

# 1 **Global decoupling of functional and phylogenetic diversity in plant** 2 **communities**

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148 **Abstract**

149 Plant communities are composed of species that differ both in functional traits and  
150 evolutionary histories. Understanding how species' traits and histories interact with the  
151 environmental conditions of a site and drive the assembly of ecological communities is the  
152 basis for predicting the impacts of climate change on biodiversity and ecosystem functioning.  
153 As species' functional traits partly result from their individual evolutionary history, the  
154 functional diversity (FD) of communities is expected, on average, to covary positively with  
155 their phylogenetic diversity (PD). However, this expectation has only been tested at local  
156 scales, for specific growth forms or specific habitat types, e.g. grasslands. Here, we compared  
157 the standardized effect sizes of FD and PD for 1,781,836 vegetation plots using the global  
158 sPlot database. In contrast to our expectations, the correlation between FD and PD was weak,  
159 not positive but negative, and these two facets of diversity were more often decoupled than  
160 coupled. While PD reflected recent climatic conditions and vegetation type, being higher in  
161 forests, FD depended on recent (1981-2010) and past climatic conditions (21,000 years ago).  
162 The independent nature of functional and phylogenetic diversity makes it crucial to consider  
163 both aspects of diversity when analyzing ecosystem functioning or prioritizing conservation  
164 efforts.

165 **Introduction**

166 Climate change and biodiversity loss are two of the most pressing environmental issues of our  
167 time, with rising temperatures and shifting precipitation patterns increasingly becoming one  
168 of the main drivers of the extinction of many plant species<sup>1</sup>. These changes have significant  
169 implications for ecosystems and human societies alike, with impacts ranging from altered  
170 agricultural yields to increased risk of natural disasters<sup>2,3</sup>. To understand and mitigate the  
171 effects of climate change and biodiversity loss, it is crucial to determine how plant species are  
172 assembled into communities and how these communities respond to changing environmental  
173 and climatic conditions<sup>4,5</sup>. This means that we need to understand the underlying mechanisms  
174 of plant community assembly, and how these mechanisms are mediated by the interactions  
175 between species' functional traits, evolutionary histories and environmental conditions<sup>6</sup>.

176 Community assembly is the net result of several processes that partially reinforce or oppose  
177 each other<sup>7</sup>. On the one hand, environmental filtering may result in a phenotypic clustering

178 of traits in a community<sup>8,9</sup>. On the other hand, biotic interactions, and in particular  
179 competitive exclusion, may limit the similarity of the phenotypes in a community, since  
180 species can more readily coexist when they have different traits, and result in trait  
181 divergence<sup>10,11</sup>. The attribution of convergence or divergence to specific mechanisms is not  
182 clearcut, however, ~~since~~ convergence could also be caused by the competitive exclusion of  
183 species whose traits are associated with low competitive abilities<sup>7</sup>, and divergence might stem  
184 from habitat filtering in case of correlated traits under different environmental controls<sup>12</sup>, or  
185 ~~In addition, trait divergence can arise~~ from interacting environmental factors that select the  
186 resident species in a community<sup>13</sup>. Whatever the underlying mechanism, species functional  
187 traits clearly play a big role in community assembly, while also being the result of the  
188 evolution of a species in its environment. In other words, functional traits are subject to  
189 selection and are often conserved within phylogenetic lineages. This means that species that  
190 are closely related on the evolutionary tree are more likely to share similar traits compared  
191 to species that are less closely related. Depending on the velocity of evolution, specific traits  
192 can be more or less conserved on the phylogenetic tree<sup>14,15</sup>. Different indices based on  
193 Brownian motion models of evolutionary model trait evolution (e.g. Blomberg's  $K$  and Pagel's  
194  $\lambda$ <sup>16,17</sup>) exist to test whether a trait is phylogenetically conserved, which are based on the  
195 correlation between the species distances in trait values and their distances in the  
196 phylogeny<sup>6,18,19</sup>.

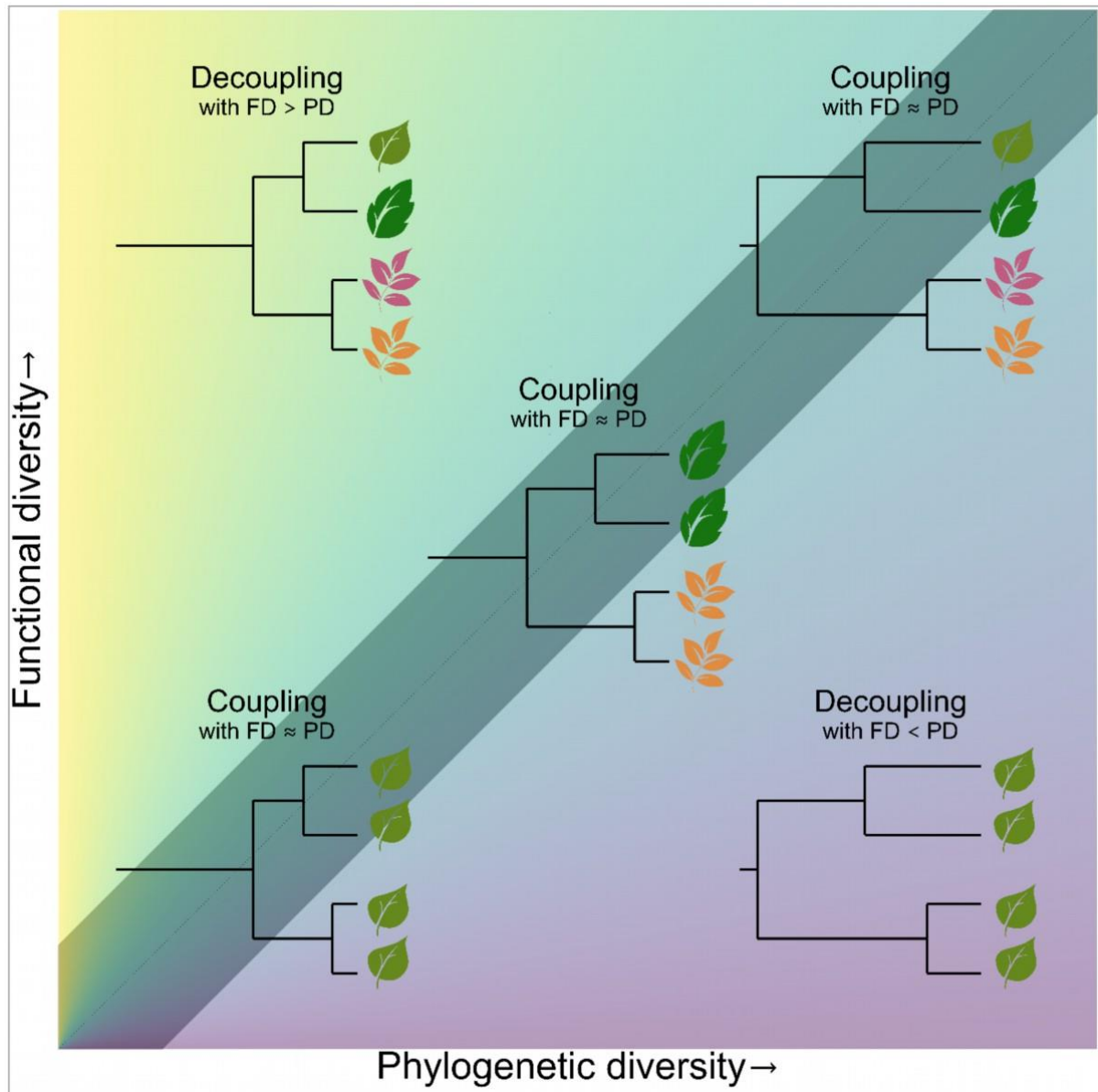
197 If species in a community share similar traits, the community is said to show phenotypic  
198 clustering, which is equivalent to having a low functional diversity (FD). Phenotypic clustering  
199 can be associated with two patterns, either a combination of phylogenetic clustering with  
200 trait conservatism (*Fig. 1*, bottom left) or a combination of phylogenetic dispersion with trait  
201 convergence (*Fig. 1*, bottom right)<sup>6,14,20</sup>. In the former case, there is a positive covariation  
202 between phylogenetic and functional distances, which is why we call the resulting  
203 communities coupled. In the latter case, the phylogenetic and functional distances are  
204 inversely related, and thus, we call the resulting communities decoupled.

205 In contrast, if species in a community have dissimilar traits, the community has a high  
206 phenotypic variation, which is equivalent to a high FD. High FD can either happen in  
207 combination with high phylogenetic variation (*Fig. 1*, top right) or phylogenetic clustering (*Fig.*  
208 *1*, top left). Again, in the former case phylogenetic and functional diversities are coupled,

209 while they are inversely related, and therefore decoupled, in the latter case<sup>20,21</sup>. Many local  
210 studies found a prevalence of coupled communities with positive covariation of functional  
211 and phylogenetic diversity (FD, PD)<sup>22–24</sup>, but negative covariations<sup>25,26</sup> and unclear patterns  
212 have also been encountered<sup>27</sup>. However, it is not yet known under which conditions  
213 communities express coupled or decoupled functional and phylogenetic diversities.

214 By calculating functional and phylogenetic diversity for 1,781,836 vegetation plots from  
215 sPlot<sup>28</sup>, the global vegetation plot database, we tested whether patterns of coupling or  
216 decoupling 1) dominate at the global level, 2) have regional patterns, 3) differ between forest  
217 and non-forest ecosystems, and 4) correlate with current and past climatic gradients. We  
218 hypothesized an overall coupled pattern of functional and phylogenetic diversity, since  
219 phylogenetic diversity has often been found to reflect functional trait diversity, especially for  
220 those phylogenetically conserved traits which are not easily measurable in plants, such as  
221 herbivore and pathogen resistance<sup>14,19,29</sup>. We expected higher phylogenetic diversity in  
222 forests than in non-forest ecosystems due to the co-occurrence of woody and non-woody  
223 plant species, given that the herbaceous habit has evolved from the ancestral woody state  
224 multiple times and in different lineages<sup>30–33</sup>. Since phylogenetic and functional diversity  
225 metrics are correlated with species richness, we used null models to calculate standardized  
226 effect sizes and quantify how much phylogenetic and functional diversity differed from  
227 random expectations, before comparing them<sup>34</sup>.





228

229 *Figure 1: Conceptual figure of the relationship between functional and phylogenetic diversity*  
 230 *after Ref. 19 & 20. If functional diversity is proportional to community phylogenetic diversity,*  
 231 *we consider the community to be coupled (diagonal). The extremes are the results either of*  
 232 *phylogenetic clustering in combination with trait convergence (bottom left) or phylogenetic*  
 233 *overdispersion in combination with trait divergence (top right). Decoupled communities can*  
 234 *be either observed if a community shows phylogenetic overdispersion in combination with*  
 235 *trait convergence (bottom right) or if it shows phylogenetic clustering with trait divergence*  
 236 *(top left).*

237

## 238 Results

### 239 The relationship of functional and phylogenetic diversity

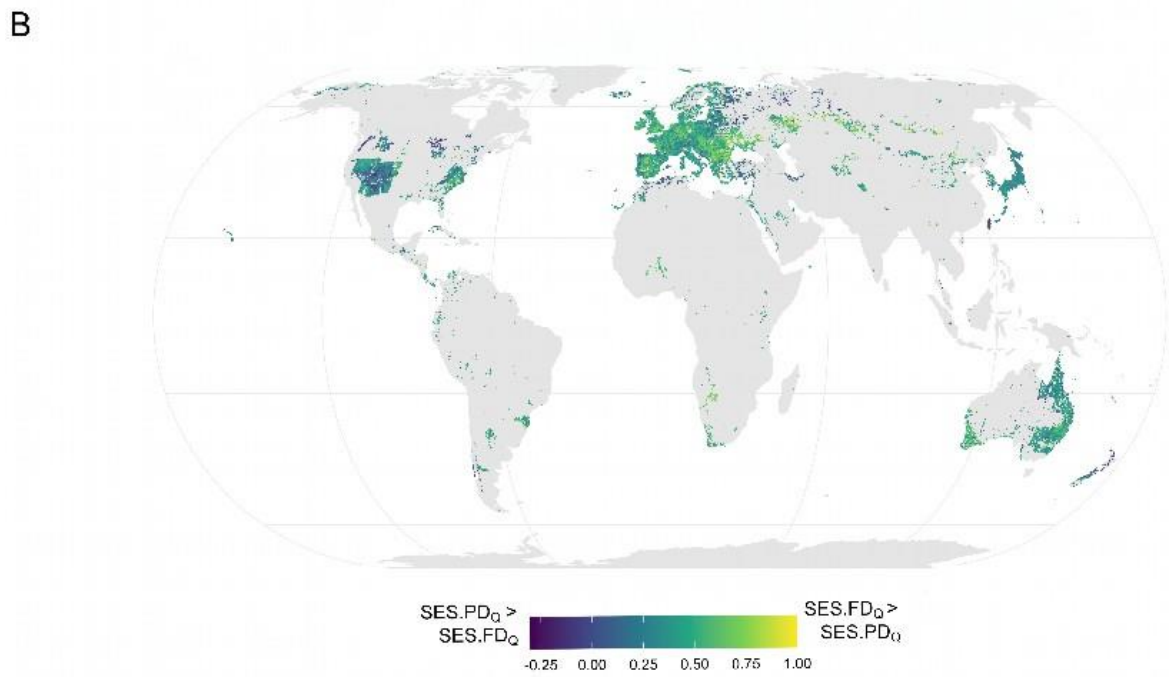
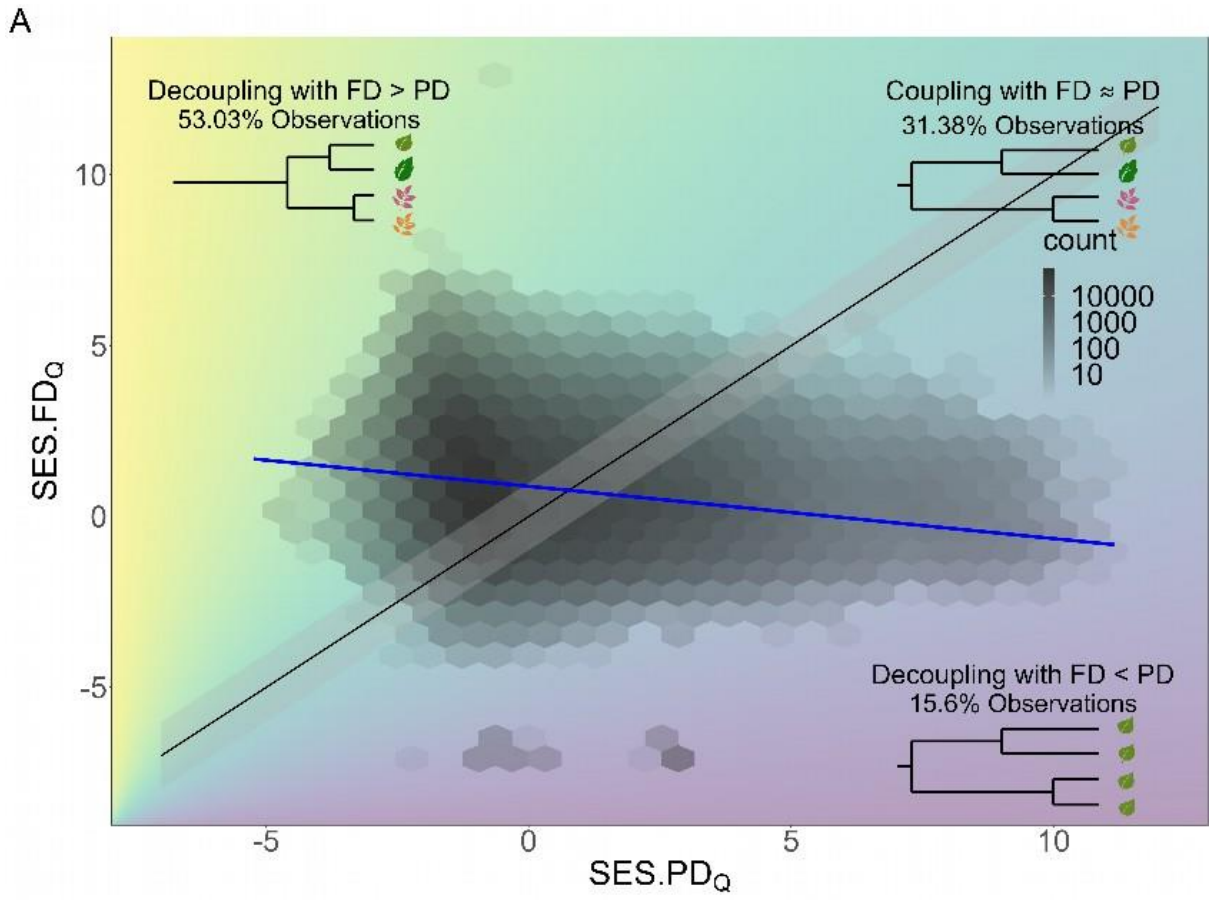
240 We modelled the relationship between functional and phylogenetic diversity indices  
241 expressed as a standardized effect size of Rao's quadratic entropy based on functional traits  
242 (SES.FD<sub>Q</sub>) and phylogenetic distances (SES.PD<sub>Q</sub>), when considering three selected functional  
243 traits representative of the main dimensions of the global spectrum of plant form and  
244 function, namely the leaf economics spectrum (specific leaf area), the size-seed mass  
245 dimension (plant height), and the root collaboration gradient (specific root length)<sup>35,36</sup>. Both  
246 indices were calculated using Rao's quadratic entropy and transformed to standardized effect  
247 sizes, based on biome-specific null models that account for the uneven species richness across  
248 plots, and use the relative frequencies of species occurrences within each biome to weight  
249 species resampling probabilities. We did this because both functional and phylogenetic  
250 diversity are tightly related to species richness. Out of 1,781,836 vegetation plots, 31.38%  
251 showed trait and phylogenetic coupling as SES.FD<sub>Q</sub> and SES.PD<sub>Q</sub> were equally high or low.  
252 53.03% of the vegetation plots had higher SES.FD<sub>Q</sub> than SES.PD<sub>Q</sub> and 15.6% had higher  
253 SES.PD<sub>Q</sub> than SES.FD<sub>Q</sub>, suggesting that decoupled plant communities are twice as common  
254 than coupled ones and that, on average, global communities are more functionally than  
255 phylogenetically diverse (*Fig. 2A*). These results did not change after removing non-significant  
256 standardized effect values, i.e. values between -1.96 and 1.96 (6.9% coupled communities,  
257 45.8% decoupled with high FD values and 17.3% decoupled with high PD values).

258 We did not find any clear geographical pattern at the global scale (*Fig. 2B*). Decoupled  
259 communities with high SES.FD<sub>Q</sub> and low SES.PD<sub>Q</sub>, (see Methods for definition of high and low  
260 values of SES.FD<sub>Q</sub> and SES.PD<sub>Q</sub>) occurred in the western USA and locally across Europe, while  
261 communities with low SES.FD<sub>Q</sub> and high SES.PD<sub>Q</sub> were found close to the Arctic circle in  
262 Scandinavia and Siberia, and in New-Zealand and Japan. Coupled communities with high  
263 values of both diversity indices were encountered in the eastern USA, Central-Europe as well  
264 as in New-Zealand and Japan.

265 Overall, we found a negative relationship between SES.FD<sub>Q</sub> and SES.PD<sub>Q</sub>. Accounting for the  
266 spatial structure of the data by adding a smoothing spline, our general additive model  
267 explained 7.8% of the deviance in SES.FD<sub>Q</sub> (*Fig. 2A*). Modelling the raw values of FD<sub>Q</sub> against

268 the raw values of  $PD_Q$ , i.e., not accounting for the effect of species richness, also returned a  
269 negative relationship with 18.5% of deviance explained (*Fig. S 1 A*). The explained deviance  
270 increased to 36.2% when the distance matrix of phylogenetic distances was square root-  
271 transformed, accounting for the non-linearity of trait evolution (*Fig. S 1 B*).

272 The negative relationship between  $SES.FD_Q$  and  $SES.PD_Q$  was robust to the use of alternative  
273 null models, diversity indices, selections of functional traits and subsets of vegetation plot  
274 data (see Methods for details). Using a null model based on a global species pool,  $SES.PD_Q$   
275 together with the spatial smoothing spline explained 5.8% of the deviance in  $SES.FD_Q$ , which  
276 increased to 6.2% when the phylogenetic distances were square root-transformed (*Fig. S 1 C*,  
277 *D*). Based on ~~a~~ biome-specific, but unweighted species pool, the explained deviance was 6.8%  
278 (*Fig. S 1 F*). When null models were constrained based on a ~~and for a~~ phylogeographic<sup>37</sup>  
279 species pool the explained deviance was 7.8% (*Fig. S 1 G*). The same negative relationship was  
280 found when using alternative indices of functional and phylogenetic diversity, i.e., when  
281 modelling standardized effect size of functional dispersion against mean pairwise distance  
282 (MPD). The explained deviance in this case was 7.1% (*Fig. S 1 E*). Considering each trait  
283 individually, or including additional traits (eight) but only for an environmentally-balanced  
284 subset of vegetation plot data (i.e., sPlotOpen<sup>38</sup>), also returned a negative relationships  
285 between  $FD_Q$  and  $PD_Q$  (*Fig. S ~~87~~, Table S 1*).



289 *Figure 2: The relationship of standardized effect size of quadratic functional (SES.FD<sub>Q</sub>) and*  
290 *phylogenetic diversity (SES.PD<sub>Q</sub>). SES.FD<sub>Q</sub> is based on three functional traits: specific leaf area,*  
291 *plant height and specific root length. A SES.FD<sub>Q</sub> as a function of SES.PD<sub>Q</sub> with the linear*  
292 *regression slope (blue) after accounting for spatial autocorrelation with a general additive*  
293 *model (7.8% explained deviance). Additionally, the line of coupling with the 1:1 relationship*  
294 *(black) and the confidence interval (grey, see Methods). 31.38% observations are lying within*  
295 *the confidence interval. 53.03% and 15.6% of all observations show decoupling, with either FD*  
296 *> PD or FD < PD, respectively. B Mean log ratio of standardized effect sizes of functional*  
297 *(SES.FD<sub>Q</sub>) and phylogenetic diversity (SES.PD<sub>Q</sub>) per raster cell (863.8 km<sup>2</sup>). Negative values*  
298 *indicate higher observed SES.PD<sub>Q</sub> than SES.FD<sub>Q</sub> and vice versa. The extracted values from the*  
299 *spatial smoothing spline from the General Additive Model (GAM) can be found in Fig. S 2 D.*

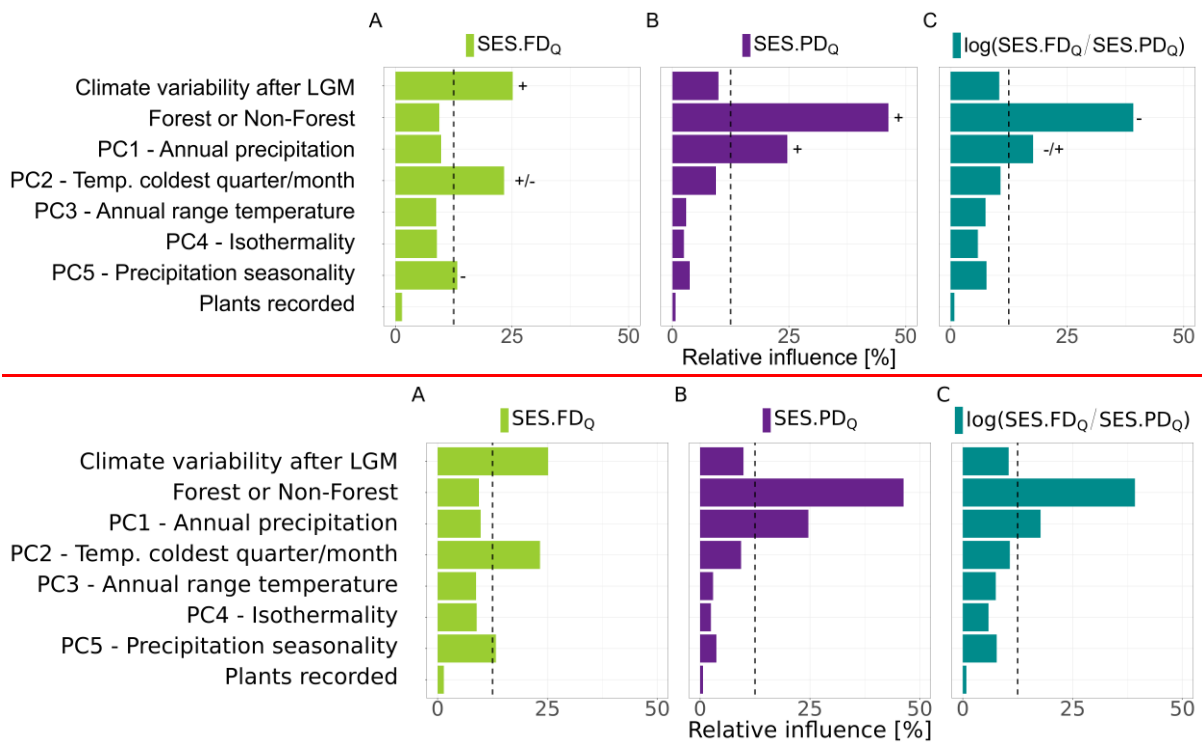
### 300 **The environmental drivers of functional and phylogenetic diversity**

301 We used Boosted Regression Trees (BRT) to select the environmental variables that best  
302 explain either SES.FD<sub>Q</sub> or SES.PD<sub>Q</sub>. The BRTs suggested climate variables to be most relevant  
303 for shaping patterns of SES.FD<sub>Q</sub> (Fig. 3 A). Temperature of the coldest quarter and coldest  
304 month (both reflected by PC2 in a principal component analysis based on 19 bioclimatic  
305 variables) had the highest relative influence on SES.FD<sub>Q</sub>, followed by the climate variability  
306 after the Last Glacial Maximum (LGM) and precipitation seasonality (PC5). Partial dependence  
307 plots suggested a predominantly positive relationship between SES.FD<sub>Q</sub> and climate variability  
308 after the LGM and a negative one with precipitation seasonality (PC5, Fig. S 3). SES.FD<sub>Q</sub> first  
309 increased and then decreased with increasing temperatures of the coldest quarter and  
310 coldest month (PC2).

311 Regarding phylogenetic diversity, SES.PD<sub>Q</sub> was especially related to the vegetation type  
312 (forest vs. non-forest, classified based on cover of the tree layer and species traits, such as  
313 growth form and height, see methods), being higher in forest compared to non-forest  
314 ecosystems, and tend to increase with annual precipitation (PC1; Fig. 3 A, Fig. S 4).

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*Figure 3: Results of the Boosted Regression Trees for **A** SES.FD<sub>Q</sub>, **B** SES.PD<sub>Q</sub> and **C** the relationship of both expressed as the logarithm of the ratio quotient between of SES.FD<sub>Q</sub> and SES.PD<sub>Q</sub>. An explanatory variable was considered relevant in the model when its relative influence was greater than 12.5%, indicated by the dashed line, which is the expected influence of a variable if all eight predictors had the same relative importance. The signs indicate the direction of the significant effects arisen from the partial dependence models (Fig. S 3 – 5).*

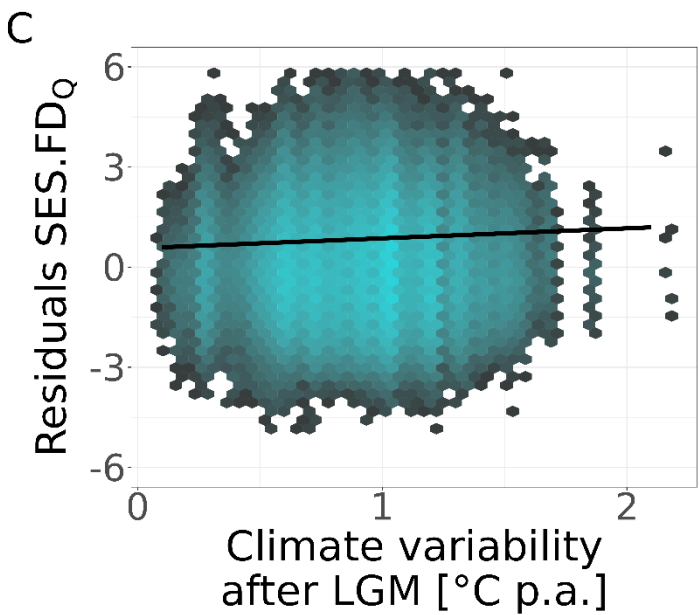
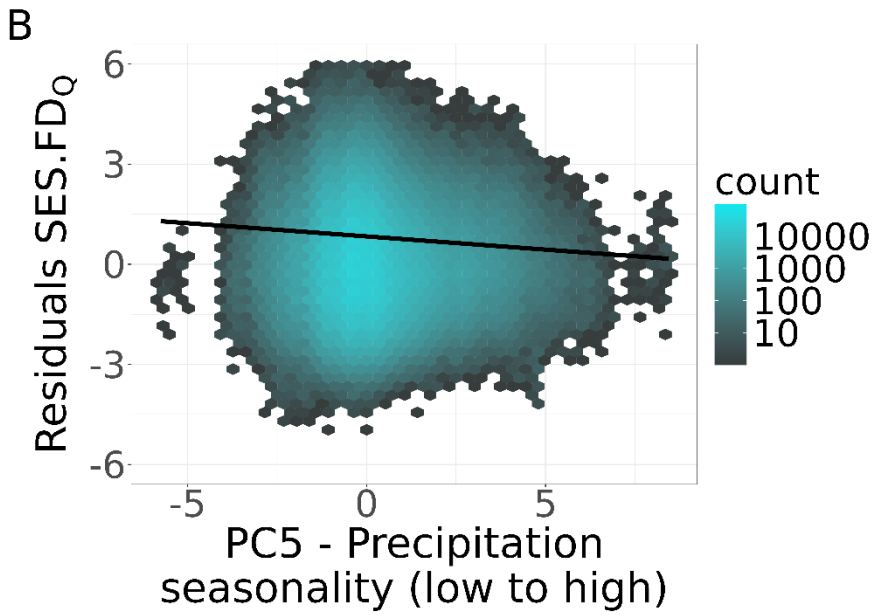
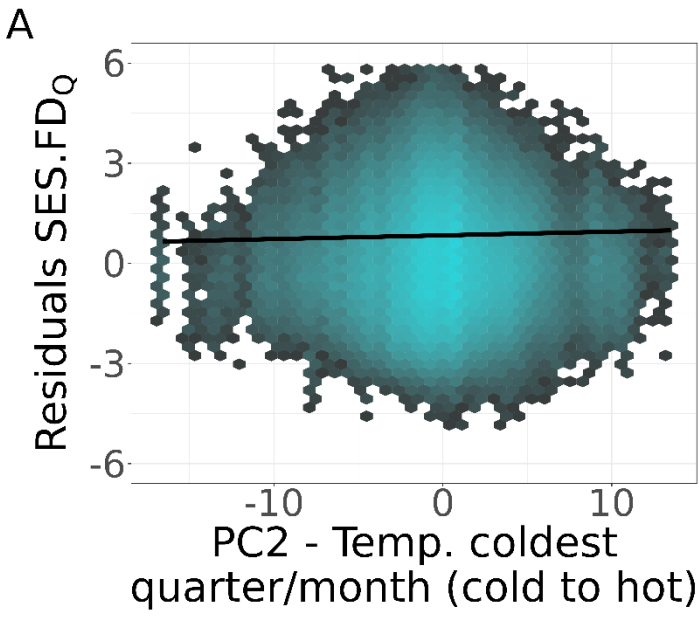
When modelling the log ratio of SES.FD<sub>Q</sub> and SES.PD<sub>Q</sub>, as log(SES.FD<sub>Q</sub>/SES.PD<sub>Q</sub>), the BRTs showed that the classification of forest or non-forest and annual precipitation (PC1) were the variables with the highest relevant influence, which was mostly equivalent to what observed for SES.PD<sub>Q</sub> (Fig. 3 B, S 5).

Only those variables with relative influence greater than 12.5%, which is the percentage of relative influence by chance (100% divided by eight explanatory variables) in the BRTs were used as predictors in the general additive models (GAM) with SES.FD<sub>Q</sub> or SES.PD<sub>Q</sub> as response variables and accounting for spatial autocorrelation. The model for SES.FD<sub>Q</sub> explained 4.6% of the deviance and suggested a positive relationship with climate variability after the LGM and temperature of the coldest quarter and month (PC2, Fig. 4). A negative relationship was shown for precipitation seasonality (PC5).

Annual precipitation (PC1), vegetation type and the spatial smoothing spline explained 37.3% of the deviance of the SES.PD<sub>Q</sub> model. SES.PD<sub>Q</sub> increased with increasing precipitation and

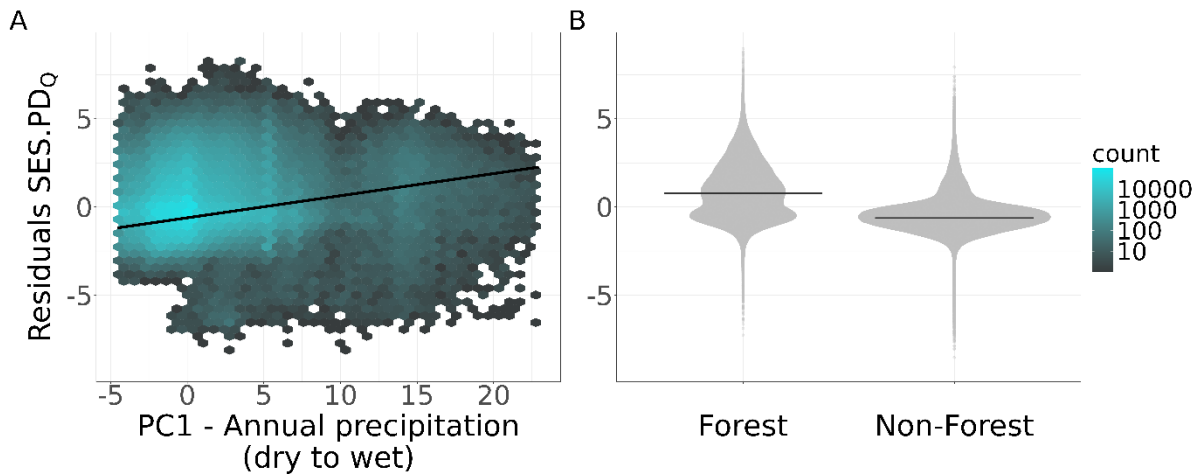
337 was higher in forests than in non-forest ecosystems (*Fig. 5*). The model of the log ~~relationship~~  
338 ratio between SES.FD<sub>Q</sub> and SES.PD<sub>Q</sub> reflected the results of SES.PD<sub>Q</sub> with an explained  
339 deviance of 30.8% (*Fig. 6*).

340 In order to explore the effect of environmental predictors on the general patterns of coupling  
341 and decoupling we modelled the relationship between SES.FD<sub>Q</sub> and SES.PD<sub>Q</sub> as an ordered  
342 categorical variable with three states, to acknowledge that while there is only one way for  
343 communities to be coupled, decoupling can come in two ways: decoupling with PD > FD, or  
344 decoupling with FD > PD. When doing so the explained deviance was 10.2% (*Fig. S 6*) with  
345 annual precipitation (PC1), precipitation seasonality (PC5) and forest or non-forest as the  
346 variables with the highest power to discriminate the three categories.

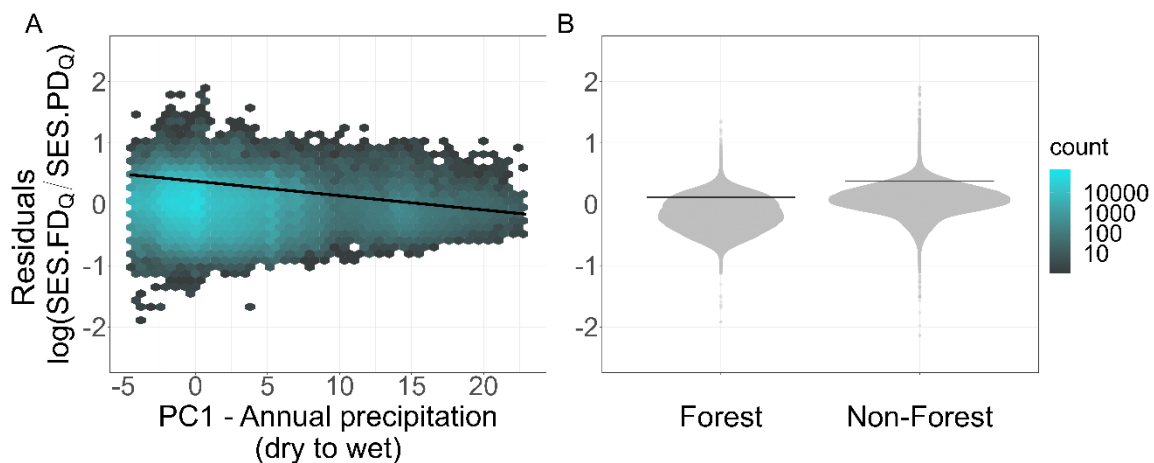




348 Figure 4: Drivers of the standardized effect size of functional diversity ( $SES.FD_Q$ ). Residuals of  
 349  $SES.FD_Q$  as a function of **A** temperature of the coldest quarter and month (PC2), **B** precipitation  
 350 seasonality (PC5), and **C** climate variability after the last glacial maximum. The general  
 351 additive model (GAM) explained 4.6% of the deviance. The solid line shows the regression  
 352 obtained from the GAM. The density hexagons show the distribution of the residuals of the  
 353 model without the explanatory variable of interest. The smooth term of  $SES.FD_Q$  can be found  
 354 in Fig. S [76 A](#).  
 355



356  
 357 Figure 5: Drivers of standardized effect size of phylogenetic diversity ( $SES.PD_Q$ ). Residuals of  
 358  $SES.PD_Q$  as a function of **A** PC1 - annual precipitation, and **B** vegetation type. The general  
 359 additive model (GAM) explained 37.3% of the deviance. The solid line shows the regression  
 360 obtained from the GAM. The density hexagons show the distribution of the residuals of the  
 361 model without the explanatory variable of interest. The smooth term of  $SES.PD_Q$  can be found  
 362 in Fig. S- [76 B](#).



363  
 364 Figure 6: Drivers of the relationship-log ratio between the standardized effect size of functional  
 365 diversity ( $SES.FD_Q$ ) and phylogenetic diversity ( $SES.PD_Q$ ). Residuals of  $\log(SES.FD_Q/SES.PD_Q)$  as  
 366 a function of **A** PC1 - annual precipitation, and **B** vegetation type based on the dominant  
 367 species. The general additive model (GAM) explained 30.8% of the deviance. The solid line  
 368 shows the regression obtained from the GAM. The density hexagons show the distribution of  
 369 the residuals of the model without the explanatory variable of interest. The smooth term of  
 370  $\log(SES.FD_Q/SES.PD_Q)$  can be found in Fig. S- [76 C](#).

## 371 Discussion

372 Plant communities differ in their functional and phylogenetic composition. Here, we modelled  
373 the relationship between functional and phylogenetic diversity in plant communities across  
374 the globe and made inferences about the drivers of these diversity facets. We showed that  
375 values of functional and phylogenetic diversity tend to be decoupled, suggesting global  
376 patterns of community assembly are primarily driven by either functional or phylogenetic  
377 diversity, less acting together. Functional diversity (FD) was driven by both recent climate  
378 conditions, as well as by past climatic events. In line with our initial hypothesis, we found high  
379 phylogenetic diversity (PD) in forest communities. The log ratio of FD and PD varied as a  
380 function of vegetation type (forest vs. non-forest), and of recent climate conditions, in line  
381 with what observed for PD.

382 Contrary to our hypothesis, we found a negative but weak relationship between FD and PD at  
383 the global scale (Fig. 2 A). As PD is often considered to be a proxy for capturing unmeasured  
384 patterns of species functional traits, we did expect a positive relationship between FD and  
385 PD<sup>39</sup>, as postulated also by theoretical studies<sup>24</sup>. The negative correlation observed at the  
386 global scale shows that functional and phylogenetic diversity are more often decoupled than  
387 coupled in plant communities, with communities either having high phylogenetic or  
388 functional diversity, which is in line with recent results in grassland communities<sup>25</sup>.  
389 Additionally, distribution of traits across phylogenies can vary at small spatial scales, including  
390 both trait clustering and overdispersion<sup>14,19</sup>. This indicates that, contrary to the expected ~~from~~  
391 ~~the~~ coupling of FD and PD, closely related species exhibit greater differences in their trait  
392 values, while phylogenetically distant species tend to share more similar trait values than  
393 expected by chance. It is possible that co-occurring species with similar traits differ in other,  
394 not easily measurable traits, e.g., herbivory resistance, which are captured by phylogeny but  
395 less so by functional traits. ~~Vice versa, phylogenetically close species tend to vary in their~~  
396 ~~functional traits. This f~~unctional clustering could be due to equalizing competitive dynamics  
397 in neutrally assembled communities<sup>40</sup> or because of broader-scale environmental filters.  
398 Additionally, when considering lineages' biogeographic histories, phylogenetic clustering  
399 could arise due to recent stochastic extinctions or limited dispersal following allopatric  
400 speciation<sup>41</sup>.

401 The negative covariation between PD and FD might primarily be explained by ~~the~~ different  
402 impacts of ~~biotic interactions~~ ~~competitive exclusion~~ and environmental filtering across  
403 communities<sup>40,42,43</sup>. In phylogenetically ~~closely related~~ clustered communities, competitive  
404 exclusion seems to be the main acting mechanism, resulting in the co-existence of species  
405 with dissimilar phenotypes and thus, higher FD. In contrast, environmental filtering seems to  
406 be the driving process in communities with low FD and high PD. Here, only species with  
407 specific phenotypes would be admitted to the community<sup>44</sup>, which however might come from  
408 different clades, thus, exhibiting functional convergence but phylogenetic variation. This  
409 pattern also suggests that ~~these~~ species would differ in features not captured by the traits  
410 we used for ~~included in~~ calculating FD<sup>45</sup>. Since most communities showed decoupling with  
411 high FD (53%), competitive exclusion seems to be the strongest driver for global plant  
412 community assembly processes. However, we have to consider that trait divergence can also  
413 arise from interacting environmental factors that filter the species in a community, ~~in~~  
414 ~~particular when these factors interact~~<sup>13</sup>. In communities with intermediate values of PD,  
415 environmental filtering and competitive exclusion seem to be equally important, thus  
416 resulting in coupled communities. However, the relative importance of such mechanisms is  
417 almost impossible to test as we do not know if species are excluded from a given community  
418 due to the environmental conditions, biotic interactions, dispersal limitation, or by the  
419 interaction between multiple factors<sup>13,46</sup>. This results in FD and PD are ~~may~~ more often  
420 ~~become~~ decoupled in communities where geographical, and ~~or~~ local drivers differentially  
421 interact with factors of biotic interactions affecting functional and phylogenetic relationships  
422 among co-occurring species.

423 We found no clear spatial patterns of functional and phylogenetic diversity, as vegetation  
424 plots with coupled ing and decoupled ing of FD and PD were observed in geographical  
425 ~~proximity~~ ~~close plant communities~~, indicating that local-scale factors dominate community  
426 assembly are the drivers of diversity within specific regions (*Fig 2 B*). Previous studies have  
427 reported geographical patterns of functional diversity based on climatic conditions, such as  
428 precipitation gradients<sup>47</sup>. Similarly, phylogenetic diversity can differ along latitudinal  
429 gradients, decreasing polewards<sup>48,49</sup>. Studies on the global distribution of PD showed striking  
430 differences across that many different ecoregions or biomes ~~are able to exhibit high values of~~  
431 phylogenetic diversity<sup>50,51</sup>. This leads to regional diversity patterns which do not translate into

432 global patterns, as the broader scale environmental conditions are unable to reflect local  
433 geographical ecological conditions—conditions are likely to be blurred by broader  
434 environmental conditions at the global scale. However, considering the relationship between  
435 functional and phylogenetic diversity as a three-level categorical variable (“Decoupling with  
436 higher PD”, “Coupling”, “Decoupling with higher FD”) we were able to show that large-scale  
437 environmental factor do play a role (Fig. S 6). This suggests that even though we are not able  
438 to explain the full range of possible combinations of FD and PD, broader patterns can be  
439 explained.

440 We were able to reveal some tendencies between SES.FD<sub>Q</sub> and environmental conditions,  
441 but not to show that SES.FD<sub>Q</sub> is strongly driven by those conditions at the global scale (Fig. 4).  
442 In particular, functional diversity was not well explained by current climatic conditions and  
443 climate variability after the Last Glacial Maximum (LGM). This is in line with studies suggesting  
444 that the functional composition of local communities depends mostly on local factors, such  
445 as land use history, soil properties and microclimatic conditions<sup>23,52</sup>. However, —a fine  
446 classification of vegetation types, as it was done in a recent Europe-wide analysis on climate-  
447 trait relationship<sup>53</sup>, could have possibly increased the explanatory power of our model.

448 Phylogenetic diversity (SES.PD<sub>Q</sub>) was consistently higher in forests compared to non-forest  
449 ecosystems, which points to the complex evolutionary structure of the different layers of  
450 forest communities (Fig. 5). Forests are normally characterized by the presence of different  
451 structural layers, with woody and non-woody species occupying different layers.  
452 Interestingly, this stratification was connected to increased phylogenetic diversity but not to  
453 higher functional diversity. We interpret this pattern as the result of the evolutionary history  
454 of trees, which significantly differs from that of the understory vegetation. Many tree species  
455 belong to families that are mostly woody, meaning they are more phylogenetically distant to  
456 other plant families which contributes to the high phylogenetic diversity found in forest  
457 ecosystems<sup>30–32</sup>. This is particularly true for conifers, which represent a clade of woody  
458 species separating from today’s angiosperms as early as 300 Mya<sup>18</sup>, and now most commonly  
459 found in forests. Furthermore, ferns and lycophods, which are typical components of the herb  
460 layer in temperate forests and typically occur as epiphytes in tropical forests, represent very  
461 distinct evolutionary histories compared to trees, contributing to the increased phylogenetic  
462 diversitydistance between co-occurring species that we observed in forests<sup>54,55</sup>. This resulted

463 in higher PD in forests where those lineages were present. Additionally, more stable  
464 microclimatic conditions under a closed canopy could have led to more favorable conditions  
465 for different species across distinct families<sup>56,57</sup>. Overall, our findings suggest that while forest  
466 ecosystems display high PD, the functional diversity of plant species ~~within these~~  
467 ~~ecosystems in forests~~ may be ~~more~~-limited ~~by the due to~~ convergence in functional traits  
468 across different layers.

469 Our work represents a first contribution to understanding the relationship between  
470 functional and phylogenetic diversity at the global scale, but it does not come without  
471 limitations. Even if sPlot is the biggest, harmonized database of global vegetation plots, the  
472 coverage is uneven across Earth's biomes and vegetation types, which may bias our results.  
473 Yet, when using an environmentally balanced subset of the data, where data from the  
474 temperate zone are downsampled in favour of data from the tropics, we observed an even  
475 stronger negative relationship between FD and PD. This suggests that tropical plant  
476 communities contribute disproportionately to this pattern. Furthermore, the data contained  
477 in sPlot were collected using different sampling protocols and approaches, for instance  
478 focusing on woody species only or using plots of various shapes and sizes. While we partially  
479 overcome this problem by including predictors related to plot record characteristics (see  
480 methods) and by calculating standardized effect sizes, it remains unknown how these biases  
481 influence the correlation between FD and PD. As species abundance data is not well  
482 standardized in sPlot, the use of presence-absence data was the robust choice, which might  
483 limit the comparison to other studies on functional and phylogenetic diversity. Also, the  
484 selection of functional traits might influence the observed relationship between functional  
485 and phylogenetic diversity, especially given that we used only three traits to calculate FD. We  
486 note, however, that our results were robust to the selection of individual traits used, either  
487 individually or jointly, ~~used~~ when calculating FD, which did not ~~indicating that the specific~~  
488 ~~trait chosen to calculate FD did not significantly~~ impact the relationship between FD and PD  
489 (*Fig. S 78, Tab. S 1*). The polytomies included in the constructed phylogeny might lead to a  
490 possible underestimation of PD<sup>58</sup>, which we accounted for by calculating standardized effect  
491 size of PD. Additionally, we found the same negative pattern when we considered functional  
492 dispersion and mean pairwise distance (*Fig. S 1 E*) as proxy for FD and PD, where the latter is  
493 known to show different dispersion patterns than FD<sub>Q</sub><sup>59</sup>. However, when including PD as an

494 explanatory variable for future studies, it is important to consider the relationship between  
495 traits and phylogeny and the potential non-linearity of trait evolution. Additionally, our  
496 analysis revealed that none of the potential traits exhibited a strong phylogenetic signal in all  
497 families considered in this study (*Fig. S 7-8 B*). Moreover, it appeared that certain families  
498 tend to possess more conserved traits compared to others. This is in line with other findings  
499 that evolutionary conservation can be associated with specific traits and lineages<sup>37</sup>, but this  
500 is not a commonly observed pattern. Consequently, depending on the sampled community  
501 and plant species, different patterns may emerge in the relationship between FD and PD.  
502 While both plant characteristics and evolutionary history are playing a crucial role in  
503 community assembly processes the underlying interacting mechanisms of biotic and abiotic  
504 factors remain unclear.

505 Our findings on the relationship of SES.FD<sub>Q</sub> and SES.PD<sub>Q</sub>, imply that ecological communities  
506 can exhibit a wide range of combinations of functional and phylogenetic diversity. The general  
507 decoupling, even with negative correlation of FD and PD found in our study ~~imply~~implies a  
508 dominant signal of competitive exclusion in plant communities. This highlights that for an  
509 effective conservation of biodiversity we need to consider both functional and phylogenetic  
510 diversity, as both seems to drive community assembly and may reflect also the adaption  
511 possibilities of the community to climate changes. However, future research is needed,  
512 especially in areas where we were able to detect communities with both high FD and PD  
513 values, to understand which regional conditions leads to those diversity hotspots.- Achieving  
514 a better understanding of the diverse and context-dependent nature of FD and PD will help  
515 us ~~shed light to better understand on~~ and protect the intricate dynamics and complexities of  
516 ecological communities.

517

## 518 **Methods**

### 519 **Species community data**

520 The vegetation plot database sPlot<sup>28</sup> ([www.idiv.de/splot](http://www.idiv.de/splot)) is a harmonized collection of  
521 national- and regional-scale vegetation-plot datasets. sPlot provides geo-referenced  
522 information on the presence and abundance of all vascular plants co-occurring in a sampling  
523 area, i.e., vegetation plot. The database version sPlot 3.0 holds a total number of 1,977,637  
524 vegetation plot records from 160 datasets collected between 1873 and 2019, across six  
525 continents and most biomes, including 76,912 vascular plant species (for version 2.1, see ref.  
526 28). The size of a plot varies according to the type of vegetation being sampled; plot size  
527 ranged from 1 m<sup>2</sup> in grasslands to 250,000 m<sup>2</sup> in forest ecosystems. The vegetation type of a  
528 plot was classified as forest and non-forest based on tree layer cover and the growth form of  
529 dominant species<sup>28</sup>. Vegetation plot records were included in the study if the cumulative  
530 coverage of species for which both trait and phylogenetic information was available  
531 accounted for at least 50% of the relative vegetation cover in that plot (see below).

532 In addition, we used sPlotOpen<sup>38</sup>, which is an environmentally balanced, open-access subset  
533 of sPlot, as a benchmark of our results, both when testing for the effect of trait selection when  
534 calculating functional diversity, and for the effect of uneven coverage of sPlot data across the  
535 Earth`s biomes.

### 536 **Functional diversity**

537 Plant functional traits were available from the gap-filled version of the TRY 5.0 database<sup>60–63</sup>.  
538 We calculated functional diversity as Rao’s quadratic entropy (FD<sub>Q</sub>) as well as functional  
539 dispersion (FDis) for all vegetation plots in sPlot 3.0. The calculation of Rao’s quadratic  
540 entropy<sup>64</sup> is based on a Gower distance matrix calculated for the species present in each  
541 vegetation plot. FDis was computed from the uncorrected species-species distance matrix  
542 with the function *dbFD* from the R-package *FD*<sup>65,66</sup>. We based this calculation on three  
543 functional traits selected to cover most of the variation within plant traits and to represent  
544 different axes in the plant economic spectrum, i.e. belowground and resource strategy of  
545 acquisition or conservation (specific root length, specific leaf area) and reproduction strategy  
546 of quality or quantity (plant height)<sup>36,67</sup>. To evaluate the influence of trait selection on the

547 relationship of functional and phylogenetic diversity, we calculated  $FD_Q$  on eight functional  
548 traits (specific leaf area, specific root length, seed mass, plant height, leaf phosphorus and  
549 nitrogen content, leaf dry matter content, chromosome number), both taken individually and  
550 jointly. We did this additional analysis based on the sPlotOpen subset only, since calculating  
551 standardized effect sizes (see below) of FD calculated on eight traits in all plots was  
552 computationally unfeasible, even using our High Performance Cluster. —Additionally,  
553 considering all eight traits for the complete dataset would have led to a loss of approximately  
554 2000 species (~10% of species considered in this study, see below) due to missing data in the  
555 TRY database.

556 Functional traits can be conserved ~~ie~~ in the phylogeny. This was tested with two evolutionary  
557 models, i.e., Blomberg's  $K$  and Pagel's  $\lambda$ , where the latter is known to be more robust against  
558 incomplete resolved phylogenies or suboptimal branch lengths<sup>16,17</sup>. Pagel's  $\lambda$  and Blomberg's  
559  $K$  were calculated using the function *phylosig* from the R-package *picante*<sup>68</sup>. In contrast to  
560 other tests for phylogenetic signals both models can be used to compare phylogenetic signals  
561 across different phylogenies<sup>16</sup>, which needs to be done as a global plant phylogeny is simply  
562 too large for an appropriate calculation of phylogenetic signals. Therefore, the phylogenetic  
563 signal for each trait was calculated within each family. All eight functional traits showed either  
564 no or low phylogenetic signals for Pagel's  $\lambda$  and Blomberg's  $K$  (Fig. S ~~7~~8 B & C). Therefore, we  
565 assume that there is also no phylogenetic signal across angiosperms for the considered traits.

## 566 **Phylogenetic diversity**

567 For all species present in sPlot, a phylogenetic tree was built using the function *phylo.maker*  
568 from the R-package *V.PhyloMaker*<sup>69</sup>. The phylogenetic backbone of the package is the  
569 combination of GenBank taxa with a backbone provided by the Open Tree of Life, version 9.1  
570 (GBOTB), for seed plants<sup>70</sup> and the clade of pteridophytes<sup>71</sup>. Missing genera were inserted to  
571 the half point of the family tree. This approach was evaluated by ref. 72, who showed that  
572 phylogenetic indices based on the calculated tree were highly correlated with indices based  
573 on the "PhytoPhylo megaphylogeny" (updated phylogenetic tree from ref. 71). Species that  
574 could not be inserted by the *phylo.maker* were bound to the half of the terminal level of a  
575 sister species if only one species was available in this genus, or to the most recent ancestor



576 (MRCA) if the genus included more than one species. This additional binding was done with  
577 the *bind.node* function from the R-package *phytools*<sup>73</sup>.

578 The computed phylogenetic tree for sPlot contained 160 families with 68,052 of 76,912  
579 species (88%) present within the database. Additional 3,802 species were included, with  
580 3,348 being bound to the node of the most recent ancestor (MRCA) of already present sister  
581 species and 454 species to the half of the terminal level on the family node. The final  
582 phylogenetic tree contained 71,854 species on 32,395 nodes. A total of 31,727 species in the  
583 phylogeny also had traits in the TRY database. Of this subset, 322 species (approx. 1%) were  
584 bound to the half of the terminal level on the family node and 2766 (approx. 9%) to the MRCA.  
585 Vegetation plot records were only included in the analysis if both trait and phylogenetic  
586 information was available for at least 50% of the total relative cover of the species in that  
587 plot. In total, 1,781,836 out of 1,977,637 plot records remained.

588 Phylogenetic diversity was calculated as Rao's quadratic entropy ( $PD_Q$ ) which amounts to the  
589 mean nearest taxon distance for presence-absence data. We used the function *raoD* from the  
590 R-package *picante*<sup>68</sup>, which is based on the cophenetic distance of all  $n$  species in the  
591 phylogeny, pruned to contain only the species in that plot. To account for the non-linearity of  
592 evolutionary histories, we also calculated  $PD_Q$  based on the square root-transformed  
593 cophenetic distance<sup>74</sup>. Additionally we calculated mean pairwise distance (MPD), to be  
594 compared with functional dispersion, as MPD could show opposite dispersion patterns than  
595  $PD_Q$ <sup>59</sup>. Only species with both trait information and known phylogeny were used to calculate  
596 functional and phylogenetic diversity.

### 597 **Standardized effect size**

598 The species richness of the vegetation plot records ranged from one to 412 species (*Fig. S 89*).  
599 Functional and phylogenetic diversity indices are known to depend on species richness<sup>75-77</sup>.  
600 Especially for functional diversity, a higher number of species in a community is more likely  
601 to return higher functional diversity values than communities with fewer species<sup>76</sup>. We  
602 controlled for species richness by calculating the standardized effect size of each diversity  
603 index for every vegetation plot record<sup>78</sup>, fixing the number of species of the plot record and  
604 drawing species randomly, which is equivalent to shuffling traits across species. As species do  
605 not equally occur across the globe, we calculated our null expectations based on biome-

606 specific species pools accounting for the frequency of species in the plot records in each  
607 biome. However, to see if the patterns also hold true for broader species pools we used the  
608 following hierarchical approach with ~~three-four~~ stages of defined species pools. For the  
609 simplest species pool, we calculated our null expectations based on all species present in the  
610 whole sPlot database, so we allowed each species to occur everywhere in the world. For a  
611 more geographically constrained approach we calculated the null expectations based on  
612 species pools within 16 phytogeographical units<sup>37</sup> (stage 2) and ten predefined biomes (stage  
613 3) in response to global climate variation<sup>28,79</sup>, namely: alpine, boreal zone, dry mid-latitudes,  
614 dry tropics and subtropics, polar and subpolar zone, subtropics with winter rain, subtropics  
615 with year-round rain, temperate mid-latitudes, tropics with summer rain, and tropics with  
616 year-round rain. The ~~third-fourth~~ and most complex null model was based on the species pool  
617 within each biome, additionally sampling the species weighted by their frequency in the plot  
618 records within each biome. This means a species that occurred more frequently within a  
619 biome was randomly drawn more often to recalculate the null diversity index, compared to a  
620 species occurring less often. For each of the ~~three-four~~ null models, we calculated the mean  
621 and standard deviation of the distribution of null functional and phylogenetic indices across  
622 499 draws. Vegetation plots only containing one species or for which trait and phylogenetic  
623 information was not available were excluded from functional or phylogenetic diversity  
624 calculations. Standardized effect sizes (SES) were obtained by subtracting the mean index of  
625 the randomized data from the observed index and dividing the result by the standard  
626 deviation of the index of the randomized data.

## 627 **Definition of coupling and decoupling**

628 To measure the percentage of coupled and decoupled communities a confidence interval was  
629 defined. We randomly drew one million values from a uniform distribution, defined between  
630 the minimum and maximum of observed standardized effect sizes of Rao's quadratic entropy  
631 based on functional traits (SES.FD<sub>Q</sub>) as explanatory variable. We created a correlated response  
632 variable by adding an error from a normal distribution, obtained from the mean and the  
633 standard deviation of the observed SES.FD<sub>Q</sub>. We fitted a linear model and extracted the  
634 intercept and the confidence interval. Communities with an observed value of SES.FD<sub>Q</sub> were  
635 considered coupled if the standardized effect sizes of Rao's quadratic entropy based on  
636 phylogenetic distance (SES.PD<sub>Q</sub>) fell within this interval. Based on this, we defined three

637 categories of community patterns, i.e. “Decoupling with higher FD than PD”, “Coupling” and  
638 “Decoupling with lower FD than PD”. This variable was later used as an ordered categorical  
639 response.

640 Additionally, we calculated the log ratio between  $SES.FD_Q$  and  $SES.PD_Q$  as  
641  $\log(SES.FD_Q/SES.PD_Q)$  after scaling the values between 0.001 and 1. Positive and negative  
642 values define the deviation with higher and lower  $SES.FD_Q$  than  $SES.PD_Q$ , respectively, from a  
643 perfect coupled community.

## 644 **Explanatory variables**

645 Current climate conditions (1981-2010) were represented by the 19 bioclimatic variables  
646 from CHELSA v.2.1<sup>80,81</sup>. A principal component analysis (PCA) was performed to reduce data  
647 dimensionality. In the following analyses, we only used the first five PCA axes, collectively  
648 accounting for 92.3% of explained variation. We interpreted the axes based on the highest  
649 loadings of the corresponding climate variable as follows: annual precipitation for PC1; mean  
650 daily air temperature of the coldest quarter and mean daily minimum air temperature of the  
651 coldest month for PC2; annual air temperature range for PC3; isothermality for PC4; and  
652 precipitation seasonality for PC5 (*Tab. S 2, Fig. S 910*).

653 Mean air temperature variability after the Last Glacial Maximum (LGM) was derived from the  
654 open-access StableClim v1.1. dataset, containing estimates from 21,000 years ago at 2.5°  
655 spatial resolution<sup>82</sup>. Climate variability represents rapid global warming during the last  
656 deglaciation during the Bølling-Allerød transition<sup>83</sup> on land and sea. The mean temperature  
657 variability between 21,000 B.P. and 100 A.D. was used as indices for the climate variability  
658 after the LGM.

659 All climate variables were extracted for each plot with the *extract* function from the R-  
660 package *raster*<sup>84</sup>.

661 Not all vegetation plot records were complete in terms of the sampled functional groups.  
662 Records from tropical forest plots often contained either only tree data, or tree and shrub  
663 data. As the exclusion of those plots would have substantially reduced the spatial coverage of  
664 our model, we added the nominal predictor variable called ‘plants recorded’ to our models  
665 to partially control for this source of bias as in ref. 35. The variable ‘plants recorded’ has four

666 values: all vascular plants, only dominant species, all woody plants, only trees. Additionally,  
667 we used the vegetation type (forest vs. non-forest) from the vegetation plot database sPlot  
668 as predictor variable.

669 In total, we prepared eight explanatory variables, five related to the current climate  
670 conditions, one to past climate variability, and two to plot record characteristics.

## 671 **Statistical modelling**

672 A generalised additive model (GAM) was used to model the relationship between functional  
673 and phylogenetic diversity, either expressed as observed Rao's quadratic entropy (for  
674 phylogenetic diversity also after a square root transformation of the distance matrix), or as  
675 standardized effect size of Rao's quadratic entropy, functional dispersion and mean pairwise  
676 distance. A GAM is a generalised linear model in which the linear response can depend on  
677 unknown smooth functions of the explanatory variables. To account for the spatial structure  
678 of the data, the spatial coordinates were included as smooth spherical splines. All GAMs  
679 included a basis penalty smoother spline on the sphere ( $bs = "sos"$ ), applied to the geographic  
680 coordinates of every plot, thus taking spatial autocorrelation into account. The explanatory  
681 variable was included as linear predictors without any smooth function. The model was  
682 performed using the function *gam* from the R-package *mgcv*<sup>85-90</sup>, defined as following:

```
683 gam( SES.FDQ ~ SES.PDQ + s(Longitude, Latitude, bs = "sos"), family = "gaussian", method =  
684 "REML")
```

685 SES.FD<sub>Q</sub> is the standardized effect size of Rao's quadratic entropy based on the three selected  
686 functional plant traits and SES.PD<sub>Q</sub> is the standardized effect size of Rao's quadratic entropy  
687 based on the phylogenetic distances of species present in the community. This step was done  
688 for the complete dataset and for the sPlotOpen subset, for which we considered the eight  
689 traits, both -individually and jointly, for calculating standardized effect size of FD.

690 To model the relationship between either functional or phylogenetic diversity and the set of  
691 the eight explanatory variables described above, we used a two-step approach. In the first  
692 step, we used Boosted Regression Trees to select relevant explanatory variables and quantify  
693 their relative influence. In the second step, we fitted GAMs using functional, phylogenetic

694 diversity or their log ratio as response variables, and the predictors selected in the first step  
695 as explanatory variables. We did this because fitting a full GAM algorithm with all predictors  
696 would lead to convergence issues, due to the huge number of data points.

697 Boosted regression trees (BRTs) are a machine-learning technique used in regression and  
698 classification having few prior assumptions and being robust against overfitting and  
699 collinearity. They are known to uncover nonlinear relationships as well as interactions among  
700 predictors. The parameters of the BRT were set as follows: a tree complexity of five and a bag  
701 fraction of 0.5. The learning rate was set to 0.01 with a maximum number of 20,000 trees.  
702 The BRTs were calculated using the *gbm.step* routine from the *dismo* package<sup>91</sup>. An  
703 explanatory variable was considered relevant in the model if its relative influence was greater  
704 than 12.5%, which is the expected influence of a variable if all the eight predictors had an  
705 equal relative importance.

706 The variables that were considered as relevant from the BRTs were then used in a second set  
707 of GAMs, having as response variable either functional diversity (SES.FD<sub>Q</sub>), phylogenetic  
708 diversity (SES.PD<sub>Q</sub>) or their log ratio, and as explanatory variables those that turned out to be  
709 relevant in the corresponding BRT. Additionally, we fitted a GAM with the ordered categorical  
710 response of coupling and decoupling against the environmental predictors, which were  
711 selected by the BRTs for functional and phylogenetic diversity. As the three categories were  
712 not equally represented, we sampled 10,000 communities for each category and repeated  
713 the GAM 100 times, besides run the same model on the complete (unbalanced) dataset. The  
714 spatial coordinates were included as smooth spherical splines in ~~the-all~~ model as explained  
715 above. As not all vegetation plot entries in sPlot are classified as forest / non-forest the  
716 number of observations for the environmental models was 1,497,238.

717 The prediction of each explanatory variable was performed using the *prediction* function from  
718 the R-package *marginaleffects*<sup>92</sup> by predicting the explanatory variable based on the  
719 sequence between the minimum and maximum of the variable in the original data and the  
720 GAM model. The plotted regressions were obtained by extracting the residuals from a GAM  
721 without the explanatory variable of interest.

722 ~~For plotting, F~~functional and phylogenetic variables were averaged ~~plotted as mean~~ for each  
723 grid cell with a size of 863.8 km<sup>2</sup>. The spatial smoother within the GAM was plotted at the  
724 same resolution based on the following model (example based on SES.FD<sub>0</sub>):

725 `gam( SES.FD0 ~ 1 + s(Longitude, Latitude, bs = "sos"), family = "gaussian", method = "REML")`

726 All analyses were performed in R 4.1.3<sup>93</sup>.

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857 **Data availability**

858 The vegetation-plot raw data contained in the sPlot database are available upon request by  
859 submitting a project proposal to sPlot's Steering Committee. The proposals should follow the  
860 Governance and Data Property Rules of the sPlot Working Group available on the sPlot  
861 website ([www.idiv.de/splot](http://www.idiv.de/splot)).

862 **Code availability**

863 All R scripts used for this study can be found in our GitHub repository at  
864 <https://github.com/georghaehn/Haehn-et-al-2023-FD-PD-coupling>.

865

866 **Method references**

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