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RESEARCH PAPER

Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics

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ABSTRACT

Aim Large trees (d.b.h. ≥ 70 cm) store large amounts of biomass. Several studies suggest that large trees may be vulnerable to changing climate, potentially leading to declining forest biomass storage. Here we determine the importance of large trees for tropical forest biomass storage and explore which intrinsic (species trait) and extrinsic (environment) variables are associated with the density of large trees and forest biomass at continental and pan-tropical scales.

Location Pan-tropical.

Methods Aboveground biomass (AGB) was calculated for 120 intact lowland moist forest locations. Linear regression was used to calculate variation in AGB explained by the density of large trees. Akaike information criterion weights (AICc-wi) were used to calculate averaged correlation coefficients for all possible multiple regression models between AGB/density of large trees and environmental and species trait variables correcting for spatial autocorrelation.

Results Density of large trees explained *c.* 70% of the variation in pan-tropical AGB and was also responsible for significantly lower AGB in Neotropical [287.95 (mean) ± 105.0 (SD) Mg ha^{-1}] versus Palaeotropical forests (Africa 418.3 ± 91.8 Mg ha^{-1}; Asia 393.3 ± 109.3 Mg ha^{-1}). Pan-tropical variation in density of large trees and AGB was associated with soil coarseness (negative), soil fertility (positive), community wood density (positive) and dominance of wind dispersed species (positive), temperature in the coldest month (negative), temperature in the warmest month (negative) and rainfall in the wettest month (positive), but results were not always consistent among continents.

Main conclusions Density of large trees and AGB were significantly associated with climatic variables, indicating that climate change will affect tropical forest biomass storage. Species trait composition will interact with these future biomass changes as they are also affected by a warmer climate. Given the importance of large trees for variation in AGB across the tropics, and their sensitivity to climate change, we emphasize the need for in-depth analyses of the community dynamics of large trees.

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Keywords

Climate, ectomycorrhizal associations, large tree density, pan-tropical analysis, soils, species traits, tree size, tropical forest biomass, wood density, wind dispersal.

INTRODUCTION

Large trees have recently started to attract the attention of biologists because they are becoming increasingly rare due to their association with globally declining areas of pristine habitat (Lindenmayer *et al.*, 2012). Large, 'old' trees are keystone components of forest ecosystems, providing nesting and sheltering cavities, creating distinct microenvironments, playing crucial roles in hydrological regimes and providing food for many animal species (Lindenmayer *et al.*, 2012). Large trees also store large quantities of carbon due to their high wood volumes. Noting the disproportionate contribution of large trees to stand level aboveground biomass (AGB), Paoli *et al.* (2008) drew attention to the much higher density of large trees in Southeast Asia than the Neotropics as a possible explanation for the observed differences in AGB between these two regions. Differences in AGB are indeed closely linked to local and regional differences in the density of large trees (DeWalt & Chave, 2004; Paoli *et al.*, 2008; Rutishauser *et al.*, 2010; Slik *et al.*, 2010), and such trees could thus be responsible for a large portion of global variation in AGB. Our first aim, therefore, is to evaluate how much of the global variation in AGB can be explained by the density of large trees.

Our second aim is to identify the potential drivers of observed differences in the density of large trees and variation in AGB across the tropics. Can these be explained by environmental conditions, such as climate and soils, or are species traits involved as well? Climate and soils have been shown to be associated with the density of large trees and AGB at local and regional spatial scales, suggesting a potential role at global scales (Laurance *et al.*, 1999; Clark & Clark, 2000; Chave *et al.*, 2004; DeWalt & Chave, 2004; Malhi *et al.*, 2006; Paoli *et al.*, 2008; Ferry *et al.*, 2010; Slik *et al.*, 2010; Baraloto *et al.*, 2011; Quesada *et al.*, 2012). For example, prolonged droughts can disproportionately increase the mortality of large trees (Slik, 2004; Nieuwstadt & Sheil, 2005; Phillips *et al.*, 2009), resulting in a lower density of large trees and AGB, while very poor, waterlogged or shallow soils can lead to stunted tree growth, suppressed maximum tree size, higher tree failure rates, reduced density of large trees and lowered AGB (Paoli *et al.*, 2008; Ferry *et al.*, 2010; Slik *et al.*, 2010; Baraloto *et al.*, 2011).

Species traits related to maximum tree size might also play a role in explaining large-scale variation in AGB (Nelson *et al.*, 1999; DeWalt & Chave, 2004; Chave *et al.*, 2006; Paoli *et al.*, 2008; Rutishauser *et al.*, 2010; Slik *et al.*, 2010; Feldpausch *et al.*, 2011). To test this we selected three traits, wood density, wind dispersal syndrome and ectomycorrhizal (ECM) associations, that can be hypothesized to affect AGB and/or the density of large trees. Slik *et al.* (2010), for example, showed that within the Asian equatorial tropics wind dispersed tree species were typically larger than non-wind dispersed species and that dominance of wind dispersed species was positively correlated with AGB. Wood density has been shown to affect AGB patterns in the Neotropics (Baker *et al.*, 2004b), and also correlates positively with drought survival of large trees (Slik, 2004; Nieuwstadt & Sheil, 2005). ECM associations have frequently been found in association with (mono-)dominance of large tree species, possibly due to increased efficiency of nutrient acquisition in low-fertility soils, leading to higher growth and survival rates (Torti *et al.*, 2001; McGuire, 2007).

Here we use a pan-tropical tree inventory data set from 120 old-growth lowland tropical moist forest locations (33 in South

America, 45 in Africa, 42 in Southeast Asia) containing 192,308 stems (≥ 10 cm stem diameter) to address the above-mentioned topics at continental and pan-tropical scales.

MATERIAL AND METHODS

Pan-tropical AGB data

We used tree inventories from old-growth (undisturbed) moist (mean annual rainfall 1500–3500 mm, number of months were evaporation exceeds rainfall < 3) lowland (below 600 m elevation) forests that included all trees with a d.b.h. ≥ 10 cm and for which the exact location (latitude and longitude) and plot size were known. Some of the inventory data came from forest plot networks (see Acknowledgements for more information). Since we used a 10 km × 10 km raster for our environmental data (climate and soils), all plots that fell within a 10 km × 10 km environmental grid cell were combined and treated as a single observation (location), i.e. all individuals within the grid cell were pooled. Only grid cells that contained at least 1 ha of tree inventories were included in the study, resulting in a total of 120 sample locations (Fig. 1, Appendix S1 in Supporting Information), 33 in America, 45 in Africa and 42 in Asia. For each of these we calculated the AGB by dividing the sum of all individual tree AGBs by the total surface area of the plots. For the AGB calculation we used the pan-tropical moist forest AGB equation given in Feldpausch *et al.* (2012) which is based on the same, but expanded, data set of destructively sampled trees from across the tropics as used for the Chave *et al.* (2005) pan-tropical AGB moist forest equation. Tree diameter–height relationships differ significantly between tropical regions, which can seriously affect regional AGB estimates (Feldpausch *et al.*, 2011, 2012; Banin *et al.*, 2012). Since most of our tree inventories lacked precisely measured tree heights, we used the regional Weibull height models given in Feldpausch *et al.* (2012) to estimate tree heights. The observed tree diameters and estimated tree heights were subsequently used as input variables in the AGB allometric equation mentioned above. Wood density values for the tree species, which are another input variable in this AGB equation, were taken from the Global Wood Density Database (Chave *et al.*, 2009; Zanne *et al.*, 2009). If species were not present in this list we used the genus-level average to estimate the species value (Chave *et al.*, 2006; Slik, 2006). For unidentified species, or species identified to family level only, we used the average wood density value of the plot in which they were found.

Tree species traits

Tree species trait data were collated from literature sources, i.e. wood density from the Global Wood Density Database (Chave *et al.*, 2009; Zanne *et al.*, 2009), ECM associations from Brundrett (2009) and wind dispersal from local floras and 'single image' by checking species fruit and seed morphology. For each location we then calculated the basal area weighted mean community value of wood density (WD) and biomass weighted percentage ECM associations and percentage wind dispersal. Wood density was weighted by basal area instead of biomass because wood density is used to calculate biomass, making these two variables dependent on each other.

Climate and soil data

We downloaded 34 climate variables from the WORLDCLIM database (http://www.worldclim.org) and 15 soil variables from the FAO database for poverty and insecurity mapping for each of the 120 locations using a *c.* 10 km × 10 km resolution (for a complete definition of each variable see Appendix S2, FAO, 2002 and Hijmans *et al.*, 2005). To reduce the number and collinearity of variables we ran a principal components analysis (PCA) (Multivariate Statistics Package MVSP, version 3.2, Kovach Computing Services, Anglesey, UK) for both the climate and soil data with the 120 locations as cases. We retained only PCA axes that explained at least 10% of data variability, resulting in three climate and four soil axes (Appendix S3). The three climate and four soil axes explained 85.1% and 74.4% of data variability, respectively. For the climate PCA axes we then selected one variable that made ecological sense in relation to AGB and tree density, was highly correlated with the concerned PCA axis, and was correlated as little as possible with the other PCA axes. This resulted in the following included climatic and soil variables: (1) *minimum temperature of the coldest month*, which was closely associated with temperature seasonality; (2) *maximum temperature of the warmest month*, which was closely associated with mean annual temperature; (3) *rainfall in the wettest month*, which was closely associated with annual rainfall; (4) *soil PCA axis 1*, which was negatively associated with soil organic carbon

Figure 1 Spatial distribution of the study sites (black dots). Due to the size of the dots they can encompass more than one location. The total number of locations is: South America 33, Africa 45, Southeast Asia 42. The extent of global moist tropical forests is indicated by grey shading.

Table 1 Mean aboveground biomass (AGB) (±SD) values (all trees, small trees and big trees) of South American, African and Asian moist tropical forests below 600 m elevation. Significant differences ($P < 0.05$) in AGB between regions were tested with one-way ANOVA followed by Bonferroni post hoc tests or Kruskal–Wallis (KW) followed by Mann–Whitney post hoc tests (if data transformation could not correct for differences in data variance between regions) and are indicated by different superscript characters (A, B) in each column.

Region	AGB all trees (Mg ha^{-1})	AGB small trees (d.b.h. < 70 cm) (Mg ha^{-1})	AGB big trees (d.b.h. ≥ 70 cm) (Mg ha^{-1})	Sample size (n)
America	287.8 ± 105.0^{A}	215.7 ± 67.5	72.2 ± 62.9^{A}	33
Asia	393.3 ± 109.3^{B}	239.4 ± 58.6	153.9 ± 87.8^{B}	42
Africa	418.3 ± 91.8^{B}	222.9 ± 37.9	186.2 ± 79.8^{B}	45
n	120	120	120	
Test statistic	17.0 (ANOVA)	3.3 (KW)	36.5 (KW)	
P	< 0.0001	n.s.	< 0.0001	

n.s., not significant.

content; (5) *soil PCA axis 2*, which was positively associated with soil water availability and storage; (6) *soil PCA axis 3*, which was positively associated with soil coarseness; (7) *soil PCA axis 4*, which was positively associated with available nutrients and pH.

Statistical analyses

Differences in AGB, density of large trees and other variables between tropical America, Africa and Asia were tested using ANOVA followed by Bonferroni post hoc tests when data variances were equal and data normally distributed. If the data variance remained unequal, even after data transformation, we used Kruskall–Wallis followed by pair-wise Mann–Whitney post hoc tests. The appropriate boundary for differentiating small and large trees was detected using cumulative addition of AGB stored in 10 cm diameter classes, performing an ANOVA test between the three main tropical regions at each cumulative step to test for significant differences in AGB between regions. This analysis showed that the three tropical regions had similar cumulative AGB values up to a diameter of 70 cm, but significantly differed at all higher cumulative AGB values (Table 1). We therefore chose 70 cm as the threshold to differentiate between small and large trees. A linear regression was performed to test the strength of the relationship between large tree (d.b.h. >= 70 cm) density and AGB.

To determine the contribution of species trait, climate and soil variables to regional and global variation in density of large trees and AGB, we computed ordinary least square (OLS) linear multiple regression models based on each possible combination of variables (1023 possible models for 10 variables) using the freely available software 'Spatial Analysis for Macroecology' (SAM), version 4.0 (Rangel *et al.*, 2010). Before we performed the OLS analyses we first tested whether regressions between the response variables and the individual predictor variables were linear and conformed to regression analysis assumptions. Our aim was not to find the single best predictive model for the response variables, but to explore the strength and direction of the predictor variables across all models using a model averaging approach based on the Akaike information criterion weight (AICc-wi). The AICc-wi represents the likelihood of a given model relative to all other models and thus varies between zero and one (Wagenmakers & Farrell, 2004), with the model with the lowest AICc having the highest AICc-wi. All model parameters were averaged across the 1023 models, weighted by their AICc-wi. A one-tailed *t*-test was used to determine whether the variation in regression coefficients observed for each variable across all models differed significantly from zero. Additionally we calculated the importance value of each predictor variable. The importance value of a predictor variable is calculated by simply adding the AICc-wi values of the models in which the variable was present, i.e. if variables were present in the most likely models they will have high importance values. Importance values vary between zero (low importance) and one (high importance).

To account for spatial autocorrelation in our OLS models we used eigenvector-based spatial filtering (SEVM) as applied in SAM version 4.0. This method extracts spatial filters using the principal components of neighbour matrices (PCNM) (Brocard & Legendre, 2002). We retained only spatial filters that reduced spatial autocorrelation with the response variable (as based on Moran's *I* values) and which alone or combined showed the lowest AICc value when regressed against the response variable. These spatial filters were subsequently added as fixed (i.e. present in all 1023 multiple regressions) predictive variables in the same model selection procedure as described above to see how this would affect the direction, strength and significance of the regression coefficients produced by the OLS regressions without spatial filters. In all but one case adding spatial filters improved the models (lower AICc values). Since the spatially corrected models are also statistically more appropriate we use the spatial models in the remainder of this paper (original OLS results can be found in Appendices S4 & S5).

All analyses, unless mentioned otherwise, were performed using the statistical software package Statgraphics Plus for Windows version 2.1 (Statpoint Technologies, Warrenton, VA, USA).

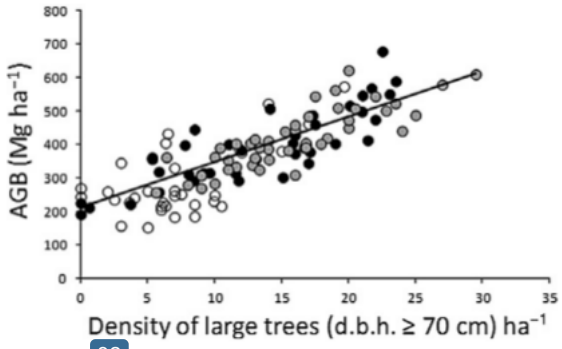

Figure 2 Relationship between density of large trees (d.b.h. ≥ 70 cm) and aboveground biomass. South American sites indicated by open circles; African sites by grey circles; Asian sites by black circles. The fitted line explains 69.8% of data variance.

RESULTS

Estimated AGB was significantly lower in South America [287.8 ± 105.0 (mean ± SD) Mg ha^{-1}] than in Africa (418.3 ± 91.8 Mg ha^{-1}) and Southeast Asia (393.3 ± 109.3 Mg ha^{-1}) (Table 1). No difference in AGB was detected between the three tropical regions when only trees up to 70 cm diameter were included in the AGB calculations, i.e. the difference in AGB was caused by the AGB stored in the largest trees (d.b.h. ≥ 70 cm) (Table 1). The lower AGB in South American forests corresponded to a significantly lower density of large trees there (density of trees with d.b.h. ≥ 70 cm in South America 7.5 ± 5.3 trees ha^{-1}, in Southeast Asia 13.4 ± 6.7 trees ha^{-1}, in Africa 15.8 ± 5.4 trees ha^{-1}; ANOVA test $n = 120$, d.f. = 2, $F = 20.8$, $P < 0.0001$). Overall, large tree density (d.b.h. ≥ 70 cm) accounted for 69.8% of pan-tropical variation in AGB (Fig. 2; linear regression results: correlation coefficient = 0.835, $R^2 = 0.698$, $F = 272.6$, $n = 120$, $P < 0.0001$).

The three tropical forest regions differed significantly in species trait values, climate variables and soil variables, with the exception of maximum rainfall of the wettest month and soil PCA axis 3 (soil texture) (Table 2). Distinctive characteristics of the South American locations included relatively high wood density, low dominance of ECM and wind dispersed trees, high maximum temperatures and high soil moisture storage combined with poor soils. Distinctive characteristics of the Asian locations included the relatively low wood density, high dominance of ECM and wind dispersed trees, low maximum temperatures combined with high minimum temperatures, high soil organic carbon, low soil water storage but high soil fertility. Distinctive characteristics of the African locations included the relatively high wood density, low minimum temperature and low soil organic carbon.

At global scales, soil variables had low to intermediate importance values as predictors for both the density of large trees and AGB, although this differed between continents (Tables 3 & 4). At the global scale, soil fertility was the most important variable, being positively correlated with both the density of large trees and AGB; however, this relationship was negative in Africa. Soil coarseness and moisture storage were less important for the density of large trees and AGB at the global scale, both decreasing with soil coarseness and moisture storage, but considerable differences existed in the strength and direction of correlation for these variables among the three continents (Tables 3 & 4). Soil carbon content was the least important soil variable at the global scale, showing no relationship with the density of large trees and a negative relationship with AGB. However, in Africa it was a strong positive correlate for the density of large trees, while in South America it was a positive correlate for AGB (Tables 3 & 4).

Species traits were strongly correlated with the density of large trees and AGB at the global and continental scales, both generally increasing with community average wood density (except Asia), ECM associations (except for AGB at global scale and Africa) and dominance of wind dispersed tree species (Tables 3 & 4). These patterns were fairly consistent within the continents, with the exception of Asia where the relationship between community average wood density and density of large trees was negative while being non-significant for AGB; and the non significant association of ECM associations with AGB in Africa and the global scale (Tables 3 & 4).

Rainfall had very high importance as a climate variable and was positively correlated with the density of large trees and AGB at the global scale. With the exception of South America this pattern was the same in most continents (Tables 3 & 4). Of the temperature variables, maximum temperature in the warmest month was the most important, being negatively correlated with the density of large trees and AGB at the global scale, but these results varied considerably between continents (Tables 3 & 4). The minimum temperature of the coldest month was negatively correlated with density of large trees and AGB at the global scale, but again varied considerably between continents (Tables 3 & 4).

Overall, the predictive models explained considerable amounts of variation in AGB and the density of large trees, with the exception of Asia, where explained variation in AGB was low (Tables 3 & 4).

DISCUSSION

Big trees as drivers of variation in AGB

Big trees accounted for more than two-thirds of sample-based pan-tropical variation in AGB, and when the three main tropical regions were compared directly they were the sole cause of the detected AGB difference between Neotropical and Palaeotropical forests. The impact of big trees on AGB also follows from the fact that they stored on average 25.1, 39.1 and 44.5% of AGB in South America, Southeast Asia and Africa respectively, but represented only 1.5, 2.4 and 3.8% of stems larger than 10 cm d.b.h. in these three respective regions. Any impacts on large trees, either by global change or other disturbances that affect the abundance and persistence of these large stems, is therefore likely to have a major impact on forest AGB.

Table 2 Comparison of species traits, climate and soil variables (mean ± SD) in the sample locations partitioned by the three main tropical regions. All tests are based on Kruskal–Wallis followed by Mann–Whitney post-hoc comparisons. Significant differences between regions in each row are indicated with different superscript characters (A, B).

	America ($n = 33$)	Asia ($n = 42$)	Africa ($n = 45$)	Test statistic	*P*-level
Wood density (g cm^{-3})	0.650 ± 0.08^{B}	0.593 ± 0.03^{A}	0.647 ± 0.04^{B}	33.9	< 0.0001
ECM (% of AGB)	2.31 ± 0.07^{A}	40.21 ± 0.18^{C}	9.77 ± 0.10^{B}	71.2	< 0.0001
Wind disp. (% of AGB)	10.62 ± 0.06^{A}	45.95 ± 0.16^{C}	19.39 ± 0.11^{B}	68.0	< 0.0001
Max. temp. (°C)	32.4 ± 7.3^{C}	30.6 ± 11.5^{A}	31.3 ± 11.5^{B}	51.7	< 0.0001
Min. temp. (°C)	19.8 ± 22.9^{A}	21.0 ± 24.9^{A}	18.3 ± 10.8^{B}	45.2	< 0.0001
Max. rain (mm month^{-1})	339.5 ± 74.2	327.7 ± 54.3	312.7 ± 76.4	1.3	NS
Soil PCA 1 (carbon)	−0.037 ± 0.123^{AB}	−0.084 ± 0.195^{A}	0.106 ± 0.174^{B}	20.7	< 0.0001
Soil PCA 2 (moisture)	0.091 ± 0.138^{C}	−0.075 ± 0.170^{A}	0.003 ± 0.135^{B}	18.1	< 0.0001
Soil PCA 3 (coarseness)	−0.046 ± 0.072	0.035 ± 0.174	0.001 ± 0.125	3.8	NS
Soil PCA 4 (fertility)	−0.045 ± 0.106^{A}	0.058 ± 0.124^{B}	−0.021 ± 0.102^{A}	18.5	< 0.0001

AGB, aboveground biomass; wood density, basal area weighted community wood density; ECM, ectomycorrhizal associations; Wind disp., trees with wind dispersal syndrome; Max. temp., temperature of the warmest month; Min. temp., temperature of the coldest month; Max. rain, rainfall in the wettest month; carbon, soil carbon content; moisture, soil moisture content; coarseness, soil particle size; fertility, soil fertility.

Table 3 The standardized regression coefficients for each predictor variable, with their importance value indicated between brackets, for density of large trees at global and continental scales as averaged over all 1023 possible models using AICc-wi (the Akiake information criterion weight) as a weighting criterion. All models were run with spatial filters to correct for effects of spatial autocorrelation on strength, direction and importance of regression coefficients.

Region		Global		Africa		America		Asia	
Soil	S1 (carbon)	−0.020	(0.244)	0.923***	(0.710)	0.037	(0.194)	0.014	(0.185)
	S2 (moisture)	−0.134**	(0.555)	0.021	(0.246)	0.023	(0.229)	−0.297**	(0.751)
	S3 (coarseness)	−0.127**	(0.577)	−0.546**	(0.715)	−0.125*	(0.200)	−0.071*	(0.212)
	S4 (fertility)	0.212**	(0.929)	−0.802**	(0.744)	0.267***	(0.363)	0.129***	(0.268)
Trait	WD	0.127**	(0.464)	0.299**	(0.562)	0.222***	(0.328)	−0.338**	(0.845)
	ECM	0.122**	(0.323)	0.194***	(0.315)	0.349**	(0.785)	0.484***	(0.794)
	Wind	0.483***	(0.997)	0.577***	(0.993)	0.092**	(0.203)	0.290**	(0.355)
Climate	T min.	−0.053*	(0.275)	0.377**	(0.688)	−0.016	(0.194)	−0.149**	(0.247)
	T max.	−0.133**	(0.466)	−0.342**	(0.758)	0.225***	(0.387)	−0.026	(0.195)
	R max.	0.197**	(0.924)	0.618**	(0.904)	−0.032	(0.180)	0.102**	(0.232)
Space	Filter 1	−0.541***	(1.000)	−0.518**	(1.000)	0.476**	(1.000)	−0.316*	(1.000)
	Filter 2	−0.134	(1.000)						
Model	AICc	743.2		273.2		211.4		288.4	
	R^2-adjusted	0.414		0.482		0.258		0.270	
	n	120		45		33		42	

AGB, aboveground biomass; WD, basal area weighted community wood density; ECM, ectomycorrhizal associations; Wind, trees with wind dispersal syndrome; T max., temperature of the warmest month; T min., temperature of the coldest month; R max., rainfall in the wettest month; carbon, soil carbon content; moisture, soil moisture content; coarseness, soil particle size; fertility, soil fertility; AICc, Akaike information criterion adjusted for small sample size.

Significance levels for non-random deviation from zero of the regression coefficients are indicated as follows: *$0.01 < P < 0.05$; **$0.001 < P < 0.01$; ***$P < 0.001$.

Climate

One obvious change that will occur in tropical forests over the next century will be an increase in temperature between 1 and 6°C (IPCC, 2007). Since tropical forests store considerable amounts of terrestrial carbon (Saatchi *et al.*, 2011) it is critical to know how temperature relates to the density of large trees and AGB across the tropics because this could indicate how tropical forests will react to rising temperatures. Although our global models show a clear negative correlation between temperature of the warmest month and the density of large trees and AGB, suggesting a loss of large trees and AGB with rising temperatures, our results are rather mixed when analysed at the continental scale. Of the three continents, only Africa shows a clear negative correlation between temperature of the warmest month and density of large trees and AGB. For the other con-

Table 4 The standardized regression coefficients for each predictor variable, with their importance value indicated between brackets, for AGB (aboveground biomass) at global and continental scales as averaged over all 1023 possible models using AICc-wi (Akaike information criterion weight) as a weighting criterion. All models were run with spatial filters to correct for effects of spatial autocorrelation on strength, direction and importance of regression coefficients.

Region		Global	Africa	America	Asia
Soil	S1 (carbon)	−0.099** (0.410)	−0.017 (0.209)	0.399*** (0.258)	−0.107** (0.240)
	S2 (moisture)	−0.039* (0.257)	0.009 (0.195)	0.077 (0.340)	−0.056 (0.204)
	S3 (coarseness)	−0.062** (0.309)	−0.176*** (0.359)	−0.406*** (0.273)	0.108** (0.239)
	S4 (fertility)	0.139** (0.676)	−0.055* (0.201)	0.312** (0.796)	0.126** (0.265)
Trait	WD	0.471*** (1.000)	0.600*** (0.997)	0.445** (0.749)	−0.049 (0.206)
	ECM	0.016 (0.234)	−0.016 (0.179)	0.227** (0.805)	0.326** (0.457)
	Wind	0.448*** (0.998)	0.631*** (0.998)	0.118*** (0.226)	0.358** (0.623)
Climate	T min.	−0.044* (0.253)	−0.052 (0.199)	−0.009 (0.140)	−0.183** (0.304)
	T max.	−0.140** (0.541)	−0.340** (0.881)	0.021 (0.131)	0.144** (0.272)
	R max.	0.225** (0.984)	0.338** (0.780)	−0.031 (0.146)	0.314** (0.652)
Space	Filter 1	−0.268* (1.000)	0.079 (1.000)	−0.484* (1.000)	−0.293* (1.000)
	Filter 2	−0.300** (1.000)		0.168 (1.000)	
	Filter 3	0.056 (1.000)		−0.127 (1.000)	
	Filter 4				
Model	AICc	1412.9	531.8	376.0	533.8
	R^2-adjusted	0.482	0.427	0.769	0.070
	n	120	45	33	42

Significance levels for non-random deviation from zero of the regression coefficients are indicated as follows: *$0.01 < P < 0.05$; **$0.001 < P < 0.01$; ***$P < 0.001$.

WD, basal area weighted community wood density; ECM, ectomycorrhizal associations; Wind, trees with wind dispersal syndrome; T max., temperature of the warmest month; T min., temperature of the coldest month; R max., rainfall in the wettest month; carbon, soil carbon content; moisture, soil moisture content; coarseness, soil particle size; fertility, soil fertility; AICc, Akaike information criterion adjusted for small sample size.

tinents the importance value for this variable was low, indicating that they were generally not selected in the best models and showed either no or a positive impact on the density of large trees and AGB. The African forest locations differed climatologically from those of the other two continents in that they had the lowest annual rainfall and are therefore generally more water limited when compared with forests in Asia and South America. This may explain the strong negative association between temperature of the warmest month and density of large trees and AGB in Africa since water stress is an important mortality factor for large tropical trees (Phillips *et al.*, 2010), especially since the water vapour pressure deficit experienced by trees increases exponentially with increasing temperature under low-humidity conditions (Boer *et al.*, 2011). Overall, however, the ambiguity in response strength and direction across continents makes it difficult to predict how the density of large trees and forest biomass will be affected by increasing temperatures in the future. So far tropical forests still seem to act as carbon sinks (Baker *et al.*, 2004a; Lewis *et al.*, 2009b), possibly due to carbon fertilization associated with the increased levels of atmospheric CO_2 (Lewis *et al.*, 2009a), but our analysis does partly indicate that this may change if temperatures keep increasing.

Annual rainfall had a high importance value and positive correlation with AGB and density of large trees, with the exception of forests in South America which showed no response. The rainfall effect was strongest in Africa, which, as mentioned earlier, has the lowest annual rainfall levels of the three tropical regions and therefore its forests can be expected to react strongly to rainfall levels. The importance of annual rainfall for AGB has been stressed by many studies (Chave *et al.*, 2004; Malhi *et al.*, 2006; Slik *et al.*, 2010; Baraloto *et al.*, 2011), and is probably related to hydraulic limitations of especially the largest trees (Lines *et al.*, 2012). Large trees are disproportionately sensitive to water stress (Slik, 2004; Nieuwstadt & Sheil, 2005), because the water tension that develops between the tree roots and canopy can cause vessel cavitation under warm and dry conditions (Hacke *et al.*, 2001), leading to lost water transport capacity and, if enough vessels are affected, to tree death. Several studies have shown that extreme or prolonged droughts do indeed increase the mortality of large trees disproportionately (Nieuwstadt & Sheil, 2005; Phillips *et al.*, 2010), resulting in considerable declines of forest AGB and density of large trees (Phillips *et al.*, 2009). On the other hand, a recent study from Ghana found that after a multidecadal decline in rainfall, tree canopy species composition shifted towards heavier wooded tree species leading to an overall increase in AGB (Fauset *et al.*, 2012), thus showing that gradual decreases in rainfall may affect tropical forests differently from intense droughts.

Soils

Our study finds relatively weak impact of soils on forest AGB and density of large trees. A problem here is that although the FAO soil data that we used are globally standardized and thus good for comparison between regions, they are also rather coarse and their local accuracy is poorly known but appears low in forested regions (e.g. Ladd *et al.*, 2013), despite the fact that extrapolation of soil variables in the FAO system is partly based on the forest types themselves. Given the notorious variability of soils over short distances, this low level of resolution could obscure otherwise strong relationships if soil data were to have been available for individual plots. Unfortunately, such data were not available for most sites included in our analysis. Good quality data are clearly urgently needed.

Relationships between soils and tropical forests show rather mixed and often conflicting results (Laurance *et al.*, 1999; DeWalt & Chave, 2004; Paoli *et al.*, 2008; Ferry *et al.*, 2010; Quesada *et al.*, 2012). This is partly because every study uses slightly different methodologies of sampling (sampling depth and intensity), includes different nutrients and differs in whether these represent available or total amounts. However, there seems to be a general pattern of increasing density of large trees and AGB with increasing soil fertility in tropical forests (Paoli *et al.*, 2008; Quesada *et al.*, 2012). Our study supports this further by identifying soil fertility (in the form of available bases) as an important positive correlate of both density of large trees and forest AGB at global scales and within South America and Asia at the continental scales. Africa formed an exception with a strong negative correlation between soil fertility and density of large trees, and to a lesser extent AGB. Shifting cultivation and migrations were very frequent in west central African forests, where most of our plots are located, before populations were forced to settle by colonial and subsequent governments (Van Gemerden *et al.*, 2003; Brncic *et al.*, 2007). We can assume that populations cultivated on the richest soils and thus reduced the number of tree stems. In these past cultivated areas, stands are still dominated by light-demanding and wind-dispersed species (Gillet & Doucet, 2012) while in the oldest forests shade tolerant species dominate, most of them being Fabaceae, often self-dispersed, gregarious, with ECM, forming large, low-diversity stands with big trees.

Species traits

Community average wood density (weighted by basal area) and dominance of wind dispersed tree species (weighted by biomass) were strong positive correlates for the density of large trees and AGB both globally and on most continents, while dominance of species with ECM associations (weighted by biomass) showed weaker, but generally also positive, correlations with density of large trees and AGB. Possession of a wind dispersal syndrome is positively associated with tree size in Asian tropical forests (Slik *et al.*, 2010), probably because the dispersal distance of wind dispersed seeds depends directly on the height from which seeds are released and exposure to wind flows (Contreras-Sanchez *et al.*, 2011). Our results show that the dominance of wind dispersed species in old-growth tropical forests is a consistent indicator of a high density of large trees and high forest AGB across all tropical continents. What is causing the dominance of wind dispersed tree species in high-biomass forests remains unclear, but deserves further study. In Asia most of the wind dispersed tree species are concentrated in the Dipterocarpaceae, which are also characterized by ECM associations. ECM associations increase nutrient availability to tree species, which, especially on poor soils, may enable them to outcompete other species with less efficient nutrient acquisition through higher survival and growth rates, potentially leading both to large tree size and a high density of large trees (Torti *et al.*, 2001; McGuire, 2007). It would be interesting to explore whether wind dispersal and ECM associations are more generally associated, as this may be one of the mechanisms explaining how wind dispersed tree species can become both dominant and large.

Wood density was another species trait that was strongly and positively correlated with the density of large trees and forest AGB, although Asian forests formed an exception to this rule. It should be noted, however, that there is a potential for artefacts in this result given that wood density is also included in the allometric equation used to calculate tree biomass. The two continents where wood density has a positive effect on forest AGB, Africa and South America, are characterized by high average wood density when compared with forests in Asia where no effect of wood density on AGB was detected. The Asian forest sites were among the coolest, wettest and least seasonal forests included in this study, which may explain their relatively low wood density, as high wood density is generally correlated with hot and drought-prone regions, either with low annual rainfall or strong seasonal patterns in rainfall (Hacke *et al.*, 2001; Malhi *et al.*, 2006; Maharjan *et al.*, 2011). Also, the areas with the highest community wood density in Asia were nutrient-poor heath forests and peat swamp forests, both of which are characterized by a low density of large trees and low to average levels of AGB (Slik *et al.*, 2010).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 List of plot locations.

Appendix S2 List of WORLDCLIM and FAO soil variable definitions.

Appendix S3 Principal components analysis climate and soil axes.

Appendix S4 Density of large trees ordinary least square regression results without correction for spatial autocorrelation.

Appendix S5 Aboveground biomass ordinary least square regression results without correction for spatial autocorrelation.

BIOSKETCH

Ferry Slik and co-authors work together with the specific aim of combining local tree data sets into larger regional and pan-tropical data sets so that large-scale patterns in tropical tree diversity, composition, traits and biomass can be studied. Such analyses are important because they can elucidate the biogeographical and environmental drivers behind these patterns, and thus might also provide insight into how global change will affect tropical tree communities. Ferry Slik and co-workers will continue to work on these questions and are currently expanding the data set significantly.

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