

Article (refereed) - postprint

Poorter, L.; van der Sande, M.T.; Thompson, J.; Arets, E.J.M.M.; Alarcón, A.; Álvarez-Sánchez, J.; Ascarrunz, N.; Balvanera, P.; Barajas-Guzmán, G.; Boit, A.; Bongers, F.; Carvalho, F.A.; Casanoves, F.; Cornejo-Tenorio, G.; Costa, F.R.C.; de Castilho, C.V.; Duivenvoorden, J.F.; Dutrieux, L.P.; Enquist, B.J.; Fernández-Méndez, F.; Finegan, B.; Gormley, L.H.L.; Healey, J.R.; Hoosbeek, M.R.; Ibarra-Manríquez, G.; Junqueira, A.B.; Levis, C.; Licona, J.C.; Lisboa, L.S.; Magnusson, W.E.; Martínez-Ramos, M.; Martínez-Yrizar, A.; Martorano, L.G.; Maskell, L.C.; Mazzei, L.; Meave, J.A.; Mora, F.; Muñoz, R.; Nytch, C.; Pansonato, M.P.; Parr, T.W.; Paz, H.; Pérez-García, E.A.; Rentería, L.Y.; Rodríguez-Velazquez, J.; Rozendaal, D.M.A.; Ruschel, A.R.; Sakschewski, B.; Salgado-Negret, B.; Schiatti, J.; Simões, M.; Sinclair, F.L.; Souza, P.F.; Souza, F.C.; Stropp, J.; ter Steege, H.; Swenson, N.G.; Thonicke, K.; Toledo, M.; Uriarte, M.; van der Hout, P.; Walker, P.; Zamora, N.; Peña-Claros, M.. 2015. **Diversity enhances carbon storage in tropical forests.** *Global Ecology and Biogeography*, 24 (11). 1314-1328.

<https://doi.org/10.1111/geb.12364>

© 2015 John Wiley & Sons Ltd

This version available <http://nora.nerc.ac.uk/id/eprint/512885/>

NERC has developed NORA to enable users to access research outputs wholly or partially funded by NERC. Copyright and other rights for material on this site are retained by the rights owners. Users should read the terms and conditions of use of this material at <http://nora.nerc.ac.uk/policies.html#access>

This document is the author's final manuscript version of the journal article, incorporating any revisions agreed during the peer review process. Some differences between this and the publisher's version remain. You are advised to consult the publisher's version if you wish to cite from this article.

The definitive version is available at

<https://onlinelibrary.wiley.com/toc/14668238/2015/24/11>

Contact CEH NORA team at

noraceh@ceh.ac.uk

Diversity enhances carbon storage in tropical forests

1
2
3 Authors: L. Poorter¹; M. T. van der Sande^{1,2}; J. Thompson^{3,4}; E. J. M. M. Arets²; A. Alarcón⁵; J. Álvarez-
4 Sánchez⁶; N. Ascarrunz⁵; P. Balvanera⁷; G. Barajas-Guzmán⁶; A. Boit⁸; F. Bongers¹; F. A. Carvalho⁹; F.
5 Casanoves¹⁰; G. Cornejo-Tenorio⁷; F. R. C. Costa⁹; C. V. de Castilho¹¹; J. F. Duivenvoorden¹²; L. P.
6 Dutrieux¹³; B. J. Enquist¹⁴; F. Fernández-Méndez¹⁵; B. Finegan¹⁶; L. H. L. Gormley¹⁷; J. R. Healey¹⁷; M.
7 R. Hoosbeek¹⁸; G. Ibarra-Manríquez⁷; A. B. Junqueira^{9,19,20}; C. Levis^{1,9}; J. C. Licona⁵; L. S. Lisboa²¹; W.
8 E. Magnusson⁹; M. Martínez-Ramos⁷; A. Martínez-Yrizar²²; L. G. Martorano²³; L. C. Maskell²⁴; L.
9 Mazzei²³; J. A. Meave⁶; F. Mora⁷; R. Muñoz⁶; C. Nytch⁴; M. P. Pansonato⁹; T. W. Parr²⁴; H. Paz⁷; M.
10 Simoes Penello²⁵; E. A. Pérez-García⁶; L. Y. Rentería⁷; J. Rodríguez-Velazquez⁷; D. M. A. Rozendaal^{1,26};
11 A. R. Ruschel²³; B. Sakschewski⁸; B. Salgado Negret²⁷; J. Schiatti⁹; F. L. Sinclair^{17,28}; P. F. Souza⁹; F. C.
12 Souza⁹; J. Stropp²⁹; H. ter Steege^{30,31}; N. G. Swenson³²; K. Thonicke⁸; M. Toledo⁵; M. Uriarte³³; P. van
13 der Hout³⁴; P. Walker³⁵; N. Zamora³⁶; M. Peña-Claros¹

¹ Forest Ecology and Forest Management Group, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands

² Alterra Wageningen UR, Wageningen, The Netherlands

³ Centre for Ecology & Hydrology, Penicuik, UK

⁴ Department of Environmental Science, University of Puerto Rico, Río Piedras, Puerto Rico

⁵ Instituto Boliviano de Investigación Forestal (IBIF), FCA-UAGRM, Santa Cruz de la Sierra, Bolivia

⁶ Facultad de Ciencias, Universidad Nacional Autónoma de México, México D.F., México

⁷ Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Morelia, México

⁸ Potsdam Institute for Climate Impact Research e.V. (PIK), Potsdam, Germany and Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), 14195 Berlin, Germany

⁹ Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil

¹⁰ Biostatistics Unit, CATIE, Turrialba, Costa Rica

¹¹ Embrapa Roraima, Boa Vista, Brazil

¹² IBED, University of Amsterdam, Amsterdam, The Netherlands

¹³ Lab of GIS and Remote-Sensing, Wageningen University, Wageningen, The Netherlands

¹⁴ Department of Ecology & Evolutionary Biology, The University of Arizona, Tucson, USA

¹⁵ Grupo de Investigación en Biodiversidad y Dinámica de Ecosistemas Tropicales, Universidad del Tolima, Ibagué, Colombia

¹⁶ Production and Conservation in Forests Programme, CATIE, Turrialba, Costa Rica

¹⁷ School of Environment, Natural Resources and Geography, Bangor University, Bangor, UK

¹⁸ Department of Soil Quality, Wageningen University, Wageningen, The Netherlands

¹⁹ Centre for Crop Systems Analysis Wageningen University, Wageningen, The Netherlands

²⁰ Knowledge, Technology and Innovation Group, Wageningen University, Wageningen, The Netherlands

²¹ ESALQ, USP, Piracicaba, Brazil

²² Instituto de Ecología, UNAM, Hermosillo, Mexico

²³ Embrapa Amazônia Oriental, Belém, Brazil

²⁴ Centre for Ecology & Hydrology (CEH), Lancaster, UK

²⁵ Embrapa Solos, Rio de Janeiro, Brazil

²⁶ Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, USA

²⁷ Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia

²⁸ World Agroforestry Centre (ICRAF), Nairobi, Kenya

²⁹ European Commission, Directorate General - Joint Research Centre, Institute for Environment and Sustainability, Ispra, Italy

14 Running title: Carbon storage in tropical forests
15
16 Corresponding author:
17
18 Lourens Poorter
19 Forest Ecology and Forest Management Group, Wageningen University
20 P.O. Box 47, 6700 AA Wageningen, The Netherlands
21 E-mail: lourens.poorter@wur.nl
22
23 Number of words in abstract: 298
24 Number of words in main body: 8679
25 Number of references: 50
26

³⁰ Naturalis Biodiversity Center, Leiden, Netherlands.

³¹ Ecology and Biodiversity Group, Utrecht University, Utrecht, The Netherlands

³² Department of Plant Biology, Michigan State University, Michigan, USA

³³ Department of Ecology, Evolution & Environmental Biology, Columbia University, New York, USA

³⁴ Van der Hout Forestry Consulting, Rotterdam, The Netherlands

³⁵ Wildtracks, P.O.Box 278, Belize City, Belize

³⁶ Instituto Nacional de Biodiversidad (INBio), Santo Domingo, Costa Rica

27 Key-words: biodiversity, biomass, scale, ecosystem functioning, Neotropics, rainfall, REDD+, soil,
28 tropical forest

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.

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

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 contiguosness 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 ≥ 5 cm 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 (≥ 60 cm 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 disproportionately 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 rainfall² as predictor variables in the analysis (Fig. 1b),
244 which allows to model such a hump-shaped relationship. The combined effect of rainfall and rainfall² 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, rainfall², 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 rainfall². 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 rainfall², 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; $\chi^2=4.95$, $P=0.176$, $df=3$), whereas the models were
306 rejected that included basal area ($\chi^2=23.10$, $P<0.001$) or stem density ($\chi^2=11.80$, $P=0.008$). 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+rainfall²’ 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+rainfall² (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

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 disproportionately 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 unimodal 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

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

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

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**

494

495 We gratefully thank all the people that have established and measured the plots, and the institutions and
496 funding agencies that supported them (e.g., CONACyT, the Darwin Initiative). This study was partly
497 funded by European Union's Seventh Framework Programme ([FP7/2007-2013]) under grant agreement
498 n° 283093; Role Of Biodiversity In climate change mitigatioN (ROBIN). We thank Nick Brokaw, Rick
499 Condit, Robin Foster, Steve Hubbell, Joe Wright and Jess Zimmerman for kindly allowing us to use their
500 (plot) data, Joe Wright and two anonymous reviewers for their very helpful comments on the manuscript,
501 and James Grace and Daniel Laughlin for their helpful advice on the SEM analysis. The Chamela plot was
502 supported by the ReserBos project (SEP-CONACyT/2009-129740). The Luquillo forest dynamics plot
503 was supported by Luquillo Long Term Ecological Research program (LTER), USA National Science
504 Foundation and others. The BCI 50-ha plot was organized by S.P. Hubbell, R.B. Foster, R. Condit, S. Lao,
505 and R. Perez under the Center for Tropical Forest Science and the Smithsonian Tropical Research in
506 Panama. Numerous organizations have provided funding, principally the U.S. National Science
507 Foundation, and hundreds of field workers have contributed.

508

509

510 **References**

511

512 Baccini, A., Goetz, S. J., Walker, W. S., Laporte, N. T., Sun, M., Sulla-Menashe, Hackler, J., Beck,
513 P.S.A., Dubayah, R., Friedl, M.A., Samanta, S. & Houghton, R. A. (2012) Estimated carbon

514 dioxide emissions from tropical deforestation improved by carbon-density maps. *Nature Climate*
515 *Change*, **2**, 182-185.

516 Baker, T. R., Phillips, O. L., Laurance, W. F., Pitman, N. C. A., Almeida, S., Arroyo, L., Difiore, A.,
517 Erwin, T., Higuchi, N., Killeen, T. J., Laurance, S. G., Nascimento, H., Monteagudo, A., Neill, D.
518 A., Silva, J. N. M., Malhi, Y., López Gonzalez, G., Peacock, J., Quesada, C. A., Lewis, S. L., &
519 Lloyd, J. (2009) Do species traits determine patterns of wood production in Amazonian forests?
520 *Biogeosciences*, **6**, 297–307.

521 Baraloto, C., Rabaud, S., Molto, Q., Blanc, L., Fortunel, C., Hérault, B., Dávila, N., Mesones, I., Rios, M.,
522 Valderrama, E. & Fine, P.V. A. (2011) Disentangling stand and environmental correlates of
523 aboveground biomass in Amazonian forests. *Global Change Biology*, **17**, 2677–2688.

524 Baruffol, M., Schmid, B., Bruelheide, H., Chi, X., Hector, A., Ma, K., Michalski, S., Tang, Z. & Niklaus,
525 P.A. (2013) Biodiversity Promotes Tree Growth during Succession in Subtropical Forest. *PLoS*
526 *ONE*, **8**, e81246.

527 Beer C, Reichstein, M., Tomelleri, E., Ciais, P., Jung, M., Carvalhais, N., Rödenbeck, C., Arain, M.A.,
528 Baldocchi, D., Bonan, G.B., Bondeau, A., Cescatti, A., Lasslop, G., Lindroth, A., Lomas, M.,
529 Luyssaert, S., Margolis, H., Oleson, K.W., Rouspard, O., Veenendaal, E., Viovy, N., Williams, C.,
530 Woodward, F.I. & Papale, D. (2010) Terrestrial Gross Carbon Dioxide Uptake: Global
531 Distribution and Covariation with Climate. *Science*, **329**, 834-838.

532 Bonan GB (2008) Forests and climate change: Forcings, feedbacks, and the climate benefits of forests.
533 *Science*, **320**, 1444-1449.

534 Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., Balvanera, P.,
535 O'Connor, M.I. & Gonzalez, A. (2011) The functional role of producer diversity in ecosystems.
536 *American Journal of Botany*, **98**, 572–92.

537 Cavanaugh, K.C., Gosnell, J.S., Davis, S.L., Ahumada, J., Boundja, P., Clark, D.B., Mugerwa, B., Jansen,
538 P. a., O'Brien, T.G., Rovero, F., Sheil, D., Vasquez, R. & Andelman, S. (2014) Carbon storage in

539 tropical forests correlates with taxonomic diversity and functional dominance on a global scale.
540 *Global Ecology and Biogeography*, **23**, 563-573.

541 Chave, J., Andalo, C., Brown, S., Cairns, M. A., Chambers, J. Q., Eames, D. Folster, H., Formard, F.,
542 Higuchi, N., Kira, T., Lescure, J. P., Nelson, B. W., Ogawa, H., Puig, H., Riera, B. & Yamakura,
543 T. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests.
544 *Oecologia*, **145**, 87-99.

545 Chisholm, R.A., Muller-Landau, H.C., Abdul Rahman, K., Bebbber, D.P., Bin, Y., Bohlman, S.A., Bourg,
546 N.A., Brinks, J., Bunyavejchewin, S., Butt, N., Cao, H., Cao, M., Cárdenas, D., Chang, L.-W.,
547 Chiang, J.-M., Chuyong, G., Condit, R., Dattaraja, H.S., Davies, S., Duque, A., Fletcher, C.,
548 Gunatilleke, N., Gunatilleke, S., Hao, Z., Harrison, R.D., Howe, R., Hsieh, C.-F., Hubbell, S.P.,
549 Itoh, A., Kenfack, D., Kiratipayoon, S., Larson, A.J., Lian, J., Lin, D., Liu, H., Lutz, J.A., Ma, K.,
550 Malhi, Y., McMahon, S., McShea, W., Meegaskumbura, M., Mohd. Razman, S., Morecroft, M.D.,
551 Nytech, C.J., Oliveira, A., Parker, G.G., Pulla, S., Punchi-Manage, R., Romero-Saltos, H., Sang,
552 W., Schurman, J., Su, S.-H., Sukumar, R., Sun, I-F., Suresh, H.S., Tan, S., Thomas, D., Thomas,
553 S., Thompson, J., Valencia, R., Wolf, A., Yap, S., Ye, W., Yuan, Z. & Zimmerman, J.K. (2013)
554 Scale-dependent relationships between tree species richness and ecosystem function in forests.
555 *Journal of Ecology*, **101**, 1214-1224.

556 Colwell, R.K. (2011) Estimates: Statistical Estimation of Species Richness and Shared Species from
557 Samples. Version 9. 2011. User's Guide and application published at <http://purl.oclc.org/estimates>

558 Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1310.

559 Diaz, S., Hector, A. & Wardle, D.A. (2009) Biodiversity in forest carbon sequestration initiatives: not just
560 a side benefit. *Current Opinion in Environmental Sustainability*, **1**, 55-60.

561 Emilio, T., C. A. Quesada, F. R. Costa, W. E. Magnusson, J. Schiatti, T. R. Feldpausch, R. J. Brienen, T.
562 R. Baker, J. Chave, & E. Álvarez. (2014). Soil physical conditions limit palm and tree basal area
563 in Amazonian forests. *Plant Ecology & Diversity*, **7**, 215-229.

564 Fauset, S., Baker, T.R., Lewis, S.L., Feldpausch, T.R., Affum-Baffoe, K., Foli, E.G., Hamer, K.C. &
565 Swaine, M.D. (2012) Drought-induced shifts in the floristic and functional composition of tropical
566 forests in Ghana. *Ecology Letters*, **15**, 1120-1129.

567 Fauset, S.; Johnson, M.O., Gloor, M., Baker, T.R., Monteagudo, A.M., Brienen, R.J.W., Feldpausch, T.R
568 *et al.* (2015) Hyperdominance in Amazonian forest carbon cycling. *Nature Communications* doi:
569 10.1038/ncomms7857

570 Fine, P. V. A., Ree, R. H., Burnham, R. J. (2008) The disparity in tree species richness among tropical,
571 temperate, and boreal biomes: the geographical area and age hypothesis. Pp 31-45 in Carson, R.
572 P., & Schnitzer, S. A. (eds.) *Tropical Forest Community Ecology*. Blackwell, Oxford, UK.

573 Gamfeldt, L., Snäll T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Fröberg,
574 M., Stendahl, J., Philipson, C.D., Mikusiński, G., Andersson, E., Westerlund, B., Andrén, H.,
575 Moberg, F., Moen, J. & Bengtsson, J. (2013) Higher levels of multiple ecosystem services are
576 found in forests with more tree species. *Nature Communications*, **4**, Art. 1340.

577 Graham, A. E., Mulkey, S. S., Kitajima, K., Phillips, N. G. & Wright, S. J. (2003) Cloud cover limits net
578 CO₂ uptake and growth of a rainforest tree during tropical rainy seasons. *Proceedings of the*
579 *National Academy of Sciences of the United States of America*, **100**, 572-576.

580 Hall, J.B. & Swaine, M.D. (1981) *Distribution and ecology of vascular plants in tropical rainforest: forest*
581 *vegetation in Ghana*. The Hague (the Netherlands): Dr W. Junk Publishers.

582 Hansen, M.C., DeFries, R.S., Townshend, J.R.G., Carroll, M. & Dimiceli, C. (2003) Global percent tree
583 cover at a spatial resolution of 500 meters: First results of the MODIS vegetation continuous fields
584 algorithm. *Earth Interactions*, **7**, 1-15.

585 Hector, A., Philipson, C., Saner, P., Chamagne, J., Dzulkipli, D., O'Brien, M., Snaddon, J.L., Ulok, P.,
586 Weilenmann, M., Reynolds, G. & Godfray, H.C.J. (2011) The Sabah Biodiversity Experiment: a
587 long-term test of the role of tree diversity in restoring tropical forest structure and functioning.
588 *Philosophical Transactions of the Royal Society*, **366**, 3303-3315.

589 Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones & Jarvis, A. (2005) Very high resolution interpolated
590 climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965-1978.

591 Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B., Scherer-Lorenzen, M.,
592 Schmid, B., Tilman, D., van Ruijven, J., Weigelt, A., Wilsey, B.J., Zavaleta, E.S. & Loreau, M.
593 (2011) High plant diversity is needed to maintain ecosystem services. *Nature*, **477**, 199-202.

594 Laurance, W.F., Fearnside, P.M., Laurance, S.G., Delamonica, P., Lovejoy, T.E., Rankin-de Merona,
595 J.M., Chambers, J.Q. & Gascon, C. (1999) Relationship between soils and Amazon forest
596 biomass: a landscape-scale study. *Forest Ecology and Management*, **118**, 127–138.

597 Lohbeck, M., Poorter, L., Martínez-Ramos, M. & Bongers, F. (2015) Biomass is the main driver of
598 changes in ecosystem process rates during tropical forest succession. *Ecology*, **96**, 1242-1252.

599 Loreau, M. & Hector, A. (2001) Partitioning selection and complementarity in biodiversity experiments.
600 *Nature*, **412**, 72–76.

601 Malhi, Y., Baker, T.R., Phillips, O.L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C.I.,
602 Fiore, A. Di, Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Montoya,
603 L.M.M., Monteagudo, A., Neill, D. a., Vargas, P.N., Patino, S., Pitman, N.C. a., Quesada, C.A.,
604 Salomao, R., Silva, J.N.M., Lezama, A.T., Martinez, R.V., Terborgh, J., Vinceti, B. & Lloyd, J.
605 (2004) The above-ground coarse wood productivity of 104 Neotropical forest plots. *Global
606 Change Biology*, **10**, 563–591.

607 Mitchard, E.T.A., Feldpausch, T.R., Brienen, R.J.W. *et al.* (2014). Markedly divergent estimates of
608 Amazon forest carbon density from ground plots and satellites. *Global Ecology and
609 Biogeography*, **23**, 935–946.

610 Nachtergaele, F., van Velthuisen, H., Verelst, L. & Wiberg, D. (2012) *Harmonized World Soil Database
611 version 1.2*. FAO, Rome and IIASA, Laxenburg, Austria.

612 Naeem, S., Bunker, D.E., Hector, A., Loreau, M. & Perrings, C. (2009) *Biodiversity, ecosystem
613 functioning, and human wellbeing. An ecological and economic perspective*. Oxford University
614 press, Oxford.

615 Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, R., O'Hara, R.B., Simpson, G.L., Solymos,
616 P., Stevens, M. H. H. & Wagner, H. (2014) Package vegan: Community ecology package. R
617 package version 2.2-0. <http://cran.r-project.org/web/packages/vegan/>.

618 Paquette, A. & Messier, C. (2011) The effect of biodiversity on tree productivity: from temperate to boreal
619 forests. *Global Ecology and Biogeography*, **20**, 170-180.

620 Pearson, R., Walker, S. & Brown, S. (005) *Source book for land use, land-use change and forestry*
621 *projects*. World Bank, Washington.

622 Quesada, C.A., Phillips, O.L., Schwarz, M., Czimczik, C.I., Baker, T.R., Patiño, S., Fyllas, N.M., Hodnett,
623 M.G., Herrera, R., Almeida, S., Alvarez Dávila, E., Arneeth, A., Arroyo, L., Chao, K.J., Dezzee,
624 N., Erwin, T., di Fiore, A., Higuchi, N., Honorio Coronado, E., Jimenez, E.M., Killeen, T.,
625 Lezama, a. T., Lloyd, G., López-González, G., Luizão, F.J., Malhi, Y., Monteagudo, A., Neill, D.
626 a., Núñez Vargas, P., Paiva, R., Peacock, J., Peñuela, M.C., Peña Cruz, A., Pitman, N., Priante
627 Filho, N., Prieto, A., Ramírez, H., Rudas, A., Salomão, R., Santos, a. J.B., Schmerler, J., Silva, N.,
628 Silveira, M., Vásquez, R., Vieira, I., Terborgh, J. & Lloyd, J. (2012) Basin-wide variations in
629 Amazon forest structure and function are mediated by both soils and climate. *Biogeosciences*, **9**,
630 2203–2246.

631 Rosseel, Y. (2012) lavaan: an R package for structural equation modeling. *Journal of Statistical Software*,
632 **48**, 1–36.

633 Sakschewski, B., von Bloh, W., Boit, A., Rammig, A., Kattge, J., Poorter, L., Peñualeas, J., Thonicke, K.
634 (2015) Leaf and stem economics spectra drive diversity of functional plant traits in a dynamic
635 global vegetation model. *Global Change Biology*, **21**, 2711–2725.

636 Santiago, L. S., Wright, S. J., Harms, K. E., Yavitt, J. B., Korine, C., Garcia, M. N. & Turner, B. L.
637 (2012). Tropical tree seedling growth responses to nitrogen, phosphorus and potassium addition.
638 *Journal of Ecology*, **100**, 309–316.

639 Slik, J.W.F, Paoli, G., McGuire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F., Boundja,
640 P., Clark, C., Collins, M., Dauby, G., Ding, Yi, Doucet, J., Eler, E., Ferreira, L., Forshed, O.,

641 Fredriksson, G., Gillet, J., Harris, D., Leal, M., Laumonier, Y., Malhi, Y., Mansor, A., Martin, E.,
642 Miyamoto, K., Araujo-Murakami, A., Nagamasu, H., Nilus, R., Nurtjahya, E., Oliveira, Á.,
643 Onrizal, O., Parada-Gutierrez, A., Permana, A., Poorter, L., Poulsen, J., Ramirez-Angulo, H.,
644 Reitsma, J., Rovero, F., Rozak, A., Sheil, D., Silva-Espejo, J., Silveira, M., Spironelo, W., Steege,
645 H., Stevart, T., Navarro-Aguilar, G.E., Sunderland, T., Suzuki, E., Tang, J., Theilade, I., van der
646 Heijden, G., van Valkenburg, J., Van Do, T., Vilanova, E., Vos, V., Wich, S., Wöll, H., Yoneda,
647 T.i, Zang, R.O, Zhang, M.G. & Zweifel, N. (2013). Large trees drive forest aboveground biomass
648 variation in moist lowland forests across the tropics *Global Ecology and Biogeography*, **22**, 1261–
649 1271.

650 Stephenson, N.L., Das, a. J., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D. a., Lines,
651 E.R., Morris, W.K., Rüger, N., Álvarez, E., Blundo, C., Bunyavejchewin, S., Chuyong, G.,
652 Davies, S.J., Duque, Á., Ewango, C.N., Flores, O., Franklin, J.F., Grau, H.R., Hao, Z., Harmon,
653 M.E., Hubbell, S.P., Kenfack, D., Lin, Y., Makana, J.-R., Malizia, A., Malizia, L.R., Pabst, R.J.,
654 Pongpattananurak, N., Su, S.-H., Sun, I.-F., Tan, S., Thomas, D., van Mantgem, P.J., Wang, X.,
655 Wiser, S.K. & Zavala, M.A. (2014) Rate of tree carbon accumulation increases continuously with
656 tree size. *Nature*, **507**, 90–93.

657 Stropp, J., Ter Steege, H. & Malhi, Y. (2009) Disentangling regional and local tree diversity in the
658 Amazon. *Ecography*, **32**, 46–54.

659 Swaine, M. D. (1996) Rainfall and soil fertility as factors limiting forest species distributions in Ghana.
660 *Journal of Ecology*, **84**, 419–428.

661 Ter Steege, H., Pitman, N., Sabatier, D., Castellanos, H., van der Hout, P., Douglas, C., Silveira, M.,
662 Phillips, O., Vasquez, R., van Andel, T., Duifenvoorden, J., de Oliveira, A. adalardo, Ek, R.,
663 Lilwah, R., Thomas, R., van Essen, J., Baider, C., Maas, P., Mori, S., Terborgh, J., Vargas, P.N.,
664 Mogollon, H. & Morawetz, W. (2003) A spatial model of tree a-diversity and tree density for the
665 Amazon. *Biodiversity and Conservation*, **12**, 2255–2277.

666 Tilman, D., Reich P.B., Knops, J., Wedin, D., Mielke, T. & Lechman, C. (2001) Diversity and
667 productivity in a long-term grassland experiment. *Science*, **294**, 843-845.

668 Toledo, M., Poorter, L., Peña-Claros, M., Alarcón, A., Balcázar, J., Leño, C., Licona, J.C., Llanque, O.,
669 Vroomans, V., Zuidema, P. & Bongers, F. (2011) Climate is a stronger driver of tree and forest
670 growth rates than soil and disturbance. *Journal of Ecology*, **99**, 254-264.

671 Vilà, M., Carillo-Gavilán, A., Vayreda, J., Bugmann, H., Fridman, J., Grodzki, W., Haase, J., Kunstler, G.,
672 Schelhaas, M.J. & Trasobares. (2013) Disentangling biodiversity and climatic determinants of
673 wood production. *PLoSone*, **8**, e53530.

674 Vitousek, P.M., Porder, S., Houlton, B.Z. & Chadwick, O.A. (2010) Terrestrial phosphorus limitation:
675 mechanisms, implications, and nitrogen–phosphorus interactions. *Ecological Applications*, **20**, 5-
676 15.

677 Yachi, S. & Loreau, M. (1999) Biodiversity and ecosystem productivity in a fluctuating environment: The
678 insurance hypothesis. *Proceedings of the National Academy of Sciences*, **96**, 1463–1468.

679 Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson
680 N.G., Wiemann M.C. & Chave, J. (2009) Data from: Towards a worldwide wood economics
681 spectrum. *Dryad Digital Repository*. <http://dx.doi.org/10.5061/dryad.234>.

682 Zhang, Y., Chen, H.Y.H. & Reich, P.B. (2012) Forest productivity increases with evenness, species
683 richness and trait variation: a global meta-analysis. *Journal of Ecology*, **100**, 742–749.

684

685

686 **Biosketch**

687 This data analysis was carried out as a collaborative research effort amongst people of the EU-funded
688 ROBIN project (the ROle of Biodiversity In climate change mitigatioN) and other forest researchers with
689 interest in the diversity and dynamics of tropical forests. We hope that such a large-scale comparative
690 approach provides a better insight into the functioning of these forests.

691 **Tables.**

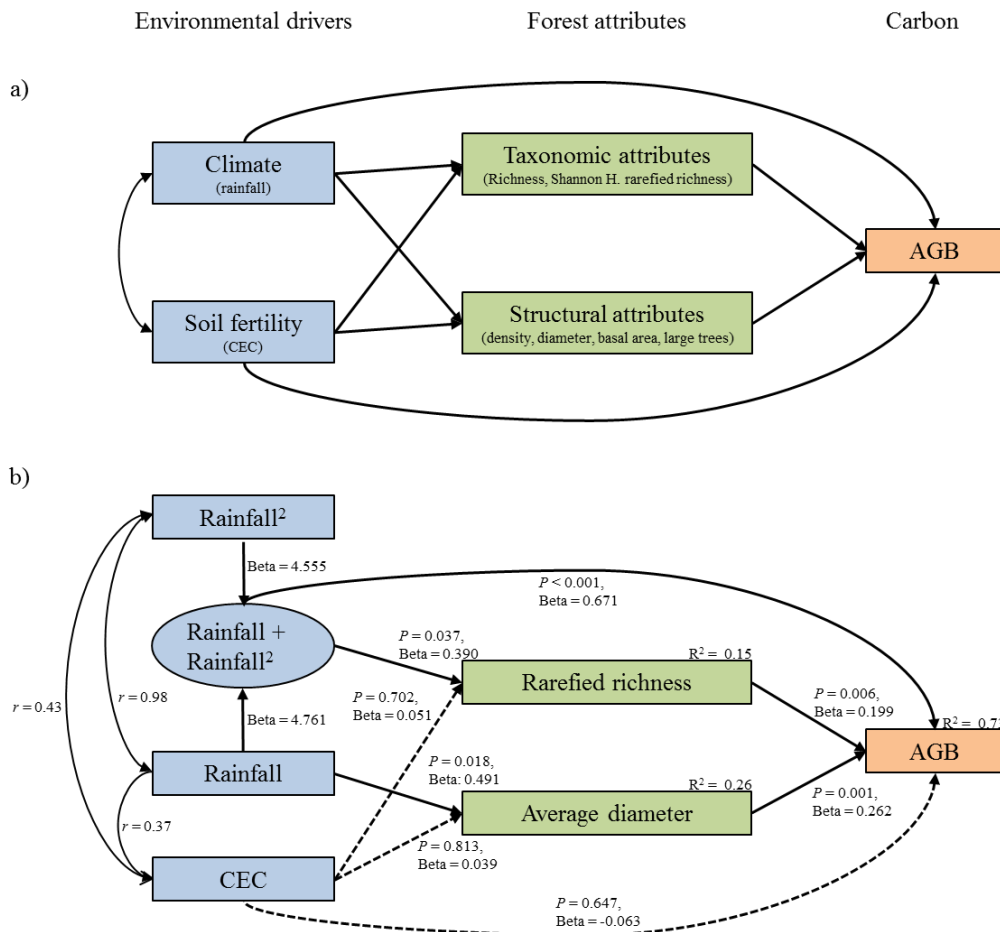
692 **Table 1:** The results of the structural equation model shown in Fig. 1b. Unstandardized coefficient, standard error, Z-
 693 value, P-value and standardized coefficient are given for each path (i.e., each arrow in Fig. 1b). These statistics are
 694 given for the composite variable, the regressions 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 ($\chi^2=4.95$, $P=0.176$), 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
<i>Composite variable:</i>						
Rainfall+Rainfall ²	Rainfall	4.44				4.76
	Rainfall ²	-0.80	0.03	-26.15	<0.001	-4.56
<i>Regressions:</i>						
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

698

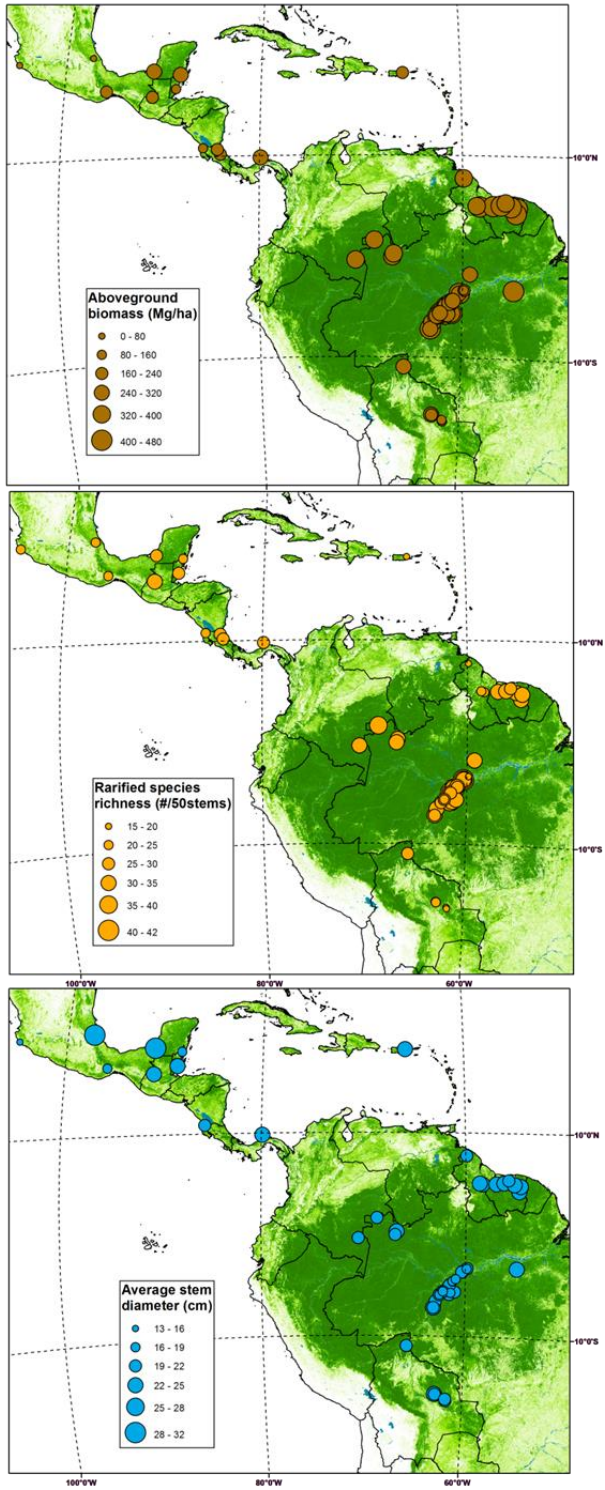
699 **Figures**

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 (rainfall²).
 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. R² indicates the total variation in a dependent variable that is explained by the combined
 711 independent variables.



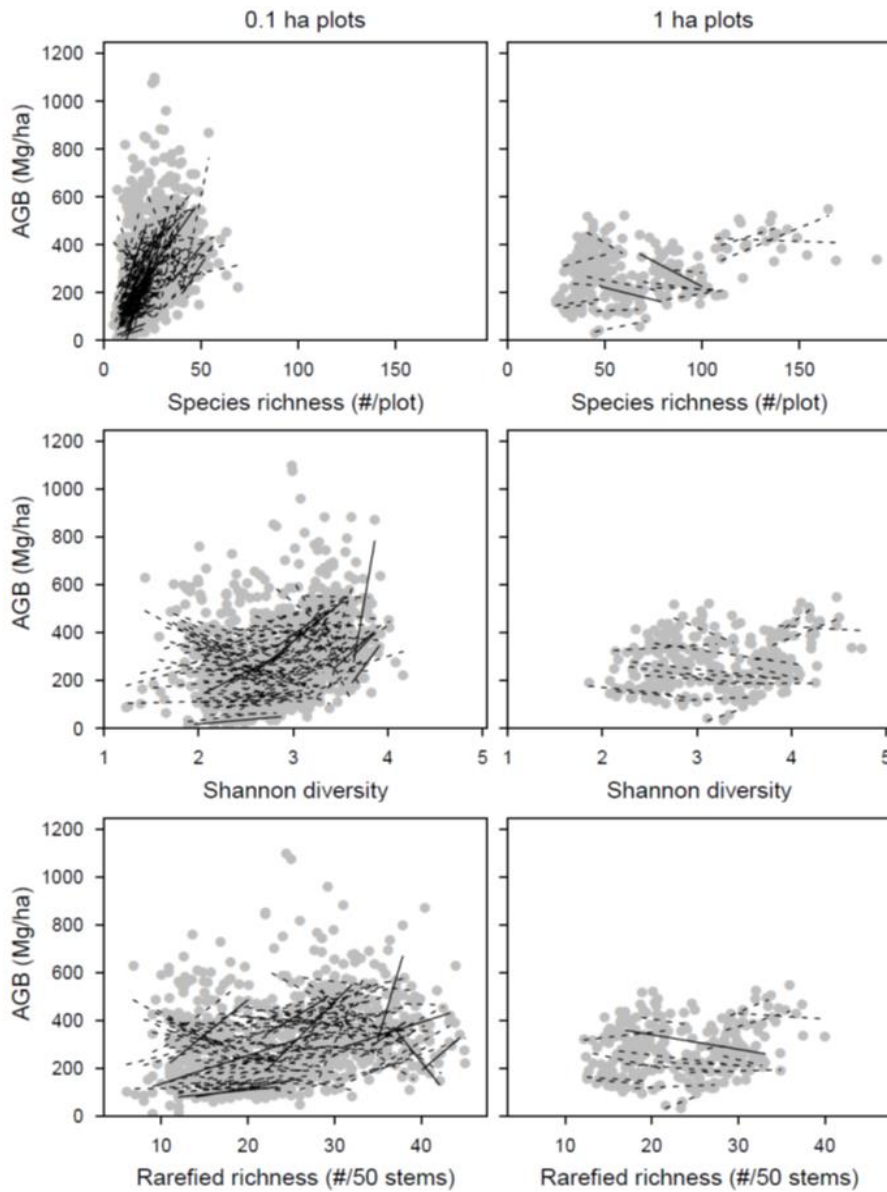
712

713 Figure 2. Map of vegetation cover in Latin America, with the location of the 60 study sites. a) above-
 714 ground biomass (AGB, Mg/ha), b) Rarefied species richness (# species/50 trees), and c) average tree
 715 diameter (cm). The size of the symbol scales with the value of the attribute. The intensity of the green
 716 color indicates the amount of forest cover. The background layer is derived from a MODerate resolution
 717 Imaging Spectroradiometer (MODIS) vegetation continuous fields (VCF) product (Hansen *et al.* 2003)



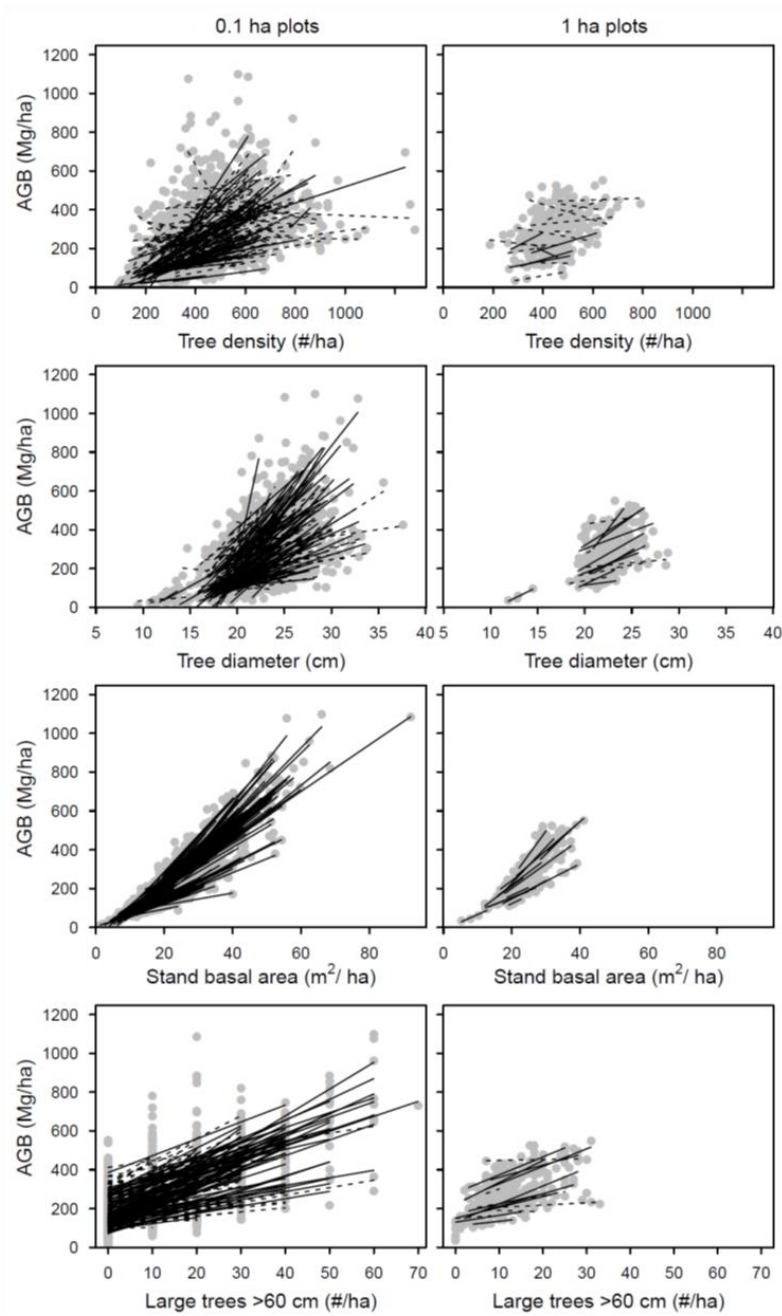
718

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 ($P > 0.05$).



726

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 ($P>0.05$).



735

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.

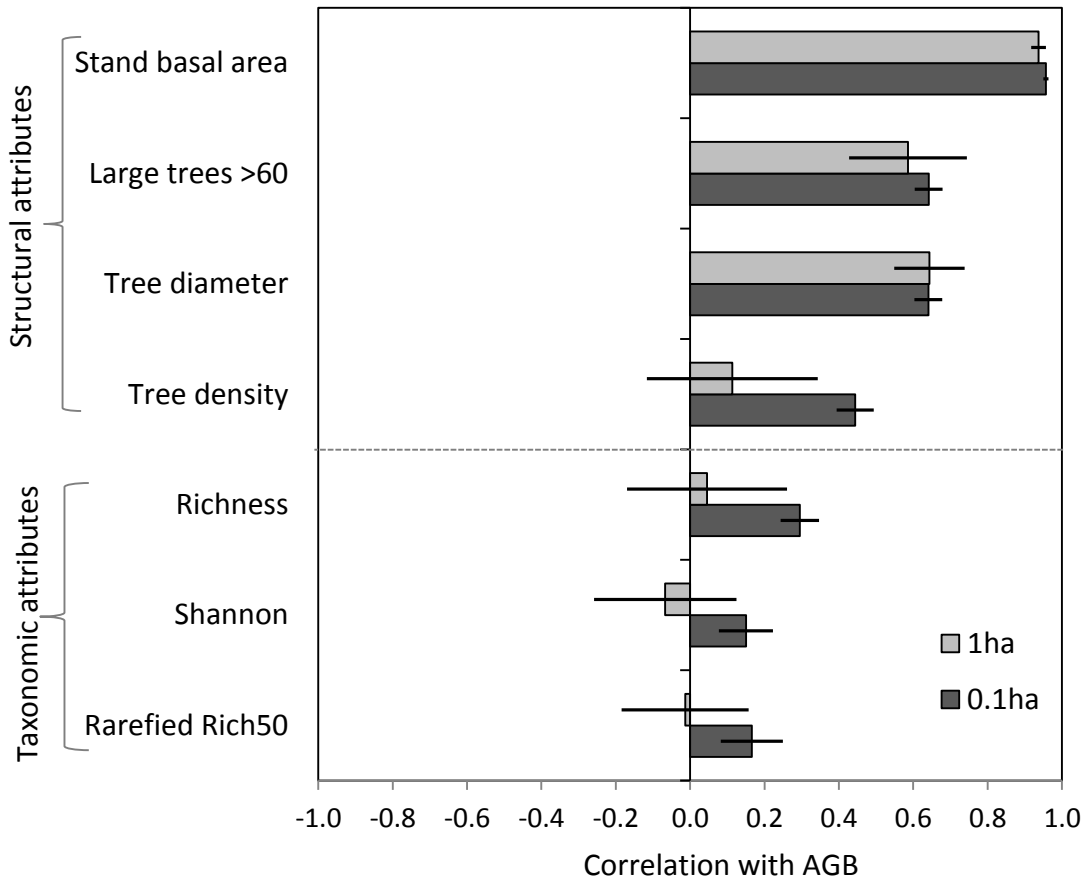
743

744

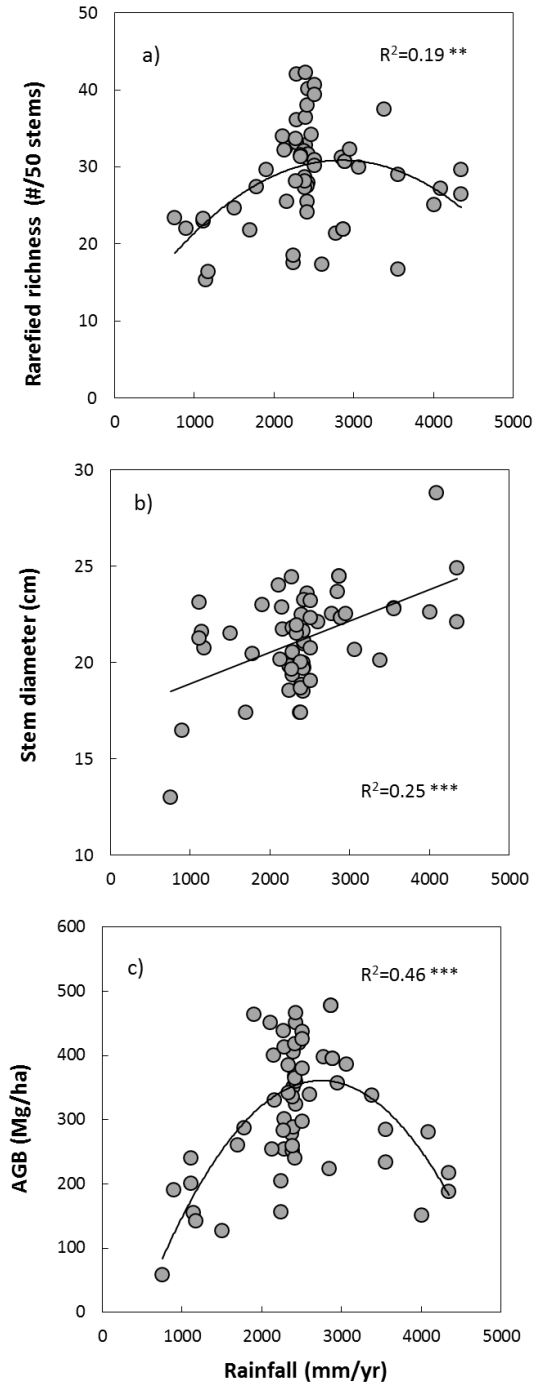
745

746

747



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. *** $P < 0.001$; ** $P < 0.01$.

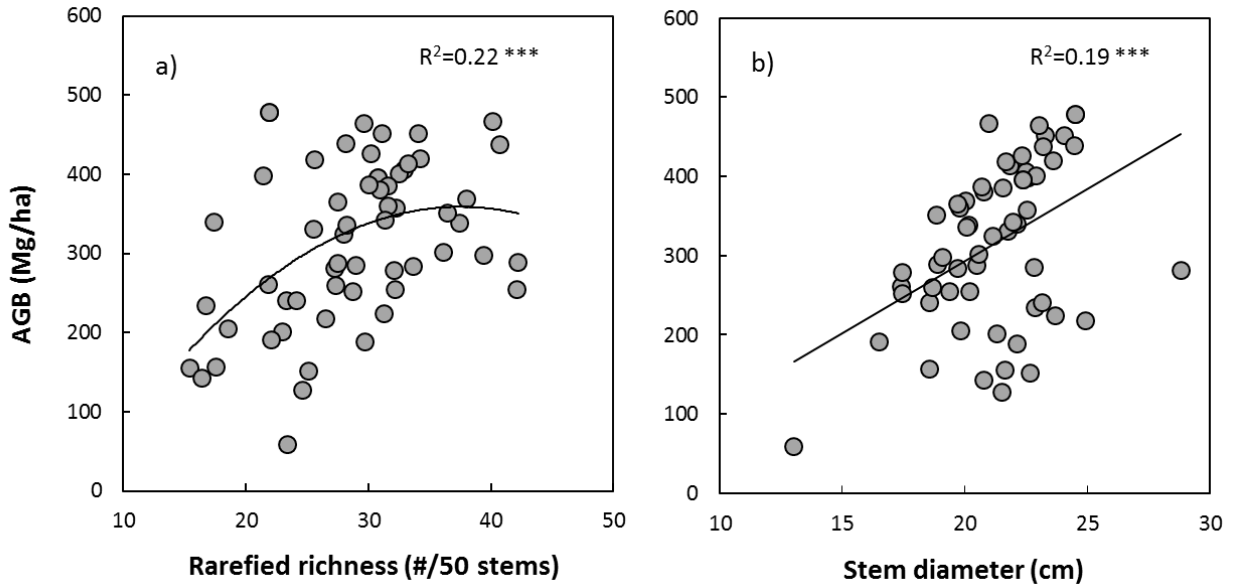


752

753

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. *** $P < 0.001$.

758



759

760

761

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 Exchange 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.