

Disentangling stand and environmental correlates of aboveground biomass in Amazonian forests

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Abstract

Tropical forests contain an important proportion of the carbon stored in terrestrial vegetation, but estimated aboveground biomass (AGB) in tropical forests varies two-fold, with little consensus on the relative importance of climate, soil and forest structure in explaining spatial patterns. Here, we present analyses from a plot network designed to examine differences among contrasting forest habitats (terra firme, seasonally flooded, and white-sand forests) that span the gradient of climate and soil conditions of the Amazon basin. We installed 0.5-ha plots in 74 sites representing the three lowland forest habitats in both Loreto, Peru and French Guiana, and we integrated data describing climate, soil physical and chemical characteristics and stand variables, including local measures of wood specific gravity (WSG). We use a hierarchical model to separate the contributions of stand variables from climate and soil variables in explaining spatial variation in AGB. AGB differed among both habitats and regions, varying from 78 Mg ha⁻¹ in white-sand forest in Peru to 605 Mg ha⁻¹ in terra firme clay forest of French Guiana. Stand variables including tree size and basal area, and to a lesser extent WSG, were strong predictors of spatial variation in AGB. In contrast, soil and climate variables explained little overall variation in AGB, though they did co-vary to a limited extent with stand parameters that explained AGB. Our results suggest that positive feedbacks in forest structure and turnover control AGB in Amazonian forests, with richer soils (Peruvian terra firme and all seasonally flooded habitats) supporting smaller trees with lower wood density and moderate soils (French Guianan terra firme) supporting many larger trees with high wood density. The weak direct relationships we observed between soil and climate variables and AGB suggest that the most appropriate approaches to landscape scale modeling of AGB in the Amazon would be based on remote sensing methods to map stand structure.

Keywords: carbon stocks, climate, flooded forest, forest structure, French Guiana, Peru, REDD, soil properties, tropical rainforest, white-sand forest, wood specific gravity

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Introduction

Tropical forests play a vital role in the global carbon cycle, as they comprise approximately 40% of all carbon estimated to be stored in terrestrial vegetation (Houghton, 2005; Malhi *et al.*, 2006). Nevertheless, there remains a large degree of uncertainty in these values, with total estimates of tropical forest biomass carbon stocks ranging from 158 to 324 Pg C (Gibbs *et al.*, 2007). The emerging

carbon trading market has underlined the urgent need to improve our understanding of the factors explaining spatial variation in aboveground biomass (AGB) in tropical forests (Gullison *et al.*, 2007), especially given recent escalations in carbon emissions resulting from deforestation, degradation, fire, and drought in tropical regions (Nepstad *et al.*, 1999; Malhi *et al.*, 2008; Phillips *et al.*, 2009). Yet despite some clear global and regional patterns (Malhi *et al.*, 2006; Lewis *et al.*, 2009; Slik *et al.*, 2010), little agreement has been reached regarding the ecological drivers for these patterns and the extent to which they can be extrapolated to construct regional planning maps (Houghton *et al.*, 2001; Gibbs *et al.*, 2007).

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Table 1 A summary of climate, soil and stand factors observed to explain spatial variation in aboveground biomass in tropical forests. ('+', positive correlation; '-', negative correlation; '*', contrasting reports)

Group	Factor	Effect	References
Climate	Total Precipitation	+	Malhi <i>et al.</i> (2006); Chave <i>et al.</i> (2004)
	Dry season length	-	Malhi <i>et al.</i> (2006); Chave <i>et al.</i> (2004)
Soil	Topography	*	Clark & Clark (2000); Ferry <i>et al.</i> (2010)
	Texture	*	Paoli <i>et al.</i> (2008); Quesada <i>et al.</i> (2009)
	Exchangeable bases	*	Laurance <i>et al.</i> (1999); Quesada <i>et al.</i> (2009)
	Labile P	*	Paoli <i>et al.</i> (2008); Quesada <i>et al.</i> (2009)
Stand	Type	*	DeWalt & Chave (2004)
	Basal area	+	Baker <i>et al.</i> (2004); Malhi <i>et al.</i> (2006); Paoli <i>et al.</i> (2008)
	Density of large trees	+	DeWalt & Chave (2004); Paoli <i>et al.</i> (2008); Rutishauser <i>et al.</i> (2010)
	Mean Tree Height	+	Chave <i>et al.</i> (2005)
	Mean Tree DBH	+	Nelson <i>et al.</i> (1999); Chave <i>et al.</i> (2005)
	Mean Wood specific gravity	*	Baker <i>et al.</i> (2004); DeWalt & Chave (2004); Stegen <i>et al.</i> (2009)

Three groups of explanatory factors have been proposed to explain regional spatial variation of AGB in tropical forests, but to date studies have provided little consensus in their relative contributions (Table 1). Among these, there appears to be concerted evidence for consistent relationships between AGB and rainfall, with moist, stable (short or no dry season) climates supporting the highest biomass in Panama, the Amazon, and Borneo (Chave *et al.*, 2004; Malhi *et al.*, 2006; Quesada *et al.*, 2009; Slik *et al.*, 2010).

Less accord exists among studies examining relationships between AGB of tropical forests and the physical and chemical factors of soils. Several studies have reported positive effects on AGB of soil fertility measures including total nitrogen (N), soil phosphorus, and exchangeable bases (Laurance *et al.*, 1999; DeWalt & Chave, 2004; Paoli *et al.*, 2008), suggesting that AGB may be limited by soil nutrient availability. However, other studies have reported lower biomass on more fertile soils, with higher turnover rates of biomass resulting in lower standing stocks (Van Schaik & Miramanto, 1985; Quesada *et al.*, 2009). Paoli *et al.* (2008) hypothesize that over large gradients in soil fertility, the true relationship with AGB may be hump-shaped, but to date this hypothesis has not been tested explicitly.

A third group of variables proposed to explain spatial patterns in AGB comprises descriptors of forest structure and composition, which we refer to as stand variables. Strong positive correlations may be expected between AGB and variables used in allometric equations, including diameter, height, and wood specific gravity (WSG) (Chave *et al.*, 2005), in addition to metrics of stem density and basal area (Chave *et al.*, 2004). Indeed, strong relationships between AGB and both basal area and large stem density have been found throughout several Neotropical forests (Chave *et al.*, 2004; DeWalt & Chave, 2004; Rutishauser *et al.*, 2010),

and appear to explain the higher AGB estimates for forests of Borneo where larger trees are more frequent (Paoli *et al.*, 2008; Slik *et al.*, 2010). Less agreement has been found for relationships between AGB and wood density. Baker *et al.* (2004) suggested that the east-west gradient in AGB across Amazonia could be explained in large part by gradients of community distributions of wood density. However, Stegen *et al.* (2009) found no consistent relationship between AGB and wood density at different spatial scales across four Neotropical forests.

The overall lack of consensus in tests linking AGB with environmental factors may be explained by three limitations of studies to date, two of which arise in large part from the difficulty of obtaining field data from remote sites. First, few sets of plots exist for which high-quality data are available describing climate, soil properties, and stand variables including species identifications and WSG measures (but see Malhi *et al.*, 2002, 2006). Second, even where these data exist, rarely do plot networks cover broad gradients that can disentangle covariation among climate, soil, forest structure, and other biogeographical factors such as floristic composition. For most lowland terra firme habitats, the east-west gradient in Amazonia represents a concomitant gradient of soil fertility, dry season length, forest turnover, and community wood density, rendering tests of the relative strengths of their relationships with AGB complicated, particularly in plot networks that do not provide replication of soil types across geographic gradients (e.g., Quesada *et al.*, 2009).

Finally, to date stand variables have been treated in the same manner as other environmental descriptors, despite the fact that they are directly or indirectly linked with the allometric calculation of AGB. Therefore, we suggest the most appropriate framework to understand processes explaining spatial patterns in AGB

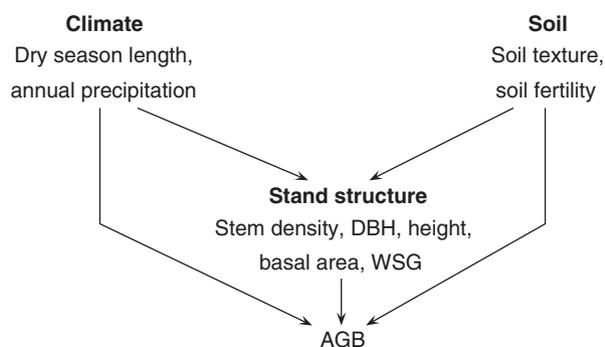


Fig. 1 A conceptual framework for studying the relationships between aboveground biomass (AGB) and stand and environmental descriptors. Previous studies have not addressed the hierarchical nature of these relationships, which results from the direct relationship between stand variables integrated into allometric relationships with AGB.

is hierarchical (Fig. 1). Higher AGB can only be achieved by increases in some stand variable, so this is the necessary first level of any analysis. The key questions then become the extent to which climate and soil explain spatial variation in AGB and the extent to which they explain stand factors which in turn explain spatial patterns in AGB. The response to these questions has important practical implications for how resources should be invested to map AGB at regional scales. If climate and/or soil are significantly correlated with either AGB or the variation in stand structure that explains AGB, then spatial interpolation of these data could be used to map AGB; if they are not, then it would be more appropriate to invest resources in remote sensing methods to map stand structure without integrating environmental data.

In this paper, we evaluate relationships between AGB and climate, soil and stand variables using a new plot network we established across strong climate and soil fertility gradients in two geographic regions of South America. We compile data from 74 plots in Loreto, Peru, and French Guiana that represent the three major lowland rain forest habitat types with contrasting edaphic environments. These three habitats are among the most common habitats in lowland Amazonia, and each has a distinctive flora (Wittman *et al.*, 2006; Fine *et al.*, 2010). First, *terra firme* forests on clay-rich soils are typical of most published studies. Here we include relatively nutrient rich and clay-dominated soils from the Pebas formation in Peru (Hoorn, 1993) in addition to brown sandy soils from Pleistocene river terraces found in Peru (Hoorn, 1993, 1994) and similar sand-silt-clay mixtures from French Guiana (ter Steege, 2000). Second, *seasonally flooded* forests include stands in which the water table is never observed to descend below 60 cm depth and remains at the soil surface for at least two

consecutive months each year (Baraloto *et al.*, 2007; Ferry *et al.*, 2010). In Peru, these include floodplain forests that are inundated during periods of heavy rains (Prance, 1979). Third, *white-sand* forests are characterized by soils with high proportions of sand and little organic material below the surface horizons. They include forests derived from podzols in Peru (Fine *et al.*, 2005; Fine *et al.*, 2010) and French Guiana (Baraloto *et al.*, 2005) as well as quartzites and weathered granite on the margin of inselbergs in French Guiana. This dataset is unique in its experimental design and its quality of data available for climate, soil and stand descriptors, to address the extent to which environment vs. biogeography contribute to spatial patterns of AGB in tropical forests. We use this design to answer three questions.

1. How does AGB vary among habitats, and are these patterns consistent across different geographic regions?
2. Are the relationships between AGB and climate, soil and stand descriptors consistent among habitats and geographic regions?
3. What are the relative contributions of stand and environmental descriptors in explaining spatial patterns of AGB?

Materials and methods

Sampling design

From 2008 to 2010, we sampled 74 stands (forested areas of ca. 20 ha) representing extremes of geographic and environmental gradients, with multiple replicates of the three broad habitat classes described above. Within each geographic region, we selected multiple zones (areas of several thousand hectares, separated by at least 50 km), within which stands corresponding to all three habitats were found (Fig. 2). In Loreto, Peru these included the Allpahuayo-Mishana Reserve in the north, the Jenaro Herrera Center of Investigation and the Matsés Reserved Zone in the south, and the Morona river basin in the west; in French Guiana these included the Laussat Conservation Area in the northwest, the Trinité Reserve in the southwest, the Nouragues Reserve in the southeast, and the Petite Montagne Tortue Conservation Area in the northeast. At each site we established two to six sample plots within different forest stands corresponding to each habitat, with at least 500 m between any two plots. All stands represent lowland forest (<500 m a.m.s.l.) with mature forest subject to natural gap-phase dynamics.

Our plot sample method represents a further modification of the Phillips *et al.* (2003) modified Gentry plots, which we designed to improve AGB estimates. The protocol aggregates ten 10 × 50 m transects within a 2 ha area (for full details, see Appendix S1). This modified 0.5-ha Gentry plot captures a gap and mature phase mosaic well and reduces the risk of sampling bias of a particular phase. Plot sites were placed following substantial prospection in zones selected from topographic

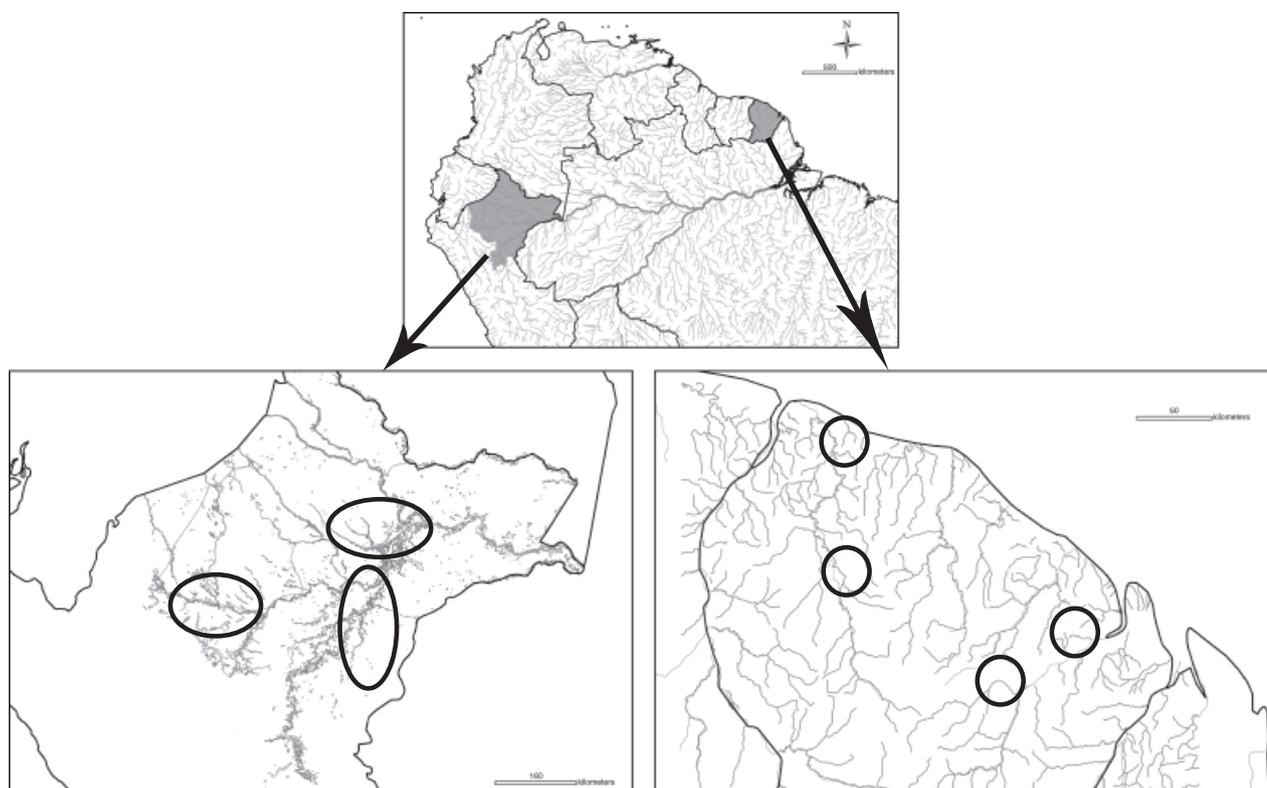


Fig. 2 Map of the Amazon region with major watersheds, illustrating zones where plots were established in Loreto, Peru and French Guiana. Within each of the seven highlighted zones, two to six plots were established in each of three lowland habitat types – seasonally flooded, terra firme clay, or white sand.

maps and satellite imagery where available. The 200×100 m plot perimeter was established to be as representative as possible of the surrounding area (ca. 10–20 ha). UTM coordinates of plots are available upon request.

Links between field and remote sensing estimates of AGB can require slope correction of field estimates to a horizontal plane (Clark & Clark, 2000). We did not correct for slope to create plots with horizontal projection equivalent to 0.5 ha, instead choosing to sample an actual field surface of 0.5 ha. We did, however, measure slope variation among transects using a hand-held clinometer. In all but four of the plots this slope was negligible ($<5^\circ$). In four plots of quartzite white sand in French Guiana, slope values varied between 15° and 27° .

Within each plot, each stem was mapped and its circumference measured to a precision of 2 mm at 1.3 m height (DBH). For stems with irregular trunks or buttresses, circumference was measured (and the point of measure marked with paint) by climbing above irregularities. Tree height was estimated visually by at least two trained persons to arrive at consensus. Visual estimation by members of our crew has been found to provide similar estimates as estimation by laser rangefinders (Figure S1).

Herbarium vouchers were collected for at least one individual of each putative morpho-species in each plot, with all other individuals referenced to this voucher. Taxonomic determinations are still underway; data presented in this paper include determinations to the family level for 99.8% of

stems, to the genus level for 94.6% of stems, to sorted morpho-species for 87.2% of stems, and matches to described species for 65.2% of stems.

Environmental variables

We calculated climatic indices using data from Météo-France in French Guiana and from the IIAP (Instituto de Investigacion de Amazonia Peruana) in Peru, in the meteorological stations nearest to each plot. In cases where weather stations were not located within 10 km of our plots, we used the mean values from any weather stations within a 50 km radius of the plot. The maximum period for which comparable data was available for all sites corresponds to the period from 1998 to 2008.

Two climatic indexes were compiled: a mean annual rainfall (hereafter 'Rain') and a dry season index (DSI). Rain was calculated as a calendar-year average. The DSI from these datasets could be calculated based on daily measurements over 11 years: we therefore calculated dry season length as the maximum number of consecutive days in each calendar year receiving <10 mm of precipitation. We report DSI as the mean value over the 11 years for which data was available from all sites.

Bulked 0–15 cm depth soil cores from each of the 10 subplots were collected and combined into a single 500 g sample that was dried at 25°C to constant mass, sieved to 2 mm, and shipped within 3 months for physical and chemical analyses

(Table 2) at the University of California, Davis DANR laboratory (for full details on laboratory protocols, see Appendix S1).

Estimating AGB

WSG varies widely within and among both species and sites (Patiño *et al.*, 2009), and error associated with WSG estimation can introduce substantial bias into AGB calculations (Sarmiento *et al.*, 2011). To avoid sampling error that can result from regional database compilation (Baraloto *et al.*, 2010b), we measured wood density directly on at least one individual of each species in each plot from the plot network (see Appendix S1 for full details).

We estimated the AGB of smaller trees with diameter at 1.3 m from the ground (DBH) between 2.5 and 10 cm, including palms, from a single equation modified from the model devised by Hughes *et al.* (1999) for a moist tropical forest of South Mexico (Chave *et al.*, 2004):

$$AGB = \frac{WSG \times e^{(-1.9703+2.1166 \times \log(DBH))}}{WSG}$$

We estimated the AGB in trees with DBH > 10 cm, including palms, using allometric formulas that integrate WSG (in g cm³), tree height (*H*, in m) and DBH (in cm) (Chave *et al.*, 2005):

$$AGB = 0.0509 \times WSG \times DBH^2 \times H.$$

We also calculated AGB for trees with DBH > 10 cm using an allometry where height was not integrated, to evaluate any

bias that might be introduced in our estimation of height and choice of allometry (Chave *et al.*, 2005):

$$AGB = WSG \times e^{(-1.499+2.148 \times \log(DBH)+0.207 \times \log(DBH)^2-0.0281 \times \log(DBH)^3)}.$$

Estimates using the allometry without height were always greater than those that included the height measure, and the bias was greatest in plots with higher AGB (Figure S1). We chose to present AGB values including height for the remainder of analyses in this study.

To permit eventual comparisons with other studies, we corrected all values to a projected horizontal surface area based on clinometers measures of slope in each plot, and we extrapolated AGB to a per-hectare basis.

Stand variables

We defined seven stand variables describing forest structure that have been linked to spatial variation in AGB (Table 1). Principal among these are basal area, mean WSG by plot, mean DBH by plot, and mean height by plot. We also included stem density in three size classes: number of stems DBH between 2.5 and 10 cm; number of stems DBH between 10 and 30 cm, and number of stems with DBH > 30 cm.

Data analysis

To study the broad patterns of regional and local variation of AGB, two-way ANOVA was used to test for AGB differences

Table 2 Environmental and geographic variables represented by the 74 0.5-ha plots in Peru and French Guiana

Group	Variable	Abbreviation	Mean	Min.	Max.
Climate	Rainfall (mm yr ⁻¹)	Rain	2923	2471	4421
	Dry Season Index (days)	DSI	22.3	15	36.8
Soil	N (%)	N	0.17	0.02	0.76
	C (%)	C	2.34	0.51	13.62
	Carbon : nitrogen	CN	15.1	1.94	28.7
	NO ₃ -N (ppm)	NO3	6.5	0.05	55.2
	Olsen P (ppm)	P	4.6	0.05	28.6
	K (mEq/100 g)	K	0.09	0.01	0.32
	Na (mEq/100 g)	Na	0.05	0.01	0.21
	Ca (mEq/100 g)	Ca	1.24	0.01	19.06
	Mg (mEq/100 g)	Mg	0.44	0.02	3.72
	Sand (%)	Sand	58.4	5.0	99.0
	Silt (%)	Silt	18.9	1.0	60.0
	Clay (%)	Clay	22.7	0.4	69.0
Stand	Basal Area (> 2.5 cm DBH) (m ² ha ⁻¹)	BA	33.0	20.1	56.3
	Stems 2.5–10 cm DBH (ha ⁻¹)	Stems2.5.10	2149	780	5760
	Stems 10–30 cm DBH (ha ⁻¹)	Stems10.30	583	284	1376
	Stems > 30 cm DBH (ha ⁻¹)	Stems.sup30	89	12	188
	Plot mean WSG	WSG	0.64	0.51	0.76
	Plot mean Height (m)	Height	13.4	8.9	17.5
	Plot mean DBH (cm)	DBH	14.5	6.4	22.8
AGB	AGB Stems > 10 cm DBH (Mg ha ⁻¹)	AGBsup10	289.1	78.6	604.9
	AGB Stems 2.5–10 cm DBH (Mg ha ⁻¹)	AGB 2.5.10	10.4	4.4	27.7
	AGB Total (Mg ha ⁻¹)	AGB	299.5	105.5	614.8

among geographic regions ($n = 2$) and habitats ($n = 3$), with Tukey post-hoc tests to compare group means.

We then investigated the relationships between each environmental variables and AGB in two steps. First, we used multiple factor analysis (MFA; Le *et al.*, 2008) to get an overview of the plots and the variables describing them. MFA is a multivariate ordination method, similar to principal component analysis (PCA), which builds axes of highest variance for different groups of variables (e.g., Baraloto *et al.*, 2010a). The advantage of MFA is that variables are separated into groups each of which is given equal weight in the analysis. In our study, this permitted us to separate stand variables that are clearly related to AGB. In addition, the relative contribution of groups with large numbers of variables is not exaggerated, as would be the case here for soil variables. Finally, MFA allows us to place groups of variables as illustrative to explore their relationships in the ordination without influencing the ordination; here, we placed the AGB group as illustrative. These analyses were conducted using the R language and environment for statistical computing version 2.11.1 (R Core Development Team, 2009), with MFA analyses using the package FACTOMINER (Le *et al.*, 2008).

We used results from the MFA to choose representative variables that represent the largest proportion of orthogonal variation in the dataset. We then employed these variables in two successive modeling approaches to examine the extent to which climate and soil explain spatial variation in stand factors, which in turn explain spatial patterns in AGB. We chose three variables describing stand structure [basal area (BA), stand mean DBH (DBH), and community-weighted mean WSG]; two variables describing climate [DSI and annual precipitation (Rain)]; and three variables describing soil properties [sand content (Sand), nitrate concentration (NO_3) and Olsen-phosphorus concentration (P)].

We first used variance partitioning by means of partial linear regression (Legendre & Legendre, 1998) to examine covariation in the relative contributions of stand, climate and soil variables on AGB. From this, it appears that stand variables alone explain more than 90% of variance, but part of this variance was shared with soil and climate factors. This led us to estimate the importance of soil and climate variables in predicting the forest structure descriptors which, in turn, predict the AGB (Fig. 1). We constrained the stand descriptors to be linear combinations of soil and climate variables, and we used a hierarchical modeling framework to write and infer the following model:

$$\text{AGB}_p = a_0 + a_1 \times \widehat{\text{BA}}_p + a_2 \times \widehat{\text{DBH}}_p + a_3 \times \widehat{\text{WSG}}_p + \varepsilon_{a_p}$$

with $\varepsilon_a \sim N(0, \sigma_a^2)$ and where (i) AGB is the above-ground biomass of plot p , (ii) a_i are the model coefficients and (iii) $\widehat{\text{BA}}$, $\widehat{\text{DBH}}$, $\widehat{\text{WSG}}$ are, respectively, the predicted values of BA, DBH, and WSG using:

$$\begin{aligned} X_p = & \beta_0 + \beta_1 \times \text{DSI}_p + \beta_2 \times \text{Rain}_p + \beta_3 \times \text{NO}_{3p} \\ & + \beta_4 \times \text{P}_p + \beta_5 \times \text{Sand}_p + \varepsilon_{b_p}, \end{aligned}$$

with $\varepsilon_b \sim N(0, \sigma_b^2)$ and where (i) X was calculated as BA, DBH or WSG data of plot p and (ii) β_i are the model coefficients.

Parameter prior distributions were chosen to be noninformative, so that parameter estimations were driven much by the data and less by the specified prior distributions:

$$a_i \sim N(0, 10^6) \beta_i \sim N(0, 10^6), \text{ and } \sigma_i \sim \text{Gamma}(0.01, 0.01).$$

Markov chain Monte Carlo simulations were performed and Gibbs sampling (Geman & Geman, 1984) was completed in WINBUGS 1.4 (Lunn *et al.*, 2000). For each model, the parameter posterior densities were obtained with 50 000 iterations after a burning step (10 000 iterations).

Results

Geographic and environmental variability of AGB

The 74 plots in our network represent a large proportion of the breadth of variation in climate and soil physical and chemical factors that has been reported for lowland forests across Amazonia (Quesada *et al.*, 2009). The different regional zones represent a two-fold gradient in annual precipitation and dry season length, which varies from nearly aseasonal forests in Loreto, Peru (16 consecutive days < 10 mm) to highly seasonal forests in eastern French Guiana (more than 35 days < 10 mm) (Table 2). Together, these sites represent three broad classes of climate – (i) moderate precipitation ($\sim 2700 \text{ mm yr}^{-1}$) with short dry seasons (< 17 days) (all Peru sites); (ii) moderate precipitation ($\sim 2500 \text{ mm yr}^{-1}$) with long dry seasons (25–36 days) (western French Guiana); and (iii) high precipitation ($> 3500 \text{ mm yr}^{-1}$) with moderate dry seasons (~ 24 days) (eastern French Guiana). In addition, the study sites cover broad gradients of soil texture, soil nitrate concentration, and soil available phosphorus (Table 2).

Across our 74 plots, AGB of stems with $\text{DBH} > 10$ cm varied by a factor of 7.8, from a minimum of 78 Mg ha^{-1} in a white sand forest in northern Loreto, Peru to a maximum of 605 Mg ha^{-1} in a terra firme clay forest of the Trinité Reserve in French Guiana (Fig. 3; Table S1). Forests in French Guiana had nearly twice the average AGB (371 Mg ha^{-1}) of forests in Loreto, Peru (215 Mg ha^{-1}). White sand forests had only about two-thirds the AGB of terra firme and seasonally flooded clay soil forests in both countries; this contrast was particularly pronounced within the French Guianan forests (Fig. 3). Seasonally flooded forests varied remarkably in AGB values, particularly within the French Guianan sites, and we did not detect an overall difference in AGB between flooded and terra firme clay forest soils (Table S1).

The contribution of stems < 10 cm DBH to total AGB was particularly pronounced in white sand forests of both countries, where smaller stems contributed on average about 10% of total AGB (vs. $< 3\%$ in terra firme

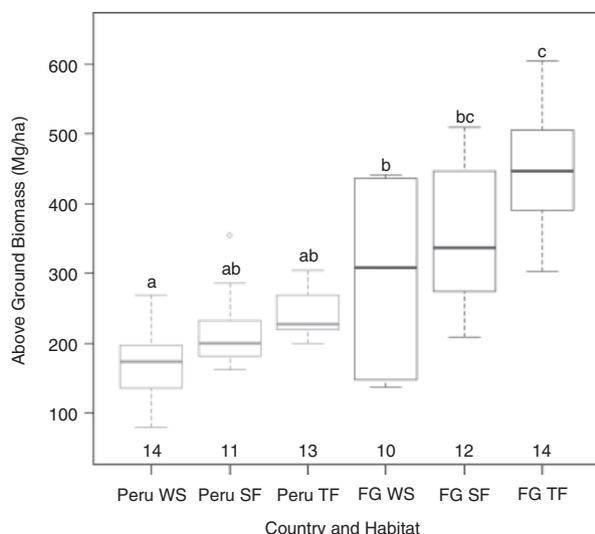


Fig. 3 Boxplot for aboveground biomass of stems >10 cm DBH ($Mg\ ha^{-1}$) in different habitats and countries (SF, seasonally flooded; TF, terra firme; WS, white sand). Letters indicate groups with different means following Tukey post-hoc tests. The number of plots represented by each group is indicated at the bottom, with 74 total plots.

clay and seasonally flooded forests; Figure S3). Nevertheless, the overall ranks of countries and habitats remained consistent for total AGB including all stems >2.5 cm DBH (Table S1).

Stand and environmental correlates of AGB

We used MFA to examine the relationships among climate, soil and stand factors in addition to their relationships with AGB. Two major gradients of environmental variation were recovered, explaining 49% of the variance in the dataset. The first MFA dimension has strong loadings of the principal components of the climate group and the forest stand group (Table S2). In particular, it represents a gradient of increasing dry season length, higher annual precipitation, and higher stand basal area (Fig. 4a). The second dimension has strong contributions of both stand and soil variables, opposing infertile sandy soils with high small stem density with fertile clay soils with larger trees (Table S2; Fig. 4a). Mean WSG was tightly positively correlated with soil sand content and soil C:N ratios and tended to increase along the first dimension of climate/geography and to decrease with increasing soil fertility (Dimension 2). Total AGB and AGB of stems with $DBH > 10\ cm$ were strongly positively correlated with the first dimension.

Ordination of the plots (Fig. 4b) reveals a clear trend of not only geographic separation by climate and stand factors (Dimension 1) but also habitat separation

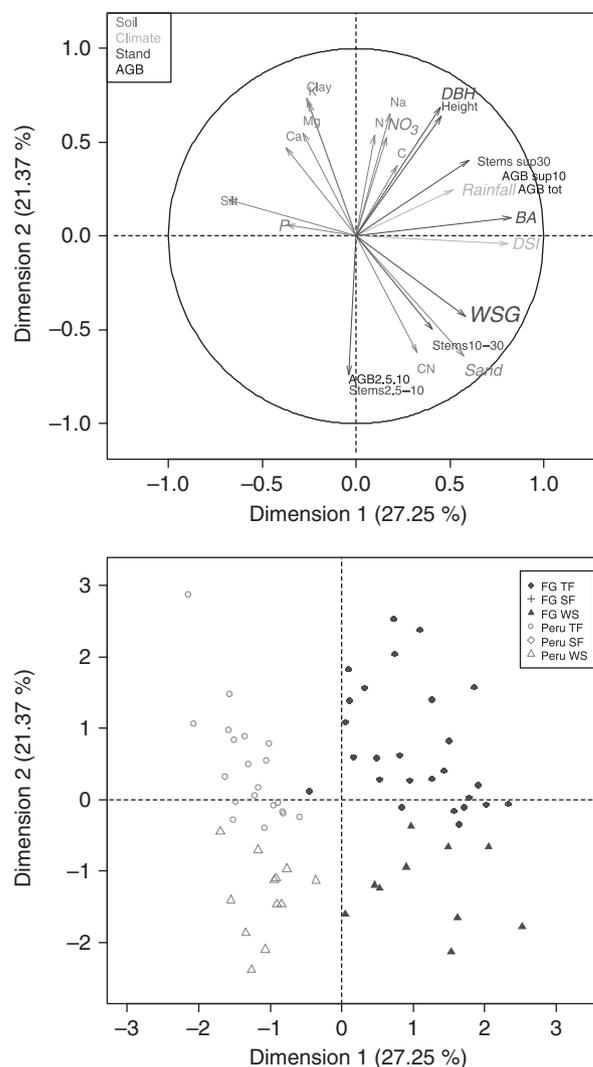


Fig. 4 Ordination of variables and forest plots using multiple factor analysis (MFA), in which aboveground biomass (AGB) variables are used in illustration along the resulting dimensions. The upper panel shows the correlation circle with groups of soil, climate, and stand variables; variables chosen for subsequent analyses are presented in bold. The lower panel shows coordinates of the 74 plots grouped in two geographic regions (Peru, French Guiana) and the three habitat types (terra firme and flooded clay forests, and white-sand forests).

between white-sand vs. clay habitats by soil texture and soil fertility (Dimension 2). Seasonally flooded and terra firme forests do not segregate within the clay-derived soils and can be considered a single group relative to the environmental variables we measured.

Most stand variables showed very strong positive relationships with AGB, confirming the ordination of the MFA analysis (Fig. 4) and the conceptual framework (Fig. 1). Average DBH and basal area were higher in French Guiana than in Peru and generally lowest in white sand forests; whereas community mean WSG was

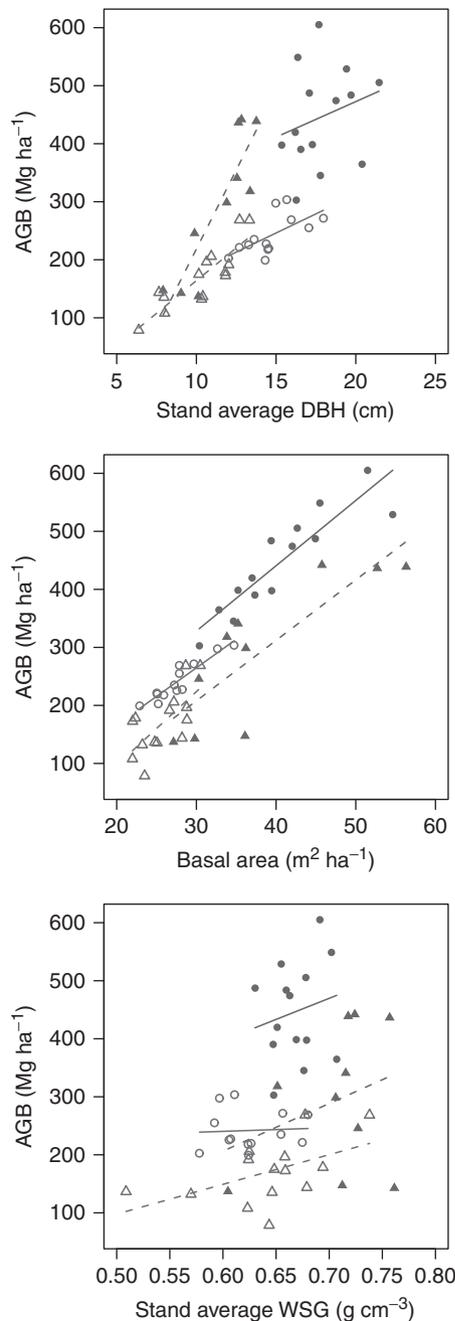


Fig. 5 Selected relationships between aboveground biomass (AGB) and stand variables. Each panel shows results for 74 plots grouped by geographic region [Peru (open), French Guiana (filled)] and habitat type [white sand (triangles) vs. terra firme and flooded clay forests (circles)]. Shown are slopes from analyses of covariance testing the interaction between forest type and stand variable on AGB.

highest in white-sand forests (Fig. 5). Despite these differences, the general relationship between these stand variables and estimated AGB was strongly congruent. Analysis of covariance revealed very strong effects of both forest type and each stand descriptor

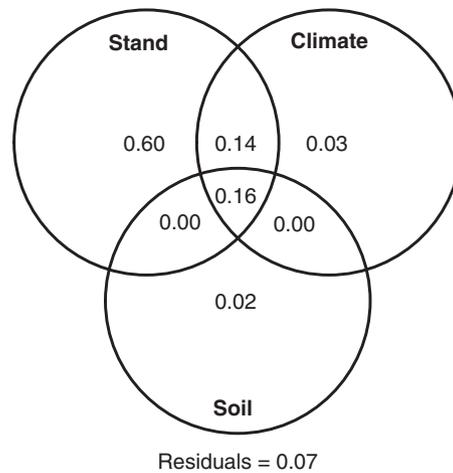


Fig. 6 Venn diagram illustrating the decomposition of spatial variation in AGB between stand, soil and climate variables. Shown are the proportions of variance explained by each combination of variable types. Note that these proportions do not necessarily sum to 1 (Legendre & Legendre, 1998).

on AGB, and the only variation in slope was the stronger slope in the relationship between DBH and AGB in white sand forests of French Guiana (Fig. 5).

The strength of these relationships was confirmed by linear model decomposition, in which 90% of spatial variation in AGB (of 93.5% total) was explained by stand variables alone, with two-thirds of this being independent of soil and climate variables (Fig. 6). Although climate and soil parameters did contribute to explain variation in AGB, this was almost entirely indirectly via covariation with stand parameters.

The Bayesian hierarchical model allowed us to detail the contributions for each climate and soil variable to the variation in stand parameters that explained spatial variation in AGB. Climate variables contributed strongly to the explanatory variation in all three stand descriptors, especially basal area (Fig. 7). Soil texture (percent sand) showed contrasting relationships, with a strong positive relationship with the explanatory variation in WSG and a strong negative relationship with the explanatory variation in stand mean DBH. Soil phosphorus showed negative relationships with the explanatory variation in all three stand descriptors, especially basal area and DBH.

Discussion

Our study provides two important advances to understanding spatial patterns of AGB in Amazonian forests. First, we present clear evidence of contrasting patterns of AGB among broad forest habitat types, in addition to confirming the strong east–west geographic gradient that has been previously described (Fig. 3). Second,

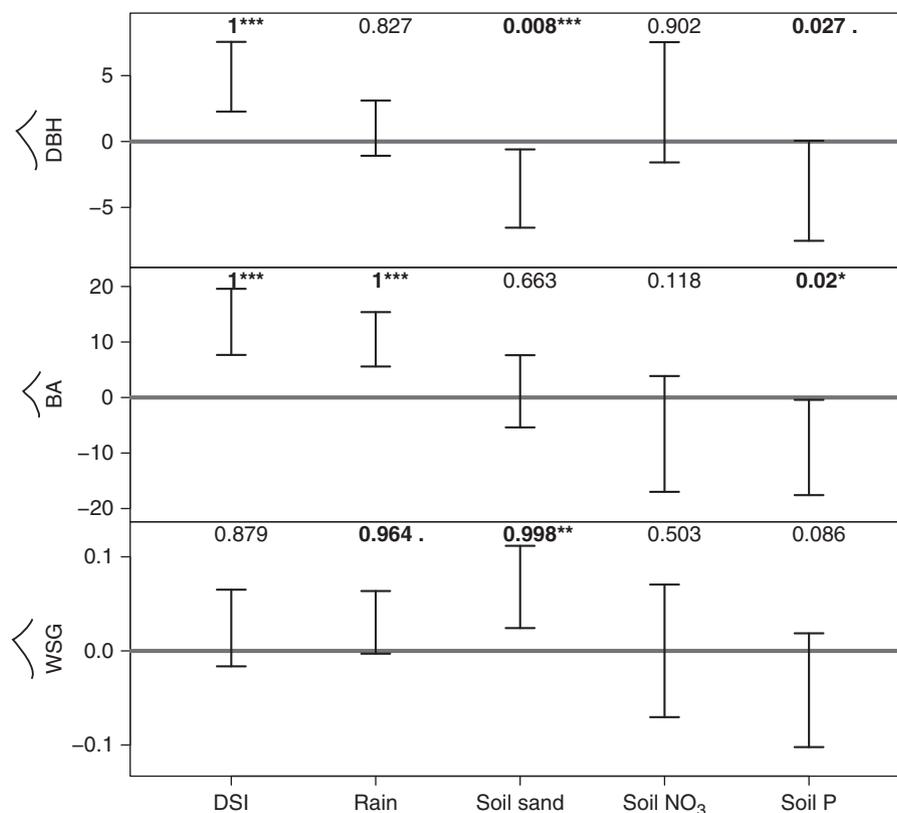


Fig. 7 Results of hierarchical Bayesian model relating five representative climate and soil variables to the variation in aboveground biomass (AGB) explained by three representative stand variables. Shown are the 95% credibility intervals of parameter estimations from the models, with the number indicating the proportion of each distribution which is greater than 0, with significant deviations from 0 shown in bold. Note that the observed values of the predictive variables were standardized to [0, 1] before running the hierarchical model, thus allowing visual comparisons of the coefficients between the predictors. WSG, wood specific gravity; BA, basal area. $P < 0.10$, $*P < 0.05$, $**P > 0.01$, $***P < 0.001$.

despite fine-scale characterization of soil and climate across these broad gradients, we did not uncover strong relationships between any soil or climate variable and AGB (Table 2). Rather, we found compelling evidence for regional and habitat patterns in stand variables describing forest structure and composition (Fig. 4) that were only partly explained by spatial variation in climate and soil physical or chemical properties (Fig. 6). The strength of the arrows in Fig. 1 could be modified to reflect these relationships with a strong arrow between stand variables and AGB; weak arrows between climate and especially soil variables and stand variables; and very weak arrows between climate and soil variables and AGB. Below we discuss these groups of variables in turn and the implications for understanding and modeling regional patterns of AGB in Amazonian forests.

Stand influence on AGB

Our analyses underline the paramount contribution of stand variables to spatial variation in AGB that has been

found in other analyses, and especially the role of larger trees (Chave *et al.*, 2004; DeWalt & Chave, 2004; Rutishauser *et al.*, 2010). This result is not surprising because diameter and height are used to estimate individual tree AGB, as illustrated by the strong linear relation between AGB and basal area (Fig. 5). Large trees (> 30 cm DBH) represented 11.4% and 16.7% of Peru and French Guiana tree samples, respectively. French Guianan forests are also characterized by higher total stem densities, especially in terra firme and seasonally flooded forests (Fig. 4); given that these forests also tend to have larger trees, they are characterized by a higher basal area and higher AGB (Fig. 5).

Our study also highlights the importance of smaller stems to carbon stocks, especially in many white-sand habitats. Overall, AGB of stems with DBH between 2.5 and 10 cm varied by a factor of more than five (Table 2), accounting for <1% in some French Guianan terra firme forests to more than 25% of total AGB in a Peruvian white-sand forest (Figure S3). This result contrasts with reports that small trees (<10 cm DBH) account for only 3% of aboveground biomass in French

Guiana (e.g., Lescure *et al.*, 1983). Eighty percent of biomass estimates in lowland tropical forests are based on measurements of trees >10 cm DBH (Keeling & Phillips, 2007). Our research shows that we should also take small trees into consideration in biomass estimations, particularly in edaphically extreme habitats such as white-sand forests. One reason that most studies may not include small trees is the time required for adequate measurement. We recommend our sampling protocol as particularly efficient to estimate rapidly the total AGB, with an average of 8 person-days to complete field sampling per plot. Still, we note that the allometries for these stems may result in overestimates because they do not include height (cf. Fig. S2), and it would be valuable to revise allometric relationships for smaller stems in future studies.

Baker *et al.* (2004) demonstrate significant differences in stand level WSG for mature forests within Amazonia, with eastern and central forests having 16% denser wood than their western counterparts. In our study, this geographic effect is confirmed, with French Guianan forests having a higher average WSG than Peruvian forests (ANOVA $P < 0.01$). However, this effect was less than half as strong as the effect of habitat (ANOVA $P < 0.001$), with white-sand forests having nearly 20% higher average wood density than terra firme and seasonally flooded forests in both countries (Fig. 5). Across all forests, these patterns explain the weaker positive correlation between WSG and AGB than has been reported in other studies across multiple Amazonian plots (Baker *et al.*, 2004; Quesada *et al.*, 2009). For example, the highest community values of WSG were found in French Guianan white-sand forests, many of which have very low AGB. Moreover, some of the French Guianan terra firme plots with the highest AGB have among the lowest community WSG values (Fig. 5). Although we concur with Baker *et al.* (2004) that patterns of species composition across the Amazon may contribute to differences in AGB because of spatial gradients in community wood density (Ter Steege *et al.*, 2006), we caution against generalizations of positive correlations between WSG and AGB, as this relationship may not be valid across all site comparisons (Stegen *et al.* 2009).

Climate, stand parameters and AGB

Few studies have attempted to relate climate with AGB, perhaps because of limited precision in climate data across tropical forest regions, especially adjacent to permanent vegetation plots. Higher rainfall and/or shorter dry seasons have been linked to higher AGB across Amazonian forests (Malhi *et al.*, 2006; Quesada *et al.*, 2009) and the Isthmus of Panama (Chave *et al.*,

2004). However, these studies could not disentangle the confounding effects of soil and stand composition from those of climate because tropical forests with the combination of high soil fertility, low precipitation and strong seasonality are rare (Quesada *et al.*, 2009). Our study sites included broad gradients of soil fertility and climate regimes (Table 2), and our statistical approach allowed us to examine the covariation among these factors.

We found very strong effects of dry season length on the stand characteristics that explained spatial variation in AGB (Fig. 7), but we note that our plot network does not cover geographic intermediates in Brazil (Fig. 2). Quesada *et al.* (2009) showed that significant correlations between dry season length and AGB dissolved after correcting for spatial autocorrelation among 59 of the RAINFOR terra firme plots. Further investigation combining these databases will be necessary to determine the relative contribution of climatic variables to spatial variation in AGB.

Soil, stand parameters and AGB

Confounding spatial effects similar to those we found with climate can impede analyses of relationships between AGB and soil parameters (Quesada *et al.*, 2009), and this may explain in part the contrasting results reported by previous studies across different spatial scales (Laurance *et al.*, 1999; DeWalt & Chave, 2004; Paoli *et al.*, 2008; Quesada *et al.*, 2009). One of the strengths of our study is the replicated sampling of contrasting soil types at different spatial scales, which reveals several consistent patterns across geographic regions and habitats. Across the entire dataset, as well as within habitats and countries, AGB decreased with increasing soil fertility as defined by Olsen-extracted phosphorus and correlated exchangeable cations (Fig. 4a) because of strong negative correlations between these soil chemical parameters and tree size and basal area (Fig. 7). Nevertheless, nitrate was positively correlated with tree size, perhaps due to accumulation of N over time in the older forests of French Guiana. Overall our results are consistent with the idea that forests on less-weathered soils have higher turnover rates which do not permit accumulation of high AGB, whereas forests on weathered soils may accumulate both standing biomass and soil nitrogen (Russo *et al.*, 2005; Quesada *et al.*, 2009).

Conclusions

Our study has strong implications both for understanding the factors explaining spatial variation in AGB in lowland tropical forests and for modeling AGB in the

Amazon. We provide sobering news for modelers seeking to use appropriate 'soil and climate functions' to refine estimates of AGB in lowland tropical forests of South America. Unlike in the forests of Borneo (Paoli *et al.*, 2008; Slik *et al.*, 2010), soil appears to exert relatively weak control over AGB across the forests studied here; and climate variables were also poorly correlated with AGB (Fig. 6). On the other hand, our study shows how stand variables may prove to be valuable tools to estimate AGB not only within terra firme forests across geographic regions, but also among contrasting habitats both within and among geographic regions (Fig. 5). Stand variables, especially canopy height, can be derived from remote sensing devices whether radar, lidar or optical (Dubayah *et al.*, 2010; Goetz *et al.*, 2009) and therefore can be used as valuable predictive variables to map and monitor forest biomass over large areas.

The weak relationships we observed between AGB and soil and climate (Fig. 6), despite fine-scale characterization across broad gradients of soil and climate, confirms previous results for little soil nutrient control over AGB in Neotropical forests (DeWalt & Chave, 2004; Quesada *et al.*, 2009). These results are generally consistent with the positive feedback hypothesis (van Schaik & Mirmanto, 1985; Quesada *et al.*, 2009), which contrasts rich soils with high turnover that support fast-growing species with smaller maximum sizes and lower wood density, vs. less fertile soils with lower turnover that support the accumulation of many, larger trees with denser wood. The model works well for both geographic contrasts (Peru vs. French Guiana) and for contrasts between seasonally flooded forests (high turnover) vs. terra firme forests (lower turnover) in the regions studied here (e.g., Ferry *et al.*, 2010) (Fig. 7). We underline the exception reported here for white-sand forests, in which strong oligotrophy and drought stress may favor investment in physical and chemical defenses (Janzen, 1974; Fine *et al.*, 2006) and traits reducing cavitation risk such as high wood density and slow growth (Chave *et al.*, 2009), resulting in the lowest AGB values ever reported (Fig. 3). The integration of forest dynamics data with the intensive measures and plot network design of our study, in collaboration with other plot networks, will permit refined tests of the positive feedback hypothesis in Amazonian forests.

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Supporting Information

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

Figure S1. Reliability of visual estimation of tree height.

Figure S2. AGB estimated without height always exceeds estimates integrating height.

Figure S3. Boxplot for aboveground biomass of stems < 10 cm DBH.

Table S1. ANOVA summary of habitat and country effects on AGB.

Table S2. Contributions of environmental variables to the MFA analysis.

Appendix S1. Details of methods.

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