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Evolutionary diversity is associated with wood productivity in Amazonian forests

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

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

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

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

Evolutionary diversity was estimated as total, neighbour and basal lineage diversity. As these metrics show strong relationships with the total taxonomic richness of communities[20,24], the effect of which we were also interested in estimating, we calculated the degree to which communities show greater or less PD, MPD and MNTD than expected given their richness (i.e. standardized phylogenetic diversity metrics)[17]. Taxonomic richness and diversity were estimated as the sum of identified genera per area, Shannon diversity, Simpson Index and Fisher's alpha. Because taxonomic and standardized phylogenetic diversity metrics represent different dimensions of biodiversity[17], with genus richness being decoupled from evolutionary diversity (i.e. gains in richness are poor predictors of gains in phylogenetic diversity)[24], we expect that they may have independent effects on ecosystem function. Changes in taxonomic diversity influence the number of functionally distinct lineages present in a community, which may influence ecosystem function via either sampling effects or complementarity. As the degree of evolutionary relatedness among tropical tree species reflects similarity in their ability to process and store carbon (i.e. closely related taxa have more similar wood density, potential tree size, growth and mortality rates)[10], we expect that communities with greater evolutionary diversity may maximize productivity and carbon storage due to complementarity in resource use. As evolutionary diversity may summarize information about a wide range of traits, species richness and composition in a single index[5], we hypothesize that evolutionary diversity would be a stronger predictor of ecosystem function than taxonomic measures of diversity[2].

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

Results

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

Climatological and soil variables were also associated with variation in productivity (Figure 3; Supplementary Figure 4 and Supplementary Table 4). Mean annual temperature, climatic water deficit, soil total phosphorus, magnesium, and potassium were all associated with productivity[25] (Figure 3), with higher rates of wood growth typical of areas in the western Amazon with low water deficit and greater nutrient availability (i.e. total phosphorus and magnesium). Although the standardized effect size of some environmental variables, such as water deficit, was large, the effect sizes of biodiversity variables in the best model were similar to some other individual environmental variables commonly considered to control variation in productivity in tropical forests, such as soil phosphorus concentrations (Figure 3; Supplementary Table 4).

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

Discussion

This study demonstrates that there is a positive, small and significant effect of both taxonomic (Simpson Index) and evolutionary (sesMNTD) measures of diversity on wood productivity, but not aboveground biomass, in tree communities across lowland, terra firme, Amazonian forests, after accounting for the influence of environmental factors, stand structural variables and spatial autocorrelation (Figures 2 and 3; Table 1; Supplementary Table 4). Although the effects of diversity on productivity were small, the strength of these effects was similar to previous studies at small experimental scales in grassland ecosystems[2–4] and is comparable to the effect of some environmental variables within this analysis, such as soil phosphorus (Figure 3).

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

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

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

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

The similar, but independent, effects of taxonomic and phylogenetic diversity for explaining variation in productivity is contrary to our initial prediction. Perhaps both variation in the relative abundance distribution among communities, best captured by Simpson's index, and the functional distinctiveness of taxa, best captured by sesMNTD, are important for determining the strength of functional complementarity within communities. In contrast, a recent subtropical biodiversity experiment found that phylogenetic diversity did not explain additional variation in rates of carbon accumulation, compared to measures of taxonomic diversity[44]**.** However, both the metrics of phylogenetic diversity and the overall level of diversity of the communities in the experimental study differ from our pan-Amazon study. Understanding the specific functional differences among genera within a community that contribute to maximizing productivity in diverse tropical forests is an important area for further research, to strengthen the links between causative mechanisms and the correlations that we report here.

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 (Figure 3; Supplementary Table 5), 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 (Figure 3). 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 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 ecosystem function[2–5], this study provides quantitative evidence for this assertion in tropical forests. Our results therefore indicate that there is a synergy between preserving diverse forests that encompass greater evolutionary heritage, and protecting ecosystem function.

Methods

Tree community data

To investigate the relationship between biodiversity and ecosystem functioning, we estimated diversity, wood productivity and aboveground biomass using data from 90 long-term forest inventory plots in the Amazon and adjacent lowland forests from the RAINFOR (Amazon Forest Inventory) network (Figure 1; Appendix 1). Data were extracted from the ForestPlots.net database, which curates tree-by-tree records from RAINFOR and other networks[51,52]. Plots were all 1 ha in size (except for two plots of 0.96 ha) and located in structurally intact and old-growth closed-canopy forest. Our analyses were restricted to continuous lowland, terra firme, moist Amazonian forests, - excluding plots in montane, swamp, seasonally dry and white-sand forests, and savannas. The ecological characteristics that influence resource uptake and thus underlie any potential relationship between ecosystem function and phylogenetic diversity may differ widely among biomes with distinct evolutionary histories[53]. For example, clades restricted to areas outside moist forests may have evolved very different unmeasured traits (e.g. higher root:shoot ratios to tolerate drought), which could lead to different relationships between evolutionary diversity and ecosystem function in comparisons across biomes. Restricting our analyses to a single biome and therefore a relatively coherent pool of genera, with similar evolutionary histories and 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 a large pan-Amazon phylogeny, including 526 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 (Supplementary Table 1). Because different metrics can reflect similar dimensions of diversity[17] (Supplementary Figure 10) we present, in the main text, the results from five diversity metrics: (1) taxonomic richness, a common and widely used diversity metric, here evaluated as the sum of all identified genera in a given community; (2) Simpson index of diversity, a common diversity metric that incorporates genus abundance, representing the probability that two stems randomly selected from a community belong to different genera; (3) total lineage diversity, the standardized effect size of phylogenetic diversity (sesPD), estimated as the sum of all branch lengths including genera within a community[16], whilst controlling for the effect of genus richness; (4) neighbour lineage diversity, which is quantified as the standardized effect size of mean nearest taxon distance (sesMNTD), whilst controlling for the effect of genus richness, which is more sensitive to relatedness near to the tips of the phylogeny[11,12] and (5) basal lineage diversity, which is quantified by mean pairwise distance (sesMPD)[11,12], whilst also controlling for the effect of genus richness and reflects phylogenetic structure at the deepest nodes[20] (see Supplementary Information for results that include all metrics).

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

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 Supplementary Information). 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 (Supplementary Table 2).

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

Statistical analyses

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

Environmental variables also influence the diversity of an ecosystem[20,64] and its ability to process and store carbon[25], and may therefore obscure relationships between diversity and ecosystem functioning. In order to account for the effect of multiple environmental variables we constructed generalised least square models where ecosystem functioning was modelled as a function of metrics related to diversity, climate, edaphic conditions, functional composition and structural variables. To avoid multicollinearity amongst variables in the model, we confirmed that variance inflation factors (VIFs) were less than five[65] for each explanatory variable. We account for spatial autocorrelation in the GLS analyses by specifying a Gaussian spatial autocorrelation structure, which is consistent with the shape of the semivariograms for biomass and productivity across this network of plots[49]. We created separate models for productivity, biomass and each diversity metric. For each response variable (productivity and biomass), we generated a set of models including all possible combinations of variables related to climate, soil, functional composition and stand structure, and selected the best model (referred to as the climate-soil-structure model) based on the Akaike Information Criterion (AIC). To investigate the additional contribution that diversity made to explain variation in both productivity and biomass, each single diversity metric was then added individually to the climate-soil-structure model. We then compared the climate-soil-structure model with models also including each single diversity metric: models with a difference in AIC greater than 2 when compared to the climate-soil-structure model, indicate models with improved support. Finally, we added pairs of diversity metrics, representing both taxonomic and evolutionary diversity (Supplementary Figure 10) into a single model to investigate whether a more complex model provides better predictive ability over single diversity metric models. Phosphorous and cation concentrations were log transformed prior to analysis. To allow comparisons of the strength of significance of the explanatory variables, they were all standardised to a mean of zero and a standard deviation of one.

We also examined the effect of the diversity metrics on wood productivity and aboveground biomass using partial correlation analyses including the variables selected in the best performing climate-soil-structure model. Partial correlation analyses are used to determine the correlation between two variables while eliminating the effect of potentially confounding variables[66].

Analyses were performed in the R Statistical software v3.1.1[67] using the vegan[68], picante[69], BiomasaFP[70], nlme[71] and ppcor[66] packages.

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

Figure 2. 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 Supplementary Information.

Figure 3. 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 water availability 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 each variable in the model, dots represent the standardized effect size and lines one standard error. In some cases, error lines are unobserved

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

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

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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. K.G.D., O.L.P., R.T.P., D.N., M.J.P.S., E.A.-D., A.A., I.A., A.A., L.E.O.C.A., A.A.M., E.J.M.M.A., L.A, G.A.A.C., O.B., C.B., J.G.B., R.G.A.B., R.J.W.B., F.B., J.L.L.C.C., W.C., J.C., A.C., J.A.C., F.C.-V., A.L.C., P.B.C., A.D.F., T.R.F., D.R.G., E.G., R.C.G., M.G., R.H., N.H., E.N.H.C., E.J.-R., T.J.K., S.L., W.F.L., G.L.-G., T.E.L., Y.M., B.S.M., B.H.M., C.M., A.M.-M., D.A.N., P.N.V., M.C.P.-M., G.P., J.J.P.III., N.C.A.P., L.P., A.P., F.R., A.R., A.Rudas., R.P.S., N.S., M.S., J.S., J.Stropp., H.T.S., J.T., R.T.-C., R.K.U., R.V.V., I.C.V., S.A.V., V.A.V., R.J.Z. and T.R.B. commented and/or approved the manuscript.

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Data availability. The permanently archived data package of the plot-level diversity, aboveground biomass, wood productivity and the genus-level phylogeny are available from https://www.forestplots.net/pt/produtos.

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