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1 **Diversity and carbon storage across the tropical forest biome**

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106 **Abstract**

107 Tropical forests are global centres of biodiversity and carbon storage. Many tropical countries aspire
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
111 inventories where carbon stocks in aboveground biomass and species identifications have been
112 simultaneously and robustly quantified. Here, we compile a unique pan-tropical dataset of 360 plots
113 located in structurally intact old-growth closed-canopy forest, surveyed using standardised methods,
114 allowing a multi-scale evaluation of diversity-carbon relationships in tropical forests. Diversity-
115 carbon relationships among all plots at 1 ha scale across the tropics are absent, and within continents
116 are either weak (Asia) or absent (Amazonia, Africa). A weak positive relationship is detectable within
117 1 ha plots, indicating that diversity effects in tropical forests may be scale dependent. The absence of
118 clear diversity-carbon relationships at scales relevant to conservation planning means that carbon-
119 centred conservation strategies alone would inevitably miss many high diversity ecosystems. As
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.

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130 Introduction

131 Biodiversity is threatened by the conversion of natural habitats and climate change¹⁻³. Tropical forests
132 are under particular pressure, whilst also being among the most diverse biomes on the planet⁴. By
133 legally protecting areas, tropical countries can safeguard ecosystems with high biodiversity value⁵,
134 and so address their policy targets to reduce biodiversity loss⁶. Likewise, carbon losses from the
135 conversion of forest to other land-uses represent major emission sources for many tropical countries⁷,
136 and so incentives such as the UN REDD+ policy framework have emerged to help safeguard areas
137 with high carbon stocks⁸. Yet the potential for protection of carbon-rich areas to directly benefit
138 biodiversity, and vice versa, depends critically on the relationship between biomass carbon and tree
139 diversity, at relevant scales. A positive relationship would indicate potential synergies while a
140 negative relationship would indicate difficult trade-offs between biodiversity and carbon conservation
141⁹. In the absence of any relationship, optimal solutions for protected area placement need to carefully
142 and separately consider the distribution of carbon stocks and the distribution of biodiversity¹⁰.
143 Understanding these distributions and potential carbon-biodiversity trade-offs is important, as
144 protecting some forest can divert threats onto other unprotected areas¹¹.

145 The expected form of diversity-carbon relationships in tropical forests and the strength and scale-
146 dependence of any underlying mechanisms are uncertain. Numerous experimental studies have
147 demonstrated that plant diversity promotes biomass production, with niche partitioning and positive
148 species interactions allowing diverse communities to exploit available resources more efficiently^{12,13}.
149 Diversity can also increase productivity through selection effects, where communities that contain a
150 larger sample of the species pool are more likely to contain high functioning species that contribute
151 strongly to ecosystem productivity¹⁴. Positive diversity-productivity relationships have been found in
152 low diversity mid-latitude forests¹⁵⁻¹⁷, potentially due to increased canopy packing through
153 complimentary canopy architecture in higher diversity forests¹⁸. Yet, it is unclear how significant
154 such mechanisms are in diverse tropical forests, as experimental and theoretical work indicates that
155 the positive effect of diversity may saturate at high species richness^{12,19}. Furthermore, additional traits
156 associated with high-productivity species could conceivably lead to a positive diversity-biomass

157 mortality relationship, as highly productive stands tend to be composed of trees with shorter biomass
158 residence times²¹. Overall, this alongside high-productivity stands consisting of smaller, lighter-
159 wooded trees²⁰, may lead to a negative diversity-biomass carbon storage relationship.

160 Previous studies investigating the tree diversity-carbon stock relationship in tropical forests have
161 reported a positive relationship at fine spatial scales^{22,23}. However, the form of the relationship at the
162 stand-level (i.e. among 1 ha plots) is less clear (Table 1), as some studies report a continued positive
163 diversity-carbon relationship among sampling locations²³⁻²⁵, while one other did not detect a
164 relationship among 1 ha subplots within 25 larger plots²². Thus, while there is some evidence that
165 higher tree diversity promotes higher carbon stocks per unit area in diverse tropical forests²²⁻²⁴, it is
166 unclear whether any positive effect is strong enough for carbon and diversity to co-vary at scales
167 relevant to conservation planning.

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

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

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193 **Results**

194 Pantropical forest carbon and diversity

195 Our standardised methods of inventory reveal great variation in both aboveground live carbon stocks
196 and tree diversity within continents and across the humid tropical forest biome. While it is possible to
197 find almost any combination of both parameters (Fig. 1), the plots reveal large differences in carbon
198 and diversity amongst the three continents (Table 2). African tropical forests are characterised by high
199 carbon storage per unit area and consistently low alpha-diversity (even the most species-rich African
200 plot had fewer species than the median species richness recorded in South America and Asia). By
201 contrast, in South American plots carbon storage per unit area was lower than in African forests (Fig.
202 1). Nevertheless both diversity and carbon vary greatly within South America, as reflects previously
203 reported gradients in species richness²⁶ and biomass^{27,28}, with some stands in the Guiana Shield
204 region containing carbon stocks comparable to forests in the paleotropics (Fig. 1). Asian forests differ
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
207 stems (Table 2), and when the analysis was repeated only including plots with >90% of stems
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

210 identification (not different amongst continents, Kruskal-Wallis test $H = 2.1$, $P = 0.335$). This
211 pantropical assessment of forest carbon stocks and diversity is consistent with previous reports from
212 individual continents, indicating high biomass in forests in Africa²⁹ and Borneo^{30,31}, high diversity in
213 central and western Amazonia³² and low diversity in Africa^{33,34}. Our analysis demonstrates that
214 forests across the Sundaland region of Southeast Asia are not only amongst the most diverse in the
215 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
219 similarity in species composition decayed most strongly with distance in South America, there was
220 weaker distance decay in Asia (Fig. 2, Supplementary Fig. 12). As a result, while adjacent stands
221 differ most in Asia, at distances $>1,000$ km plots in Asia are no more dissimilar than equidistant plot
222 pairs in South America. Differences in beta diversity could have been driven by differences in gamma
223 diversity³⁵. However, local tree communities remained more similar in Africa than other continents
224 when null models were used to account for variation in gamma diversity (Supplementary Fig. 13).
225 Gamma diversity was comparable in South America and Asia³³, so was unlikely to drive differences
226 in the distance decay of tree community similarity in those continents.

227 Large-scale diversity-carbon relationships

228 Notably, aboveground carbon stocks in live biomass per unit area was unrelated to tree species
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
231 also non-significant (Table 3, Supplementary Fig. 14). Thus, in tropical forests high values of
232 diversity and biomass carbon are associated neither at the biome nor the continental scale; instead
233 they vary independently. We note that while in both South America and Africa there is sufficient
234 statistical power to detect even small effects of diversity had they existed, in Asia power was only
235 sufficient to detect relatively large effect sizes (Table 2).

236 Since confounding environmental variables might obscure any underlying effect of tree diversity on
237 carbon stocks, we next applied multiple regression including climate and edaphic variables as
238 covariates to statistically control for environmental variation that might otherwise obscure the effect
239 of diversity. In ordinary least squares multiple regression models, there was a consistent negative
240 relationship between diversity and carbon in South America, and no significant relationship in Africa
241 and Asia (Fig. 3b). When the analysis was repeated using simultaneous autoregressive error models to
242 account for spatial autocorrelation, diversity was not supported as a predictor in South America or
243 Africa (Fig. 3c). In Asia, while there were significant positive relationships between carbon and both
244 Fisher's α and species richness (Fig. 3c), environmental variables were more important predictors of
245 carbon stocks based on their occurrence in low AIC_C models (Supplementary Table 5) and other
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
250 strongest environmental predictor of carbon stocks, as indicated by high \sum AIC_C weights (≥ 0.98), and
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
254 annual temperature (\sum AIC_C weights = 0.65).

255 Carbon stocks per unit area was also related to structural attributes, increasing with basal area and
256 basal area-weighted mean wood density, but not with stem density (Supplementary Fig. 16). While
257 consistent with previous studies²³, this is hardly surprising as both wood density and basal area are
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
261 forest stands. Stem size inequality, which has been posited as a mechanism linking diversity and
262 carbon in boreal forests³⁶, was positively related to carbon but unrelated to species richness

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

271 Fine-scale diversity-carbon relationships

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 (one-
275 sample Wilcoxon test, $P = 0.007$), and significant for plots within Africa ($n = 111$ plots, one-sample
276 Wilcoxon test, $P = 0.022$) and South America alone ($n = 118$ plots, one-sample Wilcoxon test, $P =$
277 0.013 , Fig. 4). Within these plots, 148 (55.6%) had a positive richness-carbon relationship and 118
278 (44.4%) a negative relationship (Fig. 4). Overall the richness-carbon relationship was weak but
279 positive ($\beta = 0.096 \pm 0.048$ SE). This implies that doubling species richness per 0.04 ha would
280 increase carbon stocks by 6.9%, with similar relationships for other diversity metrics (Supplementary
281 Table 7). This is consistent with an independent within-plot study of 25 plots which showed a 7%
282 effect size of diversity on aboveground biomass at the 0.04 ha spatial scale, but no relationship at the
283 1 ha scale ²².

284 Examining support for niche complementarity and selection effects

285 There was a statistically significant positive relationship between a multivariate metric of functional
286 diversity incorporating wood density and maximum diameter traits and carbon stocks at the 0.04 ha
287 scale (linear mixed effects model, $P < 0.001$, Supplementary Figure 1), but this relationship was not
288 significant in any continent at the 1 ha scale (linear regression models, $P \geq 0.139$, 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, $P \leq 0.049$, 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
295 saturate by the species richness values typical of 1 ha plots, with the exact form of this relationship
296 depending on the threshold used to define a large or dense wooded species and whether the null model
297 used to sample species randomly selected species from the pool available within a continent or
298 sampled species according to their relative frequency of occurrence (Supplementary Figures 5 – 10).
299 For example, the expected probability of sampling a tree species with maximum diameter ≥ 70 cm, as
300 assessed using a null model randomly selecting species from the pool of species recorded in plots
301 within each continent, increased from 0.760 to 0.878 over the interquartile range of species richness
302 found in 0.04 ha subplots (i.e. 11 to 18 species), but was 0.999 by the lower quartile of species
303 richness in 1 ha plots (i.e. 72 species). Likewise, there was a positive relationship between the
304 observed occurrence of potentially large tree species and species richness in 0.04 ha subplots
305 (binomial generalised linear mixed effects models, $P < 0.001$, Supplementary Figure 6), while at 1 ha
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**

309 By analysing a large, standardised, pan-tropical dataset of inventory plots we were able to explore
310 large-scale patterns in tropical forest above-ground carbon stocks per unit area and tree diversity, and
311 the large-scale and fine-scale relationships between the two. Carbon and diversity both exhibit
312 remarkable variation across the tropical forest biome. Each continent has a distinctive signature of
313 alpha diversity, beta diversity and carbon-density, and tropics-wide it is possible to find all
314 combinations of diversity and carbon. Yet, these two fundamental attributes of tropical forests are also

315 found to be largely unrelated to one another among stands, whether analysed among-continent or
316 within each one.

317 Our results contrast with those from an earlier examination of pan-tropical diversity-biomass
318 relationships reporting a positive relationship with genus level diversity²⁴ (Table 1). Although both
319 studies statistically control for the effect of climate, we also restricted our analysis to lowland plots
320 and statistically controlled for the effect of soil, which may have improved our ability to account for
321 the effect of environmental variation when examining the effect of diversity on carbon stocks.
322 Additionally, our results are based on an order of magnitude more extensive sampling of the biome
323 (166 locations and 360 plots in this study, compared to 11 locations and 59 plots in²⁴). Positive
324 stand-scale diversity-carbon stock per unit area relationships have also been reported in the neotropics
325²³ and in some Central African forests²⁵, but these positive relationships were once again not evident
326 with improved sampling across the whole domain and once spatial autocorrelation is accounted for.
327 Our neotropical dataset differs from Poorter et al.²³ by being concentrated in the Amazon basin rather
328 than including Central America and the Caribbean Islands, and by not including plots in dry forest;
329 these differences may have reduced the effects of environmental and biogeographic variation in our
330 data.

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

341 and pantropically consistent environmental driver of spatial variation in aboveground biomass carbon
342 stocks per unit area.

343 Although tree diversity and carbon stocks were uncorrelated at the stand-level, they were positively
344 correlated within forest stands, so our results are consistent with tree diversity having a positive local
345 effect on carbon in tropical forests, supporting previous studies documenting positive fine-scale
346 relationships^{22,23} (Table 1). The presence of a weakly positive (overall, South America, Africa)
347 relationship at 0.04 ha but not at 1 ha scale (overall, South America, Africa) could indicate that the
348 mechanisms driving the diversity-carbon relationship are scale dependent, or could be due to
349 environmental variation acting at larger spatial scales obscuring the mechanistic effects of diversity²².

350 Although our multiple regression models applied at 1 ha scale statistically control for important
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
353 cannot rule out the latter explanation. However, we conducted additional analyses (full details in
354 Supplementary Discussion) to examine possible mechanisms underlying the diversity effects and
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
357 (Supplementary Figure 4). The effect of functional dominance at 1 ha scale has been found before in
358 tropical forests^{24,37}, and has been interpreted to support the role of selection effects^{16,24}. However,
359 this analysis by itself is a test of the biomass ratio hypothesis³⁷. For selection effects to operate, the
360 probability of sampling a high functioning species should also increase with species richness. We
361 found that the probability of sampling species with high maximum diameters or high wood density
362 increases with species richness at diversity levels found in 0.04 ha subplots, but saturates at diversity
363 levels below those of 1 ha plots (Supplementary Figures 5 - 10), indicating that selection effects, as
364 expected, appear to be scale-dependent. Additionally, the effects of niche complementarity may also
365 saturate, as we found a positive relationship between a multivariate functional diversity metric
366 (incorporating wood density and maximum diameter traits) and carbon only at the 0.04 ha scale
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
369 neotropical rainforests³⁷. Although the saturating probability of sampling a high functioning species
370 with increasing species richness and the absence of carbon – functional diversity relationships at 1 ha
371 are consistent with both selection effects and niche complementarity being scale-dependent, they are
372 based on correlative analysis of observational data so causal inferences need to be taken cautiously.
373 Neither do our analyses test other potentially important ecosystem impacts of diversity, such as on the
374 resistance and resilience of biomass production to climate extremes³⁸. Long-term large-scale
375 experiments that manipulate tree diversity in tropical forests³⁹ will be required to provide additional
376 mechanistic insights into potential positive effects of metrics of tree diversity and their potential
377 saturation with scale.

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
380 example, Banin *et al.*⁴⁰ found a weak negative relationship between tree height and stem density,
381 meaning that allometric equations may overestimate carbon stocks in plots where stem density is
382 highest. This could increase the chances of finding a spurious positive relationship between diversity
383 and carbon, as we find a weak positive relationship between stem density and species richness
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
387 could be evaluated in the future if co-located LiDAR based aboveground biomass carbon estimates
388 and ground-based tree diversity measurements are made at sufficient sites. The uncertainty in biomass
389 carbon estimates due to using allometric equations could reduce the chance of finding diversity-
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
392 relationships (this study by number of sampling locations across the biome,²² by area sampled, see
393 Table 1) converge on a similar result with independent datasets; diversity and carbon are positively
394 related at the 0.04 ha scale but unrelated at the 1 ha scale.

395 Conservation implications

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
398 conservation can be simultaneously achieved, but only with confidence if both are considered^{9,10}. We
399 note that conservation strategies will also need to consider biodiversity of taxa other than trees, which
400 may also be unrelated to carbon stocks⁴¹, the conservation value of specific species assemblages³,
401 belowground carbon stores such as in tropical peat swamps⁴², and spatial variation in opportunity
402 costs⁴³. Methods to select protected areas that consider multiple metrics of conservation value (e.g.
403 aboveground biomass carbon and aspects of biodiversity) are available¹⁰. Our results support the use
404 of such an approach over carbon-dominated prioritisation incentivised under REDD+⁹. Applying this
405 in practice is challenging as it requires knowledge of spatial variation in tree diversity, composition
406 and carbon stocks, highlighting the importance of careful identifications to species level during forest
407 inventories. As tropical forests can have any combination of tree diversity and carbon both will
408 require explicit consideration when optimising policies to manage tropical carbon and biodiversity.

409 In sum, our large, pan-tropical analysis reveals that at small scales of less than 1 ha tree diversity is
410 weakly positively correlated with aboveground carbon stocks, potentially due to both niche
411 complementarity and sampling effects. Yet our results show that these processes do not translate to
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
418 palm 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
423 Network; www.rainfor.org,⁴⁴), AfriTRON (African Tropical Rainforest Observatory Network;
424 www.afritron.org,²⁹) and T-FORCES (Tropical Forests in the Changing Earth System;
425 www.tforces.net). The plots were all within closed-canopy lowland (maximum altitude 1217 m above
426 sea level) humid *terra firme* forest (mean annual temperature, MAT, $\geq 20^{\circ}\text{C}$ and mean annual
427 precipitation, MAP, $\geq 1300\text{mm}$), all were 1 ha, except four of 0.96 ha, and none exceeded 500 m in
428 maximum dimension. The rationale for restricting the environmental domain sampled was to
429 minimise the environmental differences among plots and thus reduce the confounding effect of
430 environmental variation on the diversity-carbon relationship; this approach contrasts with previous
431 studies that have sampled along larger elevation (and thus temperature)²⁴ and precipitation²³
432 gradients. In each plot at least 80% of stems were identified to genus and at least 60% of stems
433 identified to species (mean = 90.3% stems identified to species; 84% of plots had at least 80% stems
434 identified to species, 63% had at least 90% of stems identified to species). All stem diameter
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
437 three largest tropical humid forest blocs, with 158 plots in South America, 162 in Africa and 40 in
438 Asia (Fig. 3). These came from 166 discrete localities (South America 80, Africa 67, Asia 19), where
439 a 'locality' is defined as clusters of plots with maximum inter-plot distance of 5 km. Plot data were
440 curated in ForestPlots.net⁴⁵ or using equivalent offline procedures, with each plot following the same
441 quality control and subsequent calculation protocol. Aboveground biomass (AGB) was estimated for
442 each stem using the allometric equation $\text{AGB} = 0.0673 \times (\rho D^2 H)^{0.976}$, from⁴⁶, where ρ is stem wood
443 density (in $\text{g}\cdot\text{cm}^{-3}$) obtained from a world database^{47,48}, D is stem diameter (in cm) at 1.3m or above
444 buttresses, and H is height (in m), the latter estimated using regional height-diameter Weibull
445 equations⁴⁹. AGB values were converted to estimates of carbon using the mean carbon fraction for
446 tropical angiosperms, 47.1%, from⁵⁰. Taxon richness was estimated as the sum of identified species
447 and morphospecies plus the estimated number of unidentified taxa based on observed richness per

448 stem ratios (details in Supplementary Methods). Richness per 300 stems was estimated using
449 individual 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 square-
452 root transformed, while taxon richness was modelled using a negative binomial error distribution to
453 account for overdispersion. We used log-linear generalised linear models with binomial errors to
454 model the relationship between Sørensen index (beta diversity) and geographical distance between
455 plots in each continent, restricting this analysis to plots with >90% of stems identified to species level
456 (227 plots). Relationships among 1 ha plots were assessed using [1] bivariate Kendall's τ correlations
457 and [2] multiple regressions of carbon as a function of diversity, climate (cumulative water deficit,
458 MAT, MAP; 1 km resolution) and soil (total exchangeable bases, C:N ratio, soil texture; 0-30 cm
459 depth). We ran all predictor subsets and averaged models where cumulative AIC_c weights summed to
460 0.95. Residual spatial autocorrelation was present, so we repeated the analysis using simultaneous
461 autoregressive error models to explicitly model spatially autocorrelated errors. We also repeated the
462 analysis using structural equation models implemented in the R package lavaan⁵¹. Relationships
463 amongst 0.04 ha subplots in the 266 plots where subplot level data were also available were examined
464 using multiple regressions of ln(carbon) against ln(diversity) and ln(stem density) for each plot
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
467 mechanisms driving diversity-carbon relationships, which are described in full in the Supplementary
468 Discussion. Briefly, we produced separate models of carbon stocks as a function of the community
469 weighted mean (CWM) of wood density, the CWM of maximum stem diameter, the standard
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
472 mixed effects models with plot identity as a random effect. We related the expected probability of
473 sampling a species with large potential size or high wood density (defined as maximum diameter \geq 70
474 cm or wood density \geq 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
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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.

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687 **Tables**

688 **Table 1.** Pan-tropical and continental studies assessing the diversity-carbon relationship. Sampling locations are groups of plots in close proximity to each
 689 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
 690 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
 691 and surrounding contiguous forest, and Borneo. + indicates a positive diversity-carbon relationship, = indicates no relationship, NA indicates the relationship
 692 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
 693 plots (either 5 cm or 10 cm).

Study	Geographical scope	Number of plots		Number of sampling locations				Taxonomic level	Diversity measures	Minimum identification level	Diversity-carbon relationship	
		1 ha	0.04 ha	Total	Amazon	Congo	Borneo				Within stand	Among 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	688 ^a	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

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

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

696 ^c Relationship analysed among 1 ha plots within sampling locations, not among sampling locations.

697 ^d 0.1 ha not 0.04 ha.

698 ^e Relationship among sampling locations.

699 **Table 2.** Mean carbon stocks per unit area and tree diversity in forest inventory plots in South
 700 America (n = 158), Africa (n = 162) and Asia (n = 40). 95% confidence limits derived from 10,000
 701 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
 703 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) B
Fisher's α	80 (71 – 88) ^B	28 (26 – 30) ^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) B
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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723 **Table 3.** Correlations (Kendall's τ) between carbon and tree diversity in South America (n = 158
 724 plots), Africa (n = 162) and Asia (n = 40). Power analysis was used to estimate the minimum effect
 725 size (presented as both τ and Pearson's r) detectable with 80% power. Correlations with taxon
 726 richness per 300 stems are shown in parentheses. Correlations with other diversity metrics shown in
 727 Supplementary Table 4.

Diversity metric	South America		Africa		Asia	
	τ	<i>P-value</i>	τ	<i>P-value</i>	τ	<i>P-value</i>
Fisher's α	0.083	0.12	0.012	0.821	0.115	0.302
Species richness	0.084 (0.092)	0.12 (0.087)	0.014 (0.031)	0.788 (0.573)	0.132 (0.151)	0.230 (0.174)
Genus richness	0.066 (0.059)	0.223 (0.272)	-0.016 (0.01)	0.765 (0.859)	-0.006 (-0.051)	0.954 (0.652)
Family richness	-0.007 (-0.042)	0.893 (0.43)	-0.051 (-0.036)	0.35 (0.519)	0.087 (0.021)	0.434 (0.862)
Detectable effect size	$\tau = 0.14$ $r = 0.22$		$\tau = 0.14$ $r = 0.22$		$\tau = 0.28$ $r = 0.43$	

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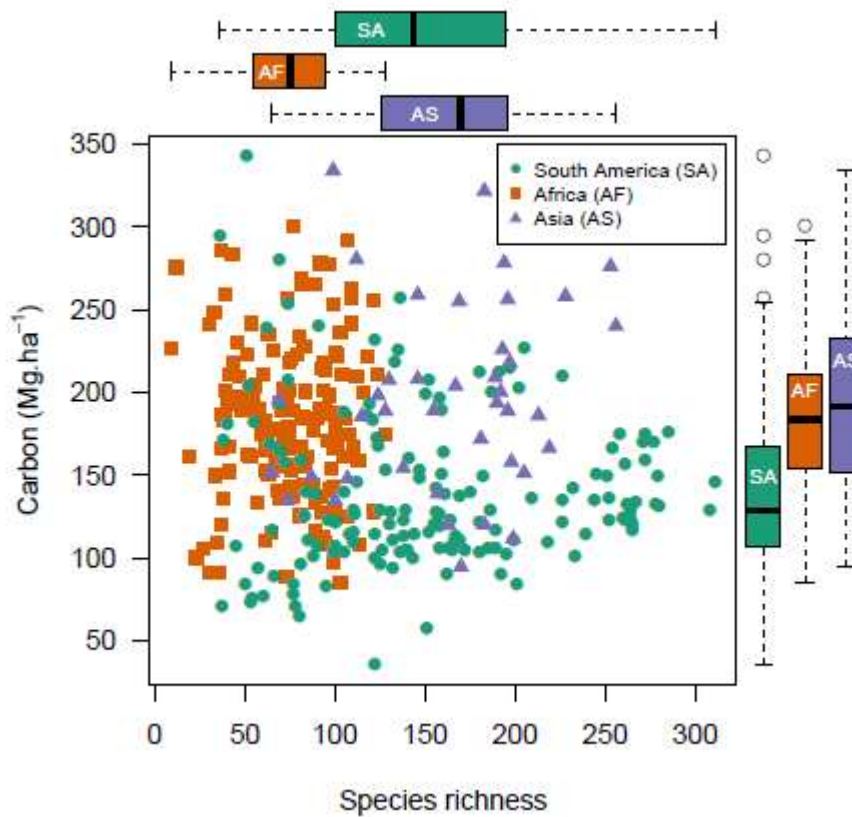
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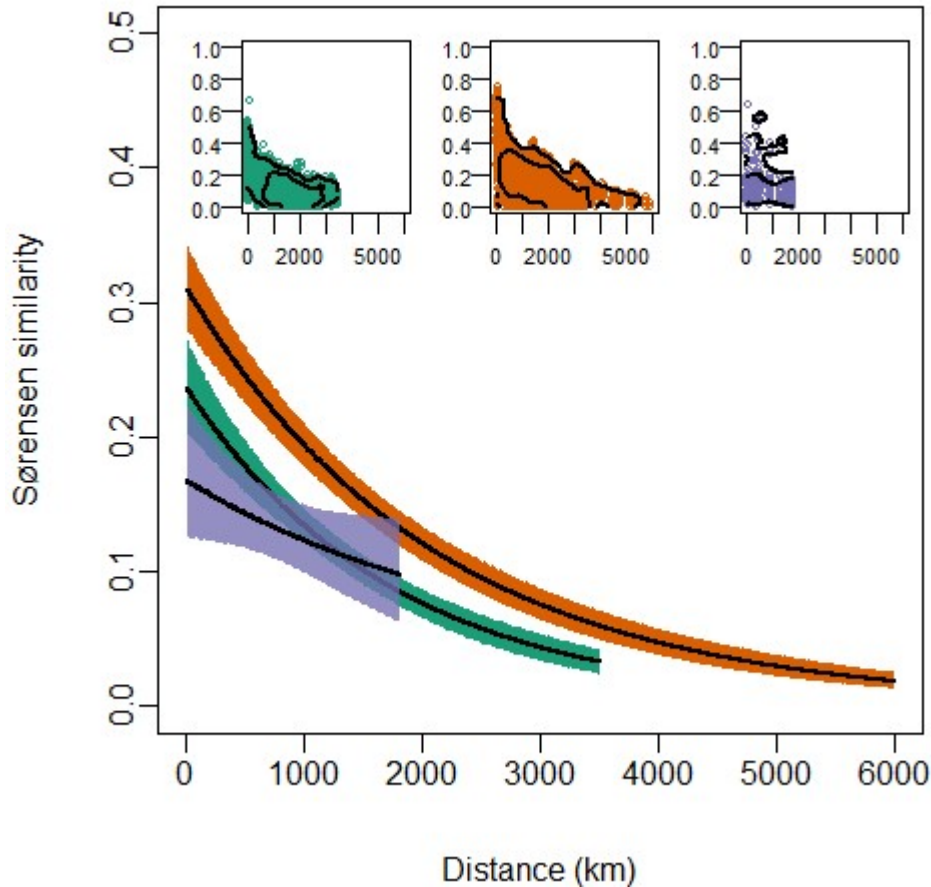
747 **Figures**

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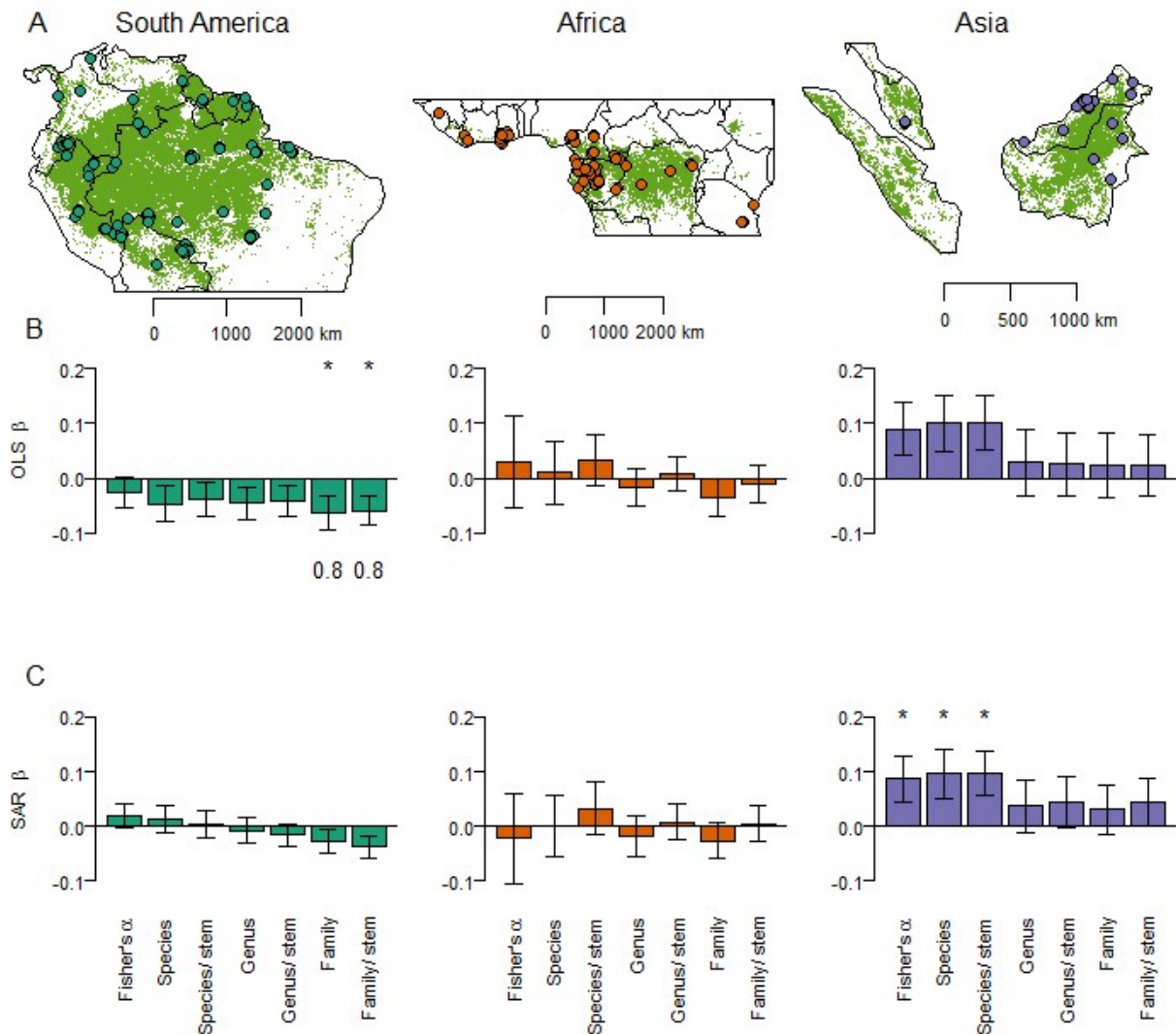
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750 **Figure 1.** The relationship between carbon stocks per unit area and tree species richness across the
 751 tropical forest biome. Green circles = plots in South America ($n = 158$), orange squares = Africa ($n =$
 752 162) and purple triangles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



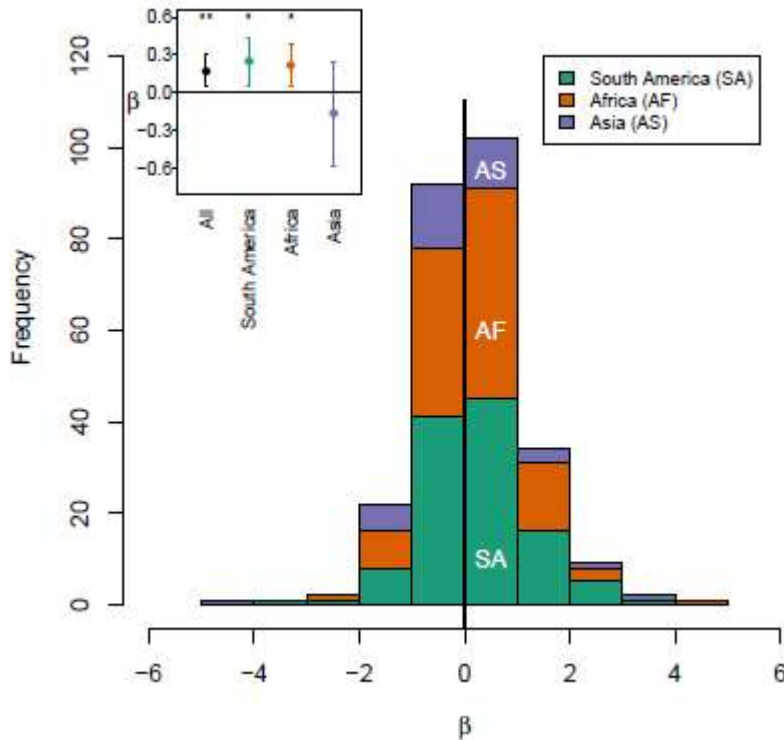
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760 **Figure 2.** Decay in similarity (Sørensen index) of tree communities with distance in South America
 761 (green), Africa (orange) and Asia (purple). Solid lines show fitted relationships of the form
 762 $\ln(\text{similarity}) = \alpha + \beta \times \text{distance} + \varepsilon$. Estimated α and β parameters for each continent are given in
 763 Supplementary Fig. S12, ε denotes binomial errors. Differences in the α parameter indicate
 764 differences in the similarity of neighbouring stands, while differences in the β parameter indicate
 765 differences in the distance decay of tree community similarity. Filled polygons show 95%
 766 confidence intervals derived from 10000 bootstrap resamples. Data underlying these relationships are
 767 shown in insets, with contours (0.05 and 0.25 quantiles) overlain to show the density of points
 768 following kernel smoothing.



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770 **Figure 3.** Stand-level effect of diversity on carbon stocks per unit area. (A) Location of clusters of
 771 forest inventory plots in South America ($n = 158$ plots), Africa ($n = 162$ plots) and Asia ($n = 40$ plots)
 772 (some cluster centroids are not visible due to over plotting). (B & C) Diversity metric coefficients in
 773 multiple regressions relating carbon to diversity, climate and soil. Results have been presented for (B)
 774 non-spatial (OLS) and (C) simultaneous autoregressive error (SAR) models. Bars show model-
 775 averaged parameter estimates, with error bars showing standard errors. Asterisks denote variables that
 776 were significant in the average model ($P < 0.05$), with the summed AIC_C weights of models in which
 777 a variable appears shown beneath bars (where >0.75). Taxa/ stem denotes richness estimates per 300
 778 stems. SAR models indicate that increasing species richness by 1 SD (from 86 to 151 species.ha⁻¹)
 779 increased carbon by 1.5 Mg.ha⁻¹ in South America, 0.2 Mg.ha⁻¹ in Africa and 15.8 Mg.ha⁻¹ in Asia
 780 (note only the relationship in Asia was statistically significant). Green shading in (A) shows the extent
 781 of broadleaved evergreen and fresh water regularly flooded forest classes from ⁵². Model coefficients
 782 are given in Supplementary Table 5. Maps were created in R version 3.02 (<http://www.R-project.org/>)
 783 ⁵³ using base maps from maps package version 2.3-9 (<http://CRAN.R-project.org/package=maps>) ⁵⁴.



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785 **Figure 4.** Variation in the coefficient (β) of the relationship between species richness and carbon
786 among 0.04 ha subplots within 266 1 ha plots. Coefficients come from multiple regression models
787 also containing the number of stems as a second-order polynomial term to allow for a saturating
788 relationship. Coefficients from plots in South America are shown in green, Africa in orange and Asia
789 in purple. Mean values of coefficients are shown in the inset, with error bars showing 95% confidence
790 intervals derived from 10000 bootstrap resamples (with replacement) of the dataset, with asterisks
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 $\ln(\text{Mg}\cdot\text{ha}^{-1}$
794 carbon) per $\ln(\text{tree species})$.