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Diversity enhances carbon storage in tropical forests

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29

30   **Abstract**

31

32   **Aim** Tropical forests store 25% of the global carbon and harbor 96% of the world's tree species, but it is

33   not clear whether this high biodiversity matters for carbon storage. Few studies have teased apart the

34   relative importance of forest attributes and environmental drivers for ecosystem functioning, and no such

35   study exists for the tropics.

36   **Location** Neotropics

37   **Methods** We relate aboveground biomass (AGB) to forest attributes (diversity and structure) and

38   environmental drivers (annual rainfall and soil fertility) using data from 144,000 trees, 2,050 forest plots

39   and 59 forest sites. The sites span the complete latitudinal and climatic gradients in the lowland

40   Neotropics, with rainfall ranging from 750 to 4350 mm/y. Relationships were analyzed within forest sites

41   at 0.1 ha and 1 ha scale, and across forest sites along large-scale environmental gradients. We used a

42   structural equation model to test the hypothesis that species richness, forest structural attributes, and

43   environmental drivers have independent, positive effects on AGB.

44   **Results** Across sites, AGB was most strongly driven by rainfall, followed by average tree stem diameter

45   and rarefied species richness, which all had positive effects on AGB. Our indicator of soil fertility (cation

46   exchange capacity) had a negligible effect on AGB, perhaps because we used a global soil database.

47   Taxonomic forest attributes (i.e., species richness, rarefied richness and Shannon diversity) had the

48   strongest relationships with AGB at small spatial scales, where an additional species can still make a

49   difference in terms of niche complementarity, whereas structural forest attributes (i.e., tree density and

50   tree size) had strong relationships with AGB at all spatial scales.

3

51 **Main conclusions** Biodiversity has an independent, positive effect on AGB and ecosystem functioning,

52 not only in relatively simple temperate systems, but also in structurally complex hyperdiverse tropical

53 forests. Biodiversity conservation should therefore be a key component of REDD+ strategies.

54

55

56 **Introduction**

57

58 Tropical forests are hotspots for carbon and biodiversity; they only cover 7-10 % of the Earth's land

59 surface, but store 25 % of the terrestrial above- and below-ground carbon (Bonan, 2008), are responsible

60 for 34 % of terrestrial primary productivity (Beer *et al.*, 2010), and harbor 96 % of the estimated 45,000

61 tree species in the world (Fine *et al.*, 2008). From a practical point of view, this provides a win-win

62 situation for the UN- Reduced Emissions from Deforestation and Degradation (REDD+) initiative, which

63 aims to conserve carbon storage of tropical forest while safeguarding biodiversity. Importantly,

64 biodiversity conservation can be much more than a side benefit alone, if a higher biodiversity enhances

65 carbon sequestration and storage (Díaz *et al.*, 2009). Forest functioning may not only be determined by

66 taxonomic attributes (i.e., measures of species identity) of the vegetation, but also by structural attributes,

67 and by the direct and indirect effects of environmental drivers (see the conceptual model in Fig. 1a).

68 Surprisingly few studies have teased apart the relative importance of these environmental drivers and

69 forest attributes for ecosystem properties and processes (but see Paquette & Messier, 2011; Vila *et al.*,

70 2013).

71 Over the past two decades there has been a strong emphasis on the role of biodiversity in

72 ecosystem properties, processes, and services (Naeem *et al.*, 2009 and references therein). Species

73 richness is thought to enhance productivity through: (1) niche complementarity, where species have

74 different niches, and are therefore able to access more of the available resources or facilitating each other,

75 thus enhancing overall productivity (Tilman *et al.,* 2001); (2) the selection effect, as by chance a very

76 productive species is included in the community (Loreau & Hector, 2001); (3) the insurance effect, as one

4

77   species contributes more to ecosystem productivity in one year, and another species in another year (Yachi

78   & Loreau, 1999; Isbell *et al.*, 2011). These hypotheses about the relationship between species richness and

79   productivity could also apply to standing biomass, as higher productivity may lead to faster biomass

80   accumulation, and productivity and biomass are therefore positively correlated in forests (Chisholm *et al.*,

81   2013).

82   Not only taxonomic attributes (i.e., species identity), but also structural attributes, such as stem

83   diameter, tree density and leaf area index, determine biomass, resource capture and productivity.

84   Vegetation structure contributes directly to biomass, but variation in structure such as leaf layering may

85   also enhance light capture and carbon gain. Structural attributes may vary more strongly within

86   communities (due to disturbances) and across communities (due to environmental gradients) than

87   taxonomic attributes, and may have a larger direct impact on biomass and ecosystem processes. A recent

88   study found, for example, that vegetation quantity (biomass) rather than vegetation quality (i.e., species

89   functional traits and variation therein) was the main driver of productivity in tropical secondary forests

90   (Lohbeck *et al.*, 2015). The question is therefore whether taxonomic attributes may explain any additional

91   variation in above-ground biomass (AGB), once the role of structural attributes has explicitly been taken

92   into account (Fig. 1a).

93   A recent meta-analysis showed that in experimental studies species richness increased primary

94   productivity and standing biomass and that biodiversity loss has, therefore, a negative effect on ecosystem

95   functioning (Cardinale *et al.*, 2011). However, most studies included in the meta-analysis were carried out

96   at small spatial scales, and involved grasslands and aquatic systems, and most experiments used a low

97   number of species (less than 10, Cardinale *et al.*, 2011), and thus the effect of high species richness can

98   not be assessed. It is not clear therefore whether the relationship between biodiversity and biomass will

99   also hold for (1) larger spatial scales -where there may be a saturating effect as the number of species rises

100   without a further increase in carbon storage, (2) areas under different environmental control, and (3)

101   hyper-diverse communities in the tropics where many species might be functionally redundant.

102   The relationships between species richness, AGB and productivity may vary with spatial scale.

103   Experimental grassland studies and many forest surveys have typically used small plots, and found that

104   the positive effect of species richness on biomass or biomass productivity saturates with only 3-8 species

105   (Tilman *et al.*, 2001; Zhang *et al.*, 2012; Gamfeldt *et al.*, 2013; Vila *et al.*, 2013). Chisholm *et al.* (2013)

106   found for temperate and tropical forests that species richness and biomass were positively related within

107   forest sites at small spatial scales (20 × 20 m), probably because in a small area with relatively few species

108   any additional species still matters for productivity and AGB. At larger spatial scales (100 × 100 m) there

109   was no consistent relationship between species richness and biomass, probably as a result of such

110   saturation effect .

111   The relationship between species richness and productivity may also vary with systems under

112   different environmental conditions. In a study using small survey plots in Canada, Paquette & Messier

113   (2011) found that in boreal forests facing harsh environmental conditions, functional tree diversity affects

114   productivity strongly and positively, whereas in benign and productive temperate forests diversity has a

115   weaker effect on productivity. Paquette & Messier hypothesized that in stressful (e.g., cold or dry)

116   environments diversity contributes to facilitation processes and, hence, to productivity, whereas in benign

117   environments diversity results in more competition. It cannot be ruled out, however, that the stronger

118   diversity effect in boreal forests is simply a result of the lower species richness there.

119   Both taxonomic and structural attributes and ecosystem properties and processes may vary along

120   environmental gradients (Fig. 1a). Species richness of tropical lowland forests tends to increase with

121   rainfall and reduced seasonality (ter Steege *et al.*, 2003). The density of large trees, forest AGB and net

122   primary productivity all increase with resource availability (annual rainfall and soil fertility), and decrease

123   with temperature (Malhi *et al.*, 2004; Baraloto *et al.*, 2011; Quesada *et al.*, 2012; Slik *et al.*, 2013). Hence,

124   environmental drivers are likely to affect AGB either directly, or indirectly via their effect on taxonomic

125   and structural forest attributes (Fig. 1a).

126   Here we relate aboveground biomass (AGB) to taxonomic and structural forest attributes, as well

127   as to rainfall and soil fertility. We use data from 144,000 trees that were sampled in 2,050 forest plots

128   established in 59 forest sites. This dataset spans the complete latitudinal and climatic gradient in the

129   lowland Neotropics (ranging from 750 to 4350 mm rainfall per year) and covers all major forest types

130   (from dry deciduous- to wet forests, Appendix S1 in Supporting Information). Relationships were

131   analyzed at a local scale under relatively homogeneous environmental conditions within forest sites (0.1

132   and 1 ha plots) and at a regional scale along large-scale environmental and biogeographical gradients

133   across forest sites.

134   We address two major questions. First, what are the effects of taxonomic and structural attributes

135   on AGB and what is their relative importance? We hypothesize that species diversity has a positive effect

136   on biomass (through niche complementarity, the selection effect, or the insurance effect) and that this

137   effect can be observed at small (0.1 ha) spatial scales (where richness is low, so an additional species still

138   makes a difference) but not at larger (1 ha) spatial scales (because of species redundancy). We predict that

139   as stem density and average stem diameter increases there will be greater AGB, and that they have

140   stronger effects on AGB than taxonomic forest attributes. Second, what are the direct effects of

141   environmental drivers on AGB, and on the taxonomic and structural attributes of the forest? We

142   hypothesize that with an increase in resource availability (water and nutrients) there will be an increase in

143   AGB, forest structure (i.e., tree size) and taxonomic diversity, and that annual rainfall will have a stronger

144   effect than soil fertility given the large climatic gradient considered.

145

146   **Methods**

147

148   *Study sites -* We compiled information on species diversity, structure and biomass from 294 1 ha plots and

149   1,975 0.1 ha plots established in 59 mature forest sites. that covered nearly the full latitudinal range of

150   Neotropical forests from Mexico to Bolivia (Fig. 2, Appendix S1). Rainfall ranged from 750 to 4350

151   mm/yr, and soil Cation Exchange Capacity (CEC) ranged from 1 to 83 cmol/kg. For all analyses we only

152   focus on trees because there was no consistent inventory data for lianas and palms, and in most forests

153   lianas and palms contribute only little to AGB. For an extensive description of the methods see Appendix

154   S2.

155

156   *Biomass calculations* - We took advantage of available plot data in mature, fully developed "old-growth"

157   forests, without visible effects of past human disturbance. The size, shape, spatial distribution and

158   contiguousness of plots varied across sites (Appendix S1). For this study, we calculated forest attributes at

159   two spatial scales (0.1 ha and 1 ha).

160   In many plots only trees ≥ 10 cm stem diameter at breast height (dbh: tree diameter at 1.3 m from

161   the ground) were measured, but in other plots data for trees ≥ 5 cm dbh. were also included as these small

162   stems can contribute a significant part of AGB in drier forests. AGB was calculated for plots of 0.1 ha and

163   1 ha, as the relationship between AGB and diversity is scale-dependent (Chisholm *et al.,* 2013). For each

164   plot, above-ground biomass was calculated for each tree using six different allometric equations. The

165   allometric equations were based on stem diameter only (Pearson, Brown *et al.,* 2005, henceforth referred

166   to as the "Brown" equations), or a combination of stem diameter and wood density (Chave *et al.,* 2005,

167   henceforth referred to as the "Chave" equations). Brown and Chave both present three different equations

168   for different forest types; dry forest, moist forest and wet forest. For use in the Chave calculations wood

169   density (WD, g cm^{-3}) data came from the local sites, or from the Neotropical data of a global WD database

170   (Zanne *et al.,* 2009, http://datadryad.org/handle/10255/dryad.235). Biomass was then summed across all

171   trees to obtain above-ground plot biomass (AGB, in Mg/ha). We first checked to what extent AGB varied

172   with the type of biomass allometric equation used, and with both diameter cutoff limits (Appendix S3).

173   The Chave and Brown estimates of plot AGB for trees ≥ 10 cm dbh were tightly related (r^2=0.81).

174   Estimated plot AGB using the Chave equations was on average 1.15 times the estimated AGB using the

175   Brown equations (paired t-test, t=16.1, P<0.001, N=480). Using the Chave equations, the estimated plot

176   AGB for trees ≥5cm dbh was on average 1.04 times the AGB of trees ≥10 cm dbh and this ratio was

177   especially large for dry forests (on average 1.178) but close to 1 for moist forests (1.033) and wet forests

178   (1.020, Appendix S3). In dry forests, small trees (5-10 cm dbh) contribute, therefore, a relatively large

179   proportion to AGB, although their absolute contribution is small. For further analysis we then used the

180   Chave equations that corresponded to the forest type (dry, moist or wet) that the plot belonged to, and we

181   used trees ≥10 cm dbh, as these data were available for all plots. We used the Chave equations because

182   they include wood density, which is an important source of large-scale variation in AGB (Mitchard *et al.,*

183   2014).

184

185   *Structural attributes -* AGB variation across forest plots is, amongst others, a function of the tree density,

186   mean stem diameter, and wood density of trees. It is therefore not the question whether these variables are

187   related to AGB, but what is their relative strength in determining AGB plot biomass. For each plot, five

188   structural attributes were calculated for which data were available and that are relevant for the biomass

189   model used: overall tree density, density of large trees (≥ 60cm dbh), mean tree diameter, and stand basal

190   area. Note that individual tree biomass is calculated based on tree diameter, and hence, tree biomass scales

191   closely with the basal area of the individual tree. This is something different from stand basal area. A high

192   stand basal area can be caused by many small trees (that each contain little biomass), or a few trees with

193   large basal area (that each contain a disproportionally large biomass).

194

195   *Taxonomic attributes-* For each plot, three taxonomic attributes were calculated: species richness per area,

196   rarefied species richness per 50 individuals, and Shannon diversity. Rarefied species richness is the

197   number of species observed when a certain number of trees is randomly drawn from a plot. Such

198   rarefaction removes the confounding effect of tree density on species richness. For rarefied richness we

199   used 50 individuals as a reference, as this number of individuals is found in both the 0.1 ha plots and 1 ha

200   plots. Calculations were made using either EstimateS 9.1.0 (Colwell, 2011) or the R package Vegan

201   (Oksanen *et al.*, 2014).

202

203   *Environmental factors-* For each site, six climatic variables were obtained from the nearest climatological

204   station, or from interpolated climatic maps from Worldclim (Hijmans *et al.,* 2005). We used mean annual

205 rainfall as the main climatic variable for subsequent analyses, because it was closely related to all other

206 climate variables, and to AGB and forest attributes. For each site six soil variables were obtained using

207 site coordinates and maps from the Harmonized World Soil Database (Nachtergaele *et al.,* 2012). Data on

208 soil N and P were not available from this database. We used CEC (in cmol/kg) as our main soil variable,

209 because it was strongly correlated with the other fertility measures and provides a straightforward measure

210 of soil fertility.

211

212 *Statistical analyses* - Pearson correlations were used to evaluate whether there was an association between

213 AGB and each of the measures of taxonomic and structural attributes *within sites* for 0.1 ha plots and 1 ha

214 plots. For the 1 ha-level, one correlation was made per site, using all 1-ha plots (with a minimum of 4

215 plots). For the 0.1 ha-level, several correlations were made per site if these small plots were nested within

216 a 1 ha plot and if several 1 ha plots were available. In that case a correlation was made per 1 ha plot using

217 all 0.1 ha subplots nested within the larger 1 ha plot, and this was repeated for all the 1 ha plots.

218 Alternatively, a single correlation was made across all plots at a site, if these small plots were not nested

219 within a single 1 ha plot. To evaluate how general these within-site correlations were, we then calculated

220 at the 0.1 ha and 1 ha level the average and 95% confidence interval of all of these correlation coefficients

221 combined, pooling all sites. If the 95% confidence interval did not overlap with zero, this means that, in

222 general, there is a significant correlation between AGB and the variable concerned. We checked the

223 consistency of the results, by repeating this analysis with a mixed linear model in which site was included

224 as a random factor, to account for the nestedness of the data (Appendix S4). For the 0.1 ha plots also the 1

225 ha plot they belonged to was included as a random factor in the model.

226 We also analyzed whether there was a relationship between AGB, taxonomic attributes and

227 structural attributes *across sites*, and therefore across the large-scale environmental gradients. Where data

228 from multiple plots were available at each site we averaged the data per site, to avoid problems with

229 nestedness. For the sites that had both 0.1 ha and 1 ha plots, we only used the average of the 1ha plots, as

230 they provide more accurate estimates of biomass and diversity. In total, data was available for 59 sites (26

231   site averages based on 1 ha plots and 33 site averages based 0.1 ha plots). One outlying site with a small

232   plot with exceptionally high AGB was removed from subsequent regression and SEM analyses.

233

234   *Structural equation modelling* - We used structural equation modelling (SEM) to test for the direct and

235   indirect effects of climate, soil fertility, and taxonomic and structural attributes on AGB (Fig. 1a). To

236   avoid complexity with nestedness of plots within sites, we based the SEM on average values for 58 sites.

237   Average site values were estimated with a different accuracy. To account for this, sites in the SEM were

238   weighted by the square root of the total plot area per site.

239   To test the conceptual model of Fig .1a, we selected only one variable per "box" (climate, soil,

240   taxonomic attributes, or structural attributes), as we had a limited number of replicates (sites). We used

241   annual rainfall as the climate variable and CEC as the soil variable. Because bivariate scatterplots

242   indicated that AGB and rarefied richness showed a hump-shaped relationship with rainfall, we included

243   for these two response variables both rainfall and rainfall^2 as predictor variables in the analysis (Fig. 1b),

244   which allows to model such a hump-shaped relationship. The combined effect of rainfall and rainfall^2 was

245   evaluated by including a composite variable (the oval box in Fig. 1b).

246   Of the three taxonomic attributes considered, we only included rarefied species richness in the

247   SEM, because it is less dependent on plot size, and multiple regressions indicated that it was the best

248   predictor of AGB (data not shown). Of the four structural attributes considered (stand basal area, average

249   tree diameter, number of trees larger than 60 cm diameter, and stem density), we did a series of SEMs

250   using the same model structure as in Fig. 1a but each time a different structural variable. The models

251   included square root-transformed AGB as the dependent variable, rarefied species richness as an

252   endogenous variable (i.e., a variable that is affected by other variables), and annual rainfall, rainfall^2, and

253   CEC as exogenous variables (i.e., independent variables that have only an effect on other variables), and

254   the composite variable combining rainfall and rainfall^2. The only model that significantly fitted the data

255   (i.e., it had a *P*-value larger than 0.05) was the model that included average tree diameter as a structural

256   attribute.

257   The indirect effects of the exogenous variables (rainfall and CEC) on AGB were calculated by

258   multiplying the standardized coefficients of all paths on one route between one of the exogenous variables

259   and AGB. All SEM analyses were performed in R 3.0.2. The models were specified with variables and

260   paths (the 'arrows' between variables) using the sem function of the lavaan package (Rosseel, 2012). The

261   replicate weights were defined using the svydesign function of the survey package, and the lavaan.survey

262   function was used to evaluate the models when taking replicate weights into account.

263

264   **Results**

265   *Within-site relations*

266   Within each study site, the AGB of the plots was regressed against the forest attributes. Within most study

267   sites, AGB tended to increase (non-significantly) with species richness, Shannon diversity and rarefied

268   richness for the 0.1 ha plots, whereas there were no clear relationships for the 1 ha plots (Fig. 3). Within

269   each study site, AGB increased consistently with average tree diameter, stand basal area, and large tree

270   density of the plots, both for 0.1 ha and 1 ha spatial scales, whereas tree density was only significant at the

271   0.1 ha scale (Fig. 4). The relationship was especially strong between AGB and stand basal area.

272   To test the generality of these relationships, we conducted a meta-analysis on the value of the

273   correlation coefficient between AGB and each of the predictor variables within each site (Fig. 5, N=103-

274   196 correlations for 0.1 ha plots, and N=16-17 correlations for 1 ha plots), and calculated the mean

275   correlation and 95% confidence intervals. This meta-analysis confirmed that, overall, there was a

276   consistent significant positive relationship between AGB and taxonomic attributes at the 0.1 scale (i.e., the

277   95% confidence interval of the average correlation coefficient did not overlap with zero), whereas this

278   relationship disappeared at the 1 ha scale. Not surprisingly, structural variables such as stand basal area,

279   average tree diameter and the density of large trees are significantly and strongly positively related to

280   AGB at both 0.1 and 1 ha spatial scales (Fig. 5). Similar results were found with a mixed linear model in

281   which site was included as a random factor, to account for the nestedness of the data (Appendix S4). The

282   strength of this within-site correlation between AGB and taxonomic diversity/stem density declined with

283   the amount of annual rainfall of the site (Appendix S5).

284

285   *Cross-site relationships between AGB and forest attributes*

286   In addition to testing within sites, we also analyzed whether there were bivariate relationships between

287   AGB, and taxonomic attributes, and structural attributes across our 58 Neotropical forest sites, and thus

288   across large-scale environmental gradients. We selected for this analysis the best scalable measure of

289   diversity (rarefied richness), and one of the best structural predictors of AGB (average tree diameter).

290   Rarefied richness varied 2.7-fold across sites (from 15 to 42 species per 50 stems, Fig. 2b), average tree

291   diameter varied 2.4-fold (from 13 to 32 cm, Fig. 2c) and AGB varied 8.1-fold (from 59 to 479 Mg/ha, Fig.

292   2a).

293   Rarefied richness (Fig. 6a) and AGB (Fig. 6c) showed a hump-backed relationship with annual

294   rainfall and peaked halfway along the rainfall gradient, between 2000 and 3000 mm/y. Average tree

295   diameter increased continuously with rainfall (Fig. 6b). All three variables tended to decrease with the

296   cation exchange capacity of the soil (Appendix 6), although the relationships were non-significant. AGB

297   was not only related to environmental variables, but also to forest attributes; AGB showed a positive

298   relationship with rarefied richness (Fig. 7a) and average stem diameter (Fig. 7b) across sites.

299

300   *Structural equation model; what are the main drivers of AGB variation?*

301   We used structural equation modelling (SEM) to evaluate our conceptual model (Fig. 1a). Our SEM

302   included six variables: annual rainfall, annual rainfall^2, cation exchange capacity (CEC), rarefied species

303   richness, average stem diameter, and AGB. Average stem diameter was selected as the structural attribute

304   because this was the only accepted model (i.e., it described the data with sufficient accuracy) with *P*-value

305   for the overall model fit larger than 0.05 (Fig. 1b; χ^2=4.95, P=0. 176. df=3), whereas the models were

306   rejected that included basal area (χ^2=23.10, P<0.001) or stem density (χ^2=11.80, P=0.008). The accepted

307 model explained 73% of the variation in AGB, 15% of the variation in rarefied richness, and 26% of the

308 variation in average stem diameter.

309   The composite variable 'rainfall+rainfall^2' had the strongest direct effect on AGB (beta=0.67, P <

310 0.001), followed by average stem diameter (beta=0.26, P=0.001), rarefied richness (beta=0.20, P=0.006),

311 and CEC (beta=-0.06, P=0.647) (Table 1, Fig. 1b). Rarefied richness was most strongly affected by

312 rainfall+rainfall^2 (beta=0.39, P=0.037), and average diameter was most strongly affected by the linear

313 effect of rainfall (beta=0.49, P=0.018). The linear effect of rainfall had, via average diameter, the strongest

314 indirect effect on AGB (beta=0.129; Appendix S7).

315

316

317 **Discussion**

318

319 Tropical forests store a significant part of global carbon and biodiversity, and the question is whether this

320 biodiversity is relevant for carbon storage? We related above-ground biomass (AGB) to forest attributes

321 and environmental drivers, and found that taxonomic attributes had the strongest relationships with AGB

322 at small spatial scales (0.1 ha), whereas structural attributes had strong relationships with AGB at both

323 spatial scales (0.1 and 1 ha). Species richness had an independent, positive effect on AGB at local scales,

324 and when sites across the continent were compared. We discuss the implications of these results for

325 conservation and REDD+ activities.

326

327 *Taxonomic attributes have the strongest relationships with AGB at small spatial scales*

328 We hypothesized that species richness and diversity would have a positive effect on biomass through

329 niche complementarity, the selection effect or the insurance effect, and that these effects would be

330 observed especially within sites at a small spatial scale (where the species richness value is low because of

331 the small sample area) but not at larger spatial scale (because of species redundancy). Indeed, within sites

332 we found positive relationships between AGB and taxonomic diversity measures at the 0.1 ha but not at

14

333   the 1 ha scale (Fig. 5). The relationship was strongest for area-based diversity measures (richness) and the

334   weakest for Shannon diversity and rarefied species richness (Fig. 5), indicating that variation in stem

335   density among plots partly drives the AGB-diversity relation. Similarly, in a global analysis of larger

336   forest plots (>16 ha), Chisholm *et al.* (2013) also found that diversity-biomass relationships were always

337   strong and positive at very small spatial scales (20x20 m), whereas at larger spatial scales (0.25 ha and 1

338   ha) there was no consistent relationship. Higher species richness enhances the variation in species traits

339   found in the community leading to niche complementarity, a higher resource capture, more efficient

340   resource use, and higher productivity. Higher species richness may also enhance facilitation (e.g., where

341   for example a nitrogen fixing species enhances soil fertility, and through this the productivity of the other

342   species). Higher species richness also increases the chance of a selection effect (in which a highly

343   productive or large species that stores a lot of biomass is included in the stand).

344   It should be acknowledged that 0.1 ha plots are rather small to accurately estimate biomass: in

345   some forests this plot size will include very few trees, or an emergent tree. This may strongly affect the

346   biomass estimate, and partly explain the large scatter in AGB at a given site. Hence, within-site

347   relationships between taxonomic diversity and AGB may be partly affected by gap dynamics and cyclic

348   succession: just after disturbance there may be a low tree species richness and biomass in the gap, whereas

349   with patch development both the number of species and their biomass increase over time, in line with the

350   intermediate disturbance hypothesis (Connell, 1978). Alternatively, the relationship between diversity and

351   AGB within sites may be driven by more permanent local environmental gradients, where areas with

352   adverse conditions, such as shallow soils (e.g., Emilio *et al.*, 2014), rocky outcrops, waterlogged areas or

353   ridge tops exposed to intense winds contain fewer stems, fewer species and lower biomass than areas with

354   deep well-developed humid and fertile soils.

355

356   *Structural attributes are tightly related to AGB at all spatial scales*

357   We expected that greater tree density and basal area of the forest would lead to an increase in AGB, as

358   structure positively influences biomass, but we did not know their relative importance. We found that

359 within sites, AGB moderately increased with increasing tree density, more strongly with large tree density

360 and most strongly with stand basal area (Fig. 5). AGB variation across forest plots is a function of the

361 stem density, and the mean stem diameter, height, crown area and wood density of trees. Biomass

362 increases exponentially with tree diameter, and large trees therefore contribute disproportionally to stand

363 biomass compared to small trees. This explains why average tree diameter, large tree density and stand

364 basal area are better predictors of AGB than overall tree density. A recent Pantropical analysis for 120

365 lowland tropical forests (Slik *et al.,* 2013) showed that 70% of the site variation in AGB was determined

366 by the density of large trees (>70 cm diameter at breast height). Because of the paucity of large trees,

367 Neotropical forest contained ca. 30% less biomass when compared to Paleotropical forests. Large trees

368 play an important role in ecosystem functioning, not only because they contribute most AGB but also

369 because they form the forest canopy, where most of the photosynthetic carbon gain is concentrated. These

370 large trees possess large and well-lit crowns, and therefore contribute most to forest primary productivity

371 (Stephenson *et al.,* 2014).

372

373 *Rainfall is a stronger driver of AGB and biodiversity than is soil fertility*

374 We hypothesized that with an increase in plant water availability (rainfall) and nutrient availability (CEC)

375 there would be an increase in AGB (Fig. 1a), whereas at very high rainfall levels we would expect that

376 soils would be highly weathered and leached (e.g., Swaine, 1996), leading to a decline in AGB. We indeed

377 found that AGB showed a unimodel relationship with the rainfall gradient across sites (Fig. 6c). Our

378 results were not due to the equations used (moist forest equations predict a higher biomass than dry and

379 wet forest equations) because when we tested this effect using the same moist forest equation for all plots,

380 then the same unimodal relationship was found (Appendix S8). In our case, the decline in AGB at high

381 rainfall was not due to leaching, as there was no relationship between rainfall and CEC in our dataset

382 (Pearson r = 0.02, n = 60, P = 0.866). A negative relationship between rainfall and soil fertility might be

383 found in geologically relatively homogeneous areas (Swaine, 1996). At the spatial scale of our study

384 across distant Neotropical forest sites, however, there is a large variation in ecological and geological

16

385   history, and parent rock material (cf. Stropp *et al.,* 2009), which may override more subtle relationships

386   between soils and rainfall.

387   Reasons for the decline of AGB at high rainfall may be due to reduced insolation because of cloud

388   cover (Graham *et al.*, 2003), or due to species composition and forest structural attributes. At intermediate

389   rainfall levels, forests are more likely to be dominated by tall and large-diameter drought-deciduous

390   canopy trees that contribute a large amount of biomass whereas at higher rainfall levels forests are more

391   dominated by shorter-statured slender trees that better compete and persist in dense and shaded closed-

392   canopy forest before they are able to access the canopy (Hall & Swaine, 1981; Fauset *et al.,* 2012). At low

393   rainfall, AGB declined, indicating that low water availability and/or a shorter length of the growing season

394   may constrain tree stature (probably because of hydraulic limitation) and tree growth (Toledo *et al.,* 2011),

395   and hence AGB stocks. It should be noted that at the same rainfall level there is a large variation in AGB

396   across forest sites (Fig. 6c) indicating that rainfall may set an upper limit to biomass stocks, but that other

397   factors (topography, shallow soils or rocky soils) may constrain biomass from reaching their potential

398   maximum value. Apart from rainfall, other climatic features that determine plant water availability, such

399   as length or severity of the dry season may explain additional variation in AGB.

400   We hypothesized that AGB would increase with soil fertility. However, we found that AGB

401   showed a non-significant decrease with increased CEC (our indicator of soil fertility, Appendix S6), and

402   CEC was neither significant in the multivariate structural equation model (Fig. 1b). Interestingly, Quesada

403   *et al.* (2012) found that forest AGB in the Amazon decreased with potassium concentration, which is one

404   of the cations that contributes to CEC. However, they also found that total available phosphorous was by

405   far the best predictor of AGB in their study, and that P had a positive effect on AGB and biomass

406   productivity. This is in line with the widely held idea that P limits productivity and biomass in tropical

407   (Vitousek *et al.*, 2010; but see Santiago *et al.,* 2012). It should be stressed that AGB is a state variable that

408   reflects the outcome of various underlying factors that affect biomass production, retention and loss.

409   Biogeographical patterns in species traits (such as maximum height, tree longevity and wood density)

410   determine biomass retention (Slik *et al.,* 2013; Fauset *et al.,* 2015); whereas recent local disturbance

17

411 history may determine biomass loss. As a result, the observed bivariate relationship between biomass and

412 any other variable is location- and scale-dependent, may be weaker than expected, and may have different

413 ultimate causes. For example, the tendency for a negative relationship between AGB and CEC that we

414 observed is not driven by a higher productivity in areas with poor soils, but likely by species having

415 adaptations to local soil conditions that enhance longevity at the species level (high WD, long lifespan),

416 and therefore biomass retention and the buildup of a larger biomass pool at the stand level (Baker *et al.,*

417 2009).

418

419 *AGB is most strongly driven by rainfall, followed by structural attributes, and taxonomic attributes*

420 We used structural equation modelling to test the independent effects of taxonomic and structural

421 attributes on AGB, and to evaluate the relative importance of biotic and environmental drivers of AGB

422 variation across sites. Standardized path coefficients indicate that AGB is most strongly driven by the

423 direct and indirect effects of rainfall (Table 1, Appendix S7, Fig. 1b), followed by average stem diameter

424 and rarefied richness, whereas CEC had a negligible effect (Fig. 1b).

425   At this continental scale, rainfall was a much stronger driver of AGB than our indicator of soil

426 fertility (CEC). It should be stressed that this may partly be the result of methodological constraints; we

427 did not use data on soil conditions at each site and for each plot, but instead used a global soil database to

428 infer soil fertility and we did not consider other nutrients, such as P. Yet, it also may indicate that rainfall

429 constrains productivity and AGB at large spatial scales, whereas soil fertility may become more important

430 at regional (Quesada *et al.,* 2012) and local scales (Laurance *et al.,* 1999).

431   Rarefied species richness has a clear, independent and positive effect on AGB at this continental

432 scale, once other structural and environmental drivers have been taken into account. To our knowledge,

433 this is the first large-scale study analyzing the multivariate relationships between AGB and its drivers

434 (environment and forest attributes) and demonstrating that biodiversity has an independent positive effect

435 on AGB of highly diverse tropical forests. Most empirical studies that have examined biodiversity effects

436 on forest AGB or productivity have ignored the effect of forest structure (e.g., Gamfeldt *et al.,* 2012), the

18

437 environment (Cavanaugh *et al.,* 2014), or both (Chisholm *et al.,* 2013). Baruffol et al. (2012) showed for a

438 single subtropical forest site that during succession diversity had an independent, positive effect on plot

439 basal area growth. Our study shows that the findings from experimental studies, temperate grasslands and

440 relatively simple temperate forests that biodiversity matters for ecosystem functioning, can therefore also

441 be extended to structurally complex, and hyperdiverse tropical forests that contain as many as 15-42

442 species per 50 stems (Appendix S1) .

443   We used a structural equation modeling approach to control as well as possible for other

444 potentially confounding factors, but correlation does not necessarily mean causation. Controlled

445 experiments (e.g., Hector *et al*., 2011), and modeling studies (e.g., Sakschewski *et al.*, 2015) are needed to

446 provide further support for a causal relationship between biodiversity and carbon storage in the tropics.

447 Our study shows that the biodiversity effect is sufficiently strong to be picked up in the real world, and to

448 be ecologically relevant.

449

450 *Implications for carbon storage and REDD+*

451 We have shown that AGB is related to the environment, as well as to structure and diversity of the forest,

452 and these results have three important implications for carbon storage in tropical forest, and the REDD+

453 program.

454   First, our results show that rainfall is the most important driver of AGB, and that AGB peaks in

455 the middle of the rainfall gradient. If AGB also scales closely with belowground biomass then this result

456 implies that, in terms of carbon storage, potential gains from REDD programs are highest in tropical moist

457 forests as these forests occur at intermediate rainfall, and store the largest amount of biomass (Fig. 2). So

458 for REDD+ , forest conservation, restoration or reforestation could best be concentrated in these areas.

459 The hump-backed relationship between AGB and rainfall means that any decrease in rainfall will have

460 different repercussions for long-term carbon storage in wet and dry forests. In currently wet forests, a

461 decline in rainfall may lead in the long-term to higher AGB (e.g., Fauset *et al.,* 2012), whereas in currently

462 moist and dry forest it may lead to lower AGB.

463   Second, structural attributes are amongst the best predictors of AGB, and they are tightly related

464   to AGB at all spatial scales assessed; from small spatial scales (Fig. 4) up to large spatial scales across the

465   continent (Fig. 1b,7). Structural attributes have the advantage that they can easily be measured in the field

466   by local communities, or assessed using remote sensing techniques. By using remote sensing techniques

467   one can easily scale up field data and produce spatially continuous AGB information over large areas

468   (Baccini *et al.*, 2012), thus providing a better assessment of global carbon storage, deforestation and forest

469   degradation, and providing benchmark maps for REDD+ monitoring reporting and verification activities.

470   Although remote sensing maps hold great promise, they may fail to capture regional gradients in biomass

471   that are driven by other forest attributes, such as forest height and wood density (Mitchard *et al.,* 2014).

472   By linking field data to remote sensing derived structural indices, one may map and detect large-scale

473   patterns in AGB while maintaining local realism.

474   A third implication for REDD+ is that areas with high diversity also tend to have a high biomass

475   (Fig. 7a), indicating that areas with a high carbon storage potential also have a high conservation potential.

476   Moreover, species richness has an independent and positive effect on AGB (Fig. 1b). Species richness

477   may also buffer ecosystem productivity against environmental change (Isbell *et al.,* 2011), and enhance

478   ecosystem resilience to disturbance (Diaz *et al.,* 2009). We found that rarefied species richness had a

479   direct effect on forest biomass, despite the very large number of species found in these hyperdiverse

480   tropical forests. The fact that in this study diversity co-determines forest functioning, indicates that the

481   conservation of biodiversity should not be considered as a simple co-benefit of REDD+ (Diaz *et al.,*

482   2009), but as an integral and crucial component of all REDD activities.

483

484   *Concluding remarks*

485   To our knowledge, this is the first study to show the relative importance of environmental conditions and

486   structural and taxonomic attributes for the amount of above ground biomass of highly diverse tropical

487   forests across large spatial scales. AGB is mainly driven by rainfall, followed by structure and species

488   richness. Species richness has an independent positive effect on AGB. From the perspective of REDD+,

489   biodiversity conservation is therefore not only a goal by itself, but it will also help to increase carbon

490   storage. Hence, conserving biodiversity is a win-win strategy because biodiversity is crucial for forest

491   functioning.

492

493   **Acknowledgements**

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510   **References**

511

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Tables.

692 **Table 1:** The results of the structural equation model shown in Fig. 1b. Unstandardized coefficient, standard error, Z-
693 value, P-value and standardized coefficient are given for each path (i.e., each arrow in Fig. 1b). These statistics are
694 given for the composite variable, the regressions between the remaining variables, and the intercepts and error
695 variances of the three dependent variables (above-ground biomass [AGB], rarefied richness and average diameter).
696 The model was accepted (χ^2=4.95, P=0.176), had 3 degrees of freedom (note that this based on the number of
697 'knowns' minus the number of free parameter in the model, not on the sample size).

| Response variable	Predictor variable	Coefficient	Std.error	Z-value	P-value	Std.Coefficient
Composite variable:						
Rainfall+Rainfall^2	Rainfall	4.44				4.76
	Rainfall^2	-0.80	0.03	-26.15	<0.001	-4.56
Regressions:						
sqrt(AGB)	Rainfall+Rainfall^2	2.61	0.28	9.24	<0.001	0.67
	ln(CEC)	-0.19	0.41	-0.46	0.647	-0.06
	Rarefied richness	0.09	0.04	2.73	0.006	0.20
	Average diameter	0.39	0.12	3.36	0.001	0.26
Rarefied richness	Rainfall+Rainfall^2	3.19	1.53	2.08	0.037	0.39
	ln(CEC)	0.32	0.83	0.38	0.702	0.05
Average diameter	Rainfall	1.21	0.51	2.37	0.018	0.49
	ln(CEC)	0.08	0.33	0.24	0.813	0.04

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Figures

700   Figure 1 (a). Conceptual diagram showing how environmental drivers (rainfall, soil fertility) affect forest
701   attributes (taxonomic and structural attributes), and how environmental drivers and forest attributes
702   together affect carbon storage in above-ground biomass (AGB). The two types of forest attributes are
703   characterized by their magnitude (e.g., species richness, basal area) and their variation (e.g., species
704   diversity, density of large trees). (b) Final structural equation model relating AGB to biotic drivers
705   (rarefied richness and average tree diameter [average dbh) and abiotic drivers (rainfall and cation
706   exchange capacity [CEC]). Biomass and rarefied richness show a hump-backed relationship with rainfall
707   (see also Fig. 6a,c), and are therefore modeled as a function of rainfall and the square of rainfall (rainfall^2).
708   Significant paths (continuous arrows), non-significant paths (broken arrows) and correlations (double-
709   sided arrows) are shown. For each path the significance level (P) and standardized regression coefficient
710   are shown. R^2 indicates the total variation in a dependent variable that is explained by the combined
711   independent variables.

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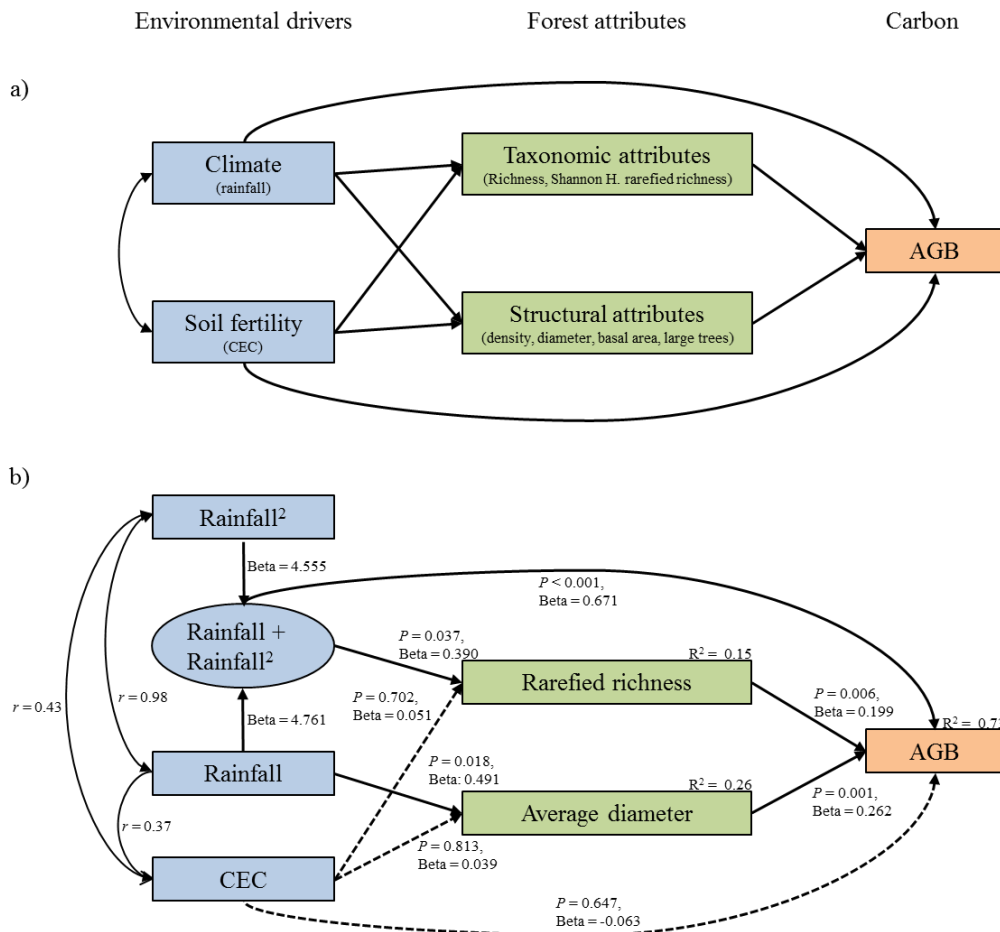
Figure 2. Map of vegetation cover in Latin America, with the location of the 60 study sites. a) above-ground biomass (AGB, Mg/ha), b) Rarefied species richness (# species/50 trees), and c) average tree diameter (cm). The size of the symbol scales with the value of the attribute. The intensity of the green color indicates the amount of forest cover.The background layer is derived from a MODerate resolution Imaging Spectroradiometer (MODIS) vegetation continuous fields (VCF) product (Hansen *et al.* 2003)
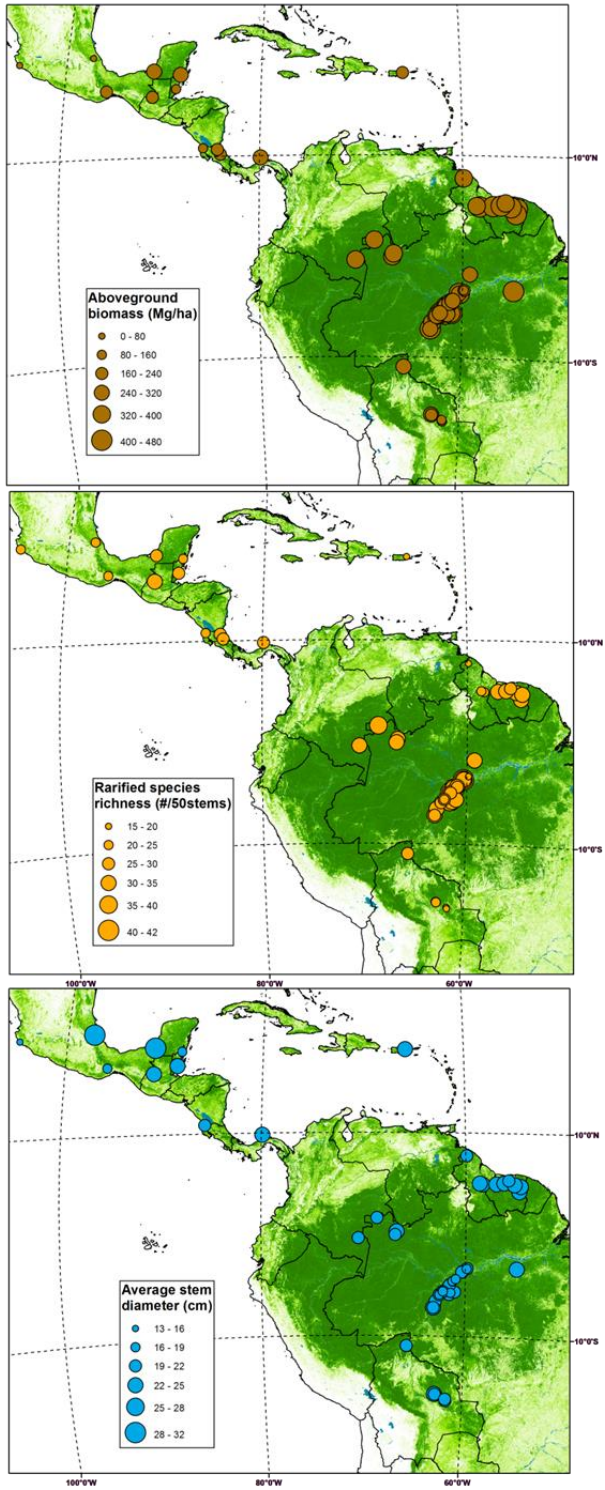
719 Figure 3. Relationship between above-ground biomass (AGB) and three taxonomic attributes; species
720 richness per unit area (top panels), Shannon diversity (middle panels), and rarefied species richness per 50
721 stems (bottom panels). Relationships are shown for 0.1 ha plots (left panels, N= 47-53 sites and 916-1837
722 plots) and 1 ha plots (right panels N= 25 sites and 294 plots). All data are based on trees ≥10 cm dbh. Dots
723 indicate the observed values. Regression lines are shown for each site (for the 1-ha plots), or several
724 regression lines are shown per site (0.1 ha plots within a 1 ha plot). Continuous regression lines are
725 significant, broken regression lines are not significant (P>0.05).
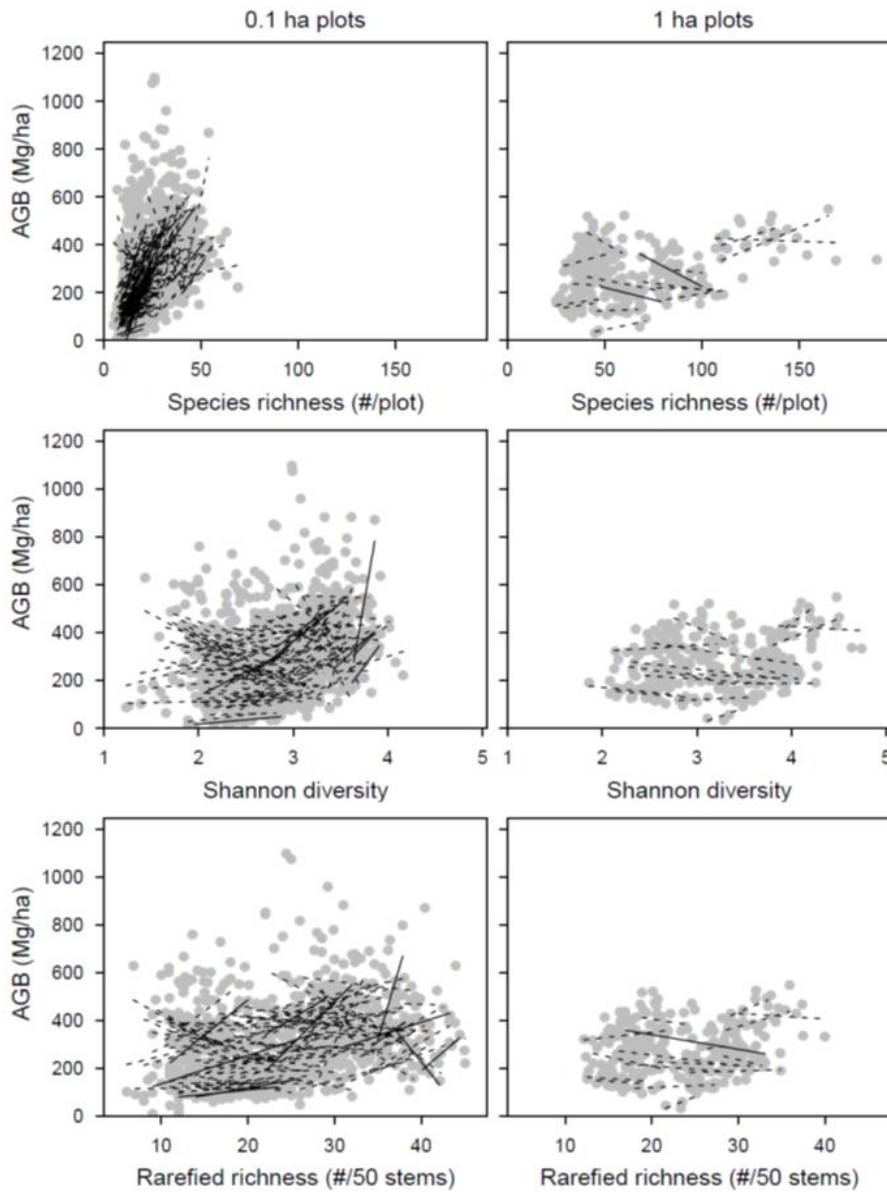
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727 Figure 4. Relationship between above ground biomass (AGB) and four structural attributes; tree density
728 (top panels), average tree diameter (upper middle panels), stand basal area (lower middle panels), and
729 density of large trees (≥60 cm dbh) (bottom panels). Relationships are shown for 0.1 ha plots (left panels,
730 N= 53 sites and 1837 plots) and 1 ha plots (right panels N= 25 sites and 294 plots). All data are based on
731 trees ≥10 cm dbh, with the exception of the density of large trees. Dots indicate the observed values.
732 Regression lines are shown for each site (for the 1-ha plots), or several regression lines are shown per site
733 (0.1 ha plots within a 1 ha plot). Continuous regression lines are significant, broken regression lines are
734 not significant (P>0.05).
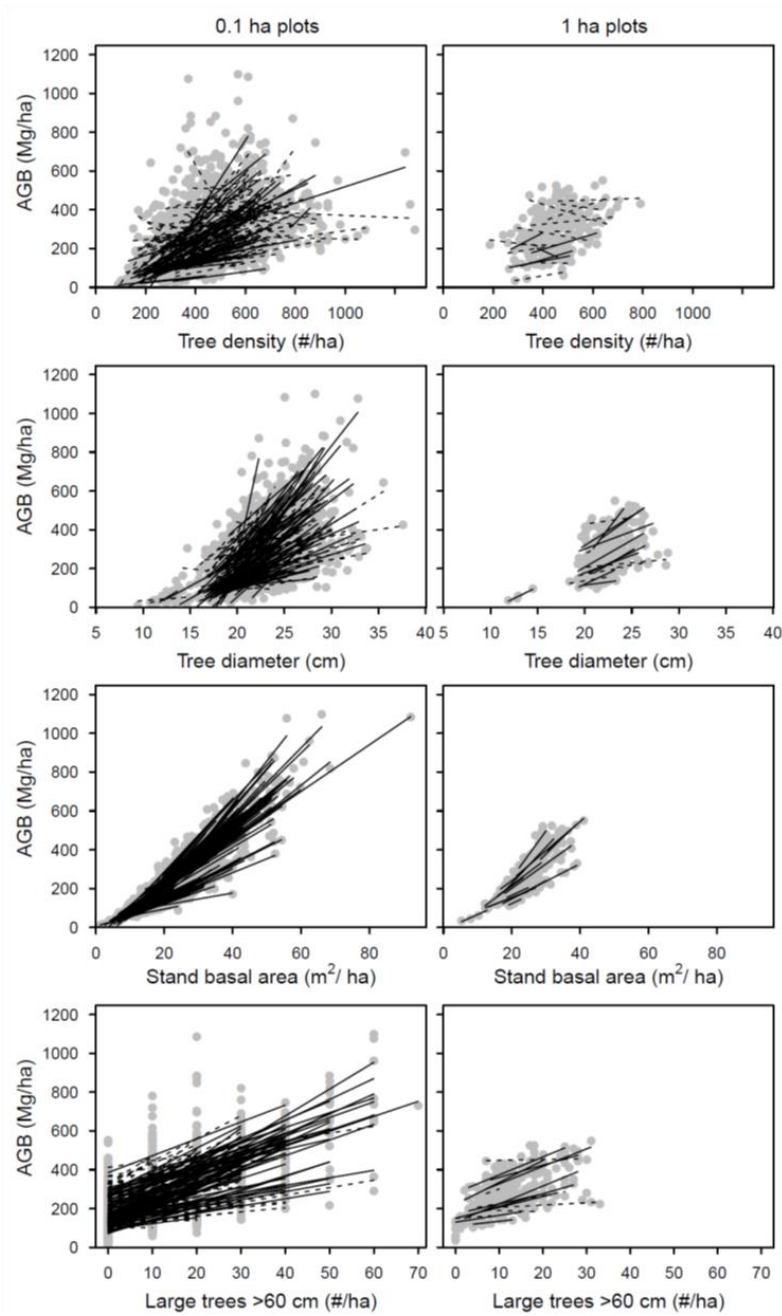
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736 Figure 5. Meta-analysis of the within-site correlation between above-ground biomass (AGB) and
737 taxonomic attributes and structural attributes. Correlations are shown at two spatial scales; 0.1 ha plots
738 (black bars) and 1 ha plots (grey bars). Taxonomic attributes (shown below the dashed line) are rarefied
739 species richness at 50 stems (Rarefied Rich50), Shannon diversity (Shannon), species richness (Richness).
740 Structural attributes (shown above the dashed line) are tree density, average tree diameter, density of large
741 trees ≥ 60 cm dbh, and stand basal area. Means and 95 percent confidence intervals are shown. N = 103-
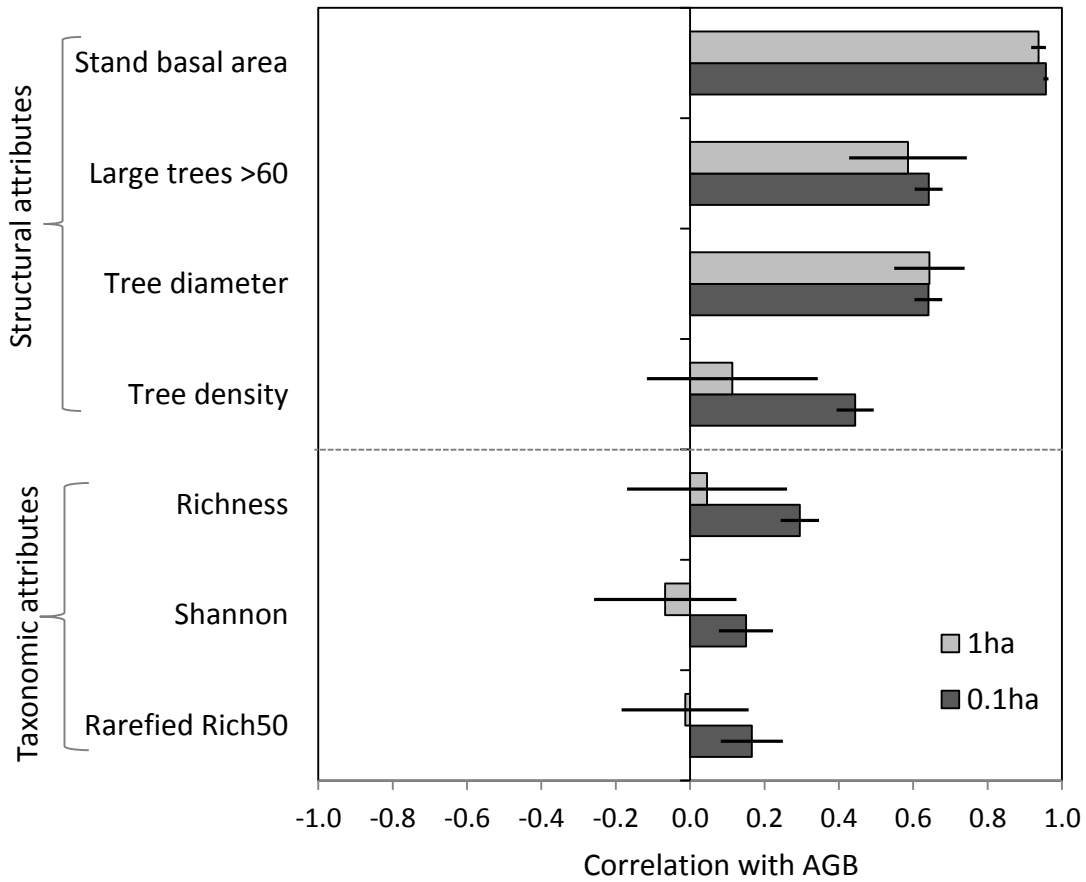742 196 correlations for 0.1 ha plots, and N = 16-17 correlations for 1 ha plots.

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748   Figure 6. Relationship between annual rainfall and a) rarefied species richness; b) average tree diameter,
749   and c) above-ground biomass (AGBs) for 58 Neotropical forest sites. For each site, average values were
750   calculated for the largest plot size available (1 ha plots or 0.1 ha plots). All data are based on trees ≥10 cm
751   dbh. Regression lines and coefficients of determination (R^2) are shown. *** P<0.001; ** P<0.01.
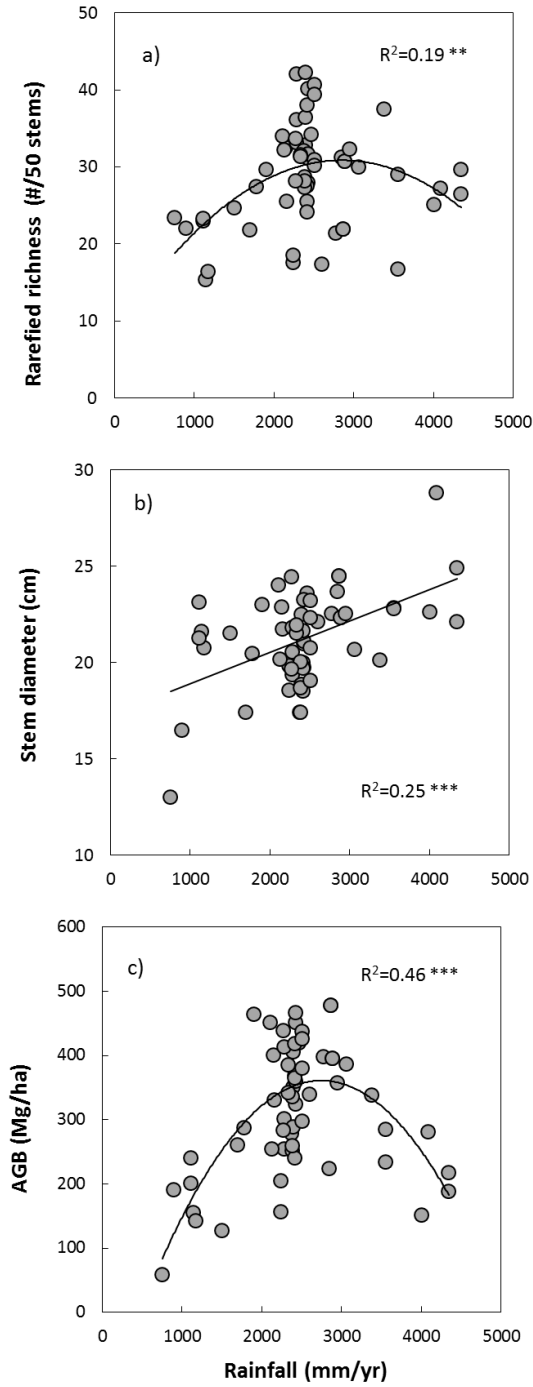

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754 Figure 7. Relationship between above-ground biomass (AGB) and a) rarefied species richness; b), average
755 tree diameter for 58 Neotropical forest sites. For each site, average values were calculated for the largest
756 plot size available (1 ha plots or 0.1 ha plots). All data are based on trees ≥10 cm dbh. Regression lines
757 and coefficients of determination (R^2) are shown. *** P<0.001.

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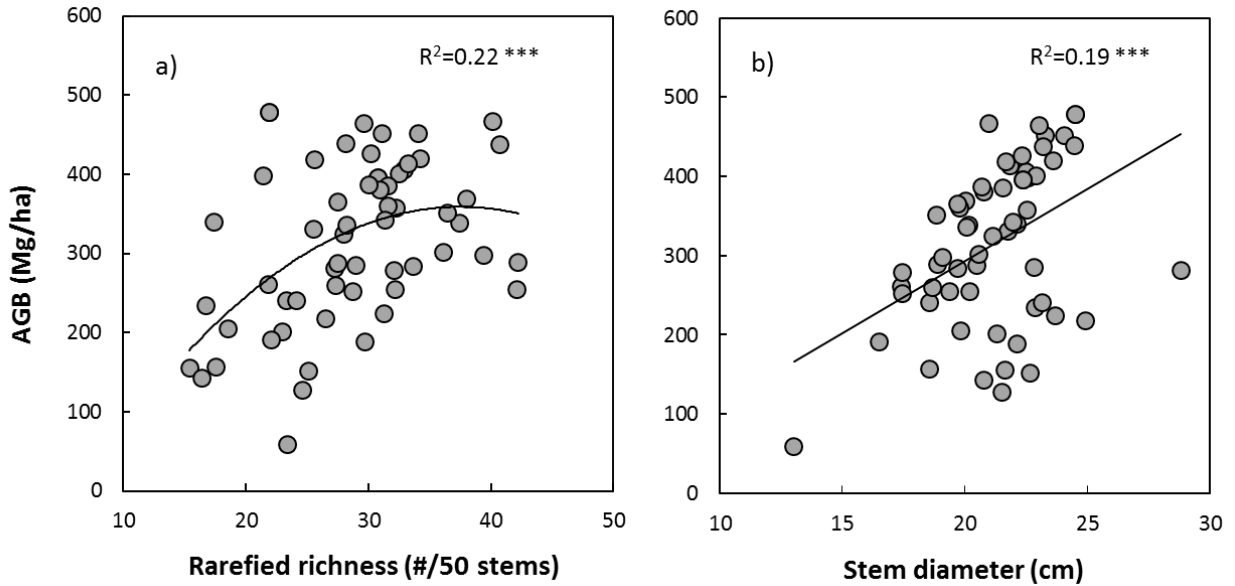
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762 **Supporting information**

763 Appendix S1. Overview of sites included in the study.

764 Appendix S2. Extended methods.

765 Appendix S3. Above-ground plot biomass estimates using the Chave and Brown equations and using
766 different diameter cutoff limits.

767 Appendix S4. Mixed linear model results of the relationship between above-ground biomass and
768 taxonomical and structural forest attributes at the 0.1 ha and 1 ha level.

769 Appendix S5. Strength of the relation between aboveground biomass, species richness and stem density
770 versus annual rainfall of the sites.

771 Appendix 6. Relationship between Cation Ecxhancge Capacity and rarefied richness, average stem
772 diameter and aboveground biomass.

773 Appendix S7. Standardized coefficients of the indirect paths in the structural equation model.

774 Appendix S8. Relationship between average above-ground biomass at a site and annual rainfall.