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# 1 Taxonomic and phylogenetic diversity are associated with wood productivity in 2 Amazonian forests

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79 Higher levels of taxonomic and evolutionary diversity are expected to maximize  
80 ecosystem function, yet the relative importance of these different aspects of diversity  
81 for driving variation in ecosystem function at large scales in diverse forests is unknown.  
82 We explored this issue within Amazonian forests, which play a major role in the global  
83 carbon cycle and harbour a remarkable diversity of angiosperm lineages and species.  
84 Using 90 inventory plots across intact, lowland, *terra firme*, Amazonian forests and a  
85 new phylogeny including 582 angiosperm genera, we investigated the association  
86 between taxonomic and evolutionary metrics of diversity and two key measures of  
87 ecosystem function - aboveground wood productivity and biomass storage - whilst  
88 accounting for the effects of climatic and edaphic variables. While taxonomic and  
89 phylogenetic diversity were not important predictors of variation in biomass, both  
90 emerge as independent predictors of wood productivity. Amazon forests that contain  
91 greater evolutionary diversity and a higher proportion of rare species have higher  
92 productivity. Whilst climatic and edaphic variables are together the strongest  
93 predictors of productivity, our results demonstrate that the evolutionary diversity of tree  
94 species in diverse forest stands also influences productivity. As our models accounted  
95 for wood density and tree size, they also suggest that additional, unstudied,  
96 evolutionarily correlated traits have significant effects on ecosystem function in tropical  
97 forests. Overall, our pan-Amazonian analysis shows that greater phylogenetic  
98 diversity translates into higher levels of ecosystem function: tropical forest  
99 communities with more distantly related taxa have greater wood productivity.

100 **Main text**

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

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

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

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



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

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

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

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

## 199 **Results**

200 Individually, both taxonomic and evolutionary measures of diversity showed strong  
201 positive, bivariate relationships with productivity (Fig. 1; Table S3). Because climate,  
202 soil, forest structure, functional composition and spatial autocorrelation might obscure  
203 the underlying effect of diversity on wood productivity we also controlled for variation  
204 in these variables by including them as model covariates. Using linear models, we  
205 found that the best statistical model of productivity (based on AIC values) contained  
206 both evolutionary (sesMNTD) and taxonomic (Simpson index) measures of diversity  
207 ( $R^2 = 0.47$ ;  $\Delta AIC = -2.5$  in relation to the model excluding both taxonomic and  
208 evolutionary diversity metrics; Fig. 2; Table 1). This shows that these metrics reflect  
209 distinct aspects of diversity that are both important for understanding patterns of  
210 productivity (Fig. S11). Partial correlation analysis produced similar results to the  
211 model selection approach (Table S4): sesMNTD ( $\tau=0.15$ ;  $p=0.044$ ) and Simpson's  
212 index ( $\tau=0.15$ ;  $p=0.046$ ) both showed significant partial correlations with productivity  
213 after accounting for other variables (Table S4). In contrast, **diversity represented as**  
214 the number of genera in each community had no effect on productivity after accounting  
215 for environmental and structural factors, using either the model selection approach  
216 ( $p=0.51$ ) or partial correlation analysis ( $p=0.57$ ) (Table 1, full coefficients from the  
217 models are shown in Appendix 4).

218 Climatological and soil variables were also associated with variation in productivity  
219 (Fig. 2 and S5; Tables S2 and S4). Mean annual temperature, climatic water deficit,  
220 soil total phosphorus, magnesium, and potassium were all associated with  
221 productivity<sup>25</sup> (Fig. 2), with higher rates of wood growth typical of areas in the western  
222 Amazon with low water deficit and greater nutrient availability (i.e. total phosphorus  
223 and magnesium). Although the standardized effect size of some environmental

224 variables, such as water deficit, was large, the effect sizes of biodiversity variables in  
225 the best model were similar to some other individual environmental variables  
226 commonly considered to control variation in productivity in tropical forests, such as soil  
227 phosphorus concentrations (Fig. 2; Table S4).

228 Bivariate correlations indicated significant negative associations between biomass  
229 and all diversity metrics (Fig. S6; Table S3). However, biodiversity and biomass were  
230 almost completely unrelated after accounting for variation in climate, soil, forest  
231 structure and mean functional composition (Fig 2; Table S5), in contrast to the positive,  
232 significant biodiversity-productivity relationships (Table S4). Instead, biomass was  
233 largely determined by variation in wood density (Fig. 2 and. S8; Table S5). The model  
234 selection approach also suggested that variation in temperature, stem abundance and  
235 magnesium concentration had a small, significant effect on biomass (Fig 2; Appendix  
236 4), but these results were not supported by the partial correlation analysis (Table S5).

## 237 **Discussion**

238 This study demonstrates that there is a positive, small and significant effect of both  
239 taxonomic (Simpson Index) and evolutionary (sesMNTD) measures of diversity on  
240 wood productivity, but not aboveground biomass, in tree communities across lowland,  
241 *terra firme*, Amazonian forests, after accounting for the influence of environmental  
242 factors, stand structural variables and spatial autocorrelation (Fig. 1 and 2; Table 1;  
243 Table S4). Although the effects of diversity on productivity were small, the strength of  
244 these effects was similar to previous studies at small experimental scales in grassland  
245 ecosystems<sup>2-4</sup> and is comparable to the effect of some environmental variables within  
246 this analysis, such as soil phosphorus (Fig 2).

247 A range of mechanisms may underlie the significant relationships between neighbour  
248 lineage diversity (sesMNTD), Simpson index and productivity (Fig. 1, Tables 1 and S4)  
249 including both sampling effects (**i.e. the presence of species with particularly**  
250 **important functional traits within a community**) and functional complementarity. In  
251 general, the contribution of sesMNTD **and Simpson index** to explaining variation in  
252 productivity, even after accounting for two major stand structural attributes (wood  
253 density and tree size), suggests that among lineages, there are additional functional  
254 characteristics that are related to phylogenetic relationships among taxa that promote  
255 productivity within plots. Since the evolutionary relationships among species tend to  
256 reflect their similarity in functional traits<sup>10,31,32</sup> and because evolutionary diversity  
257 explicitly incorporates species differences, the effect of sesMNTD on productivity is  
258 likely to be a result of increased functional complementarity among lineages<sup>1,2</sup>. **Higher**  
259 **values of the Simpson index, which indicate a more even distribution of**  
260 **abundances among genera<sup>33</sup>, may also increase niche complementarity.**  
261 Alternatively, the weak positive effects of sesMNTD **and Simpson index** on  
262 productivity could be due to sampling effects, but this is unlikely as tropical forests are  
263 sufficiently diverse at the 1 ha plot scale **such that** sampling effects saturate; these  
264 diverse forests comprise taxa from the entire phylogeny at this scale, and include  
265 genera that have both fast and slow demographic traits<sup>26</sup>. Moreover, lineages that  
266 contribute disproportionately to the diversity/productivity relationship<sup>8</sup> are scattered  
267 across the phylogeny and there is no phylogenetic signal for the contribution of  
268 different lineages to the effect of Simpson Index or sesMNTD on wood productivity  
269 (see SI text and Fig. S12). These results suggest that greater phylogenetic diversity is  
270 not related to a higher probability of sampling functionally dominant lineages that  
271 disproportionately contribute to the relationship between evolutionary and taxonomic

272 diversity, and productivity. Because of this, complementarity appears to be the most  
273 likely mechanism to explain the positive biodiversity effects we observe (see SI for  
274 further analyses and discussion).

275 One potentially key unmeasured trait that may underlie an increase in functional  
276 complementarity and productivity in more diverse communities is variation in canopy  
277 structure. Canopy structure is a key determinant of productivity in temperate forests<sup>34</sup>  
278 and experiments with young trees<sup>35</sup> demonstrate that mixtures of species with  
279 complementary crown morphologies and branching patterns have denser canopies<sup>35–</sup>  
280 <sup>37</sup>, because species distribute their branches and leaves in complementary height  
281 layers of the canopy. As a result, both light interception and productivity are  
282 enhanced<sup>36</sup>. In Amazonian forests, there is a wide range of canopy architecture among  
283 species and complementarity in crown shape may enable trees to utilize canopy space  
284 more efficiently. For example, for 2457 trees in Madre de Dios in the Peruvian  
285 Amazon<sup>38,39</sup> crown architecture varies widely among families (Fig. S9). Differences in  
286 crown architecture among genera from different families may enhance canopy space  
287 filling and resource uptake. There may also be variation among communities in other  
288 unstudied, evolutionarily correlated traits such as below ground resource allocation,  
289 tree height/diameter allometry, hydraulic traits or functional groups (e.g. nitrogen/non-  
290 nitrogen fixers) that may affect productivity.

291 The effect of sesMNTD and Simpson index on productivity could also reflect pathogen  
292 dilution in more diverse communities. Host ranges of most tree pests and pathogens  
293 show a clear phylogenetic signal, with co-occurring, closely related plant lineages  
294 being more vulnerable to similar natural enemies than distant relatives<sup>40,41</sup>. A  
295 community with greater sesMNTD (i.e. comprising more distantly related lineages) is  
296 therefore expected to be less susceptible to disease pressure<sup>41</sup>, and thus needs fewer

297 resources invested in defence, which in turn allows faster growth rates<sup>42</sup>. In tropical  
298 regions, where strong conspecific negative density dependence is observed<sup>43</sup>,  
299 individual trees tend to have lower performance (e.g. growth and survival) when  
300 growing near conspecific neighbours. **At the community level, a species may**  
301 **therefore have a better performance in forests that contain fewer close relatives.**  
302 **Similar arguments may also apply to communities with higher values of**  
303 **Simpson's index: a greater proportion of rare species may reduce the**  
304 **probability of an individual tree being attacked by species-specific pathogens**  
305 **and/or herbivores, and increase community-level productivity.**

306 **The similar, but independent, effects of taxonomic and phylogenetic diversity**  
307 **for explaining variation in productivity is contrary to our initial prediction.**  
308 **Perhaps both variation in the relative abundance distribution among**  
309 **communities, best captured by Simpson's index, and the functional**  
310 **distinctiveness of taxa, best captured by sesMNTD, are both important for**  
311 **determining the strength of functional complementarity within communities. In**  
312 **contrast, a recent subtropical biodiversity experiment found that phylogenetic**  
313 **diversity did not explain additional variation in rates of carbon accumulation,**  
314 **compared to measures of taxonomic diversity<sup>44</sup>. However, both the metrics of**  
315 **phylogenetic diversity and the overall level of diversity of the communities in**  
316 **the experimental study differ from our observational study. Understanding the**  
317 **specific functional differences among genera within a community that**  
318 **contribute to maximizing productivity in diverse tropical forests is an important**  
319 **area for further research to strengthen the links between causative mechanisms**  
320 **and the correlations that we report here.**

321 Both taxonomic and evolutionary diversity had no effect on aboveground biomass in

322 intact forests in Amazonia. These results are supported by a previous pan-tropical  
323 study that used an overlapping dataset to investigate the role of taxonomic diversity  
324 on biomass<sup>26</sup>, and a recent study that investigated the role of evolutionary diversity on  
325 biomass during forest succession and found that despite a positive effect of  
326 phylogenetic diversity on biomass in early successional forests, there is no effect at  
327 later stages of forest succession<sup>45</sup>. Not surprisingly, but contrary to the positive effect  
328 of taxonomic and evolutionary diversity on productivity, biomass was strongly  
329 determined by functional characteristics (Fig. 2; Table S5), with variation in wood  
330 density being the most important variable in controlling patterns of biomass in these  
331 forests<sup>15,26,46</sup>. To a much lesser extent and consistent with previous findings<sup>47</sup>, the  
332 number of stems had a marginal and positive effect on biomass (Fig. 2). These results  
333 corroborate a recent meta-analysis in tropical forests, which found that stand structural  
334 (e.g. number of stems) **and community mean functional trait (e.g. wood density)**  
335 **variables** are more important than taxonomic diversity for predicting variation in  
336 biomass<sup>48</sup>. In general, as variation in stem mortality rates is a better predictor of  
337 variation in stand biomass among plots than productivity<sup>49</sup> and tree death is a highly  
338 stochastic process<sup>50</sup>, any positive effect of tree diversity on biomass through increased  
339 productivity is likely obscured by the impact of variation in stem mortality rates among  
340 plots.

341 Overall, our results suggest that multiple facets of diversity have a small, positive effect  
342 on present-day functioning of the world's largest tropical forest. In particular, this study  
343 provides the first evidence that evolutionary diversity is weakly, but significantly,  
344 related to ecosystem functioning at large scales in natural ecosystems. While  
345 evolutionary diversity has previously been suggested as a factor to consider in the  
346 identification of priority areas for conservation because of its role in enhancing



347 ecosystem function<sup>2-5</sup>, this study provides quantitative evidence for this assertion in  
348 tropical forests. Our results therefore indicate that there is a synergy between  
349 preserving diverse forests that encompass greater evolutionary heritage, and  
350 protecting ecosystem function.

## 351 **Methods**

### 352 **Tree community data**

353 To investigate the relationship between biodiversity and ecosystem functioning, we  
354 estimated diversity, wood productivity and aboveground biomass using data from 90  
355 long-term forest inventory plots in the Amazon and adjacent lowland forests from the  
356 RAINFOR (Amazon Forest Inventory) network (Appendix 1; Fig. S1). Data were  
357 extracted from the ForestPlots.net database, which curates tree-by-tree records from  
358 RAINFOR and other networks<sup>51,52</sup>. Plots were all 1 ha in size (except for two plots of  
359 0.96 ha) and located in structurally intact and old-growth closed-canopy forest. Our  
360 analyses were restricted to continuous lowland, *terra firme*, moist Amazonian forests,  
361 - excluding plots in montane, swamp, seasonally dry and white-sand forests, and  
362 savannas. The ecological characteristics that influence resource uptake and thus  
363 underlie any potential relationship between ecosystem function and phylogenetic  
364 diversity may differ widely among biomes with distinct evolutionary histories<sup>53</sup>. For  
365 example, clades restricted to areas outside moist forests may have evolved very  
366 different unmeasured traits (e.g. higher root:shoot ratios to tolerate drought), which  
367 could lead to different relationships between evolutionary diversity and ecosystem  
368 function in comparisons across biomes. Restricting our analyses to a single biome and  
369 therefore a relatively coherent pool of genera, with similar evolutionary histories and  
370 proven ability to disperse and mix across Amazonia over geological timescales<sup>54</sup>,

371 allowed us to limit the potentially confounding effect of large, cross-biome differences  
372 in phylogenetic composition on the relationship between diversity and ecosystem  
373 function.

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

## 382 **Phylogenetic tree**

383 To calculate metrics of evolutionary diversity, we constructed the largest pan-Amazon  
384 phylogeny to date, including 582 genera based on two chloroplast DNA gene regions:  
385 *rbcL* and *matK*, following protocols from Gonzalez et al.<sup>56</sup>. Full details of the temporally  
386 calibrated, ultrametric phylogeny construction can be found in the Supplementary  
387 Material. Our analyses included only those genera where we have phylogenetic data:  
388 90.4% of the total number of genera in the plots, which encompass 98.0% of all  
389 identified stems.

## 390 **Biodiversity metrics**

391 To represent the different aspects of biodiversity, we calculated ten genus-level  
392 diversity metrics, including taxonomic diversity indices and metrics that incorporate the  
393 evolutionary history within communities (Table S1). Because different metrics can  
394 reflect similar dimensions of diversity<sup>17</sup> (Fig. S11) we present, in the main text, the

395 results from five diversity metrics: (1) taxonomic richness, a common and widely used  
396 diversity metric, here evaluated as the sum of all identified genera in a given  
397 community; (2) Simpson index of diversity, a common diversity metric that  
398 incorporates genus abundance, representing the probability that two stems randomly  
399 selected from a community belong to different genera; (3) total lineage diversity, the  
400 standardized effect size of phylogenetic diversity (sesPD), estimated as the sum of all  
401 branch lengths including genera within a community<sup>16</sup>, whilst controlling for the effect  
402 of genus richness; (4) neighbour lineage diversity, which is quantified as the  
403 standardized effect size of mean nearest taxon distance (sesMNTD), whilst controlling  
404 for the effect of genus richness, which is more sensitive to relatedness near to the tips  
405 of the phylogeny<sup>11,12</sup> and (5) basal lineage diversity, which is quantified by mean  
406 pairwise distance (sesMPD)<sup>11,12</sup>, whilst also controlling for the effect of genus richness  
407 and reflects phylogenetic structure at the deepest nodes<sup>20</sup> (see SI for results that  
408 include all metrics).

409 Because the null expectation for the evolutionary diversity metrics of communities (i.e.  
410 PD, MNTD and MPD) necessarily shows strong relationships with the total taxonomic  
411 richness of communities, we quantified their standardized values: the degree to which  
412 communities show greater (+) or less (-) PD, MNTD or MPD than expected given their  
413 genus richness. We calculated the standardised effect sizes, sesPD, sesMNTD and  
414 sesMPD by first generating a null expectation via randomly shuffling genera tip labels  
415 in the phylogeny 999 times. The effect size was then calculated as the difference  
416 between the observed and expected values, the latter being the mean across  
417 randomizations, and dividing this difference by the standard deviation of values across  
418 the randomisations. These standardized metrics represent the residuals from the  
419 relationship between each evolutionary diversity metric and genus richness within

420 each plot and allow us to identify areas with high or low evolutionary diversity whilst  
421 accounting for the effect of richness.

## 422 **Wood productivity and aboveground biomass**

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

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

## 445 **Environmental variables**

446 Because variation in both productivity and biomass in Amazonian forests is expected  
447 to be mediated by soil and climate<sup>25</sup>, we included environmental variables as  
448 covariates in our models. For climate data, to avoid collinearity among explanatory  
449 variables, we selected mean annual temperature (MAT °C), extracted from the  
450 WorldClim dataset at 30' ( $\approx$  1km) resolution<sup>27</sup> and maximum climatic water deficit  
451 (CWD), a measure of water stress, extracted from a global gridded layer<sup>60</sup>. For soil  
452 data, we used average values for each plot, calculated at 0-30 cm depth, for soil  
453 texture, total phosphorus ( $\text{mg kg}^{-1}$ ), potassium, magnesium, calcium, and sodium  
454 concentrations ( $\text{mmol}_{\text{eq}} \text{kg}^{-1}$ ) collated at ForestPlots.net and based on intensive soil  
455 sampling from each RAINFOR plot that used standardised field and analytical  
456 protocols<sup>25,28</sup>. Because silt, clay and sand content (%) are strongly correlated, soil  
457 texture was expressed as the first two axes of a principal component analysis (PCA).  
458 The first axis was negatively strongly related with sand content and the second  
459 negatively with clay (Table S2).

## 460 **Stand structure variables**

461 We also included descriptors of stand structure as covariates in our models, including  
462 mean wood density, mean potential tree size and number of stems, all of which have  
463 been shown to shape productivity and biomass in tropical tree communities<sup>15</sup>. We  
464 extracted wood density data from the Global Wood Density database<sup>29,61</sup> selecting  
465 data for Mexico, Central America and South America. The data were matched to each  
466 stem in the plot data at the species-level, and in cases where this information was  
467 unavailable, matched to the average of species values for that genus. We then  
468 calculated the mean wood density value across all stems in a plot. To estimate  
469 potential tree size, we used data from Coelho de Souza et al.<sup>10</sup> spanning 577 single

470 census plots from across Amazonia, for the potential size that each genus could  
471 achieve. These values were assigned to each individual tree based on its identity. We  
472 then derived mean potential tree size for each plot, averaged across stems. The  
473 number of stems per plot was calculated as the average number of individuals with  
474 dbh greater than 10 cm across multiple censuses.

## 475 **Statistical analyses**

476 To investigate the strength of the relationship between each measure of ecosystem  
477 functioning (i.e. productivity and biomass) and the set of diversity metrics in each plot,  
478 we conducted: (1) bivariate Kendall's  $\tau$  non-parametric correlation tests; (2)  
479 generalised least squares modelling (GLS) and (3) Kendall's  $\tau$  pairwise partial  
480 correlation tests. For bivariate correlations, as testing the relationships for the range  
481 of biodiversity metrics involved ten tests for each dependent variable, P-values were  
482 adjusted for multiple comparisons using the false discovery rate<sup>63</sup> (Table S3).

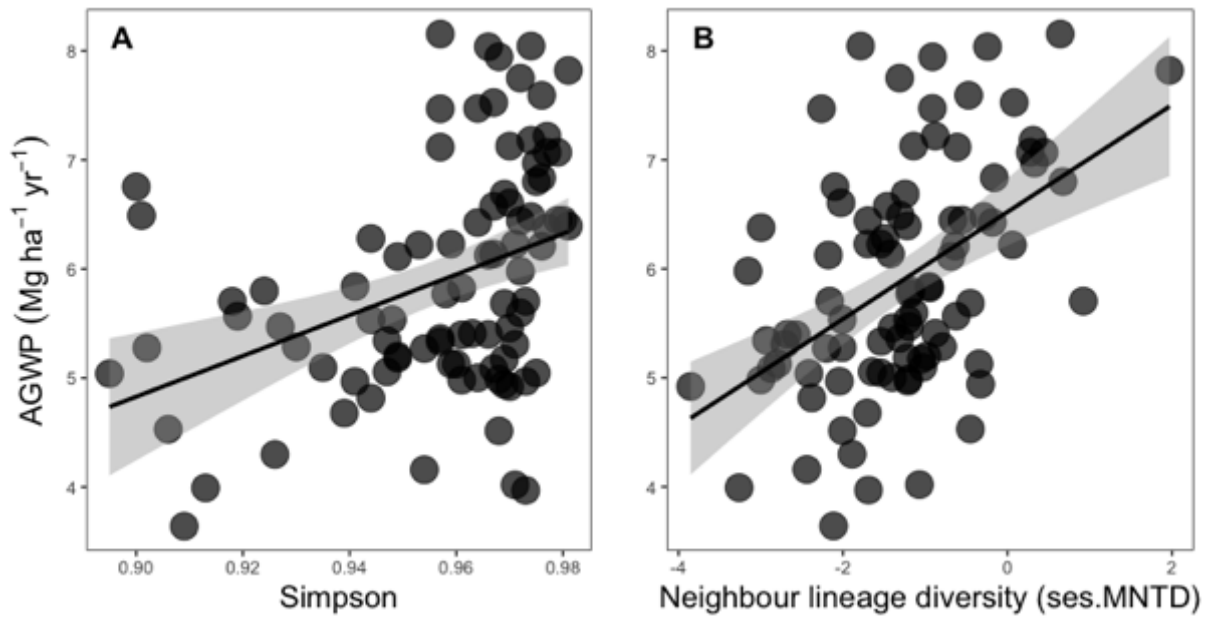
483 Environmental variables also influence the diversity of an ecosystem<sup>20,64</sup> and its ability  
484 to process and store carbon<sup>25</sup>, and may therefore obscure relationships between  
485 diversity and ecosystem functioning. In order to account for the effect of multiple  
486 environmental variables we constructed generalised least square models where  
487 ecosystem functioning was modelled as a function of metrics related to diversity,  
488 climate, edaphic conditions, functional composition and structural variables. To avoid  
489 multicollinearity amongst variables in the model, we confirmed that variance inflation  
490 factors (VIFs) were less than five<sup>65</sup> for each explanatory variable. We account for  
491 spatial autocorrelation in the GLS analyses by specifying a Gaussian spatial  
492 autocorrelation structure, which is consistent with the shape of the semivariograms for  
493 biomass and productivity across this network of plots<sup>49</sup>. We created separate models  
494 for biomass, productivity and each diversity metric. For each response variable

495 (productivity and biomass), we generated a set of models including all possible  
496 combinations of variables related to climate, soil, functional composition and stand  
497 structure, and selected the best model (referred to as the climate-soil-structure model)  
498 based on the Akaike Information Criterion (AIC). To investigate the additional  
499 contribution that diversity made to explain variation in both productivity and biomass,  
500 each single diversity metric was then added individually to the climate-soil-structure  
501 model. We then compared the climate-soil-structure model with models also including  
502 each single diversity metric: models with a difference in AIC greater than 2 when  
503 compared to the climate-soil-structure model, indicate models with improved support.  
504 Finally, we added pairs of diversity metrics, representing both taxonomic and  
505 evolutionary diversity (Fig. S11) into a single model to investigate whether a more  
506 complex model provides better predictive ability over single diversity metric models.  
507 Phosphorous and cation concentrations were log transformed prior to analysis. To  
508 allow comparisons of the strength of significance of the explanatory variables, they  
509 were all standardised to a mean of zero and a standard deviation of one.

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

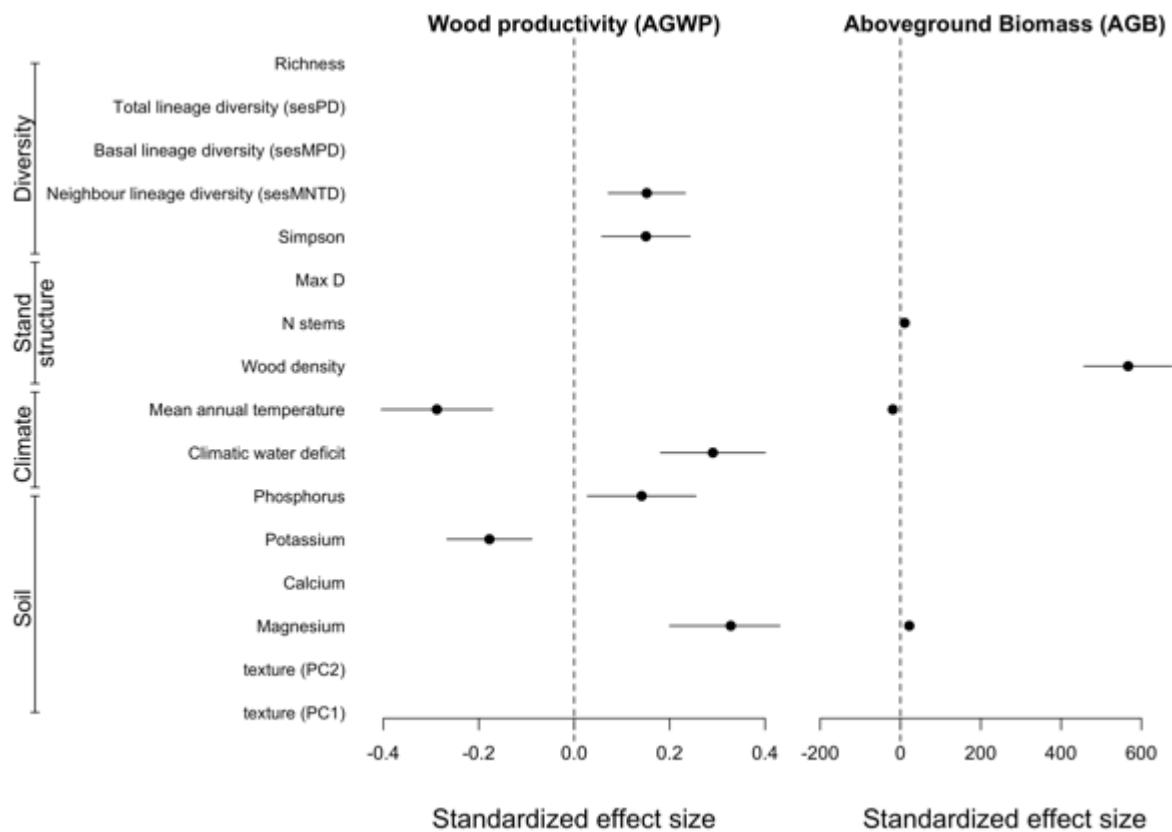
515 Analyses were performed in the R Statistical software v3.1.1<sup>67</sup> using the *vegan*<sup>68</sup>,  
516 *picante*<sup>69</sup>, *BiomasaFP*<sup>70</sup>, *nlme*<sup>71</sup> and *ppcor*<sup>66</sup> packages.





517

518 **Figure 1.** Bivariate relationships between aboveground wood productivity (AGWP)  
 519 and the diversity variables included in the best performing model: A) Simpson Index  
 520 and B) Neighbour lineage diversity from 90 single hectare plots across Amazonia.  
 521 Shaded area represents 95% confidence interval. Relationships for the other  
 522 taxonomic and phylogenetic diversity metrics are included in the SI.



523

524 Figure 2. Standardised effect sizes for the best fit generalised least square model  
 525 across plots for both aboveground wood productivity (AGWP) and aboveground  
 526 biomass (AGB) as a function of diversity metrics, structural attributes, climate and soil  
 527 variables selected based on the lowest AIC values and largest proportion of the  
 528 variance explained ( $R^2$ ). The best model for AGWP includes neighbour lineage  
 529 diversity and Simpson index as biodiversity metrics mean annual temperature, climatic  
 530 water deficit, total phosphorus, magnesium and potassium. Greater productivity is  
 531 found in plots with lower mean annual temperature, higher precipitation and on soils  
 532 with greater amounts of soil phosphorus, magnesium and lower amounts of  
 533 potassium. The best model for AGB included wood density, number of stems,  
 534 magnesium, and mean annual temperature. The relationship between AGB and WD  
 535 is non-linear and in all AGB analyses, WD was specified with linear and quadratic  
 536 terms, but for clarity, in the graph, effect size is shown only for the quadratic term. For

537 each variable in the model, dots represent the standardized effect size and lines one  
538 standard error. In some cases, error lines are unobserved due to very small standard  
539 errors. See graphs S5 and S8 for detailed bivariate correlations and Appendix 4 for all  
540 the coefficients of the models.

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

Model	AGWP			AGB		
	R <sup>2</sup>	AIC	$\Delta$ AIC	R <sup>2</sup>	AIC	$\Delta$ AIC
Climate-soil-structure model + sesMNTD + Simpson	<b>0.47</b>	<b>199.08</b>	<b>-2.51</b>	-	-	-
Climate-soil-structure model + sesMNTD	0.45	205.04	3.45	0.74	973.99	1.99
Climate-soil-structure model + Simpson	0.44	200.73	-0.86	0.74	973.78	1.78
Climate-soil-structure model + sesPD	0.46	201.13	-0.46	0.74	973.72	1.72
Climate-soil-structure model + sesMPD	0.44	203.57	4.48	0.74	973.97	1.97
Climate-soil-structure model + richness	0.44	203.12	1.53	0.74	971.03	-0.97
Climate-soil-structure model	0.44	201.59	0.00	<b>0.74</b>	<b>972.00</b>	<b>0</b>

556

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## 573 Author contributions

574 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.  
575 designed the study. F.C.S., K.G.D. and T.R.B. produced the phylogeny; F.C.S.  
576 analyzed data and wrote the paper; all co-authors collected field data or data  
577 management. O.L.P., Y.M. and Jon Lloyd conceived the RAINFOR forest census plot  
578 network. All co-authors commented and/or approved the manuscript.

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