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Evolutionary diversity is associated with wood productivity in Amazonian forests

Fernanda Coelho de Souza[1*], Kyle G. Dexter[2,3], Oliver L. Phillips[1], R. Toby Pennington[3,4], Danilo Neves[5], Martin J. P. Sullivan[1], Esteban Alvarez-Davila[6], Átila Alves[7], Ieda Amaral[7], Ana Andrade[8], Luis E. O. C. Aragao[4,9], Alejandro Araujo-Murakami[10], Eric J. M. M. Arets[11], Luzmilla Arroyo[10], Gerardo A. Aymard C.[12], Olaf Bánki[13], Christopher Baraloto[14], Jorcely G. Barroso[15], Rene G. A. Boot[16], Roel J. W. Brienen[1], Foster Brown[17], José Luís C. Camargo[8], Wendeson Castro[18], Jerome Chave[19], Alvaro Cogollo[20], James A. Comiskey[21,22], Fernando Cornejo-Valverde[23], Antonio Lola da Costa[24], Plínio B. de Camargo[25], Anthony Di Fiore[26], Ted R. Feldpausch[4], David R. Galbraith[1], Emanuel Gloor[1], Rosa C. Goodman[27], Martin Gilpin[1], Rafael Herrera[28,29], Niro Higuchi[30], Eurídice N. Honorio Coronado[31], Eliana Jimenez-Rojas[32], Timothy J. Killeen[33], Susan Laurance[34], William F. Laurance[34], Gabriela Lopez-Gonzalez[1], Thomas E. Lovejoy[35], Yadvinder Malhi[36], Beatriz S. Marimon[37], Ben Hur Marimon-Junior[37], Casimiro Mendoza[38], Abel Monteagudo-Mendoza[39], David A. Neill[40], Percy Núñez Vargas[41], Maria C. Peñuela Mora[42], Georgia C. Pickavance[1], John J. Pipoly III[43], Nigel C. A. Pitman[44], Lourens Poorter[45], Adriana Prieto[46], Freddy Ramirez[47], Anand Roopsind[48], Agustin Rudas[46], Rafael P. Salomão[49,50], Natalino Silva[50], Marcos Silveira[51], James Singh[52], Juliana Stropp[53], Hans ter Steege[13,54], John Terborgh[55,56], Raquel Thomas-Caesar[57], Ricardo K. Umetsu[37], Rodolfo V. Vasquez[39], Ima Célia-Vieira[49], Simone A. Vieira[58], Vincent A. Vos[59,60], Roderick J. Zagt[16] and Timothy R. Baker[1]

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 emerged as independent predictors of wood productivity. Amazon forests that contain greater evolutionary diversity and a higher proportion of rare species have higher productivity. While climatic and edaphic variables are together the strongest predictors of productivity, our results show 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.

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 were associated with greater biomass and productivity and variability in the amount of evolutionary history shared within a group of species was 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 generalized, 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

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A full list of affiliations appears at the end of the paper.

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 (for example, 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 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, as well as the relative abundance of major clades in the community[20]. All of these metrics attain higher values in communities comprising 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 (Fig. 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 phylogenetic diversity, MPD and MNTD than expected given their richness (that is, 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 (that is, variation in richness is a poor predictor of variation 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 (that is, 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 hypothesized that evolutionary diversity would be a stronger predictor of ecosystem function than taxonomic measures of diversity[2].

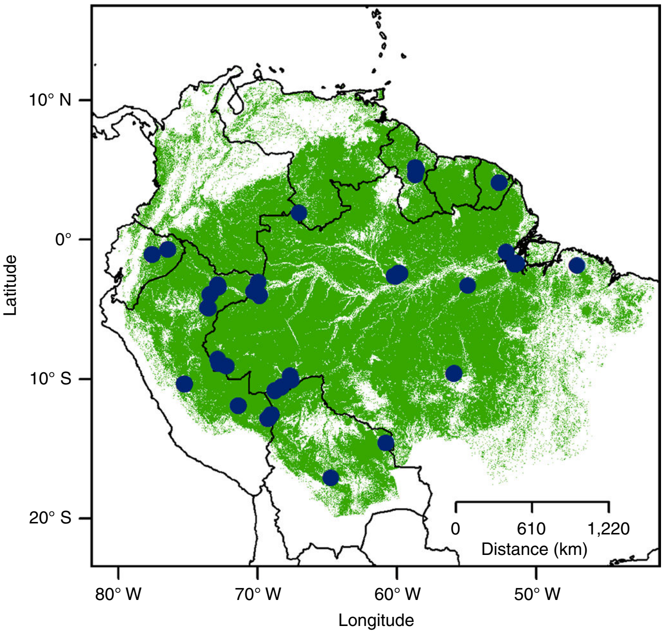

Fig. 1 | Location of plots. Location of 90 1-ha permanent inventory plots shown on a forest cover map[72] produced from global land cover data. Plots are all located in lowland moist forests on well-drained soils across the Amazon Basin (see Methods for details).

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 accounted for variation in these factors in all of 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 the Simpson index. Taxon richness was chosen because it is widely used in comparative studies, and the Simpson index was chosen 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 of 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

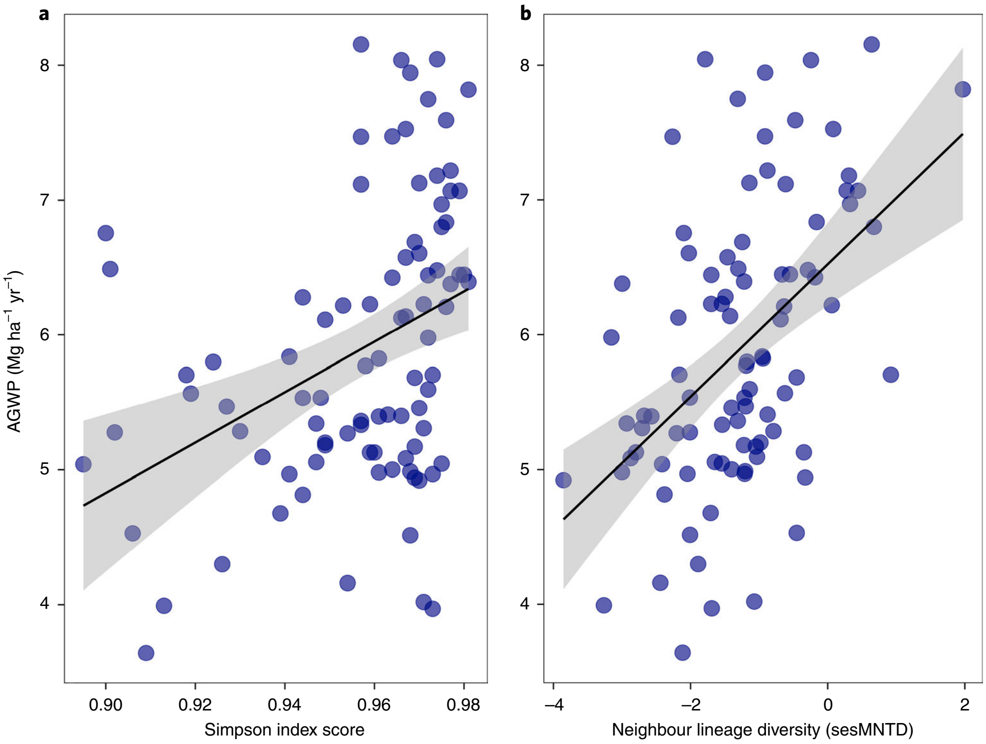

Fig. 2 | Bivariate relationships between aboveground wood productivity (AGWP) and the diversity variables included in the best-performing model. **a**,**b**, Relationship between AGWP and Simpson index (**a**) and neighbour lineage diversity (**b**), using data from 90 1-ha plots across Amazonia. Shaded areas represent 95% confidence intervals. Solid lines indicate significant bivariate correlations between productivity and diversity metrics. Relationships for the other taxonomic and phylogenetic diversity metrics are included in the Supplementary Information.

(Fig. 2 and 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 Akaike information criterion (AIC) values) contained both evolutionary (standardized effect size of MNTD (sesMNTD)) and taxonomic (Simpson index) measures of diversity (correlation coefficient $R^2 = 0.47$; $\Delta\mathrm{AIC} = -2.5$, in relation to the model excluding both taxonomic and evolutionary diversity metrics; Fig. 3 and Table 1). This shows that these metrics reflect distinct aspects of diversity that are both important for understanding patterns of productivity (Supplementary Fig. 10). Partial correlation analysis produced similar results to the model selection approach (Supplementary Table 4): sesMNTD (Kendall's $\tau = 0.15$; $P = 0.044$) and the Simpson index ($\tau = 0.15$; $P = 0.046$) 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 Supplementary Appendix 4).

Climatological and soil variables were also associated with variation in productivity (Fig. 3, Supplementary Fig. 4 and Supplementary Table 4). Mean annual temperature, climatic water deficit, and soil total phosphorus, magnesium and potassium were all associated with productivity[25] (Fig. 3), with higher rates of wood growth typical of areas in the western Amazon with low water deficit and greater nutrient availability (that is, total phosphorus and magnesium). Although the standardized effect sizes of some environmental variables, such as water deficit, were 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 (Fig. 3 and Supplementary Table 4).

Bivariate correlations indicated significant negative associations between biomass and all diversity metrics (Supplementary Fig. 5 and Supplementary Table 3). However, biodiversity and biomass were almost completely unrelated after accounting for variation in climate, soil, forest structure and mean functional composition (Fig. 3 and Supplementary Table 5), in contrast with the positive, significant biodiversity–productivity relationships (Supplementary Table 4). Instead, biomass was largely determined by variation in wood density (Fig. 3, Supplementary Fig. 7 and 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 (Fig. 3 and Supplementary Appendix 4), but these results were not supported by the partial correlation analysis (Supplementary Table 5).

Discussion

This study shows 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 (Figs. 2 and 3, Table 1 and 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 comparable to the effects of some environmental variables within this analysis, such as soil phosphorus (Fig. 3).

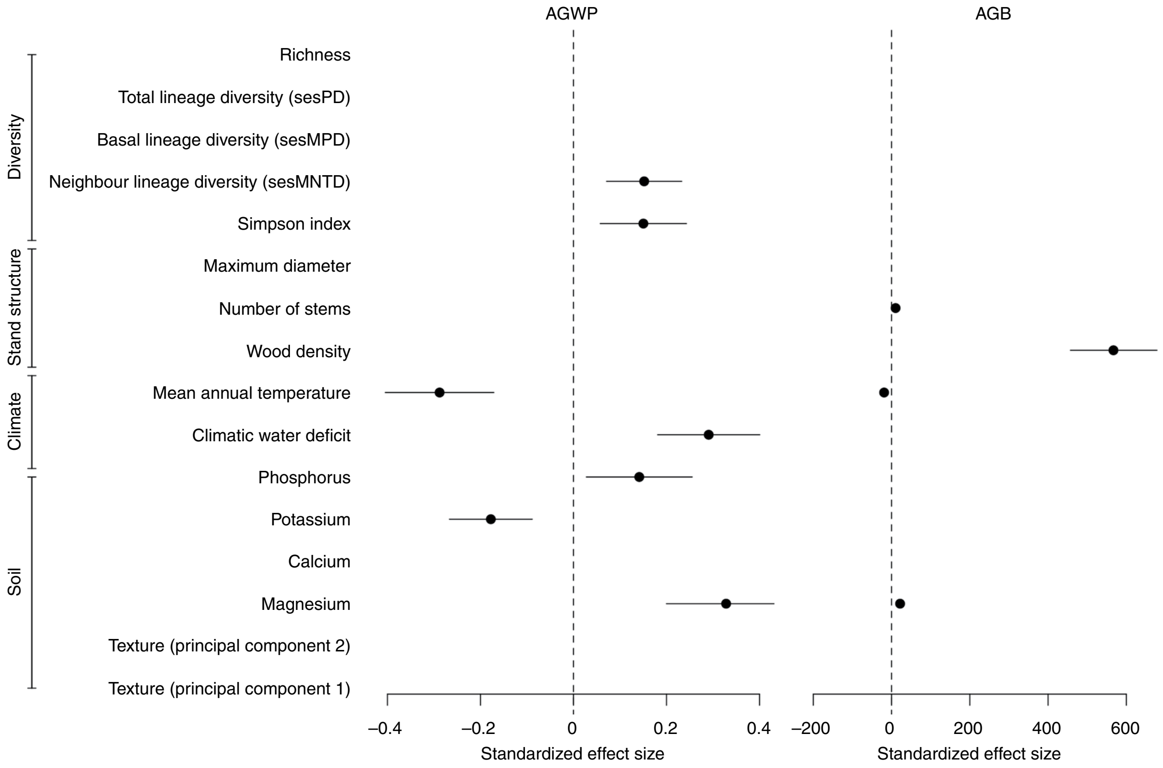

Fig. 3 | Standardized effect sizes for the best-fit model for both wood productivity and aboveground biomass. Both models include diversity metrics, structural attributes, climate and soil variables selected based on the lowest AIC values and largest proportion of variance explained. The best model for AGWP includes neighbour lineage diversity and the Simpson index as biodiversity metrics, as well as mean annual temperature, climatic water deficit, total phosphorus, magnesium and potassium. Greater productivity is found in plots with lower mean annual temperature and higher water availability, and on soils with greater amounts of soil phosphorus and magnesium and lower amounts of potassium. The best model for aboveground biomass (AGB) included wood density, number of stems, magnesium and mean annual temperature. The relationship between AGB and wood density is nonlinear. In all AGB analyses, wood density was specified with linear and quadratic terms, but for clarity, in the graph, the effect size is shown only for the quadratic term. For each variable in the model, dots represent the standardized effect size and lines represent 1 s.d. In some cases, error lines are unobserved due to very small standard deviations. See Supplementary Figs. 4 and 7 for detailed bivariate correlations, and Supplementary Appendix 4 for all of the coefficients of the models.

Table 1 | Results for GLS models across 90 1-ha plots for AGWP and AGB.

Model	AGWP			AGB		
	R^2	AIC	ΔAIC	R^2	AIC	ΔAIC
Climate–soil–structure model + sesMNTD + Simpson index	**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 index	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	**0.74**	**972.00**	**0**

Biomass and productivity were modelled as a function of diversity metrics, structural and compositional attributes, and climate and soil variables, and accounted for spatial autocorrelation using a Gaussian correlations structure. The best model for AGWP is the climate–soil–structure model + sesMNTD + Simpson index. The best model for AGB is the climate–soil–structure model. Full coefficients are taken from the models shown in Supplementary Appendix 4. The results are 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. ΔAIC 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, and total phosphorus, magnesium and potassium. For AGB, the climate–soil–structure model includes wood density, number of stems, magnesium and mean annual temperature.

A range of mechanisms may underlie the significant relationships between neighbour lineage diversity (sesMNTD), Simpson index and productivity (Fig. 2, Table 1 and Supplementary Table 4), including both sampling effects (that is, 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 the 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 the Simpson index or sesMNTD on wood productivity (see Supplementary Text and Supplementary Fig. 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] show 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 2,457 trees in Madre de Dios in the Peruvian Amazon[38,39], crown architecture varies widely among families (Supplementary Fig. 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 belowground resource allocation, tree height/diameter allometry, hydraulic traits or functional groups (for example, nitrogen/non-nitrogen fixers) that may affect productivity.

The effect of sesMNTD and the 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 (that is, 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 (for example, 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 the Simpson 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 are in contrast with our initial prediction. Perhaps both variation in the relative abundance distribution among communities (best captured by the Simpson 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 with 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 differed 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], as well as 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 in contrast with the positive effect of taxonomic and evolutionary diversity on productivity, biomass was strongly determined by functional characteristics (Fig. 3 and 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 (Fig. 3). These results corroborate a recent meta-analysis in tropical forests, which found that stand structural (for example, number of stems) and community mean functional trait variables (for example, wood density) 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 probably 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 (Fig. 1 and Supplementary 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 (for example, higher root-to-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 of 16.1 years in total (range: 2.0–28.6 years), with regular recensuses. All trees and palms with diameter at breast height 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 genus level, with a minimum of 70% identified to genus level 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 Information. Our analyses included only those genera for which 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 Fig. 10) we present 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) the 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] while controlling for the effect of genus richness); (4) neighbour lineage diversity (quantified as the sesMNTD while 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 (quantified by the standardized effect size of the mean pairwise distance (sesMPD)[11,12] while also controlling for the effect of genus richness, and reflecting 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 (that is, phylogenetic diversity, 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 (−) phylogenetic diversity, MNTD or MPD than expected given their genus richness. We calculated the standardized 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) divided by the standard deviation of values across the randomizations. 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 while 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: (1) the sum of tree growth alive in the first and last censuses; (2) the growth of trees that recruited during the census interval; (3) estimates of unobserved growth of trees that died during the census interval; and (4) 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 the census interval length (see Supplementary Information for details).

Aboveground biomass per stem was estimated using a pan-tropical, three-parameter equation $\mathrm{AGB} = 0.0673 \times (\mathrm{WD}\, D^2 H)^{0.976}$ from Chave et al.[60], where WD is the stem wood density (in g cm^{-3}) from the Global Wood Density database[29,61], D is the tree diameter (in cm) at 1.3 m or above the buttress, and H is the tree height (in m). Tree height was estimated based on regional diameter–height Weibull equations[62]. Similar to productivity, to reduce the influence of potential stochastic changes, and due to variation in the census interval within plots, we estimated biomass per plot using a weighted average across multiple censuses (see Supplementary Information for details). We extracted wood density data 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 the mean annual temperature (°C; extracted from the WorldClim dataset at 30 s (~1 km^2) resolution[27]) and maximum climatic water deficit (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}), and potassium, magnesium, calcium and sodium concentrations (mmol$_{\mathrm{eq}}$ kg^{-1}), collated at ForestPlots.net and based on intensive soil sampling from each RAINFOR plot that used standardized 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. The first axis was negatively and strongly correlated with sand content, whereas the second was negatively correlated 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. In cases where this information was unavailable, data were 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 the 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 the 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 a diameter at breast height >10 cm across multiple censuses.

Statistical analyses. To investigate the strength of the relationship between each measure of ecosystem functioning (that is, productivity and biomass) and the set of diversity metrics in each plot, we conducted: (1) bivariate Kendall's τ non-parametric correlation tests; (2) generalized least-squares (GLS) modelling; 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. To account for the effects of multiple environmental variables, we constructed GLS 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 among variables in the model, we confirmed that variance inflation factors 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 of the 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 AIC. To investigate the additional contribution that diversity made to explaining 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: a difference in AIC > 2 compared with the climate–soil–structure model indicated that a model had improved support. Finally, we added pairs of diversity metrics, representing both taxonomic and evolutionary diversity (Supplementary Fig. 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 before analysis. To allow comparisons of the strength of significance of the explanatory variables, they were all standardized to a mean of zero and a standard deviation of one.

We also examined the effects 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 were used to determine the correlation between two variables while eliminating the effect of potentially confounding variables[66].

Analyses were performed with the R statistical software (version 3.1.1)[67], using the vegan[68], picante[69], BiomasaFP[70], nlme[71] and ppcor[66] packages.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

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

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Author contributions

F.C.d.S., R.T.B. and K.G.D. conceived the study. F.C.d.S., R.T.B., O.L.P. and K.G.D. designed the study. F.C.d.S., K.G.D. and R.T.B. produced the phylogeny. F.C.d.S. analysed the data and wrote the paper. All co-authors collected field data or managed data. O.L.P. and Y.M. conceived the RAINFOR forest census plot network. K.G.D., O.L.P., R.T.P., D.N., M.J.P.S., E.Á.-D., A.Alves, I.A., A.Andrade, 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.C.C., W.C., J.C., A.C., J.A.C., F.C.-V., A.L.d.C., P.B.d.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.-J., C.M., A.M.-M., D.A.N., P.N.V., M.C.P.M., G.C.P., J.J.P., N.C.A.P., L.P., A.P., F.R., A.Roopsind, A.Rudas, R.P.S., N.S., M.S., J.Singh, 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 R.T.B. commented and/or approved the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Correspondence and requests for materials should be addressed to F.C.

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[1]School of Geography, University of Leeds, Leeds, UK. [2]School of Geosciences, University of Edinburgh, Edinburgh, UK. [3]Royal Botanic Garden Edinburgh, Edinburgh, UK. [4]Geography Department, College of Life and Environmental Sciences, University of Exeter, Exeter, UK. [5]Department of Botany, Federal University of Minas Gerais, Belo Horizonte, Brazil. [6]Escuela de Ciencias Agropecuarias y Ambientales, Universidad Nacional Abierta y a Distancia, Sede José Celestino Mutis, Bogotá, Colombia. [7]Projeto TEAM—Manaus, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil. [8]Biological Dynamics of Forest Fragment Project, INPA and STRI, Manaus, Brazil. [9]National Institute for Space Research, São José dos Campos, Brazil. [10]Museo de Historia Natural Noel Kempff Mercado, Universidad Autonoma Gabriel Rene Moreno, Santa Cruz, Bolivia. [11]Wageningen Environmental Research, Wageningen University and Research, Wageningen, the Netherlands. [12]UNELLEZ-Guanare, Programa del Agro y del Mar, Herbario Universitario PORT, Mesa de Cavacas, Venezuela. [13]Naturalis Biodiversity Center, Leiden, the Netherlands. [14]International Center for Tropical Botany, Department of Biological Sciences, Florida International University, Miami, FL, USA. [15]Universidade Federal do Acre, Rio Branco, Brazil. [16]Tropenbos International, Wageningen, the Netherlands. [17]Woods Hole Research Center, Boston, MA, USA. [18]Programa de Pós-Graduação em Ecologia e Manejo de Recursos Naturais, Universidade Federal do Acre, Rio Branco, Brazil. [19]Laboratoire Evolution et Diversité Biologique, Université Toulouse III Paul Sabatier, Toulouse, France. [20]Jardín Botánico de Medellín Joaquín Antonio Uribe, Medellin, Colombia. [21]National Park Service, Fredericksburg, VA, USA. [22]Smithsonian Institution, Washington DC, USA. [23]Proyecto Castaña, Madre de Dios, Peru. [24]Centro de Geociencias, Universidade Federal do Para, Belem, Brazil. [25]Centro de Energia Nuclear na Agricultura, Universidade de São Paulo, São Paulo, Brazil. [26]Department of Anthropology, University of Texas at Austin, Austin, TX, USA. [27]Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden. [28]Centro de Ecología, IVIC, Caracas, Venezuela. [29]Institut für Geographie und Regionalforschung, Univerity of Vienna, Vienna, Austria. [30]Instituto Nacional de Pesquisas da Amazônia, Manaus, Brasil. [31]Instituto de Investigaciones de la Amazonia Peruana, Iquitos, Peru. [32]Universidad Nacional de Colombia, Bogotá, Colombia. [33]GTECA—Amazonica, Santa Cruz, Bolivia. [34]Centre for Tropical Environmental and Sustainability Science and College of Science and Engineering, James Cook University, Cairns, Queensland, Australia. [35]Environmental Science and Policy Department, George Mason University, Washington DC, USA. [36]Environmental Change Institute, School of Geography and the Environment, University of Oxford, Oxford, UK. [37]Universidade do Estado de Mato Grosso, Nova Xavantina, Brazil. [38]Unidad Académica del Trópico, Escuela de Ciencias Forestales, Universidad Mayor de San Simón, Sacta, Bolivia. [39]Jardín Botánico de Missouri, Pasco, Peru. [40]Facultad de Ingeniería Ambiental, Universidad Estatal Amazónica, Puyo, Ecuador. [41]Universidad Nacional San Antonio Abad del Cusco, Cusco, Peru. [42]Universidad Regional Amazónica Ikiam, Tena, Ecuador. [43]Broward County Parks and Recreation Division, Davie, FL, USA. [44]Center for Tropical Conservation, Duke University, Durham, NC, USA. [45]Forest Ecology and Forest Management Group, Wageningen University and Research, Wageningen, the Netherlands. [46]Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogota, Colombia. [47]Universidad Nacional de la Amazonía Peruana, Iquitos, Peru. [48]Department of Biological Sciences, Boise State University, Boise, ID, USA. [49]Museu Paraense Emilio Goeldi, Belém, Brazil. [50]Universidade Federal Rural da Amazônia, Belém, Brasil. [51]Museu Universitário, Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre, Rio Branco, Brazil. [52]Guyana Forestry Commission, Georgetown, Guyana. [53]Institute of Biological and Health Sciences, Federal University of Alagoas Maceio, Maceio, Brazil. [54]Systems Ecology, Vrije Universiteit, Amsterdam, the Netherlands. [55]Department of Biology and Florida Museum of Natural History, University of Florida, Gainesville, FL, USA. [56]School of Science and Engineering, James Cook University, Cairns, Queensland, Australia. [57]Iwokrama International Centre for Rainforest Conservation and Development, Georgetown, Guyana. [58]Núcleo de Estudos e Pesquisas Ambientais, Universidade Estadual de Campinas, Campinas, Brazil. [59]Centro de Investigación y Promoción del Campesinado—Regional Norte Amazónico, Riberalta, Bolivia. [60]Universidad Autónoma del Beni, Riberalta, Bolivia. *e-mail: fecoelhos@gmail.com

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Corresponding author(s): Fernanda Coelho de Souza

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Software and code

Policy information about availability of computer code

Data collection	No software was used for data collection.
Data analysis	- Multiple DNA sequence alignments, were conducted using MAFFT (v.6.8226) followed by manual adjustments in Mesquite; - To generate a maximum likelihood tree, rbcL and matK sequences were combined using RAxML v.7.2.7 on the Cipres server (https://www.phylo.org); - Bayesian Markov Chain Monte Carlo (MCMC) was conducted using BEAST (v.1.8.2) on the CIPRES server; - Branch-lengths and divergence times were assigned using TreeAnnotator; - Taxonomic diversity metrics were calculated using vegan package (v. 2.0-1.0) in the R statistical software (v. 3.1.1); - Phylogetneic diversity metrics were calculates using picante package (v. 1.6-2) in R; - Aboveground biomass and wood productivity were calculated using BiomsaFP package (v. 1.1) in R; - Generalised Least Square models were conducted using nlme package (v. 3.1-117) in R; - Model selection was conducted using MuMIn package (v. 1.15.1) in R; - Partial correlation analyses were conducted using ppcor (v. 1.0) in R.

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Once the paper is accepted the permanently archived data package of the plot-level diversity, aboveground biomass, wood productivity and the genus-level phylogeny will be available from https://www.forestplots.net/pt/produtos.

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We used a newly constructed pan-Amazon phylogeny including 526 genera based on two chloroplast DNA gene regions and 90 long-term monitoring plots across Amazonia to investigate the relationships between tree diversity and ecosystem function. This study provides the first evidence that evolutionary diversity is related to wood productivity at large spatial scales in natural ecosystems, suggesting that there is a synergy between preserving diverse forests that encompass greater evolutionary heritage and protecting ecosystem function.
Research sample	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.
Sampling strategy	We used all 90 inventory plots from lowland moist forests on well-drained soils across the Amazon Basin.
Data collection	Forest plots were established between 1975-2010 and were all monitored for at least two years, with regular recensuses and a mean total monitoring period of 16.1 years. All trees and palms with diameter at breast height (dbh) greater than 10 cm were included in the analyses, records of tree mortality and identifications of recruits were conducted using uniform and standardized protocols. Data were extracted from the ForestPlots.net database, which curates tree-by-tree records.
Timing and spatial scale	Plots were established between 1975-2010, monitored for at least 2 years and all 1 ha in size (except for two plots of 0.96).
Data exclusions	Our analyses were restricted to continuous lowland, terra firme, moist Amazonian forests and restricted to a single biome with relatively coherent pool of genera with similar evolutionary stories and ability to disperse and mix across Amazonia over geological timescales. We excluded plots in montane, swamp, seasonally dry, white-sand and savannas.
Reproducibility	All attempts to repeat the analyses were successful.
Randomization	We included environmental variables as covariates in our Generalized Least Square models.
Blinding	Blinding was not used in this study as it is not appropriate in a large-scale ecological study such as this.

Did the study involve field work? ☐ Yes ☐ No

Field work, collection and transport

Field conditions	This study was conducted in structurally intact and old-growth closed-canopy forest with mean annual temperature varying from 23.8 to 27.2 Celsius degrees and cumulative watter deficit from 0 to - 473.4.
Location	Forest plots were all located in Amazonia lowland old-growth forests, please see Appendix 1 for detailed information.
Access and import/export	Fieldwork in Amazonia has been conducted by, and in collaboration with, many South American institutions over many years to generate the long-term inventory record, in compliance with appropriate national laws. Permits for fieldwork iclude: Peru, from the Peruvian Protected Areas Authorithy (SERNANP), permits 001-2011, 008-2013, 021-2014; from the Peruvian Forest Service (SERFOR) permits 0198-2011, 0148-2012, 383-2012, 077-2014; Bolivia, from Ministerio de Medio Ambiente y Agua (MMAyA) permit (026/2009); and Brazil, from the Brazilian Research Council (CNPq) permit (00048/2013-5).
Disturbance	No disturbance were caused by the study.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging