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## Evolutionary diversity is associated with wood productivity in Amazonian forests

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# 1 Evolutionary diversity is associated with wood productivity in Amazonian 2 forests

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80 Higher levels of taxonomic and evolutionary diversity are expected to maximize  
81 ecosystem function, yet their relative importance in driving variation in ecosystem  
82 function at large scales in diverse forests is unknown. Using 90 inventory plots  
83 across intact, lowland, *terra firme*, Amazonian forests and a new phylogeny including  
84 526 angiosperm genera, we investigated the association between taxonomic and  
85 evolutionary metrics of diversity and two key measures of ecosystem function -  
86 aboveground wood productivity and biomass storage. While taxonomic and  
87 phylogenetic diversity were not important predictors of variation in biomass, both  
88 emerge as independent predictors of wood productivity. Amazon forests that contain  
89 greater evolutionary diversity and a higher proportion of rare species have higher  
90 productivity. Whilst climatic and edaphic variables are together the strongest  
91 predictors of productivity, our results demonstrate that the evolutionary diversity of  
92 tree species in diverse forest stands also influences productivity. As our models  
93 accounted for wood density and tree size, they also suggest that additional,  
94 unstudied, evolutionarily correlated traits have significant effects on ecosystem  
95 function in tropical forests. Overall, our pan-Amazonian analysis shows that greater  
96 phylogenetic diversity translates into higher levels of ecosystem function: tropical  
97 forest communities with more distantly related taxa have greater wood productivity.

98 **Main text**

99 Higher levels of taxonomic and phylogenetic diversity play important and  
100 independent roles in determining ecosystem function<sup>1-3</sup>. In experimental studies of  
101 temperate grasslands, higher levels of taxonomic and evolutionary diversity are  
102 associated with greater biomass and productivity<sup>2-4</sup>. In particular, the structure of  
103 evolutionary diversity, measured by the variability in evolutionary history shared  
104 within a group of species, is often a better predictor of productivity than the number  
105 of species<sup>2-4</sup>, consistent with the hypothesis that evolutionary dissimilarity is related  
106 to niche complementarity<sup>1-5</sup>. However, although the results of a range of biodiversity  
107 experiments<sup>2-7</sup> suggest that communities with distantly related lineages have greater  
108 carbon stocks and productivity, the effect of phylogenetic diversity on measures of  
109 ecosystem function remains controversial. Positive relationships are common, but  
110 not a rule, and negligible effects of evolutionary diversity on productivity and biomass  
111 have been reported in some cases<sup>8,9</sup>. Therefore, it is still unclear whether these  
112 relationships can be generalised, and the extent to which evolutionarily diverse  
113 communities maximize function is unknown, particularly at large scales relevant to  
114 conservation planning.

115 The total amount of phylogenetic diversity represented by species within a  
116 community may be valuable for understanding how diversity affects ecosystem  
117 function because these properties tend to reflect variation in the functional diversity  
118 of these communities. This is because evolutionary relationships can capture  
119 information about multiple traits<sup>5,10-12</sup>, including those that are difficult to measure.  
120 For instance, in an experimental study of grassland communities, evolutionary  
121 diversity was a better predictor of productivity than some easily measured, or 'soft',  
122 functional traits (e.g. specific leaf area, seed weight and height), suggesting that

123 unmeasured traits that are significantly related to phylogenetic relationships, such as  
124 root architecture, root morphology, resource requirements or other critical functional  
125 differences, could contribute to maximizing productivity<sup>3</sup>. Evolutionary diversity  
126 metrics that encompass the full breadth of functional diversity may be more  
127 informative about how much species contribute to ecosystem function, particularly in  
128 hyperdiverse communities such as tropical forests where the links between soft  
129 traits, such as specific leaf area and wood density<sup>13,14</sup>, and ecosystem functions,  
130 such as productivity, are typically weak<sup>15</sup>.

131 The evolutionary diversity of a community can be measured in different ways to  
132 reflect distinct aspects of biodiversity<sup>11,16,17</sup>, and these metrics may all relate in  
133 different ways to variation in functional traits, life-history strategies, and, as a result  
134 ecosystem function<sup>2,3,5,18</sup>. Phylogenetic diversity (PD) is the sum of the total  
135 evolutionary history, or amount of the tree of life present in a given community and is  
136 quantified as the sum of the branch lengths, which are measured in units of time,  
137 from a phylogeny that represents all species in a given community (total lineage  
138 diversity)<sup>16</sup>. A second aspect of evolutionary diversity is the extent to which  
139 communities are dominated by closely related species (neighbour lineage diversity),  
140 which can be quantified by mean nearest taxon distance (MNTD)<sup>11,12</sup>. Finally,  
141 another dimension of the evolutionary history of a community is whether it contains a  
142 balanced proportion of the major lineages of organisms (basal lineage diversity)<sup>19,20</sup>,  
143 which can be represented by the mean phylogenetic distance (MPD) between all  
144 pairs of species<sup>11</sup>. MPD is strongly affected by branch lengths at the deepest nodes  
145 of the phylogeny and the relative abundance of major clades in the community<sup>20</sup>. All  
146 of these metrics attain higher values in communities comprised of more distantly  
147 related individuals.

148 Amazonian forests provide an ideal context for exploring the link between tree  
149 diversity and ecosystem functioning because these forests include some of the most  
150 species-rich ecosystems on earth<sup>21</sup> and contain a wide variety of angiosperm  
151 lineages<sup>20</sup>. They also play a key role in regulating planetary biogeochemical cycles,  
152 including fixing as much carbon annually as the human economy emits globally<sup>22</sup>,  
153 and storing an order of magnitude more<sup>23</sup>. Here, we construct a pan-Amazon  
154 angiosperm phylogeny and use this in conjunction with data from 90 long-term  
155 monitoring plots across Amazonia (Figure 1) to investigate the relationships between  
156 tree diversity and ecosystem function. We investigate the role of taxonomic and  
157 evolutionary diversity in promoting aboveground wood productivity (hereafter  
158 productivity) and aboveground biomass (hereafter biomass).

159 Evolutionary diversity was estimated as total, neighbour and basal lineage diversity.  
160 As these metrics show strong relationships with the total taxonomic richness of  
161 communities<sup>20,24</sup>, the effect of which we were also interested in estimating, we  
162 calculated the degree to which communities show greater or less PD, MPD and  
163 MNTD than expected given their richness (i.e. standardized phylogenetic diversity  
164 metrics)<sup>17</sup>. Taxonomic richness and diversity were estimated as the sum of identified  
165 genera per area, Shannon diversity, Simpson Index and Fisher's alpha. Because  
166 taxonomic and standardized phylogenetic diversity metrics represent different  
167 dimensions of biodiversity<sup>17</sup>, with genus richness being decoupled from evolutionary  
168 diversity (i.e. gains in richness are poor predictors of gains in phylogenetic  
169 diversity)<sup>24</sup>, we expect that they may have independent effects on ecosystem  
170 function. Changes in taxonomic diversity influence the number of functionally distinct  
171 lineages present in a community, which may influence ecosystem function via either  
172 sampling effects or complementarity. As the degree of evolutionary relatedness

173 among tropical tree species reflects similarity in their ability to process and store  
174 carbon (i.e. closely related taxa have more similar wood density, potential tree size,  
175 growth and mortality rates)<sup>10</sup>, we expect that communities with greater evolutionary  
176 diversity may maximize productivity and carbon storage due to complementarity in  
177 resource use. As evolutionary diversity may summarize information about a wide  
178 range of traits, species richness and composition in a single index<sup>5</sup>, we hypothesize  
179 that evolutionary diversity would be a stronger predictor of ecosystem function than  
180 taxonomic measures of diversity<sup>2</sup>.

181 As environmental factors<sup>25,26</sup>, stand structure and mean functional composition  
182 (number of stems, wood density and potential tree size)<sup>15</sup> are also associated with  
183 both productivity and biomass, we account for variation in these factors in all our  
184 analyses using available climate data<sup>27</sup>, locally collected soil data<sup>28</sup> and stand  
185 structural and functional characteristics<sup>10,29</sup>. We explore the effects of taxonomic and  
186 evolutionary diversity metrics on ecosystem function using partial correlations, and in  
187 linear models of productivity and biomass that account for the influence of climate,  
188 soil, forest structure and functional composition, as these variables might obscure  
189 any underlying effect of diversity on ecosystem function (see Methods for details).  
190 We focus our results and discussion on the influence of standardized phylogenetic  
191 diversity metrics<sup>17,30</sup> and on two common taxonomic metrics of diversity: taxon  
192 richness and Simpson Index. Taxon richness was chosen because it is widely used  
193 in comparative studies and Simpson Index because it was included in the best model  
194 that explained the greatest variance in the data. Analyses incorporating Shannon  
195 Index, Fisher's Alpha and raw phylogenetic diversity metrics gave broadly similar  
196 results and are presented in the supplementary information. All the analyses were  
197 conducted at the genus-level due to the resolution of the phylogeny.



## 198 **Results**

199 Individually, both taxonomic and evolutionary measures of diversity showed strong  
200 positive, bivariate relationships with productivity (Figure 2; Supplementary Table 3).  
201 Because climate, soil, forest structure, functional composition and spatial  
202 autocorrelation might obscure the underlying effect of diversity on wood productivity  
203 we also controlled for variation in these variables by including them as model  
204 covariates. Using linear models, we found that the best statistical model of  
205 productivity (based on AIC values) contained both evolutionary (sesMNTD) and  
206 taxonomic (Simpson index) measures of diversity ( $R^2 = 0.47$ ;  $\Delta AIC = -2.5$  in relation  
207 to the model excluding both taxonomic and evolutionary diversity metrics; Figure 3;  
208 Table 1). This shows that these metrics reflect distinct aspects of diversity that are  
209 both important for understanding patterns of productivity (Supplementary Figure 10).  
210 Partial correlation analysis produced similar results to the model selection approach  
211 (Supplementary Table 4): sesMNTD ( $r=0.15$ ;  $p=0.044$ ) and Simpson's index ( $r=0.15$ ;  
212  $p=0.046$ ) both showed significant partial correlations with productivity after  
213 accounting for other variables (Supplementary Table 4). In contrast, genus richness  
214 had no effect on productivity after accounting for environmental and structural  
215 factors, using either the model selection approach ( $p=0.51$ ) or partial correlation  
216 analysis ( $p=0.57$ ) (Table 1, full coefficients from the models are shown in Appendix  
217 4).

218 Climatological and soil variables were also associated with variation in productivity  
219 (Figure 3; Supplementary Figure 4 and Supplementary Table 4). Mean annual  
220 temperature, climatic water deficit, soil total phosphorus, magnesium, and potassium  
221 were all associated with productivity<sup>25</sup> (Figure 3), with higher rates of wood growth  
222 typical of areas in the western Amazon with low water deficit and greater nutrient

223 availability (i.e. total phosphorus and magnesium). Although the standardized effect  
224 size of some environmental variables, such as water deficit, was large, the effect  
225 sizes of biodiversity variables in the best model were similar to some other individual  
226 environmental variables commonly considered to control variation in productivity in  
227 tropical forests, such as soil phosphorus concentrations (Figure 3; Supplementary  
228 Table 4).

229 Bivariate correlations indicated significant negative associations between biomass  
230 and all diversity metrics (Supplementary Figure 5; Supplementary Table 3).  
231 However, biodiversity and biomass were almost completely unrelated after  
232 accounting for variation in climate, soil, forest structure and mean functional  
233 composition (Figure 3; Supplementary Table 5), in contrast to the positive, significant  
234 biodiversity-productivity relationships (Supplementary Table 4). Instead, biomass  
235 was largely determined by variation in wood density (Figure 3 and Supplementary  
236 Figure 7; Supplementary Table 5). The model selection approach also suggested  
237 that variation in temperature, stem density and magnesium concentration had a  
238 small, significant effect on biomass (Figure 3; Appendix 4), but these results were  
239 not supported by the partial correlation analysis (Supplementary Table 5).

## 240 **Discussion**

241 This study demonstrates that there is a positive, small and significant effect of both  
242 taxonomic (Simpson Index) and evolutionary (sesMNTD) measures of diversity on  
243 wood productivity, but not aboveground biomass, in tree communities across  
244 lowland, *terra firme*, Amazonian forests, after accounting for the influence of  
245 environmental factors, stand structural variables and spatial autocorrelation (Figures  
246 2 and 3; Table 1; Supplementary Table 4). Although the effects of diversity on  
247 productivity were small, the strength of these effects was similar to previous studies

248 at small experimental scales in grassland ecosystems<sup>2-4</sup> and is comparable to the  
249 effect of some environmental variables within this analysis, such as soil phosphorus  
250 (Figure 3).

251 A range of mechanisms may underlie the significant relationships between neighbour  
252 lineage diversity (sesMNTD), Simpson index and productivity (Figure 2, Table 1 and  
253 Supplementary Table 4) including both sampling effects (i.e. the presence of  
254 particular species with relevant functional traits within a community) and functional  
255 complementarity. In general, the contribution of sesMNTD and Simpson index to  
256 explaining variation in productivity, even after accounting for two major stand  
257 structural attributes (wood density and tree size), suggests that among lineages,  
258 there are additional functional characteristics that are related to phylogenetic  
259 relationships among taxa that promote productivity within plots. Since the  
260 evolutionary relationships among species tend to reflect their similarity in functional  
261 traits<sup>10,31,32</sup> and because evolutionary diversity explicitly incorporates species  
262 differences, the effect of sesMNTD on productivity is likely to be a result of increased  
263 functional complementarity among lineages<sup>1,2</sup>. Higher values of the Simpson index,  
264 which indicate a more even distribution of abundances among genera<sup>33</sup>, may also  
265 increase niche complementarity. Alternatively, the weak positive effects of sesMNTD  
266 and Simpson index on productivity could be due to sampling effects, but this is  
267 unlikely as tropical forests are sufficiently diverse at the 1 ha plot scale such that  
268 sampling effects saturate; these diverse forests comprise taxa from the entire  
269 phylogeny at this scale, and include genera that have both fast and slow  
270 demographic traits<sup>26</sup>. Moreover, lineages that contribute disproportionately to the  
271 diversity/productivity relationship<sup>8</sup> are scattered across the phylogeny and there is no  
272 phylogenetic signal for the contribution of different lineages to the effect of Simpson

273 Index or sesMNTD on wood productivity (see Supplementary text and  
274 Supplementary Figure 12). These results suggest that greater phylogenetic diversity  
275 is not related to a higher probability of sampling functionally dominant lineages that  
276 would in turn disproportionately contribute to the relationship between evolutionary  
277 and taxonomic diversity, and productivity. Because of this, complementarity appears  
278 to be the most likely mechanism to explain the positive biodiversity effects we  
279 observe (see Supplementary Information for further analyses and discussion).

280 One potentially key unmeasured trait that may underlie an increase in functional  
281 complementarity and productivity in more diverse communities is variation in canopy  
282 structure. Canopy structure is a key determinant of productivity in temperate forests<sup>34</sup>  
283 and experiments with young trees<sup>35</sup> demonstrate that mixtures of species with  
284 complementary crown morphologies and branching patterns have denser  
285 canopies<sup>35-37</sup>, because species distribute their branches and leaves in  
286 complementary height layers of the canopy. As a result, both light interception and  
287 productivity are enhanced<sup>36</sup>. In Amazonian forests, there is a wide range of canopy  
288 architecture among species and complementarity in crown shape may enable trees  
289 to utilize canopy space more efficiently. For example, for 2457 trees in Madre de  
290 Dios in the Peruvian Amazon<sup>38,39</sup> crown architecture varies widely among families  
291 (Supplementary Figure 8). Differences in crown architecture among genera from  
292 different families may enhance canopy space filling and resource uptake. There may  
293 also be variation among communities in other unstudied, evolutionarily correlated  
294 traits such as below ground resource allocation, tree height/diameter allometry,  
295 hydraulic traits or functional groups (e.g. nitrogen/non-nitrogen fixers) that may affect  
296 productivity.

297 The effect of sesMNTD and Simpson index on productivity could also reflect  
298 pathogen dilution in more diverse communities. Host ranges of most tree pests and  
299 pathogens show a clear phylogenetic signal, with co-occurring, closely related plant  
300 lineages being more vulnerable to similar natural enemies than distant relatives<sup>40,41</sup>.  
301 A community with greater sesMNTD (i.e. comprising more distantly related lineages)  
302 is therefore expected to be less susceptible to disease pressure<sup>41</sup>, and thus needs  
303 fewer resources invested in defence, which in turn allows faster growth rates<sup>42</sup>. In  
304 tropical regions, where strong conspecific negative density dependence is observed,  
305 individual trees tend to have lower performance (e.g. growth and survival) when  
306 growing near closely related neighbours<sup>43</sup>. At the community level, a species may  
307 therefore perform better in forests that contain fewer close relatives. Similar  
308 arguments may also apply to communities with higher values of Simpson's index: a  
309 greater proportion of rare species may reduce the probability of an individual tree  
310 being attacked by species-specific pathogens and/or herbivores, and increase  
311 community-level productivity.

312 The similar, but independent, effects of taxonomic and phylogenetic diversity for  
313 explaining variation in productivity is contrary to our initial prediction. Perhaps both  
314 variation in the relative abundance distribution among communities, best captured by  
315 Simpson's index, and the functional distinctiveness of taxa, best captured by  
316 sesMNTD, are important for determining the strength of functional complementarity  
317 within communities. In contrast, a recent subtropical biodiversity experiment found  
318 that phylogenetic diversity did not explain additional variation in rates of carbon  
319 accumulation, compared to measures of taxonomic diversity<sup>44</sup>. However, both the  
320 metrics of phylogenetic diversity and the overall level of diversity of the communities  
321 in the experimental study differ from our pan-Amazon study. Understanding the

322 specific functional differences among genera within a community that contribute to  
323 maximizing productivity in diverse tropical forests is an important area for further  
324 research, to strengthen the links between causative mechanisms and the  
325 correlations that we report here.

326 Both taxonomic and evolutionary diversity had no effect on aboveground biomass in  
327 intact forests in Amazonia. These results are supported by a previous pan-tropical  
328 study that used an overlapping dataset to investigate the role of taxonomic diversity  
329 on biomass<sup>26</sup>, and a recent study that investigated the role of evolutionary diversity  
330 on biomass during forest succession and found that despite a positive effect of  
331 phylogenetic diversity on biomass in early successional forests, there is no effect at  
332 later stages of forest succession<sup>45</sup>. Not surprisingly, but contrary to the positive effect  
333 of taxonomic and evolutionary diversity on productivity, biomass was strongly  
334 determined by functional characteristics (Figure 3; Supplementary Table 5), with  
335 variation in wood density being the most important variable in controlling patterns of  
336 biomass in these forests<sup>15,26,46</sup>. To a much lesser extent and consistent with previous  
337 findings<sup>47</sup>, the number of stems had a marginal and positive effect on biomass  
338 (Figure 3). These results corroborate a recent meta-analysis in tropical forests, which  
339 found that stand structural (e.g. number of stems) and community mean functional  
340 trait (e.g. wood density) variables are more important than taxonomic diversity for  
341 predicting variation in biomass<sup>48</sup>. In general, as variation in stem mortality rates is a  
342 better predictor of variation in stand biomass among plots than productivity<sup>49</sup> and  
343 tree death is a highly stochastic process<sup>50</sup>, any positive effect of tree diversity on  
344 biomass through increased productivity is likely obscured by the impact of variation  
345 in stem mortality rates among plots.

346 Overall, our results suggest that multiple facets of diversity have a small, positive  
347 effect on present-day functioning of the world's largest tropical forest. In particular,  
348 this study provides evidence that evolutionary diversity is weakly, but significantly,  
349 related to ecosystem functioning at large scales in natural ecosystems. While  
350 evolutionary diversity has previously been suggested as a factor to consider in the  
351 identification of priority areas for conservation because of its role in enhancing  
352 ecosystem function<sup>2-5</sup>, this study provides quantitative evidence for this assertion in  
353 tropical forests. Our results therefore indicate that there is a synergy between  
354 preserving diverse forests that encompass greater evolutionary heritage, and  
355 protecting ecosystem function.

## 356 **Methods**

### 357 **Tree community data**

358 To investigate the relationship between biodiversity and ecosystem functioning, we  
359 estimated diversity, wood productivity and aboveground biomass using data from 90  
360 long-term forest inventory plots in the Amazon and adjacent lowland forests from the  
361 RAINFOR (Amazon Forest Inventory) network (Figure 1; Appendix 1). Data were  
362 extracted from the ForestPlots.net database, which curates tree-by-tree records from  
363 RAINFOR and other networks<sup>51,52</sup>. Plots were all 1 ha in size (except for two plots of  
364 0.96 ha) and located in structurally intact and old-growth closed-canopy forest. Our  
365 analyses were restricted to continuous lowland, *terra firme*, moist Amazonian forests,  
366 - excluding plots in montane, swamp, seasonally dry and white-sand forests, and  
367 savannas. The ecological characteristics that influence resource uptake and thus  
368 underlie any potential relationship between ecosystem function and phylogenetic  
369 diversity may differ widely among biomes with distinct evolutionary histories<sup>53</sup>. For

370 example, clades restricted to areas outside moist forests may have evolved very  
371 different unmeasured traits (e.g. higher root:shoot ratios to tolerate drought), which  
372 could lead to different relationships between evolutionary diversity and ecosystem  
373 function in comparisons across biomes. Restricting our analyses to a single biome  
374 and therefore a relatively coherent pool of genera, with similar evolutionary histories  
375 and proven ability to disperse and mix across Amazonia over geological  
376 timescales<sup>54</sup>, allowed us to limit the potentially confounding effect of large, cross-  
377 biome differences in phylogenetic composition on the relationship between diversity  
378 and ecosystem function.

379 Plots were established between 1975 and 2010 and monitored for an average 16.1  
380 years in total (range 2.0 to 28.6 years), with regular recensuses. All trees and palms  
381 with diameter at breast height (dbh) greater than 10 cm were included in the  
382 analyses. In the dataset, all recorded species and genus names were checked and  
383 standardized using the Taxonomic Name Resolution Service<sup>55</sup>. Across all plots  
384 94.9% of stems were identified to the genus level, with a minimum of 70% identified  
385 to genus per plot. We excluded all individuals not identified to genus-level (5.1%)  
386 from biodiversity metric calculations.

### 387 **Phylogenetic tree**

388 To calculate metrics of evolutionary diversity, we constructed a large pan-Amazon  
389 phylogeny, including 526 genera based on two chloroplast DNA gene regions: *rbcL*  
390 and *matK*, following protocols from Gonzalez et al.<sup>56</sup>. Full details of the temporally  
391 calibrated, ultrametric phylogeny construction can be found in the Supplementary  
392 Material. Our analyses included only those genera where we have phylogenetic  
393 data: 90.4% of the total number of genera in the plots, which encompass 98.0% of all  
394 identified stems.



## 395 **Biodiversity metrics**

396 To represent the different aspects of biodiversity, we calculated ten genus-level  
397 diversity metrics, including taxonomic diversity indices and metrics that incorporate  
398 the evolutionary history within communities (Supplementary Table 1). Because  
399 different metrics can reflect similar dimensions of diversity<sup>17</sup> (Supplementary Figure  
400 10) we present, in the main text, the results from five diversity metrics: (1) taxonomic  
401 richness, a common and widely used diversity metric, here evaluated as the sum of  
402 all identified genera in a given community; (2) Simpson index of diversity, a common  
403 diversity metric that incorporates genus abundance, representing the probability that  
404 two stems randomly selected from a community belong to different genera; (3) total  
405 lineage diversity, the standardized effect size of phylogenetic diversity (sesPD),  
406 estimated as the sum of all branch lengths including genera within a community<sup>16</sup>,  
407 whilst controlling for the effect of genus richness; (4) neighbour lineage diversity,  
408 which is quantified as the standardized effect size of mean nearest taxon distance  
409 (sesMNTD), whilst controlling for the effect of genus richness, which is more  
410 sensitive to relatedness near to the tips of the phylogeny<sup>11,12</sup> and (5) basal lineage  
411 diversity, which is quantified by mean pairwise distance (sesMPD)<sup>11,12</sup>, whilst also  
412 controlling for the effect of genus richness and reflects phylogenetic structure at the  
413 deepest nodes<sup>20</sup> (see Supplementary Information for results that include all metrics).

414 Because the null expectation for the evolutionary diversity metrics of communities  
415 (i.e. PD, MNTD and MPD) necessarily shows strong relationships with the total  
416 taxonomic richness of communities, we quantified their standardized values: the  
417 degree to which communities show greater (+) or less (-) PD, MNTD or MPD than  
418 expected given their genus richness. We calculated the standardised effect sizes,  
419 sesPD, sesMNTD and sesMPD by first generating a null expectation via randomly

420 shuffling genera tip labels in the phylogeny 999 times. The effect size was then  
421 calculated as the difference between the observed and expected values, the latter  
422 being the mean across randomizations, and dividing this difference by the standard  
423 deviation of values across the randomisations. These standardized metrics represent  
424 the residuals from the relationship between each evolutionary diversity metric and  
425 genus richness within each plot and allow us to identify areas with high or low  
426 evolutionary diversity whilst accounting for the effect of richness.

## 427 **Wood productivity and aboveground biomass**

428 Aboveground wood productivity was estimated as the rate of gain in biomass during  
429 each census interval. Because longer census intervals increase the proportion of  
430 productivity that cannot be directly detected due to trees growing and dying during  
431 the census interval<sup>57</sup>, productivity was corrected for varying census interval lengths.  
432 Following the methodology developed by Talbot et al.<sup>58</sup> estimates of annualized  
433 productivity per plot were computed as: i) the sum of tree growth alive in the first and  
434 in the last censuses, ii) growth of trees that recruited during the census interval, iii)  
435 estimates of unobserved growth of trees that died during the census interval and iv)  
436 estimates of unobserved trees that both recruited and died between census periods.  
437 Census-interval length is expected to affect the estimates of productivity, while plots  
438 monitored over short total census lengths are more likely to be affected by stochastic  
439 changes over time and measurement errors<sup>59</sup>. Productivity estimates were weighted  
440 by the cubic root of census-interval length (details in Supplementary Information).

441 Aboveground biomass per stem was estimated using a pan-tropical, three parameter  
442 equation  $AGB = 0.0673 * (wd D^2 H)^{0.976}$ , from Chave et al.<sup>60</sup>, where  $wd$  is the stem  
443 wood density (in  $g.cm^3$ ) from the Global Wood Density<sup>29,61</sup>,  $D$  is the tree diameter (in  
444 cm) at 1.3 m or above the buttress and  $H$  tree height (in m). Tree height was  
445 estimated based on regional diameter-height Weibull equations<sup>62</sup>. Similar to  
446 productivity, in order to reduce the influence of potential stochastic changes and due  
447 to variation in census interval within plots, we estimated biomass per plot using a  
448 weighted average across multiple censuses (details in Supplementary Information).  
449 We extracted wood density from the Global Wood Density database<sup>29,61</sup>.

## 450 **Environmental variables**

451 Because variation in both productivity and biomass in Amazonian forests is expected  
452 to be mediated by soil and climate<sup>25</sup>, we included environmental variables as  
453 covariates in our models. For climate data, to avoid collinearity among explanatory  
454 variables, we selected mean annual temperature (MAT °C), extracted from the  
455 WorldClim dataset at 30' ( $\approx$  1km) resolution<sup>27</sup> and maximum climatic water deficit  
456 (CWD), a measure of water stress, extracted from a global gridded layer<sup>60</sup>. For soil  
457 data, we used average values for each plot, calculated at 0-30 cm depth, for soil  
458 texture, total phosphorus ( $\text{mg kg}^{-1}$ ), potassium, magnesium, calcium, and sodium  
459 concentrations ( $\text{mmol}_{\text{eq}} \text{kg}^{-1}$ ) collated at ForestPlots.net and based on intensive soil  
460 sampling from each RAINFOR plot that used standardised field and analytical  
461 protocols<sup>25,28</sup>. Because silt, clay and sand content (%) are strongly correlated, soil  
462 texture was expressed as the first two axes of a principal component analysis (PCA).  
463 The first axis was negatively strongly related with sand content and the second  
464 negatively with clay (Supplementary Table 2).

## 465 **Stand structure variables**

466 We also included descriptors of stand structure as covariates in our models,  
467 including mean wood density, mean potential tree size and number of stems, all of  
468 which have been shown to shape productivity and biomass in tropical tree  
469 communities<sup>15</sup>. We extracted wood density data from the Global Wood Density  
470 database<sup>29,61</sup> selecting data for Mexico, Central America and South America. The  
471 data were matched to each stem in the plot data at the species-level, and in cases  
472 where this information was unavailable, matched to the average of species values  
473 for that genus. We then calculated the mean wood density value across all stems in  
474 a plot. To estimate potential tree size, we used data from Coelho de Souza et al.<sup>10</sup>

475 spanning 577 single census plots from across Amazonia, for the potential size that  
476 each genus could achieve. These values were assigned to each individual tree  
477 based on its identity. We then derived mean potential tree size for each plot,  
478 averaged across stems. The number of stems per plot was calculated as the  
479 average number of individuals with dbh greater than 10 cm across multiple  
480 censuses.

### 481 **Statistical analyses**

482 To investigate the strength of the relationship between each measure of ecosystem  
483 functioning (i.e. productivity and biomass) and the set of diversity metrics in each  
484 plot, we conducted: (1) bivariate Kendall's  $\tau$  non-parametric correlation tests; (2)  
485 generalised least squares modelling (GLS) and (3) Kendall's  $\tau$  pairwise partial  
486 correlation tests. For bivariate correlations, as testing the relationships for the range  
487 of biodiversity metrics involved ten tests for each dependent variable, P-values were  
488 adjusted for multiple comparisons using the false discovery rate<sup>63</sup> (Supplementary  
489 Table 3).

490 Environmental variables also influence the diversity of an ecosystem<sup>20,64</sup> and its  
491 ability to process and store carbon<sup>25</sup>, and may therefore obscure relationships  
492 between diversity and ecosystem functioning. In order to account for the effect of  
493 multiple environmental variables we constructed generalised least square models  
494 where ecosystem functioning was modelled as a function of metrics related to  
495 diversity, climate, edaphic conditions, functional composition and structural variables.  
496 To avoid multicollinearity amongst variables in the model, we confirmed that variance  
497 inflation factors (VIFs) were less than five<sup>65</sup> for each explanatory variable. We  
498 account for spatial autocorrelation in the GLS analyses by specifying a Gaussian  
499 spatial autocorrelation structure, which is consistent with the shape of the

500 semivariograms for biomass and productivity across this network of plots<sup>49</sup>. We  
501 created separate models for productivity, biomass and each diversity metric. For  
502 each response variable (productivity and biomass), we generated a set of models  
503 including all possible combinations of variables related to climate, soil, functional  
504 composition and stand structure, and selected the best model (referred to as the  
505 climate-soil-structure model) based on the Akaike Information Criterion (AIC). To  
506 investigate the additional contribution that diversity made to explain variation in both  
507 productivity and biomass, each single diversity metric was then added individually to  
508 the climate-soil-structure model. We then compared the climate-soil-structure model  
509 with models also including each single diversity metric: models with a difference in  
510 AIC greater than 2 when compared to the climate-soil-structure model, indicate  
511 models with improved support. Finally, we added pairs of diversity metrics,  
512 representing both taxonomic and evolutionary diversity (Supplementary Figure 10)  
513 into a single model to investigate whether a more complex model provides better  
514 predictive ability over single diversity metric models. Phosphorous and cation  
515 concentrations were log transformed prior to analysis. To allow comparisons of the  
516 strength of significance of the explanatory variables, they were all standardised to a  
517 mean of zero and a standard deviation of one.

518 We also examined the effect of the diversity metrics on wood productivity and  
519 aboveground biomass using partial correlation analyses including the variables  
520 selected in the best performing climate-soil-structure model. Partial correlation  
521 analyses are used to determine the correlation between two variables while  
522 eliminating the effect of potentially confounding variables<sup>66</sup>.

523 Analyses were performed in the R Statistical software v3.1.1<sup>67</sup> using the vegan<sup>68</sup>,  
524 picante<sup>69</sup>, BiomasaFP<sup>70</sup>, nlme<sup>71</sup> and ppcor<sup>66</sup> packages.

525 **Figure 1.** Location of 90 one-hectare permanent inventory plots shown on the forest  
526 cover map<sup>72</sup> produced from Global Land Cover<sup>73</sup>. Plots are all located in lowland  
527 moist forests on well-drained soils across the Amazon Basin (please see methods  
528 for details).

529 **Figure 2.** Bivariate relationships between aboveground wood productivity (AGWP)  
530 and the diversity variables included in the best performing model: A) Simpson Index  
531 and B) Neighbour lineage diversity from 90 single hectare plots across Amazonia.  
532 Shaded area represents 95% confidence interval. Relationships for the other  
533 taxonomic and phylogenetic diversity metrics are included in the Supplementary  
534 Information.

535 **Figure 3.** Standardised effect sizes for the best fit generalised least square model  
536 across plots for both aboveground wood productivity (AGWP) and aboveground  
537 biomass (AGB) as a function of diversity metrics, structural attributes, climate and  
538 soil variables selected based on the lowest AIC values and largest proportion of the  
539 variance explained ( $R^2$ ). The best model for AGWP includes neighbour lineage  
540 diversity and Simpson index as biodiversity metrics, mean annual temperature,  
541 climatic water deficit, total phosphorus, magnesium and potassium. Greater  
542 productivity is found in plots with lower mean annual temperature, higher water  
543 availability and on soils with greater amounts of soil phosphorus, magnesium and  
544 lower amounts of potassium. The best model for AGB included wood density,  
545 number of stems, magnesium, and mean annual temperature. The relationship  
546 between AGB and WD is non-linear and in all AGB analyses, WD was specified with  
547 linear and quadratic terms, but for clarity, in the graph, effect size is shown only for  
548 the quadratic term. For each variable in the model, dots represent the standardized  
549 effect size and lines one standard error. In some cases, error lines are unobserved

550 due to very small standard errors. See Supplementary Figures 4 and 7 for detailed  
551 bivariate correlations and Appendix 4 for all the coefficients of the models.

552 **Table 1.** Results for generalised least square (GLS) models across 90, one ha plots  
553 for aboveground wood productivity (AGWP) and aboveground biomass (AGB) as a  
554 function of diversity metrics, structural and compositional attributes, climate, soil  
555 variables, and accounting for spatial autocorrelation (Gaussian correlation structure).  
556 The best models for both AGWP and AGB are highlighted in bold - full coefficients  
557 from the models shown in Appendix 4. Results are shown for the best-fit model, with  
558 lowest AIC values, incorporating environmental variables (climate and soil),  
559 functional attributes (mean wood density, potential tree size and number of stems),  
560 and spatial autocorrelation. Delta AIC values refer to the comparison between each  
561 model that includes the diversity variables and the climate-soil-structure model,  
562 which excludes diversity. For AGWP, the climate-soil-structure model includes mean  
563 annual temperature, climatic water deficit, total phosphorus, magnesium and  
564 potassium. For AGB, the climate-soil-structure model includes wood density, number  
565 of stems, magnesium, and mean annual temperature.



566

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586 **Author contributions**

587 F.C.S, T.R.B. and K.G.D. conceived the study, F.C.S, T.R.B., O.L.P. and K.G.D.  
588 designed the study. F.C.S., K.G.D. and T.R.B. produced the phylogeny; F.C.S.  
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601 **Data availability.** The permanently archived data package of the plot-level diversity,  
602 aboveground biomass, wood productivity and the genus-level phylogeny are  
603 available from <https://www.forestplots.net/pt/produtos>.

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