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1 Diversity and carbon storage across the tropical forest biome

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106 Abstract

Tropical forests are global centres of biodiversity and carbon storage. Many tropical countries aspire 107 108 to protect forest to fulfil biodiversity and climate mitigation policy targets, but the conservation 109 strategies needed to achieve these two functions depend critically on the tropical forest tree diversity-110 carbon storage relationship. Assessing this relationship is challenging due to the scarcity of inventories where carbon stocks in aboveground biomass and species identifications have been 111 112 simultaneously and robustly quantified. Here, we compile a unique pan-tropical dataset of 360 plots located in structurally intact old-growth closed-canopy forest, surveyed using standardised methods, 113 allowing a multi-scale evaluation of diversity-carbon relationships in tropical forests. Diversity-114 carbon relationships among all plots at 1 ha scale across the tropics are absent, and within continents 115 116 are either weak (Asia) or absent (Amazonia, Africa). A weak positive relationship is detectable within 1 ha plots, indicating that diversity effects in tropical forests may be scale dependent. The absence of 117 clear diversity-carbon relationships at scales relevant to conservation planning means that carbon-118 centred conservation strategies alone would inevitably miss many high diversity ecosystems. As 119 120 tropical forests can have any combination of tree diversity and carbon stocks both will require explicit 121 consideration when optimising policies to manage tropical carbon and biodiversity. 122 123 124 125

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130 Introduction

Biodiversity is threatened by the conversion of natural habitats and climate change ¹⁻³. Tropical forests 131 are under particular pressure, whilst also being among the most diverse biomes on the planet ⁴. By 132 legally protecting areas, tropical countries can safeguard ecosystems with high biodiversity value ⁵, 133 and so address their policy targets to reduce biodiversity loss ⁶. Likewise, carbon losses from the 134 conversion of forest to other land-uses represent major emission sources for many tropical countries ⁷, 135 136 and so incentives such as the UN REDD+ policy framework have emerged to help safeguard areas with high carbon stocks⁸. Yet the potential for protection of carbon-rich areas to directly benefit 137 biodiversity, and vice versa, depends critically on the relationship between biomass carbon and tree 138 diversity, at relevant scales. A positive relationship would indicate potential synergies while a 139 140 negative relationship would indicate difficult trade-offs between biodiversity and carbon conservation ⁹. In the absence of any relationship, optimal solutions for protected area placement need to carefully 141 and separately consider the distribution of carbon stocks and the distribution of biodiversity ¹⁰. 142 Understanding these distributions and potential carbon-biodiversity trade-offs is important, as 143 144 protecting some forest can divert threats onto other unprotected areas ¹¹.

The expected form of diversity-carbon relationships in tropical forests and the strength and scale-145 dependence of any underlying mechanisms are uncertain. Numerous experimental studies have 146 147 demonstrated that plant diversity promotes biomass production, with niche partitioning and positive species interactions allowing diverse communities to exploit available resources more efficiently ^{12,13}. 148 Diversity can also increase productivity through selection effects, where communities that contain a 149 larger sample of the species pool are more likely to contain high functioning species that contribute 150 strongly to ecosystem productivity ¹⁴. Positive diversity-productivity relationships have been found in 151 low diversity mid-latitude forests ¹⁵⁻¹⁷, potentially due to increased canopy packing through 152 complimentary canopy architecture in higher diversity forests ¹⁸. Yet, it is unclear how significant 153 154 such mechanisms are in diverse tropical forests, as experimental and theoretical work indicates that the positive effect of diversity may saturate at high species richness ^{12,19}. Furthermore, additional traits 155 associated with high-productivity species could conceivably lead to a positive diversity-biomass 156

mortality relationship, as highly productive stands tend to be composed of trees with shorter biomass
residence times ²¹. Overall, this alongside high-productivity stands consisting of smaller, lighterwooded trees ²⁰, may lead to a negative diversity-biomass carbon storage relationship.

160 Previous studies investigating the tree diversity-carbon stock relationship in tropical forests have reported a positive relationship at fine spatial scales ^{22,23}. However, the form of the relationship at the 161 stand-level (i.e. among 1 ha plots) is less clear (Table 1), as some studies report a continued positive 162 diversity-carbon relationship among sampling locations ²³⁻²⁵, while one other did not detect a 163 relationship among 1 ha subplots within 25 larger plots ²². Thus, while there is some evidence that 164 higher tree diversity promotes higher carbon stocks per unit area in diverse tropical forests ²²⁻²⁴, it is 165 unclear whether any positive effect is strong enough for carbon and diversity to co-vary at scales 166 relevant to conservation planning. 167

Here we analyse a unique dataset of 360 inventory plots across the three major tropical forest blocs in 168 169 the Americas, Africa, and the Sundaland biogeographic region in Southeast Asia (subsequently 170 referred to as Asia). Importantly, this dataset greatly improves sampling of the two most extensive 171 contiguous areas of tropical forest in the world, centred on the Amazon and Congo Basins (Table 1). Each plot was surveyed by standardised methods and is of uniform size, allowing robust 172 quantification of co-located aboveground live carbon and tree diversity estimates. We analyse this 173 174 standardised, multi-continental dataset at three spatial scales. Firstly, we explore forest carbon and diversity patterns within South America, Africa and Asia, in order to characterise among-continent 175 variations in tree alpha diversity, beta diversity, and carbon stocks. Secondly, we assess stand-level (1 176 ha) diversity-carbon relationships within each of the continents, initially by looking at the bivariate 177 association of tree diversity metrics and carbon stocks per unit area, and then re-examining the 178 relationships after controlling for potentially confounding environmental variation and residual spatial 179 autocorrelation. Finally, we investigate fine-scale relationships between tree diversity and carbon 180 181 within 0.04 ha subsections of 1 ha plots, where environmental differences that may obscure a positive diversity effect on carbon are accounted for. This approach allows us to (1) examine basic patterns of 182 diversity and carbon across the biome, (2) test if more diverse tropical forests are also in fact more 183

184 carbon dense, and (3) explore whether relationships between diversity and carbon-storage, after accounting for the effect of potentially confounding variables, are consistent with tree diversity 185 having a positive effect on carbon in tropical forests. We conduct additional analyses to assess support 186 for the operation of selection effects and niche complementarity at different spatial scales. We focus 187 188 on carbon in aboveground live biomass derived using allometric relationships, and diversity metrics relating to taxon richness. We also repeat analyses using alternative diversity metrics that consider 189 species abundance and functional diversity for which results and inferences are similar (see 190 Supplementary Information). 191

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193 Results

194 Pantropical forest carbon and diversity

Our standardised methods of inventory reveal great variation in both aboveground live carbon stocks 195 and tree diversity within continents and across the humid tropical forest biome. While it is possible to 196 find almost any combination of both parameters (Fig. 1), the plots reveal large differences in carbon 197 198 and diversity amongst the three continents (Table 2). African tropical forests are characterised by high carbon storage per unit area and consistently low alpha-diversity (even the most species-rich African 199 plot had fewer species than the median species richness recorded in South America and Asia). By 200 contrast, in South American plots carbon storage per unit area was lower than in African forests (Fig. 201 202 1). Nevertheless both diversity and carbon vary greatly within South America, as reflects previously reported gradients in species richness ²⁶ and biomass ^{27,28}, with some stands in the Guiana Shield 203 region containing carbon stocks comparable to forests in the paleotropics (Fig. 1). Asian forests differ 204 205 again, having on average both high carbon storage per unit area and high tree diversity. These 206 differences in diversity amongst continents remain when diversity metrics are standardised per 300 stems (Table 2), and when the analysis was repeated only including plots with >90% of stems 207 208 identified to species level (Supplementary Table 3), thus are robust to differing stem numbers (lower 209 in Africa, negative binomial GLM $\chi^2 = 188.6$, P < 0.001), and are unaffected by levels of tree

identification (not different amongst continents, Kruskal-Wallis test H = 2.1, P = 0.335). This pantropical assessment of forest carbon stocks and diversity is consistent with previous reports from individual continents, indicating high biomass in forests in Africa ²⁹ and Borneo ^{30,31}, high diversity in central and western Amazonia ³² and low diversity in Africa ^{33,34}. Our analysis demonstrates that forests across the Sundaland region of Southeast Asia are not only amongst the most diverse in the tropics, as noted elsewhere³³, but also amongst the most carbon-dense.

216 Beta-diversity also showed contrasting patterns amongst continents. Tree communities in

217 neighbouring forests were least similar in Asia and most similar in Africa, where diversity rapidly

218 saturates over geographic distance and plots (Fig. 2, Supplementary Fig. 11). However while

similarity in species composition decayed most strongly with distance in South America, there was
weaker distance decay in Asia (Fig. 2, Supplementary Fig. 12). As a result, while adjacent stands
differ most in Asia, at distances >1,000 km plots in Asia are no more dissimilar than equidistant plot
pairs in South America. Differences in beta diversity could have been driven by differences in gamma
diversity ³⁵. However, local tree communities remained more similar in Africa than other continents
when null models were used to account for variation in gamma diversity (Supplementary Fig. 13).

225 Gamma diversity was comparable in South America and Asia ³³, so was unlikely to drive differences

in the distance decay of tree community similarity in those continents.

227 Large-scale diversity-carbon relationships

Notably, aboveground carbon stocks in live biomass per unit area was unrelated to tree species 228 229 richness amongst 1 ha plots, whether analysed within continents or when combining all data in a pan-230 tropical analysis (Fig. 1, Table 3). Correlations with other diversity metrics varied in sign but were also non-significant (Table 3, Supplementary Fig. 14). Thus, in tropical forests high values of 231 diversity and biomass carbon are associated neither at the biome nor the continental scale; instead 232 they vary independently. We note that while in both South America and Africa there is sufficient 233 statistical power to detect even small effects of diversity had they existed, in Asia power was only 234 sufficient to detect relatively large effect sizes (Table 2). 235

236 Since confounding environmental variables might obscure any underlying effect of tree diversity on carbon stocks, we next applied multiple regression including climate and edaphic variables as 237 covariates to statistically control for environmental variation that might otherwise obscure the effect 238 of diversity. In ordinary least squares multiple regression models, there was a consistent negative 239 240 relationship between diversity and carbon in South America, and no significant relationship in Africa and Asia (Fig. 3b). When the analysis was repeated using simultaneous autoregressive error models to 241 account for spatial autocorrelation, diversity was not supported as a predictor in South America or 242 Africa (Fig. 3c). In Asia, while there were significant positive relationships between carbon and both 243 Fisher's α and species richness (Fig. 3c), environmental variables were more important predictors of 244 carbon stocks based on their occurrence in low AIC_C models (Supplementary Table 5) and other 245 246 diversity metrics were not supported as predictors of carbon stocks (Fig. 3c). Thus, overall no 247 consistent pan-tropically applicable relationship between diversity and carbon stocks was observed. 248 Instead, carbon stocks per unit area was influenced by climate and soil (Supplementary Fig. 15, 249 Supplementary Table 5). In South America and Africa annual cumulative water deficit was the strongest environmental predictor of carbon stocks, as indicated by high $\sum AIC_c$ weights (≥ 0.98), and 250 251 in South America a positive effect of soil fertility was also evident (Supplementary Fig. 15, 252 Supplementary Table 5). In Asia, where no plots experienced cumulative water deficit, carbon stocks 253 per unit area increased with mean annual precipitation ($\sum AIC_C$ weights = 1) and declined with mean annual temperature ($\sum AIC_C$ weights = 0.65). 254

255 Carbon stocks per unit area was also related to structural attributes, increasing with basal area and basal area-weighted mean wood density, but not with stem density (Supplementary Fig. 16). While 256 consistent with previous studies²³, this is hardly surprising as both wood density and basal area are 257 258 constituents of biomass estimates. Critically, these two structural attributes of carbon stocks per unit 259 area were themselves largely unrelated to species richness (Supplementary Fig. 16), indicating that 260 diversity is not a correlate of the key structural factors that lead to high biomass in some tropical forest stands. Stem size inequality, which has been posited as a mechanism linking diversity and 261 carbon in boreal forests ³⁶, was positively related to carbon but unrelated to species richness 262

263 (Supplementary Fig. 17). Inclusion of mean wood density (a proxy for stem turnover) in multiple regression models did not affect diversity-carbon relationships (Supplementary Table 6), indicating 264 that the lack of a consistent diversity-carbon relationship is unlikely to be due to variation in 265 mortality. Finally, we also used structural equation modelling to examine the relationship between 266 267 diversity and carbon while explicitly modelling the effect of climate and soil on both tree species richness and carbon stocks. In this modelling framework, there were non-significant positive 268 relationships between species richness and carbon in Africa and Asia and a significant negative 269 relationship in South America (Supplementary Figure 18). 270

271 <u>Fine-scale diversity-carbon relationships</u>

272 Amongst 0.04 ha subplots within each plot most environmental differences in climate and soil are 273 implicitly accounted for. Here, relationships between species richness and carbon were on average 274 significantly positive when considering all 266×1 ha plots for which we had subplot-scale data (onesample Wilcoxon test, P = 0.007), and significant for plots within Africa (n = 111 plots, one-sample 275 Wilcoxon test, P = 0.022) and South America alone (n = 118 plots, one-sample Wilcoxon test, P =276 277 0.013, Fig. 4). Within these plots, 148 (55.6%) had a positive richness-carbon relationship and 118 (44.4%) a negative relationship (Fig. 4). Overall the richness-carbon relationship was weak but 278 positive ($\beta = 0.096 \pm 0.048$ SE). This implies that doubling species richness per 0.04 ha would 279 280 increase carbon stocks by 6.9%, with similar relationships for other diversity metrics (Supplementary Table 7). This is consistent with an independent within-plot study of 25 plots which showed a 7% 281 effect size of diversity on aboveground biomass at the 0.04 ha spatial scale, but no relationship at the 282 1 ha scale 22 . 283

284 Examining support for niche complementarity and selection effects

There was a statistically significant positive relationship between a multivariate metric of functional diversity incorporating wood density and maximum diameter traits and carbon stocks at the 0.04 ha scale (linear mixed effects model, P < 0.001, Supplementary Figure 1), but this relationship was not significant in any continent at the 1 ha scale (linear regression models, $P \ge 0.139$, Supplementary 289 Figure 1). Carbon stocks increased with the community weighted means of both wood density and 290 maximum diameter traits at both 0.04 ha (linear mixed effects models, P < 0.001, Supplementary 291 Figure 4) and 1 ha scales (linear regression models, $P \le 0.049$, Supplementary Figure 4), indicating 292 that carbon stocks was positively related to the functional dominance of potentially large and dense 293 wooded species. The probability of sampling a species with large maximum size or dense wood 294 increased through the range of species richness values typical of 0.04 ha subplots, but tended to saturate by the species richness values typical of 1 ha plots, with the exact form of this relationship 295 depending on the threshold used to define a large or dense wooded species and whether the null model 296 used to sample species randomly selected species from the pool available within a continent or 297 sampled species according to their relative frequency of occurrence (Supplementary Figures 5 - 10). 298 For example, the expected probability of sampling a tree species with maximum diameter ≥ 70 cm, as 299 300 assessed using a null model randomly selecting species from the pool of species recorded in plots within each continent, increased from 0.760 to 0.878 over the interquartile range of species richness 301 found in 0.04 ha subplots (i.e. 11 to 18 species), but was 0.999 by the lower quartile of species 302 richness in 1 ha plots (i.e. 72 species). Likewise, there was a positive relationship between the 303 observed occurrence of potentially large tree species and species richness in 0.04 ha subplots 304 (binomial generalised linear mixed effects models, P < 0.001, Supplementary Figure 6), while at 1 ha 305 306 scale this relationship was no longer evident as all but one 1 ha plot contained a potentially large 307 species. Further details and interpretation of these analyses are given in Supplementary Discussion.

308 Discussion

By analysing a large, standardised, pan-tropical dataset of inventory plots we were able to explore large-scale patterns in tropical forest above-ground carbon stocks per unit area and tree diversity, and the large-scale and fine-scale relationships between the two. Carbon and diversity both exhibit remarkable variation across the tropical forest biome. Each continent has a distinctive signature of alpha diversity, beta diversity and carbon-density, and tropics-wide it is possible to find all combinations of diversity and carbon. Yet, these two fundamental attributes of tropical forests are also found to be largely unrelated to one another among stands, whether analysed among-continents orwithin each one.

317 Our results contrast with those from an earlier examination of pan-tropical diversity-biomass relationships reporting a positive relationship with genus level diversity ²⁴ (Table 1). Although both 318 studies statistically control for the effect of climate, we also restricted our analysis to lowland plots 319 and statistically controlled for the effect of soil, which may have improved our ability to account for 320 321 the effect of environmental variation when examining the effect of diversity on carbon stocks. Additionally, our results are based on an order of magnitude more extensive sampling of the biome 322 (166 locations and 360 plots in this study, compared to 11 locations and 59 plots in ²⁴). Positive 323 stand-scale diversity-carbon stock per unit area relationships have also been reported in the neotropics 324 ²³ and in some Central African forests ²⁵, but these positive relationships were once again not evident 325 326 with improved sampling across the whole domain and once spatial autocorrelation is accounted for. Our neotropical dataset differs from Poorter et al. ²³ by being concentrated in the Amazon basin rather 327 than including Central America and the Caribbean Islands, and by not including plots in dry forest; 328 329 these differences may have reduced the effects of environmental and biogeographic variation in our 330 data.

Our best sampled regional domains - the world's two largest contiguous regions of tropical forest -331 332 show no within-continent diversity-carbon relationship at the 1 ha scale. In our dataset, tropical carbon remained positively but weakly related to diversity in Asia, and this was the exception among 333 major tropical forest regions. Importantly, this lack of a consistent positive relationship between 334 diversity and carbon is robust to analysis method, persisting whether data are analysed using simple 335 bivariate correlations, or with multiple regressions to account for environmental drivers, or by 336 simultaneous autoregressive models to also account for spatial autocorrelation, or when constructing 337 structural equation models to account for environmental effects on diversity. Instead, we found that 338 339 moisture availability (annual cumulative water deficit in South America and Africa, mean annual precipitation in Asia where plots did not experience cumulative water deficit) was the most important 340

and pantropically consistent environmental driver of spatial variation in aboveground biomass carbonstocks per unit area.

343 Although tree diversity and carbon stocks were uncorrelated at the stand-level, they were positively correlated within forest stands, so our results are consistent with tree diversity having a positive local 344 effect on carbon in tropical forests, supporting previous studies documenting positive fine-scale 345 relationships ^{22,23} (Table 1). The presence of a weakly positive (overall, South America, Africa) 346 347 relationship at 0.04 ha but not at 1 ha scale (overall, South America, Africa) could indicate that the mechanisms driving the diversity-carbon relationship are scale dependent, or could be due to 348 environmental variation acting at larger spatial scales obscuring the mechanistic effects of diversity²². 349 Although our multiple regression models applied at 1 ha scale statistically control for important 350 351 variation in climate, soil texture and soil chemistry, it is clearly not possible to capture all 352 environmental variation that may influence carbon stocks, such as local disturbance history, so we cannot rule out the latter explanation. However, we conducted additional analyses (full details in 353 Supplementary Discussion) to examine possible mechanisms underlying the diversity effects and 354 355 explore their putative scale-dependency. Carbon stocks increased with the functional dominance of 356 species with high wood density and large maximum diameter at both 0.04 ha and 1 ha scales (Supplementary Figure 4). The effect of functional dominance at 1 ha scale has been found before in 357 tropical forests ^{24,37}, and has been interpreted to support the role of selection effects ^{16,24}. However, 358 this analysis by itself is a test of the biomass ratio hypothesis ³⁷. For selection effects to operate, the 359 probability of sampling a high functioning species should also increase with species richness. We 360 found that the probability of sampling species with high maximum diameters or high wood density 361 increases with species richness at diversity levels found in 0.04 ha subplots, but saturates at diversity 362 363 levels below those of 1 ha plots (Supplementary Figures 5 - 10), indicating that selection effects, as expected, appear to be scale-dependent. Additionally, the effects of niche complementarity may also 364 saturate, as we found a positive relationship between a multivariate functional diversity metric 365 (incorporating wood density and maximum diameter traits) and carbon only at the 0.04 ha scale 366 367 (Supplementary Figure 1). The absence of a significant relationship between tree functional diversity

368 and carbon stocks per unit area at 1 ha scale is consistent with a previous analysis from three neotropical rainforests ³⁷. Although the saturating probability of sampling a high functioning species 369 370 with increasing species richness and the absence of carbon – functional diversity relationships at 1 ha are consistent with both selection effects and niche complementarity being scale-dependent, they are 371 372 based on correlative analysis of observational data so causal inferences need to be taken cautiously. Neither do our analyses test other potentially important ecosystem impacts of diversity, such as on the 373 resistance and resilience of biomass production to climate extremes ³⁸. Long-term large-scale 374 experiments that manipulate tree diversity in tropical forests ³⁹ will be required to provide additional 375 mechanistic insights into potential positive effects of metrics of tree diversity and their potential 376 saturation with scale. 377

378 A caveat with this and other studies using allometric equations to estimate above-ground biomass 379 carbon is that allometric equations do not allow variation in tree architecture with forest structure. For example, Banin et al. 40 found a weak negative relationship between tree height and stem density, 380 meaning that allometric equations may overestimate carbon stocks in plots where stem density is 381 382 highest. This could increase the chances of finding a spurious positive relationship between diversity and carbon, as we find a weak positive relationship between stem density and species richness 383 384 (Supplementary Figure 16). This potential bias is unlikely to have impacted our results, as we still 385 find a weak positive diversity-carbon relationship within plots and no relationship among plots when 386 diversity metrics are standardised per *n* stems (Table 3, Supplementary Table 7). Such potential biases could be evaluated in the future if co-located LiDAR based aboveground biomass carbon estimates 387 and ground-based tree diversity measurements are made at sufficient sites. The uncertainty in biomass 388 carbon estimates due to using allometric equations could reduce the chance of finding diversity-389 390 carbon relationships by adding noise to the data. Whilst this highlights the need to maximise statistical 391 power with large datasets, we note that the two largest studies investigating diversity-carbon relationships (this study by number of sampling locations across the biome, ²² by area sampled, see 392 Table 1) converge on a similar result with independent datasets; diversity and carbon are positively 393 394 related at the 0.04 ha scale but unrelated at the 1 ha scale.

395 <u>Conservation implications</u>

396 Despite the absence of a stand-level diversity-carbon relationship, some forest stands certainly do 397 combine high tree diversity and biomass (Fig. 1), indicating that high value carbon and biodiversity conservation can be simultaneously achieved, but only with confidence if both are considered ^{9,10}. We 398 note that conservation strategies will also need to consider biodiversity of taxa other than trees, which 399 400 may also be unrelated to carbon stocks ⁴¹, the conservation value of specific species assemblages ³, belowground carbon stores such as in tropical peat swamps ⁴², and spatial variation in opportunity 401 costs ⁴³. Methods to select protected areas that consider multiple metrics of conservation value (e.g. 402 aboveground biomass carbon and aspects of biodiversity) are available ¹⁰. Our results support the use 403 of such an approach over carbon-dominated prioritisation incentivised under REDD+⁹. Applying this 404 405 in practice is challenging as it requires knowledge of spatial variation in tree diversity, composition and carbon stocks, highlighting the importance of careful identifications to species level during forest 406 inventories. As tropical forests can have any combination of tree diversity and carbon both will 407 require explicit consideration when optimising policies to manage tropical carbon and biodiversity. 408 409 In sum, our large, pan-tropical analysis reveals that at small scales of less than 1 ha tree diversity is weakly positively correlated with aboveground carbon stocks, potentially due to both niche 410 complementarity and sampling effects. Yet our results show that these processes do not translate to 411

412 patterns at scales that matter practically for conservation: tree diversity and carbon vary

413 independently among sites, both within continents and across the whole tropical forest biome. Despite

414 the general lack of association between diversity and carbon, our analysis demonstrates that forests in

415 Asia are not only amongst the most diverse in the tropics but also amongst the most carbon-dense.

416 Thus at a global scale a clear synergy emerges, with forests in Asia being both highly speciose and

417 extremely carbon-dense. Asian forests are under substantial threat, particularly from conversion to oil

- 418palm plantations and more intensive logging than elsewhere in the tropics. As a triple hotspot for
- 419 biodiversity, carbon and threat, there is a compelling global case for prioritising their conservation.

420 Methods

421 To permit comparisons among and within continents we utilised 360 forest inventory plots, surveyed 422 using uniform standardised protocols, from three networks, RAINFOR (Amazon Forest Inventory Network; www.rainfor.org, 44), AfriTRON (African Tropical Rainforest Observatory Network; 423 www.afritron.org, ²⁹) and T-FORCES (Tropical Forests in the Changing Earth System; 424 425 www.tforces.net). The plots were all within closed-canopy lowland (maximum altitude 1217 m above sea level) humid *terra firme* forest (mean annual temperature, MAT, $\geq 20^{\circ}$ C and mean annual 426 precipitation, MAP, \geq 1300mm), all were 1 ha, except four of 0.96 ha, and none exceeded 500 m in 427 maximum dimension. The rationale for restricting the environmental domain sampled was to 428 minimise the environmental differences among plots and thus reduce the confounding effect of 429 environmental variation on the diversity-carbon relationship; this approach contrasts with previous 430 studies that have sampled along larger elevation (and thus temperature)²⁴ and precipitation²³ 431 432 gradients In each plot at least 80% of stems were identified to genus and at least 60% of stems identified to species (mean = 90.3% stems identified to species; 84% of plots had at least 80% stems 433 identified to species, 63% had at least 90% of stems identified to species). All stem diameter 434 435 measurements follow standard (above buttress) methods (see Supplementary Methods for full 436 protocols). All stems ≥ 10 cm d.b.h. were measured. Sampling was distributed across the world's three largest tropical humid forest blocs, with 158 plots in South America, 162 in Africa and 40 in 437 Asia (Fig. 3). These came from 166 discrete localities (South America 80, Africa 67, Asia 19), where 438 a 'locality' is defined as clusters of plots with maximum inter-plot distance of 5 km. Plot data were 439 440 curated in ForestPlots.net ⁴⁵ or using equivalent offline procedures, with each plot following the same quality control and subsequent calculation protocol. Aboveground biomass (AGB) was estimated for 441 each stem using the allometric equation AGB = $0.0673 \text{ x} (\rho D^2 H)^{0.976}$, from ⁴⁶, where ρ is stem wood 442 density (in g.cm⁻³) obtained from a world database ^{47,48}, D is stem diameter (in cm) at 1.3m or above 443 buttresses, and H is height (in m), the latter estimated using regional height-diameter Weibull 444 equations ⁴⁹. AGB values were converted to estimates of carbon using the mean carbon fraction for 445 tropical angiosperms, 47.1%, from ⁵⁰. Taxon richness was estimated as the sum of identified species 446 and morphospecies plus the estimated number of unidentified taxa based on observed richness per 447

stem ratios (details in Supplementary Methods). Richness per 300 stems was estimated usingindividual based rarefaction.

450 Differences in diversity and carbon among continents were assessed using analysis of variance. To 451 meet model assumptions, carbon stocks per unit area was log-transformed and Fisher's alpha squareroot transformed, while taxon richness was modelled using a negative binomial error distribution to 452 account for overdispersion. We used log-linear generalised linear models with binomial errors to 453 454 model the relationship between Sørensen index (beta diversity) and geographical distance between plots in each continent, restricting this analysis to plots with >90% of stems identified to species level 455 (227 plots). Relationships among 1 ha plots were assessed using [1] bivariate Kendall's τ correlations 456 and [2] multiple regressions of carbon as a function of diversity, climate (cumulative water deficit, 457 458 MAT, MAP; 1 km resolution) and soil (total exchangeable bases, C:N ratio, soil texture; 0-30 cm depth). We ran all predictor subsets and averaged models where cumulative AIC_c weights summed to 459 0.95. Residual spatial autocorrelation was present, so we repeated the analysis using simultaneous 460 autoregressive error models to explicitly model spatially autocorrelated errors. We also repeated the 461 analysis using structural equation models implemented in the R package lavaan ⁵¹. Relationships 462 amongst 0.04 ha subplots in the 266 plots where subplot level data were also available were examined 463 using multiple regressions of ln(carbon) against ln(diversity) and ln(stem density) for each plot 464 465 individually, as well as for all plots using a random coefficients mixed effect model with plot identity 466 as a random effect. Finally, we conducted a series of analyses to assess support for possible mechanisms driving diversity-carbon relationships, which are described in full in the Supplementary 467 468 Discussion. Briefly, we produced separate models of carbon stocks as a function of the community weighted mean (CWM) of wood density, the CWM of maximum stem diameter, the standard 469 470 deviation of wood density and a functional diversity metric including both these traits. Relationships 471 at 1 ha were modelled using linear regression, relationships at 0.04 ha were modelled using linear mixed effects models with plot identity as a random effect. We related the expected probability of 472 473 sampling a species with large potential size or high wood density (defined as maximum diameter ≥ 70 474 cm or wood density ≥ 0.8 g.cm⁻³ respectively, other thresholds were also examined) to species

475 richness using null models, and also used binomial generalised linear mixed-effects models to relate 476 the occurrence of these species in 0.04 ha subplots to species richness. Significance testing is based on 477 two-tailed tests, with $\alpha = 0.05$ used to determine statistical significance. See Supplementary Methods 478 for full details of methods.

479

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518 Author contributions

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535 Competing financial interests statement

536 The authors declare no competing financial interests.

537 **References**

538	1	Dirzo, R. et al. Defaunation in the Anthropocene. Science 345, 401-406,							
539		doi:10.1126/science.1251817 (2014).							
540	2	Thomas, C. D. et al. Extinction risk from climate change. Nature 427, 145-148,							
541		doi:http://www.nature.com/nature/journal/v427/n6970/suppinfo/nature02121_S1.html							
542		(2004).							
543	3	ter Steege, H. et al. Estimating the global conservation status of more than 15,000							
544		Amazonian tree species. Science Advances 1, doi:10.1126/sciadv.1500936 (2015).							
545	4	Lewis, S. L., Edwards, D. P. & Galbraith, D. Increasing human dominance of tropical forests.							
546		Science 349, 827-832, doi:10.1126/science.aaa9932 (2015).							
547	5	Moilanen, A. et al. Prioritizing multiple-use landscapes for conservation: methods for large							
548		multi-species planning problems. Vol. 272 (2005).							
549	6	Chape, S., Harrison, J., Spalding, M. & Lysenko, I. Measuring the extent and effectiveness of							
550		protected areas as an indicator for meeting global biodiversity targets. Philosophical							
551		Transactions of the Royal Society B: Biological Sciences 360 , 443-455,							
552		doi:10.1098/rstb.2004.1592 (2005).							
553	7	Matthews, H. D. et al. National contributions to observed global warming. Environmental							
554		Research Letters 9 , 014010 (2014).							
555	8	United Nations Framework Convention on Climate Change. (ed Conference of the Parties							
556		Twenty-first session) (2015).							
557	9	Gardner, T. A. <i>et al.</i> A framework for integrating biodiversity concerns into national REDD+							
558		programmes. <i>Biol. Conserv.</i> 154, 61-71, doi:10.1016/j.biocon.2011.11.018 (2012).							
559	10	Thomas, C. D. et al. Reconciling biodiversity and carbon conservation. Ecology Letters 16, 39-							
560		47, doi:10.1111/ele.12054 (2013).							
561	11	Ewers, R. M. & Rodrigues, A. S. L. Estimates of reserve effectiveness are confounded by							
562		leakage. Trends in Ecology & Evolution 23, 113-116,							
563		doi: <u>http://dx.doi.org/10.1016/j.tree.2007.11.008</u> (2008).							
564	12	Cardinale, B. J. et al. Biodiversity loss and its impact on humanity. Nature 486, 59-67,							
565		doi:http://www.nature.com/nature/journal/v486/n7401/abs/nature11148.html#supplemen							
566		tary-information (2012).							

- Tilman, D., Isbell, F. & Cowles, J. M. Biodiversity and Ecosystem Functioning. *Annual Review of Ecology, Evolution, and Systematics* 45, 471-493, doi:10.1146/annurev-ecolsys-120213 091917 (2014).
- 57014Loreau, M. & Hector, A. Partitioning selection and complementarity in biodiversity571experiments. Nature 412, 72-76, doi:10.1038/35083573 (2001).
- Morin, X., Fahse, L., Scherer-Lorenzen, M. & Bugmann, H. Tree species richness promotes
 productivity in temperate forests through strong complementarity between species. *Ecology Letters* 14, 1211-1219, doi:10.1111/j.1461-0248.2011.01691.x (2011).
- 57516Ruiz-Benito, P. *et al.* Diversity increases carbon storage and tree productivity in Spanish576forests. Global Ecology and Biogeography 23, 311-322, doi:10.1111/geb.12126 (2014).
- Jucker, T., Bouriaud, O., Avacaritei, D. & Coomes, D. A. Stabilizing effects of diversity on
 aboveground wood production in forest ecosystems: linking patterns and processes. *Ecology Letters* 17, 1560-1569, doi:10.1111/ele.12382 (2014).
- Jucker, T., Bouriaud, O. & Coomes, D. A. Crown plasticity enables trees to optimize canopy
 packing in mixed-species forests. *Functional Ecology* 29, 1078-1086, doi:10.1111/13652435.12428 (2015).
- Liang, J. J., Zhou, M., Tobin, P. C., McGuire, A. D. & Reich, P. B. Biodiversity influences plant
 productivity through niche-efficiency. *Proc. Natl. Acad. Sci. U. S. A.* **112**, 5738-5743,
 doi:10.1073/pnas.1409853112 (2015).
- 586 20 Keeling, H. C. & Phillips, O. L. The global relationship between forest productivity and biomass. *Global Ecology and Biogeography* 16, 618-631, doi:10.1111/j.1466588 8238.2007.00314.x (2007).
- 589 21 Galbraith, D. *et al.* Residence times of woody biomass in tropical forests. *Plant Ecology & Diversity* 6, 139-157, doi:10.1080/17550874.2013.770578 (2013).
- 591 22 Chisholm, R. A. *et al.* Scale-dependent relationships between tree species richness and
 592 ecosystem function in forests. *Journal of Ecology* **101**, 1214-1224, doi:10.1111/1365593 2745.12132 (2013).
- 59423Poorter, L. *et al.* Diversity enhances carbon storage in tropical forests. *Global Ecology and*595*Biogeography*, n/a-n/a, doi:10.1111/geb.12364 (2015).
- 59624Cavanaugh, K. C. *et al.* Carbon storage in tropical forests correlates with taxonomic diversity597and functional dominance on a global scale. *Global Ecology and Biogeography* 23, 563-573,598doi:10.1111/geb.12143 (2014).
- 599 25 Day, M., Baldauf, C., Rutishauser, E. & Sunderland, T. Relationships between tree species
 600 diversity and above-ground biomass in Central African rainforests: implications for REDD.
 601 *Environmental Conservation* 41, 64-72, doi:doi:10.1017/S0376892913000295 (2014).
- Ter Steege, H. *et al.* A spatial model of tree α-diversity and tree density for the Amazon.
 Biodiversity & Conservation 12, 2255-2277, doi:10.1023/a:1024593414624 (2003).
- Quesada, C. A. *et al.* Basin-wide variations in Amazon forest structure and function are
 mediated by both soils and climate. *Biogeosciences* 9, 2203-2246, doi:10.5194/bg-9-22032012 (2012).
- 60728Baraloto, C. *et al.* Disentangling stand and environmental correlates of aboveground biomass608in Amazonian forests. *Global Change Biology* **17**, 2677-2688, doi:10.1111/j.1365-6092486.2011.02432.x (2011).
- Lewis, S. L. *et al.* Above-ground biomass and structure of 260 African tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368,
 doi:10.1098/rstb.2012.0295 (2013).
- 61330Banin, L. *et al.* Tropical forest wood production: a cross-continental comparison. Journal of614Ecology 102, 1025-1037, doi:10.1111/1365-2745.12263 (2014).
- Slik, J. W. F. *et al.* Environmental correlates of tree biomass, basal area, wood specific gravity
 and stem density gradients in Borneo's tropical forests. *Global Ecology and Biogeography* 19,
 50-60, doi:10.1111/j.1466-8238.2009.00489.x (2010).

618 32 Gentry, A. H. Tree species richness of upper Amazonian forests. Proceedings of the National 619 Academy of Sciences 85, 156-159 (1988). Slik, J. W. F. et al. An estimate of the number of tropical tree species. Proceedings of the 620 33 National Academy of Sciences, doi:10.1073/pnas.1423147112 (2015). 621 622 Parmentier, I. et al. The odd man out? Might climate explain the lower tree α -diversity of 34 623 African rain forests relative to Amazonian rain forests? Journal of Ecology 95, 1058-1071, 624 doi:10.1111/j.1365-2745.2007.01273.x (2007). 625 35 Kraft, N. J. B. *et al.* Disentangling the Drivers of β Diversity Along Latitudinal and Elevational 626 Gradients. Science 333, 1755-1758, doi:10.1126/science.1208584 (2011). 627 Zhang, Y. & Chen, H. Y. H. Individual size inequality links forest diversity and above-ground 36 628 biomass. Journal of Ecology 103, 1245-1252, doi:10.1111/1365-2745.12425 (2015). 629 37 Finegan, B. et al. Does functional trait diversity predict above-ground biomass and 630 productivity of tropical forests? Testing three alternative hypotheses. Journal of Ecology 103, 631 191-201, doi:10.1111/1365-2745.12346 (2015). 632 38 Isbell, F. et al. Biodiversity increases the resistance of ecosystem productivity to climate 633 extremes. Nature 526, 574-577, doi:10.1038/nature15374 (2015). 634 39 Hector, A. et al. The Sabah Biodiversity Experiment: a long-term test of the role of tree 635 diversity in restoring tropical forest structure and functioning. Philosophical Transactions of the Royal Society of London B: Biological Sciences 366, 3303-3315 (2011). 636 637 40 Banin, L. et al. What controls tropical forest architecture? Testing environmental, structural 638 and floristic drivers. Global Ecology and Biogeography 21, 1179-1190, doi:10.1111/j.1466-639 8238.2012.00778.x (2012). 640 41 Beaudrot, L. et al. Limited carbon and biodiversity co-benefits for tropical forest mammals 641 and birds. Ecological Applications (2015). 642 42 Draper, F. C. et al. The distribution and amount of carbon in the largest peatland complex in 643 Amazonia. Environmental Research Letters 9, 124017 (2014). 644 43 Balmford, A., Gaston, K. J., Blyth, S., James, A. & Kapos, V. Global variation in terrestrial 645 conservation costs, conservation benefits, and unmet conservation needs. Proceedings of 646 the National Academy of Sciences 100, 1046-1050, doi:10.1073/pnas.0236945100 (2003). 647 44 Malhi, Y. et al. An international network to monitor the structure, composition and dynamics 648 of Amazonian forests (RAINFOR). Journal of Vegetation Science 13, 439-450, 649 doi:10.1111/j.1654-1103.2002.tb02068.x (2002). 650 45 Lopez-Gonzalez, G., Lewis, S. L., Burkitt, M. & Phillips, O. L. ForestPlots.net: a web application 651 and research tool to manage and analyse tropical forest plot data. Journal of Vegetation 652 *Science* **22**, 610-613, doi:10.1111/j.1654-1103.2011.01312.x (2011). Chave, J. et al. Improved allometric models to estimate the aboveground biomass of tropical 653 46 654 trees. Global Change Biology 20, 3177-3190, doi:10.1111/gcb.12629 (2014). 47 Chave, J. et al. Towards a worldwide wood economics spectrum. Ecology Letters 12, 351-655 656 366, doi:10.1111/j.1461-0248.2009.01285.x (2009). 657 48 Zanne, A. E. *et al.* (Dryad Data Repository, 2009). 658 49 Feldpausch, T. R. et al. Tree height integrated into pantropical forest biomass estimates. 659 Biogeosciences 9, 3381-3403 (2012). 660 50 Thomas, S. C. & Martin, A. R. Carbon Content of Tree Tissues: A Synthesis. Forests 3, 332-352 661 (2012). 662 51 Rosseel, Y. lavaan: An R Package for Structural Equation Modeling. 2012 48, 36, 663 doi:10.18637/jss.v048.i02 (2012). 664 52 Bartholomé, E. & Belward, A. S. GLC2000: a new approach to global land cover mapping 665 from Earth observation data. International Journal of Remote Sensing 26, 1959-1977, 666 doi:10.1080/01431160412331291297 (2005).

- 66753R: A Language and Environment for Statistical Computing, R Core Team, R Foundation for668Statistical Computing, Vienna, Austria (2016) https://www.R-project.org.
- 669 54 Original S code by Richard A. Becker and Allan R. Wilks. R version by Ray Brownrigg.
 670 Enhancements by Thomas P Minka. maps: Draw Geographical Maps. R package version 2.3671 9. (2014) http://CRAN.R-project.org/package=maps.

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687 Tables

Table 1. Pan-tropical and continental studies assessing the diversity-carbon relationship. Sampling locations are groups of plots in close proximity to each

other (individual large plots in 22 , TEAM core study sites in 24 , "forest sites" in 23 , groups of plots within 5 km of each other in this study). The number of sampling locations in the largest blocs of forest in each continent are given, these are the Amazon basin and surrounding contiguous forest, the Congo basin

and surrounding contiguous forest, and Borneo. + indicates a positive diversity-carbon relationship, = indicates no relationship, NA indicates the relationship

was not studied at the given scale. In this study, 22 and 24 all stems ≥ 10 cm d.b.h. were measured, in 23 the minimum stem diameter measured varied among

was not studied at the given scale. In this study, and an stems ≤ 10 cm 0.0.11, were measured, in the minimum stem dameter measured varied and

693 plots (either 5 cm or 10 cm).

Study	Geographical scope	Number of plots		Number of sampling locations			ons	Taxonomic level	Diversity measures	Minimum identification	Diversity-carbon relationship	
	-	1 ha	0.04 ha	Total	Amazon	Congo	Borneo			level	Within	Among
											stand	stands
This study	Tropics	360	6536	166	77	52	18	Species, genus and family	Richness, rarefied richness, Shannon diversity, Simpson diversity, Fisher's alpha and functional diversity	60 % stems to species, 80 % to genus	+	=
22	Tropical and temperate	688ª	17200 ª	25	2	1	1	Species	Richness ^b	Not stated	+	= ^c
24	Tropics	59	NA	11	3	2	0	Genus	Richness, Shannon diversity, functional diversity	80 % stems to family	NA	+
23	Tropical America	294	1975 ^d	59	47	0	0	Species	Richness, rarefied richness and Shannon diversity	Not stated	+	+ e

^a Sample size not stated, so maximum possible number of 1 ha and 0.04 ha subplots given.

^b Stem density was included as a covariate in analysis.

^cRelationship analysed among 1 ha plots within sampling locations, not among sampling locations.

697 ^d 0.1 ha not 0.04 ha.

^e Relationship among sampling locations.

Table 2. Mean carbon stocks per unit area and tree diversity in forest inventory plots in South

America (n = 158), Africa (n = 162) and Asia (n = 40). 95% confidence limits derived from 10,000

bootstrap resamples of the data (sampling with replacement) are shown in parentheses. Different

702 letters indicate significant differences between continents (ANOVA and subsequent Tukey's all-pair

comparison, P < 0.05). Data for other diversity metrics shown in Supplementary Table 2.

Variable	South America	Africa	Asia
Carbon (Mg ha ⁻¹)	140 (133 – 148) ^A	183 (176 – 190) ^B	197 (180 - 215) в
Fisher's α	80 (71 – 88) ^B	$28(26-30)^{\text{A}}$	84 (73 - 96) ^B
Species richness (ha ⁻¹)	152 (141 – 163) ^B	$74(70-78)^{A}$	162 (147 - 177) ^B
(300 stems ⁻¹)	109 (102 – 116) ^B	$65(62-69)^{A}$	120 (111 - 130) в
Genus richness (ha-1)	91 (86 – 96) ^B	59 (56 – 62) ^A	87 (81 - 93) ^B
(300 stems^{-1})	72 (68 – 75) ^B	54 (51 – 56) ^A	71 (66 - 75) ^B
Family richness (ha ⁻¹)	38 (37 – 39) ^B	$28(27-28)^{A}$	40 (38 - 42) ^B
(300 stems ⁻¹)	$33(32-34)^{B}$	$26(25-27)^{A}$	35 (34 - 37) ^B

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Table 3. Correlations (Kendall's \tau) between carbon and tree diversity in South America (n = 158
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- plots), Africa (n = 162) and Asia (n = 40). Power analysis was used to estimate the minimum effect
- size (presented as both τ and Pearson's r) detectable with 80% power. Correlations with taxon

richness per 300 stems are shown in parentheses. Correlations with other diversity metrics shown inSupplementary Table 4.

Diversity metric	South America		Africa		Asia		
	τ	P-value	τ	P-value	τ	P-value	
Fisher's α	0.083	0.12	0.012	0.821	0.115	0.302	
Species richness	0.084	0.12	0.014	0.788	0.132	0.230	
	(0.092)	(0.087)	(0.031)	(0.573)	(0.151)	(0.174)	
Genus richness	(0.066)	(0.223)	-0.016	(0.765)	-0.006	(0.954)	
Family richness	-0.007	0.893	-0.051	0.35	0.087	0.434	
1 uning 110111000	(-0.042)	(0.43)	(-0.036)	(0.519)	(0.021)	(0.862)	
Detectable	$\tau = 0.14$		$\tau = 0.14$		$\tau = 0.28$		
effect size	r = 0.22		r = 0.22		r = 0.43		
8							
9							
n							

747 Figures

748



750 Figure 1. The relationship between carbon stocks per unit area and tree species richness across the tropical forest biome. Green circles = plots in South America (n = 158), orange squares = Africa (n = 158) 751 752 162) and purple triangles = Asia (n =40). Boxplots show variation in species richness and biomass 753 carbon stocks in each continent. Both carbon and species richness varied significantly between continents (Table 2), but no significant correlation exists between carbon and species richness, 754 755 whether within each continent ($\tau \le 0.132$, $P \ge 0.12$) nor across all three continents (linear regression weighted by sampling density in each continent, $\beta < 0.001$, t = 0.843, P = 0.4, weights = 1.2 for South 756 757 America, 0.6 for Africa and 1.8 for Asia). Relationships for other diversity metrics are similar (Supplementary Fig. S13). 758



Distance (km)









784

Figure 4. Variation in the coefficient (β) of the relationship between species richness and carbon 785 among 0.04 ha subplots within 266 1 ha plots. Coefficients come from multiple regression models 786 787 also containing the number of stems as a second-order polynomial term to allow for a saturating relationship. Coefficients from plots in South America are shown in green, Africa in orange and Asia 788 in purple. Mean values of coefficients are shown in the inset, with error bars showing 95% confidence 789 intervals derived from 10000 bootstrap resamples (with replacement) of the dataset, with asterisks 790 791 denoting significant differences from zero (one-sample Wilcoxon test, ** P < 0.01, * P < 0.05). 792 Across all plots, doubling species richness increased carbon by 6.9 %. The horizontal line in the inset 793 and bold vertical line in the main figure show where coefficients = 0. β is in units of ln(Mg.ha⁻¹

794 carbon) per ln(tree species).