RESEARCH PAPER

Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests

J. W. F. Slik[1]*, Shin-Ichiro Aiba[2], Francis Q. Brearley[3], Chuck H. Cannon[1,4], Olle Forshed[5], Kanehiro Kitayama[6], Hidetoshi Nagamasu[7], Reuben Nilus[8], John Payne[9], Gary Paoli[10,11], Axel D. Poulsen[12], Niels Raes[13], Douglas Sheil[14], Kade Sidiyasa[15], Eizi Suzuki[2] and Johan L. C. H. van Valkenburg[16]

[1]*Key Laboratory in Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Yunnan 666303, China,* [2]*Faculty of Science, Kagoshima University, Kagoshima 890-8580, Japan,* [3]*Department of Environmental and Geographical Sciences, Manchester Metropolitan University, Manchester M1 5GD, UK,* [4]*Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409-3131, USA,* [5]*Department of Forest Ecology and Management, Faculty of Forest Sciences, Swedish University of Agricultural Sciences, SE-90183 Umea, Sweden,* [6]*Center for Ecological Research, Kyoto University, Otsu 520-2113, Japan,* [7]*Department of Botany, Kyoto University, Kyoto 606-8502, Japan,* [8]*Forest Research Centre, Sabah Forestry Department, 90000 Sandakan, Sabah, Malaysia,* [9]*World Wide Fund for Nature–Malaysia, 88800 Kota Kinabalu, Sabah, Malaysia,* [10]*Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109-1048, USA,* [11]*Indonesian Resource Institute, Bogor 16113, Indonesia,* [12]*Royal Botanic Garden Edinburgh, Edinburgh EH3 5LR, UK,* [13]*Nationaal Herbarium Nederland, Leiden University, 2333 CC Leiden, The Netherlands,* [14]*Institute of Tropical Forest Conservation, Mbarara University of Science and Technology, PO BOX 1410, Kabale, Uganda,* [15]*Wanariset-Samboja Herbarium, KM38 Samboja, Indonesia,* [16]*Plant Protection Service, 6700 HC Wageningen, The Netherlands*

*Correspondence: Ferry Slik, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan 666303, China.
E-mail: ferryslik@hotmail.com

ABSTRACT

Aim Tropical forests have been recognized as important global carbon sinks and sources. However, many uncertainties about the spatial distribution of live tree above-ground biomass (AGB) remain, mostly due to limited availability of AGB field data. Recent studies in the Amazon have already shown the importance of large sample size for accurate AGB gradient analysis. Here we use a large stem density, basal area, community wood density and AGB dataset to study and explain their spatial patterns in an Asian tropical forest.

Location Borneo, Southeast Asia.

Methods We combined stem density, basal area, community wood density and AGB data from 83 locations in Borneo with an environmental database containing elevation, climate and soil variables. The Akaike information criterion was used to select models and environmental variables that best explained the observed values of stem density, basal area, community wood density and AGB. These models were used to extrapolate these parameters across Borneo.

Results We found that wood density, stem density, basal area and AGB respond significantly, but differentially, to the environment. AGB was only correlated with basal area, but not with stem density and community wood specific gravity.

Main conclusions Unlike results from Amazonian forests, soil fertility was an important positive correlate for AGB in Borneo while community wood density, which is a main driver of AGB in the Neotropics, did not correlate with AGB in Borneo. Also, Borneo's average AGB of 457.1 Mg ha^{-1} was *c.* 60% higher than the Amazonian average of 288.6 Mg ha^{-1}. We find evidence that this difference might be partly explained by the high density of large wind-dispersed Dipterocarpaceae in Borneo, which need to be tall and emergent to disperse their seeds. Our results emphasize the importance of Bornean forests as carbon sinks and sources due to their high carbon storage capacity.

Keywords

Above ground biomass, basal area, Borneo, carbon storage, REDD, stem density, tropical forest, wood density.

INTRODUCTION

Ongoing negotiations on greenhouse gas reductions leading up to a new climate agreement to be formulated in Copenhagen in December 2009 might compensate those countries that ensure protection of their old-growth forests and the carbon stored in them. The 'reduced emission from deforestation and degradation' (REDD) scheme has been proposed as a possible mechanism to realize this (Putz *et al.*, 2008). Given the high rates of deforestation in tropical Asia and the limited extent of old-growth forests that persist there (Sodhi *et al.*, 2004), mapping of above-ground biomass (AGB) is of immediate priority for Southeast Asia. So far the most comprehensive attempts to map AGB in Asia have been made by Brown *et al.* (1993) and Gibbs *et al.* (2007). These studies captured most of the large-scale variation in AGB across tropical Asia, but due to scarcity of inventory data they may have underestimated its regional variability.

Important progress has recently been made in formulating accurate AGB equations for trees across the tropics (Chave *et al.*, 2005). Here we make use of these new equations and apply them to a large dataset of 83 tree inventories spread across the island of Borneo. We combined this large AGB dataset with environmental data on soils, elevation and climate at a 5-arcmin resolution (*c.* 10 × 10 km at the equator) for an AGB modelling approach. Our aim was to produce a map of potential biomass that can serve as a baseline for determining local loss or gain of tree biomass within Borneo. Our secondary aim was to identify the most important regional-scale environmental correlates for AGB. Since AGB is closely linked to community-wide wood density, tree-stem density and basal area (Malhi *et al.*, 2006; Saatchi *et al.*, 2007), we included these variables to determine how they interact with AGB. Additionally, we explore the possible contribution of the wind-dispersed emergent dipterocarp trees to observed AGB patterns in Borneo, since Paoli *et al.* (2008) suggested that this might explain some of the observed differences in AGB between Borneo and the Neotropics.

MATERIALS AND METHODS

Environmental GIS layers

Climate and altitude can have a profound impact on AGB (Takyu *et al.*, 2003; Malhi *et al.*, 2006) so we included a digital elevation model and the four least correlated bioclimatic variables of the WORLDCLIM dataset (http://www.worldclim.org/) for Borneo (Hijmans *et al.*, 2005) in the environmental database: temperature seasonality, temperature annual range, annual rainfall and rainfall seasonality (Fig. 1). Since droughts have been shown to increase large tree mortality in tropical forests, and could thus affect above-ground biomass (Slik & Eichhorn, 2003; van Nieuwstadt & Sheil, 2005; Rolim *et al.*, 2005), we added a data layer representing El Niño–Southern Oscillation (ENSO) drought stress defined as the relative difference between the normalized difference vegetation index (NDVI) of a severe ENSO year (July 1982–June 1983) and a non-ENSO year (July 1981–June 1982) (Fig. 1). We chose the period 1982–83 because it has the oldest available remote sensing data for a severe El Nino, and because during that period Borneo's old-growth forests were still relatively intact.

Soils are known to affect AGB as well (Castilho *et al.*, 2006; Paoli *et al.*, 2008), so additionally we selected 15 soil variables from the UN Food and Agriculture Organization (FAO) database for poverty and insecurity mapping (for an exact definition of each variable see FAO, 2002). Principal components analysis (PCA) was used to summarize the soil data in five independent soil axes that together explained 83% of soil data variance (Table 1, Fig. 1). Soil axis 1 (31.6% data variance) was positively correlated with topsoil cation exchange capacity, organic carbon pool, soil moisture storage, easily available water and topsoil nitrogen content, but negatively with soil drainage; soil axis 2 (22.5% data variance) was negatively correlated with topsoil base saturation, pH and soil production index; soil axis 3 (16.6% data variance) was negatively correlated with cation exchange capacity of the clay topsoil and top- and subsoil texture coarseness; soil axis 4 (7.5% data variance) was negatively correlated with soil depth; while soil axis 5 (4.9% of data variance) was positively correlated with soil C:N ratio, but negatively with topsoil organic carbon content.

All data had a 5-arcmin resolution (*c.* 10 km at the equator) covering Borneo with 8577 grid cells. Our final data selection contained 11 environmental variables (Fig. 1). All data mapping exercises were performed with Manifold GIS (Manifold Net Ltd).

Old-growth forest inventory data and AGB

Tree inventory data in this study represent old-growth forests only, meaning that the selected locations showed no signs of human disturbance. We were able to assemble a dataset of 83 old-growth forest locations for which we had one of the following reliable tree [diameter at breast height (d.b.h.) ≥ 10 cm] datasets: (1) complete lists of trees with their identification and d.b.h. (59 locations), (2) stem density, basal area and complete lists of trees with their identifications but no stem specific d.b.h. values (10 locations), and (3) stem density and basal area values only (14 locations) (Fig. 1a, Appendix S1 in Supporting Information). These locations were assigned longitude and latitude values that corresponded to the centre of the grid cells in which the inventories were located to make them compatible with our environmental data for Borneo.

For the 69 locations with complete tree inventories, we determined the oven-dry wood density of each species from the literature (Oey, 1990; Suzuki, 1999; Osunkoya *et al.*, 2007); this sometimes involved converting air-dry wood densities into oven-dry values using the conversion equation given in Reyes *et al.* (1992). For species without known wood density, we used the average wood density of the species' genus, which has been shown to capture up to 70% of wood density variability in Indonesian tree species (Slik, 2006). Together with tree d.b.h., the oven-dry wood density values can be used to estimate tree AGB for Borneo's lowland forests with the moist forest equation
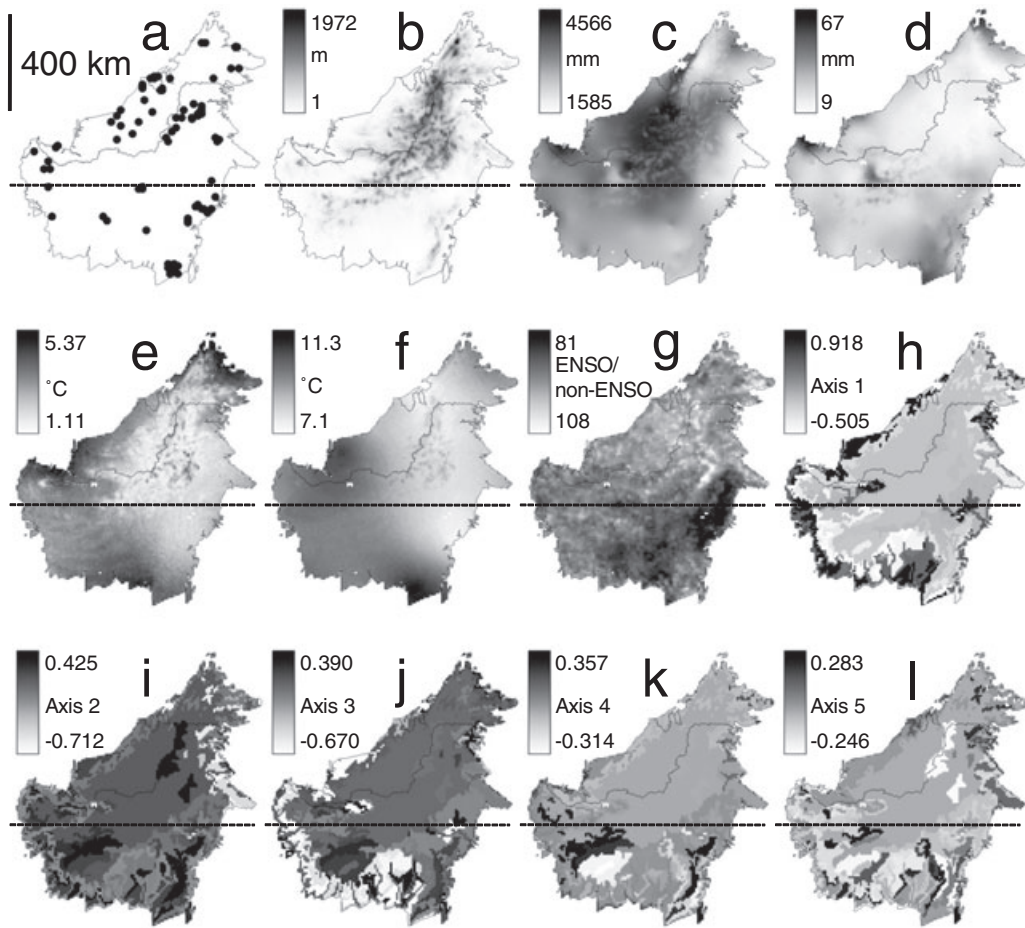
Figure 1 Data locations and environmental variables used in this study (based on averages for *c*. 10 × 10 km grid cells): (a) locations with scale bar; (b) altitude (m above sea level); (c) annual rainfall (mm year^{-1}); (d) rainfall seasonality (coefficient of monthly rainfall variation); (e) temperature seasonality (standard deviation of average yearly temperature); (f) temperature annual range (maximum – minimum monthly temperature); (g) El Niño–Southern Oscillation (ENSO) drought impact [relative difference between the normalized difference vegetation index (NDVI) of a severe ENSO year (July 1982–June 1983) and a non-ENSO year (July 1981–June 1982)]; (h) soil axis 1 [coordinate on principal components analysis (PCA) axis 1]; (i) soil axis 2 (coordinate on PCA axis 2); (j) soil axis 3 (coordinate on PCA axis 3); (k) soil axis 4 (coordinate on PCA axis 4); (l) soil axis 5 (coordinate on PCA axis 5). The Equator is indicated with a dashed line.

Table 1 Principal components analysis (PCA) factor loadings for the five soil axes (between brackets the amount of explained data variance) used in this study. The highest or lowest factor loading per soil variable is indicated in bold.

Factor	Axis 1 (31.6%)	Axis 2 (22.5%)	Axis 3 (16.6%)	Axis 4 (7.5%)	Axis 5 (4.9%)
Base saturation topsoil	−0.047	**−0.462**	0.042	0.135	0.350
CEC clay topsoil	0.262	−0.189	**−0.336**	0.313	−0.082
CEC soil topsoil	**0.342**	−0.106	0.148	0.035	0.137
C:N ratio topsoil	0.234	0.159	−0.267	−0.287	**0.623**
Easy available water	**0.362**	−0.260	−0.027	0.123	−0.091
Effective soil depth	0.112	−0.171	−0.094	**−0.793**	−0.272
Nitrogen topsoil	**0.338**	0.133	0.232	0.145	−0.234
Organic carbon topsoil	0.254	0.289	0.207	0.065	**−0.349**
Organic carbon pool	**0.350**	0.216	0.157	−0.089	0.078
pH topsoil	−0.202	**−0.370**	0.086	0.203	−0.091
Soil drainage	**−0.382**	0.121	−0.096	−0.062	−0.292
Soil moisture storage	**0.327**	−0.295	0.005	−0.018	−0.186
Soil production index	−0.022	**−0.470**	0.046	−0.236	−0.152
Textural class subsoil	0.133	0.017	**−0.555**	0.030	−0.158
Textural class topsoil	0.018	0.100	**−0.578**	0.142	−0.155

C, carbon; CEC, cation-exchange-capacity; N, nitrogen.

given in Chave *et al.* (2005). For forests located at elevations higher than 1000 m, we used the wet forest equation given in Chave *et al.* (2005), as this better approximates the AGB of montane forests (J. Chave, pers. comm.). Total AGB ha^{-1} for each location was calculated by summing the AGB values of all trees in a site and dividing this value by the total survey area (ha) sampled. For each location we also calculated stem density ha^{-1}, the average wood density of all stems and basal area (m^2) ha^{-1} (Appendix S1).

We could not calculate AGB directly for 24 locations due to lack of stem-specific d.b.h. values. Instead we applied multiple regression analysis with AGB as the dependent variable and stem density and basal area as the predictor variables (based on the 59 locations for which we had these three values). This analysis showed that AGB was highly predictable for Borneo's old-growth forests (R^2-adjusted = 0.92, F-ratio = 333.0, $P < 0.0001$, n = 59) if stem density and basal area for a location were known. We therefore used the derived multiple regression equation to estimate AGB for the 24 sites where we could not calculate it directly, increasing our AGB sample size to 83 locations.

Correcting for sampling bias

We also tested whether community average oven-dry wood density, stem density, basal area and AGB were dependent on total tree sample size and survey area of the locations using multiple regression analysis (with tree sample size and survey area log-transformed). This analysis showed that both the community average oven-dry wood density (R^2-adjusted = 0.11, F-ratio = 5.0, $P = 0.0093$, $n = 68$) and basal area (R^2-adjusted = 0.13, F-ratio = 6.8, $P = 0.0018$, $n = 68$) of the locations were significantly correlated with tree sample size and survey area. We corrected for this sampling bias by subtracting predicted values from the observed values. These residuals were subsequently used in the modelling exercise.

Correlations between community wood density, stem density, basal area and AGB

To get some basic idea of the relationships between community wood density, stem density, basal area and AGB, we applied linear regression between all possible pairwise combinations of these variables. This analysis was performed with the sample bias corrected location data that were used in the modelling exercise.

Model selection procedure

The relationships between environmental variables, community average oven-dry wood density, stem density, basal area and AGB were determined with the Akaike information criterion (AIC) using the model selection application in the Spatial Analysis in Macroecology program (sam, version 3.0; Rangel *et al.*, 2006). The model selection application in sam first calculates multiple regression models for all possible combinations of variables, i.e. for our 11 environmental variables there were 2047

possible combinations, and then ranks these models from best to worst according to their AIC score. We considered all models with ΔAIC < 3 as equally informative and determined the importance of the explanatory variables for each dependent variable (community oven-dry wood density, stem density, basal area and AGB) by determining their frequency of occurrence in these models.

For each of the selected models we determined the multiple regression equations via ordinary least squares regression (OLS), or, when we detected significant spatial autocorrelation of residuals, via simultaneous autoregressive regression (SAR). Since we obtained several multiple regression models for each dependent variable, we could calculate multiple community oven-dry wood density, stem density, basal area and AGB estimates for each grid cell in Borneo. These data were summarized by averaging all estimates per grid cell because this has been shown to provide a good consensus value for summarizing the results of multiple, equally likely models (Marmion *et al.*, 2009). It has the additional advantage that the standard deviations of these average values give an indication of the reliability of the final estimate in each grid cell.

The fit between our averaged estimates and the observed data (correlation coefficients, R^2-adjusted, F-ratio and P-values) was determined by regressing estimated against observed values. Moran's I was used to test for residual spatial autocorrelation of our estimates for community average oven-dry wood density, stem density, basal area and AGB.

RESULTS

The AGB values in Borneo were unrelated to community-wide wood density and stem density, but were significantly positively related with basal area (Fig. 2). Basal area itself was also significantly positively correlated with stem density (Fig. 2). Community average oven-dry wood density, stem density, basal area and AGB were all significantly correlated with environmental variables (Table 2).

Tree community oven-dry wood density was explained by 97 equally likely models and was most frequently correlated with increasing elevation, coarseness of soil texture and ENSO drought stress (Table 2). Other less frequent correlates for community-wide oven-dry wood density were soil fertility (negative), soil depth (negative), rainfall seasonality (positive), temperature seasonality (positive), annual rainfall (positive) and soil drainage (positive). Annual temperature range and soil C:N ratio showed mixed results, being both positively and negatively correlated with community average oven-dry wood density. No spatial autocorrelation of residuals was detected at any distance class (Table 2).

Tree-stem density was explained by 13 equally likely models and was most frequently correlated with increasing temperature seasonality, decreasing rainfall seasonality and increasing elevation (Table 2). Other, less frequent correlates for stem density were ENSO drought stress (negative), soil C:N ratio (positive), annual rainfall (positive), soil depth (negative), soil texture coarseness (positive), temperature annual range (positive), soil
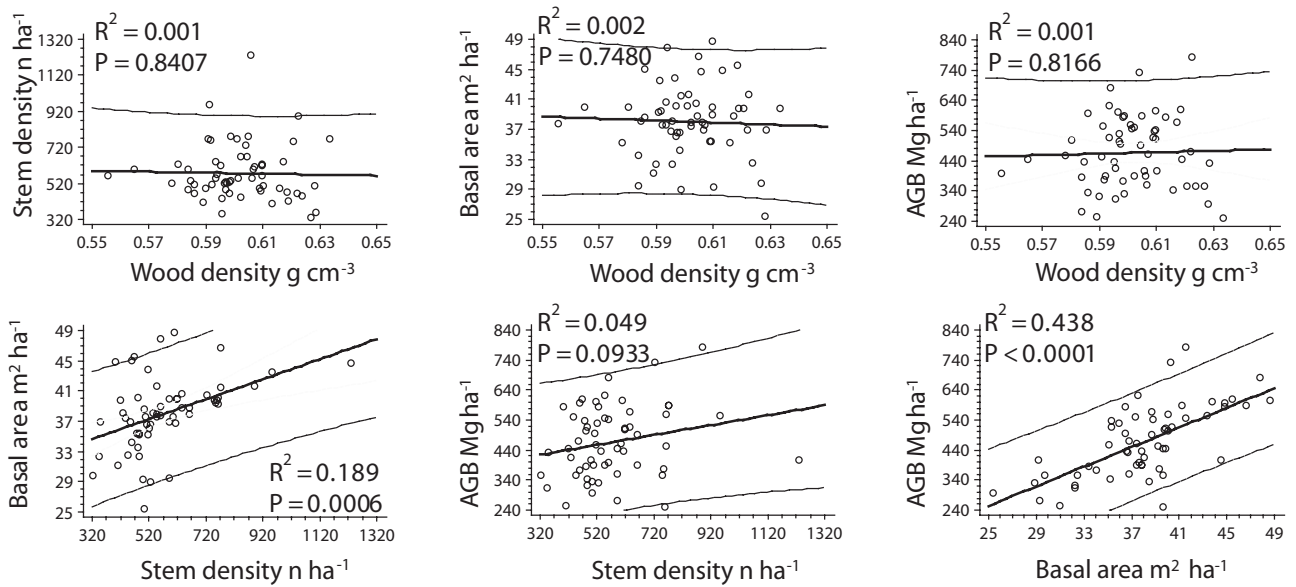
Figure 2 Linear regressions between community average wood density, stem density, basal area and above-ground biomass (AGB) based on 59 locations for which all of these variables were available. Comparisons are based on values that are corrected for plot sampling bias. The thin, dashed line indicates the 95% prediction limits of the regression line (i.e. there is 95% chance that a new observation will fall within these lines).

fertility (positive) and soil drainage (negative). No spatial auto-correlation of residuals was detected at any distance class (Table 2).

Tree basal area was explained by 15 equally likely models and was most frequently correlated with increasing annual rainfall, soil fertility, soil C:N ratio, elevation and annual temperature range (Table 2). Other less frequently selected correlates were soil drainage (positive), temperature seasonality (positive), rainfall seasonality (negative), ENSO drought stress (negative), soil depth (positive) and soil texture coarseness (negative). There was limited short- and long-distance spatial autocorrelation of residuals.

Tree AGB was explained by 56 equally likely models and was most frequently correlated with increasing annual rainfall, soil fertility and soil drainage (Table 2). Other less frequent selected correlates were soil C:N ratio (positive), soil texture coarseness (negative), soil depth (positive), rainfall seasonality (negative) and temperature seasonality (negative). Elevation, ENSO drought stress and annual temperature range were both positively and negatively correlated with AGB. There was limited short- and long-distance spatial autocorrelation of residuals.

Extrapolation of the multiple regression equations across all Bornean grid cells resulted in the patterns shown in Fig. 3 (grid cell values provided in Appendix S2). Community average oven-dry wood density is predicted to be especially high in peat swamp and montane forests. Tree densities are predicted to be highest at high elevations, while they are predicted to be lowest in south-eastern Borneo where ENSO drought stress is largest. Basal area is generally predicted to be highest in central and northern Borneo, but shows some exceptionally low and high values in areas with extreme soil pH and fertility values. AGB

shows patterns similar to the basal area map, but predicts an even higher concentration of biomass in central and northern Borneo, while peat swamps are predicted to contain relatively low AGB. Again, some very high and low AGB values are associated with extreme values of soil fertility and pH. Model uncertainties are generally highest in high-elevation forests, peat swamps and heath forests. AGB predictions show additional high levels of uncertainty based on soil types.

DISCUSSION

AGB and basal area gradients

Both basal area and AGB were strongly positively correlated with annual rainfall but negatively correlated with increasing rainfall seasonality. This confirms the importance of a stable, wet climate for the accumulation of biomass in tropical forests (Brown *et al.*, 1993; Malhi *et al.*, 2006; Saatchi *et al.*, 2007). The correlation with rainfall patterns was combined with a strong positive impact of soil fertility on basal area and AGB in Borneo, which contradicts results from the Amazon where the highest AGB was found to occur on relatively poor soils characterized by slow-growing tree communities with high wood densities (Malhi *et al.*, 2006; Saatchi *et al.*, 2007). In the Amazon, tree community wood density patterns strongly influenced AGB gradients (Baker *et al.*, 2004), but in Borneo this relationship was not significant. On the contrary, the slowest growing, least dynamic forests growing on the poorest Bornean soils (peat swamps, heath forests) were characterized by relatively low AGB, even though the wood density of these tree communities was among the highest. It remains unclear why soil fertility does not

Table 2 Fit between the predicted values and the observed values, percentage of models that included each variable and the direction of the correlation, and residual spatial autocorrelation (RSA) (Moran's *I* values, significant values in bold).

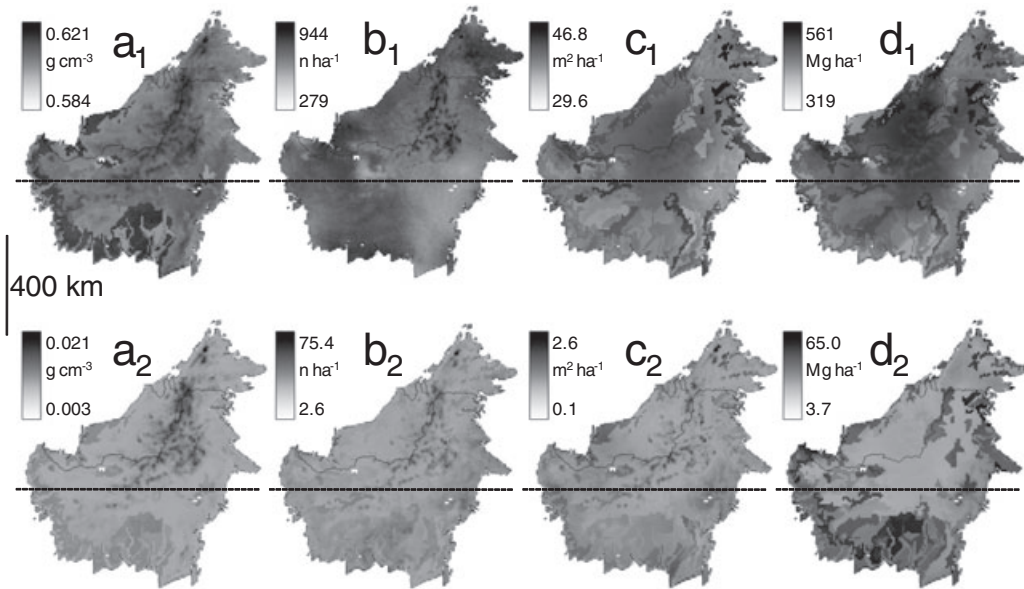|	Tree community oven-dry wood density	Tree-stem density	Tree basal area	Tree AGB
Total no. of models selected	97	13	15	56
Correlation coefficient	0.43	0.53	0.48	0.42
R^2-adjusted	16.9	26.9	22.4	17.0
F-ratio	14.6	30.5	24.1	17.1
n	69	83	83	82
P	0.0003	< 0.0001	< 0.0001	0.0001
Variable importance				
Variable 1	(93.8) (+) Elevation	(100.0) (+) Temp. seas.	(100.0) (+) Annual rain	(92.9) (+) Annual rain
Variable 2	(71.1) (−) Soil 3	(100.0) (−) Rain seas.	(100.0) (−) Soil 2	(66.1) (−) Soil 2
Variable 3	(52.6) (+) ENSO	(84.6) (+) Elevation	(100.0) (+) Soil 5	(55.4) (−) Soil 1
Variable 4	(30.9) (+) Soil 2	(23.1) (−) ENSO	(80.0) (+) Elevation	(42.9) (+) Soil 5
Variable 5	(26.8) (+) Soil 4	(23.1) (+) Soil 5	(53.3) (+) Temp. range	(33.9) (+) Soil 3
Variable 6	(24.7) (±) Soil 5	(15.4) (+) Annual rain	(26.7) (−) Soil 1	(25.0) (−) Soil 4
Variable 7	(23.7) (±) Temp. range	(7.7) (+) Soil 4	(20.0) (+) Temp. seas.	(25.0) (−) Rain seas.
Variable 8	(18.6) (+) Rain seas.	(7.7) (−) Soil 3	(13.3) (−) Rain seas.	(14.3) (−) Temp. seas.
Variable 9	(15.5) (+) Temp. seas.	(7.7) (+) Temp. range	(6.7) (−) ENSO	(7.1) (±) Elevation
Variable 10	(14.4) (±) Annual rain	(7.7) (−) Soil 2	(6.7) (+) Soil 4	(7.1) (±) ENSO
Variable 11	(13.4) (−) Soil 1	(7.7) (+) Soil 1	(6.7) (+) Soil 3	(7.1) (±) Temp. range
RSA test distances (km)			Moran's *I*	Moran's *I*
58	n.s.	n.s.	0.073	**0.097**
167	n.s.	n.s.	**−0.1268**	0.005
252	n.s.	n.s.	−0.078	−0.072
318	n.s.	n.s.	0.070	0.042
383	n.s.	n.s.	0.010	−0.007
447	n.s.	n.s.	−0.082	−0.110
530	n.s.	n.s.	−0.067	−0.032
620	n.s.	n.s.	−0.013	**−0.143**
693	n.s.	n.s.	**0.125**	0.007
766	n.s.	n.s.	−0.025	0.047
990	n.s.	n.s.	−0.005	0.025

AGB, aboveground biomass; 'Soil *x*', soil principal components axis *x*; ENSO, El Niño–Southern Oscillation drought stress defined as the relative difference between the normalized difference vegetation index of a severe ENSO year and a non-ENSO year. n.s., not significant.

affect AGB gradients in the Amazon more strongly. A possible explanation might be related to the fact that most Amazonian forests are characterized by seasonal rainfall patterns while most of Borneo is always wet with very few areas receiving a long-term average of less than 100 mm of rain per month during the whole year, a value that compensates for evapotranspiration in the tropics (Walsh, 1996). The seasonal rainfall climate in the Neotropics might form a limiting factor for biomass accumulation that obscures the impact of soil fertility on AGB gradients there.

Another conspicuous difference between Borneo and the Amazon that we detected was that average AGB in Borneo (457.1 Mg ha⁻¹) was *c.* 60% higher than the Amazonian average of 288.6 Mg ha⁻¹ (value based on 227 plots from 105 locations taken from Malhi *et al.*, 2006). This observation agrees with findings by Paoli *et al.* (2008) who found stem densities for large trees (d.b.h. > 70 cm) to be up to three times higher in Borneo than in the Neotropics. As most AGB is stored in these large trees, this might explain the observed difference in AGB between

Borneo and the Amazon. One of the hypotheses that Paoli *et al.* (2008) suggested to explain the difference in large tree density between Borneo and the Neotropics is the dominance of the dipterocarp family in Borneo; this family consists of huge emergent trees that are rare and endemic in the Neotropics (Ashton, 1982; Gentry, 1988). We did find some support for this hypothesis when we plotted the percentage of dipterocarp trees in the d.b.h. > 70 cm diameter class against AGB, which resulted in a significant positive correlation between these two variables (R^2-adjusted = 0.26, *F*-ratio = 8.9, *P* = 0.0071, *n* = 23, using only sites with more than five stems in both the dipterocarp and non-dipterocarp category) (Fig. 4). Interestingly, the *y*-intercept of this relationship, where the percentage of dipterocarps is zero, was 229.1 Mg ha⁻¹, a value close to the Amazonian average.

A possible explanation for the high AGB in dipterocarp-dominated forests could be related to the wind dispersal strategy of dipterocarps, i.e. they need to be tall and emergent to effectively disperse their seeds. When we compared the maximum
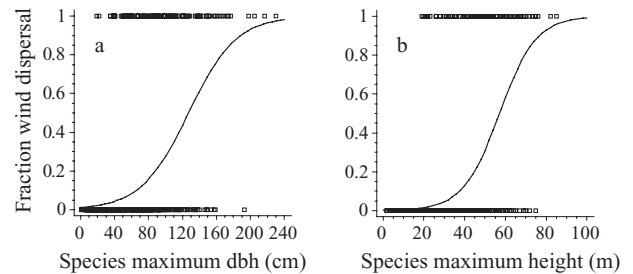
Figure 3 Extrapolated results for: (a_1) tree community oven-dry wood density and its (a_2) standard deviation (average 0.602 ± 0.006 g cm^{-3}); (b_1) stem density and its (b_2) standard deviation (average 602 ± 17.8 stems ha^{-1}); (c_1) basal area and its (c_2) standard deviation (average 37.1 ± 0.7 m^2 ha^{-1}); and (d_1) above-ground biomass and its (d_2) standard deviation (average 445 ± 23.4 Mg ha^{-1}). The Equator is indicated with a dashed line.
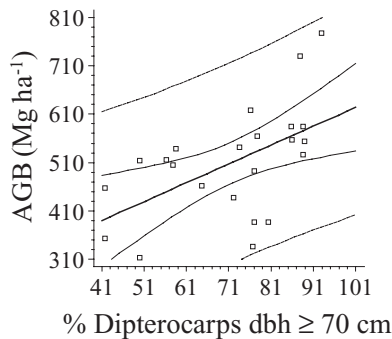
Figure 4 The linear relationship between AGB and percentage of stems in the diameter at breast height (d.b.h.) ≥ 70 cm class belonging to the Dipterocarpaceae [regression line (bold) with 95% confidence limits (thin) and 95% prediction limits (dashed)].

Figure 5 Logistic regression between the presence of a seed wind dispersal syndrome and tree species potential maximum diameter at breast height (d.b.h.) (a) and height (b). The *y*-axis represents the chance that a species has wind-dispersed seeds given its maximum potential d.b.h. (a) and height (b).

diameter and height of tree species with tree dispersal syndrome for 978 Bornean tree species (data taken from Slik, 2009), we did indeed find a highly significant correlation between presence of wind dispersal and maximum tree diameter (logistic regression between wind dispersal strategy and maximum d.b.h.: odds ratio = 1.036, $\chi^2 = 180.2$, $P < 0.0001$, $n = 978$) and height (odds ratio = 1.120, $\chi^2 = 220.5$, $P < 0.0001$, $n = 978$) (Fig. 5), indicating that wind-dispersed trees generally attain larger sizes than trees with other dispersal syndromes. Since Neotropical forests are generally dominated by animal dispersed trees while Borneo's forests are dominated by the wind dispersed Dipterocarpaceae (Gentry, 1988), this might partly explain the higher density of big trees and AGB in Borneo. This finding stresses the impor-

tance of including species traits and shifts in species composition as explanations of AGB gradients in tropical forests.

Comparing our results with the previous Asian AGB maps by Brown *et al.* (1993) and the updated version by Gibbs *et al.* (2007) is complicated because these studies combined below- and above-ground carbon values. They do show that Borneo has exceptionally high biomass within Asia, but the AGB patterns detected within Borneo show limited spatial variability. Our study shows much higher spatial variability and resolution in AGB gradients across Borneo, which is probably related to the fact that we used many more AGB sample sites within Borneo. The patterns that we found within Borneo differ considerably from the earlier studies by identifying the highest AGB values more to the north of Borneo, but this might be related to the fact that these earlier maps combined soil carbon and AGB.

Southern Borneo is dominated by peat swamps that contain large amounts of below-ground biomass stored as peat layers with a thickness of sometimes more than 20 m.

Community average wood density gradients

Patterns in community-wide wood density have mainly been linked to forest disturbance regimes and productivity (ter Steege & Hammond, 2001; Baker *et al.*, 2004; Malhi *et al.*, 2004; Slik *et al.*, 2008), but also to annual rainfall gradients, rainfall seasonality and droughts (Hacke *et al.*, 2001; Baker *et al.*, 2004; Slik, 2004; van Nieuwstadt & Sheil, 2005). Disturbance regimes are thought to influence tree community wood density by increasing the abundance of fast-growing tree species with relatively low wood densities. Given the generally negative relationship between disturbance and community wood density it is interesting to note that our study shows that ENSO droughts, as a large-scale infrequent disturbance, seem to result in the opposite relationship. The areas that were hit hardest during the severe 1982–83 ENSO-associated drought were shown to have among the highest community average wood densities in Borneo. This corresponds to observations made during the severe 1997–98 ENSO-associated drought that found that the drought disproportionately increased the mortality of large trees with low wood densities (Slik, 2004; van Nieuwstadt & Sheil, 2005). Resistance to xylem embolism/implosion probably explains this difference in drought tolerance in relation to wood density (Hacke *et al.*, 2001).

Soils also played an important role in explaining observed community-wide wood density gradients. Our study predicts high community wood densities on coarse sandy soils (heath forests) and in the peat swamps that are widespread along the western and southern coastal lowlands of Borneo. These forests are growing on extremely nutrient-poor acidic soils, resulting in slow tree growth rates (Nishimura *et al.*, 2007). The species composition in these forests is characterized by a phylogenetically diverse subset of tree species found in the surrounding dry-land forests (Slik *et al.*, 2009). Since the forests in peat swamps are among the least productive in Borneo (Nishimura *et al.*, 2007), this does correspond to the negative correlation found between wood density and forest productivity in the Neotropics (Malhi *et al.*, 2004).

Community-wide wood density is usually found to correlate neutrally or negatively with elevation (Chave *et al.*, 2006; Moser *et al.*, 2008). However, our study finds a positive correlation due to increasing dominance of heavy wooded species (i.e. *Leptospermum* spp., *Lithocarpus* spp., *Syzygium* spp., *Tristaniopsis* spp.) at higher elevations. The low growth rates at higher elevation, in combination with occasional drought mortality due to drying out of shallow soils along ridges (Ashton, 2003), might explain this trend of increasing dominance of heavy wooded species with increasing elevation.

Tree-stem density gradients

Temperature and rainfall seasonality were strongly associated with stem density gradients in Borneo, indicating that climate plays an important role in explaining these gradients (see also Takyu *et al.*, 2005). Our results confirm findings from the Amazon where stem densities were shown to be negatively correlated with dry month length and positively with annual rainfall (ter Steege *et al.*, 2003), although the relative positive contribution of annual rainfall to increasing stem density in Borneo is small. The importance of rainfall for tree density gradients is emphasized by the negative relationship that we detected between stem density and severe droughts that are associated with ENSO events in Borneo.

Stem densities were positively correlated with temperature seasonality and elevation, which is also a temperature proxy. The positive impact of elevation on stem densities corresponds to results found across the tropics (Givnish, 1999; Takyu *et al.*, 2005; Lovett *et al.*, 2006). These changes in stem density are probably related to lowered temperatures and energy inputs at higher elevations, as Takyu *et al.* (2005) found strong similarity in forest structure changes, including stem density, along latitudinal and elevational gradients when they expressed these environmental variables in a shared warmth index (temperature sum during the growing season). Forests at lower temperatures show lower growth and productivity than those at high temperatures, which might contribute to the stunted high-elevation forests with high stem densities.

Soils seem to have a limited impact on stem densities in Borneo when compared with climatic factors. However, stem density was found to increase with increasing soil C:N ratio, sandiness and fertility, while it decreased with soil depth and drainage. Again, water availability seems a key factor, with drier, well-drained coarse-textured soils supporting lower stem densities. Indeed, several studies have reported high stem densities in heath and peat-swamp forests on poorly drained sandy soils in Borneo (Proctor *et al.*, 1983; Nishimura *et al.*, 2007). Our results also indicate a weak relationship between increasing stem density and increasing soil fertility, which might be related to the fact that more fertile soils generally support more dynamic forests with high turnover rates (Phillips *et al.*, 1994; Malhi *et al.*, 2004). More dynamic and productive forests of the western Amazon also show relatively high stem densities (ter Steege *et al.*, 2003; Malhi *et al.*, 2004), although this effect is difficult to distinguish from the confounding influence of the relatively high annual rainfall there.

Data limitations

Although our analysis is one of the most comprehensive for Borneo so far, there are some limitations to the data that may have influenced our results. One of the most important is the fact that the inventory data do not cover all vegetation types and environmental variables equally well (see also Slik *et al.*, 2009). For example, peat swamp forest, mangroves and heath forests were underrepresented, possibly explaining why we often detected large uncertainty in our predictions (as expressed in high SD values) for these forest types. Also, most inventories were from lowland sites, which might have resulted in altitudinal biases in our results.

Another problem with the data is related to a mismatch between the spatial scale of the inventories (usually several hectares or less) and the environmental variables (10×10 km grid). Although our large sample size ensured that we picked up most of the important large-scale environmental correlates for stem density, community wood density, basal area and AGB, it is likely that considerably more and stronger spatial heterogeneity in AGB can be detected if the resolution of the AGB sample sites and environmental data were to match more closely.

We also found a limited amount of residual spatial autocorrelation in both basal area and AGB gradients, which violates the assumption that residuals should be independent and results in inflated type 1 errors (Dormann *et al.*, 2007). Fortunately, short-distance residual spatial autocorrelation (RSA), while causing inflated type 1 errors, does not seriously affect the interpretation of the regression coefficients estimated by ordinary least squares regressions (Diniz-Filho *et al.*, 2007; Hawkins *et al.*, 2007), meaning that our predictions do reflect meaningful environmental patterns, even if they have some spatial autocorrelation in residuals.

Implications for carbon trading

Our study shows that the environment plays a significant role in explaining patterns in the AGB of old-growth forests in Borneo. This means that potential AGB gradients can be predicted with some certainty for areas without AGB measurements. This is important, because many areas in Borneo and Southeast Asia have already been deforested, converted into agricultural use or more or less disturbed, meaning that the original AGB present in these areas can no longer be assessed by field sampling. Using our modelling approach we were able to predict the potential AGB for these areas, which can be used as a reference value for determining how much AGB has been lost due to land-use changes. It can also be used to calculate how much AGB is preserved when an old-growth forest is protected. This could provide an objective way to assign carbon credits to countries that preserve their old-growth forests as is suggested in the 'reduced carbon emission from deforestation and degradation' (REDD) scheme. Interestingly, Borneo's forests seem, on average, to contain almost 60% more AGB per surface area than comparable forests in the Amazon, indicating the importance of Bornean forests as carbon sinks and sources.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Old-growth forest tree inventory locations with their sample details.
Appendix S2 Listing of longitude, latitude, predicted stem density, basal area, community wood density and above-ground biomass (AGB) for each 10×10 km grid cell in Borneo.

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BIOSKETCH

The authors of this article regularly cooperate to share inventory data from the island of Borneo with the purpose of studying large-scale patterns in tree floristics, diversity and structural parameters so that our understanding of how these patterns have come about is increased. Author contributions: F.S. analysed data and wrote the article, N.R. provided GIS environmental data, while all other authors contributed inventory data and commented on draft versions of the manuscript.

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