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Taxonomic and phylogenetic diversity are associated with wood productivity in 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.

4

Main text

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

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

5

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[3]. 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[13,14], and ecosystem functions, such as productivity, are typically

132　weak[15].

133　The evolutionary diversity of a community can be measured in different ways to reflect

134　distinct aspects of biodiversity[11,16,17], 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[2,3,5,18]. 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)[16]. 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)[11,12]. 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)[19,20], which can be represented by the mean

145　phylogenetic distance (MPD) between all pairs of species[11]. 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[20]. 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[21] and contain a wide variety of angiosperm lineages[20]. 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[22], and storing an order

154   of magnitude more[23]. 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[20,24], 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)[17].

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[17] with richness being decoupled from evolutionary diversity (i.e.**

169   **gains in richness are poor predictors of gains in phylogenetic diversity)[24], 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

7

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)[10], **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[2].**

182 As environmental factors[25,26], stand structure and mean functional composition

183 (number of stems, wood density and potential tree size)[15] 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[27], locally collected soil data[28] and stand

186 structural and functional characteristics[10,29]. 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[17,30] 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.

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; ΔAIC = -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 (τ=0.15; p=0.044) and Simpson's

212 index (τ=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[25] (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[2–4] 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[10,31,32] 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[1,2]. **Higher**

259   **values of the Simpson index, which indicate a more even distribution of**

260   **abundances among genera[33], 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[26]. Moreover, lineages that

266   contribute disproportionately to the diversity/productivity relationship[8] 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

11

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[34]

278 and experiments with young trees[35] demonstrate that mixtures of species with

279 complementary crown morphologies and branching patterns have denser canopies[35–

280 37], 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[36]. 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[38,39] 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[40,41]. A

295 community with greater sesMNTD (i.e. comprising more distantly related lineages) is

296 therefore expected to be less susceptible to disease pressure[41], and thus needs fewer

297 resources invested in defence, which in turn allows faster growth rates[42]. In tropical

298 regions, where strong conspecific negative density dependence is observed[43],

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[44]. 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

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

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

347 ecosystem function[2–5], 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[51,52]. 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[53]. 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[54],

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

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

Phylogenetic tree

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

Biodiversity metrics

To represent the different aspects of biodiversity, we calculated ten genus-level diversity metrics, including taxonomic diversity indices and metrics that incorporate the evolutionary history within communities (Table S1). Because different metrics can reflect similar dimensions of diversity[17] (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[16], 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[11,12] and (5) basal lineage diversity, which is quantified by mean

406   pairwise distance (sesMPD)[11,12], whilst also controlling for the effect of genus richness

407   and reflects phylogenetic structure at the deepest nodes[20] (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.

Wood productivity and aboveground biomass

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

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

Environmental variables

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

Stand structure variables

We also included descriptors of stand structure as covariates in our models, including mean wood density, mean potential tree size and number of stems, all of which have been shown to shape productivity and biomass in tropical tree communities[15]. We extracted wood density data from the Global Wood Density database[29,61] selecting data for Mexico, Central America and South America. The data were matched to each stem in the plot data at the species-level, and in cases where this information was unavailable, matched to the average of species values for that genus. We then calculated the mean wood density value across all stems in a plot. To estimate potential tree size, we used data from Coelho de Souza et al.[10] 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 τ non-parametric correlation tests; (2)

479   generalised least squares modelling (GLS) and (3) Kendall's τ 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[63] (Table S3).

483   Environmental variables also influence the diversity of an ecosystem[20,64] and its ability

484   to process and store carbon[25], 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[65] 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[49]. 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[66].

515   Analyses were performed in the R Statistical software v3.1.1[67] using the vegan[68],

516   picante[69], BiomasaFP[70], nlme[71] and ppcor[66] packages.

517
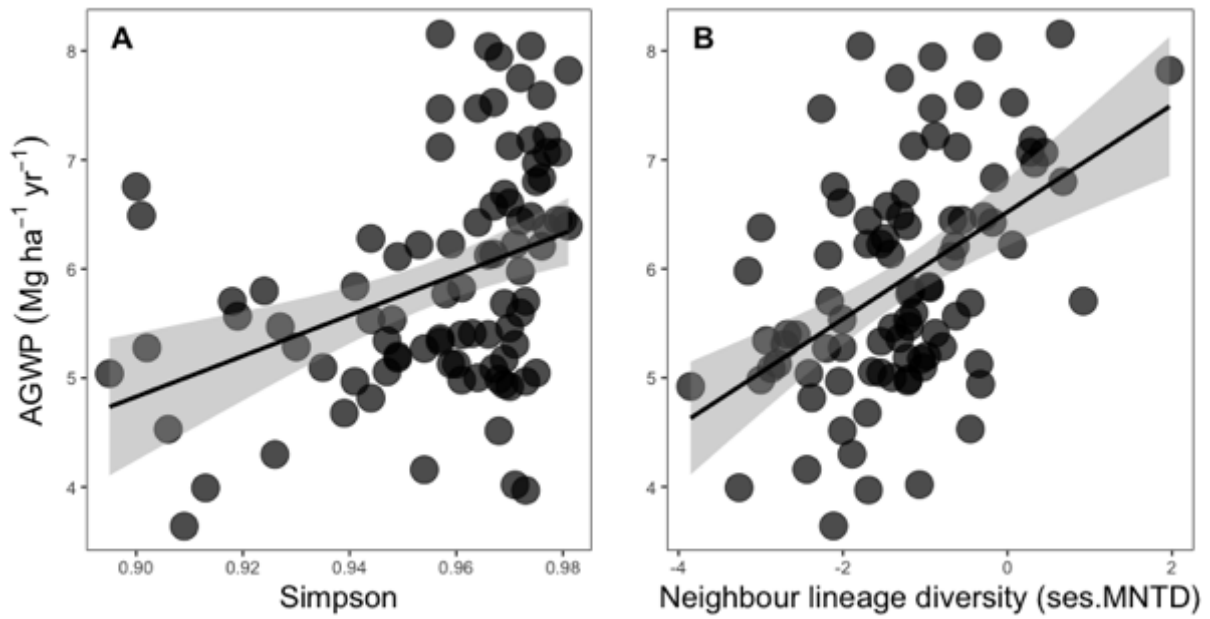
Figure 1. Bivariate relationships between aboveground wood productivity (AGWP) and the diversity variables included in the best performing model: A) Simpson Index and B) Neighbour lineage diversity from 90 single hectare plots across Amazonia. Shaded area represents 95% confidence interval. Relationships for the other taxonomic and phylogenetic diversity metrics are included in the SI.
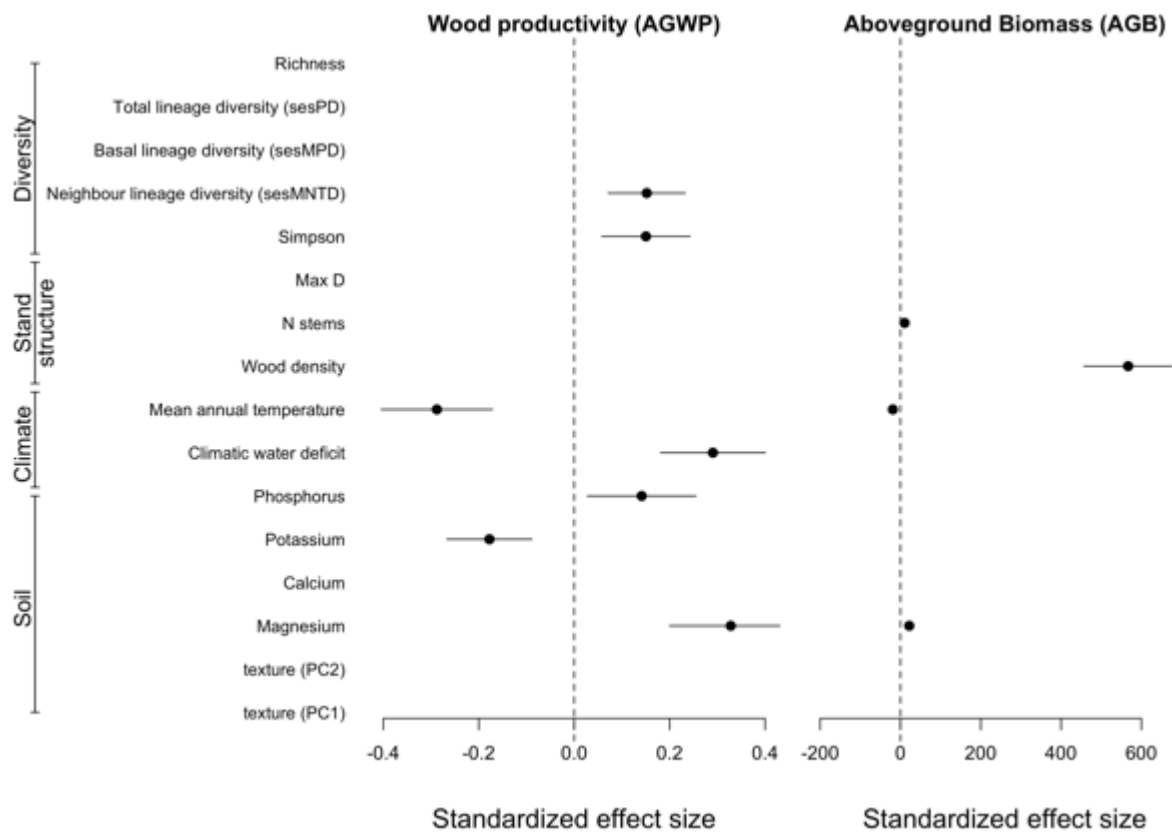
Figure 2. Standardised effect sizes for the best fit generalised least square model across plots for both aboveground wood productivity (AGWP) and aboveground biomass (AGB) as a function of diversity metrics, structural attributes, climate and soil variables selected based on the lowest AIC values and largest proportion of the variance explained (R^2). The best model for AGWP includes neighbour lineage diversity and Simpson index as biodiversity metrics mean annual temperature, climatic water deficit, total phosphorus, magnesium and potassium. Greater productivity is found in plots with lower mean annual temperature, higher precipitation and on soils with greater amounts of soil phosphorus, magnesium and lower amounts of potassium. The best model for AGB included wood density, number of stems, magnesium, and mean annual temperature. The relationship between AGB and WD is non-linear and in all AGB analyses, WD was specified with linear and quadratic terms, but for clarity, in the graph, effect size is shown only for the quadratic term. For

24

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^2	AIC	Δ AIC	R^2	AIC	ΔAIC
Climate-soil-structure model + sesMNTD + Simpson	**0.47**	**199.08**	**-2.51**	-	-	-
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	**0.74**	**972.00**	**0**

Author contributions

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

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