed the results, revised manuscript 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. ⁴⁷.



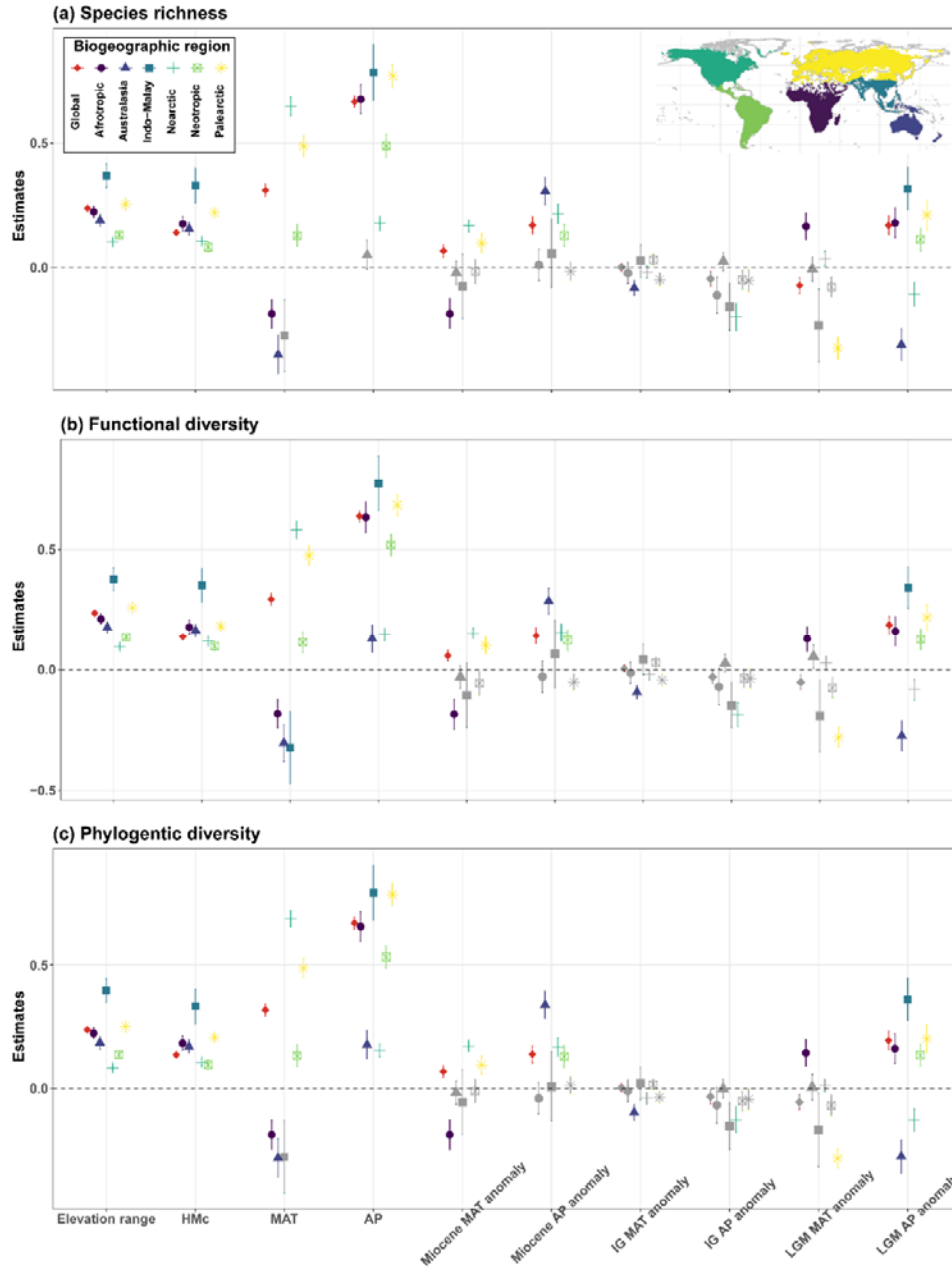
863 **Figures**

864

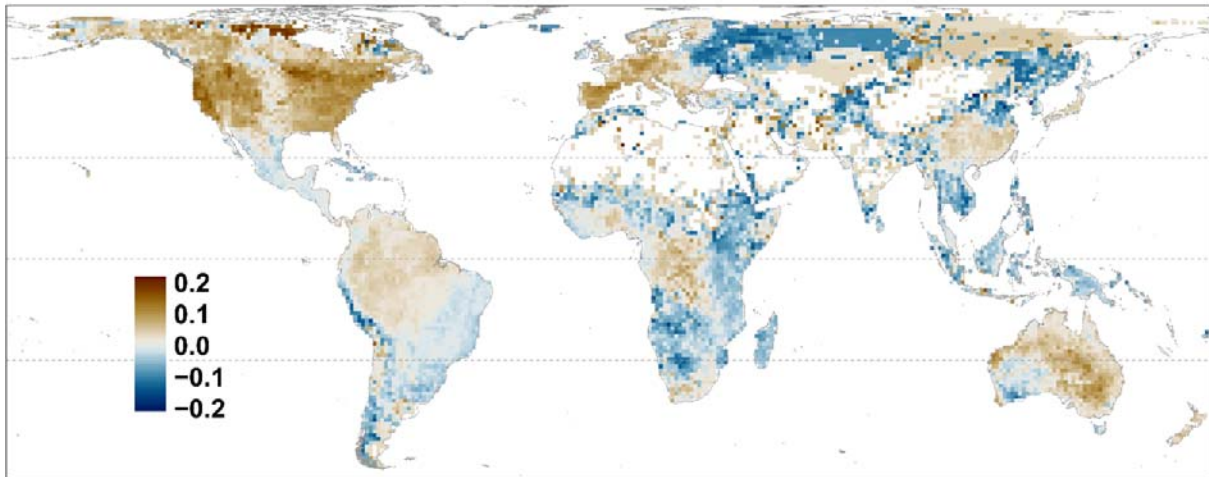
865 **Fig. 1** Global patterns of tree (a) species richness, (c) functional diversity, and (e) phylogenetic diversity. In

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.

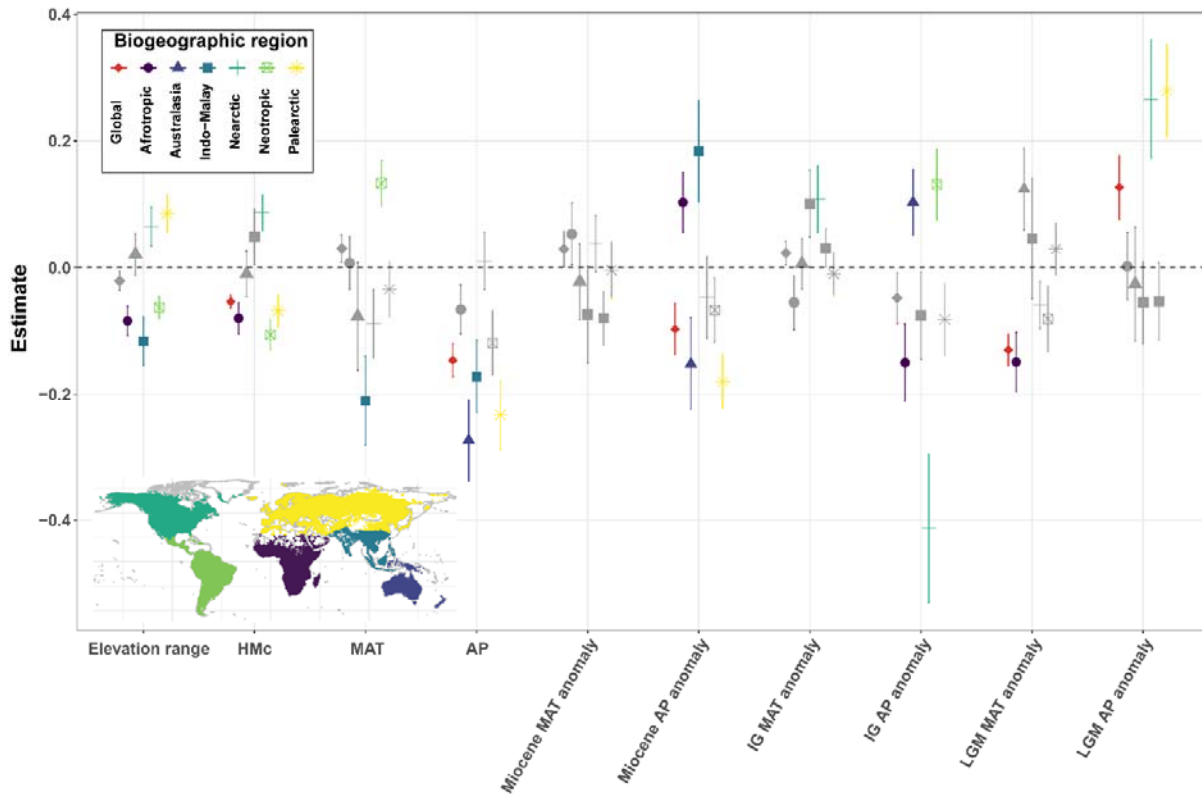


868 **Fig. 2** Effects of the tested environmental variables on tree (a) specie richness (SR), (b) functional diversity
869 (FD) and (c) phylogenetic diversity (PD). Estimates (± 1 standard error) of effects were obtained from
870 simultaneous autoregressive (SAR) models. Different colors and shapes 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.



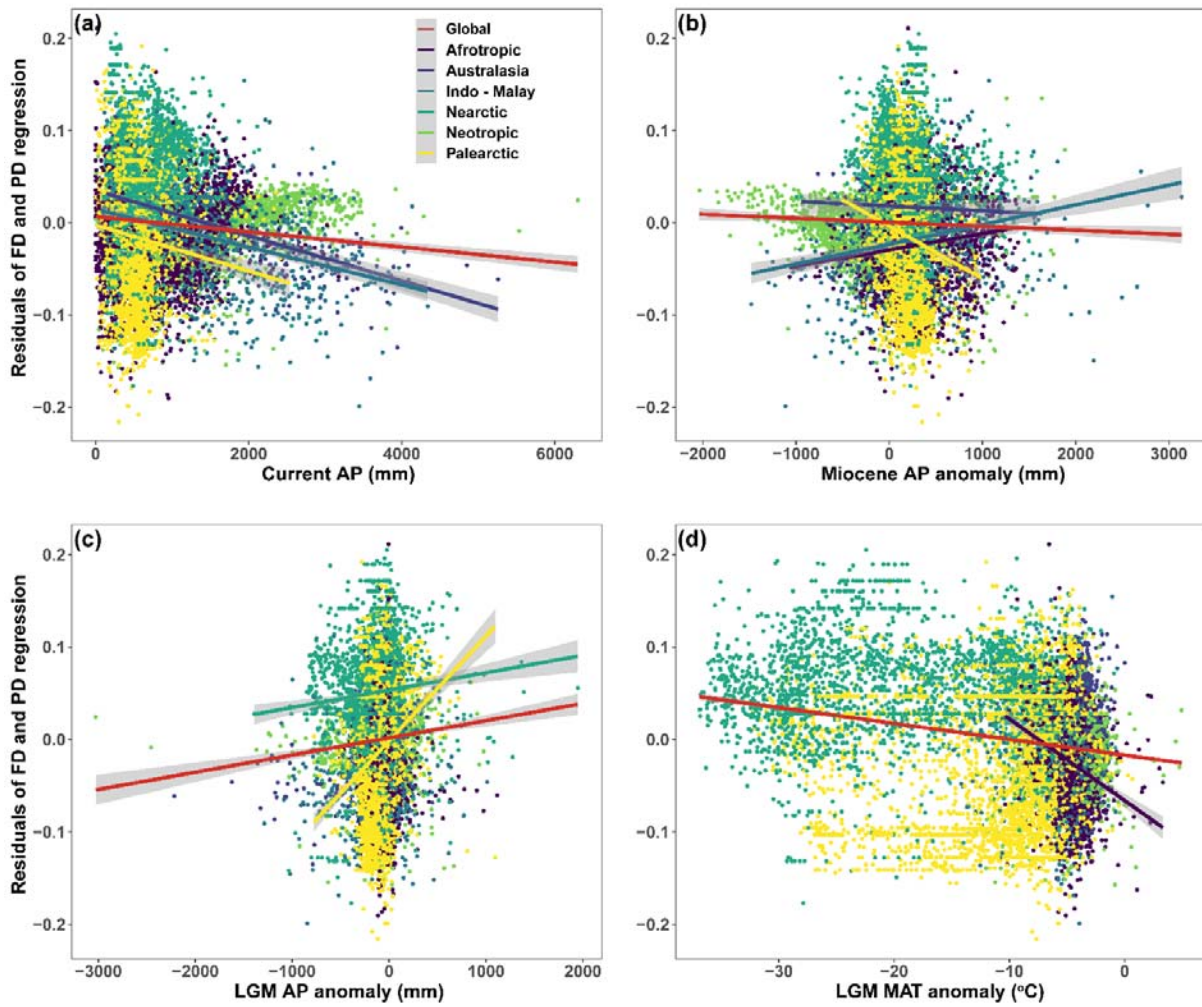
874

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 Behrman 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 (± 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, $p < 0.05$).