

Forest structure along a 600 km transect of natural disturbances and seasonality gradients in central-southern Amazonia

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Summary

1. A negative relationship between stand biomass and the density of stems is expected to develop during the self-thinning process in resource-limited forests; this leads to a large proportion of the total biomass occurring in large trees. Nevertheless, frequent disturbance regimes can reduce self-thinning and the accumulation of large trees.

2. We investigated size–density relationships and the contribution of large trees (dbh $\geq$ 70 cm) to stand biomass in 55 1-ha plots along a 600 km transect in central-southern Amazonia. The effects of natural-disturbance gradients (frequency of storms and soil characteristics) and seasonality on forest-structure components (density of stems and mean individual mass) and stand biomass were examined.

3. Contrary to self-thinning predictions, stand biomass increased in forests with higher stem densities. Large trees contained only an average of 5% of stand biomass, and half of the stand biomass was represented by small trees with diameters $<$ 27 cm. These findings indicate that persistent or strong disturbance plays a critical role in forest structure and biomass in the central-southern Amazon. Frequent storms were identified as an important source of disturbance in the region. Forests under higher frequency of storms had trees with lower individual mass and higher stem packing. More physically restrictive soils seem to magnify the effects of exogenous disturbances limiting individual tree size.

4. Forests in areas with longer dry seasons had lower stem densities; however, individual mass was higher in these areas. These structural components of biomass seem to counterbalance each other in generating total stand biomass. Seasonality affected forest structural components but not stand biomass.

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5. Synthesis. Forests of central-southern Amazonia are not resource limited and accumulate most part of their biomass in small- to mid-sized trees. The effects of environmental gradients on specific structural components of stand biomass differ such that strong positive effects on one component can mitigate strong negative effects on other component. Future work on the determinants of stand biomass should investigate forest structure and the contributions of individual components to stand biomass.

Key-words: above-ground biomass, carbon stocks, density of stems, determinants of plant community diversity and structure, Purus–Madeira interfluvium, soil, storms, tropical forest

Introduction

Stand biomass is mainly a product of average plant biomass and the density of stems. Therefore, these two forest-structure components are fundamental to understand and to estimate stand-biomass variation. Despite the recognized importance of environmental gradients and disturbance regimes for forest structure and biomass variation (Urquiza-Haas, Dolman & Peres 2007; Slik *et al.* 2010), a general principle based on resource limitation may determine space occupation and biomass accumulation. As a stand develops, trees increase in size and there is less space for individuals, resulting in density-dependent mortality due to competition between crowded stems (i.e. ‘stand self-thinning’; Yoda *et al.* 1963; Westoby 1984). Over time or across different communities, the average individual size increases with decrease in density of stems (Westoby 1984). The self-thinning relationship has been found in many planted and natural stands, and also in assemblages composed of mixed species and ages across space (White 1981; Westoby 1984; Niklas, Midgley & Enquist 2003a; Luyssaert *et al.* 2008).

The self-thinning model allows predictions about stand-biomass accumulation. The negative size–density relationship leads stand biomass to increase as maximum density of individuals decreases (Weller 1987; Petraitis 1995), despite differences in forest age and stem density (Luyssaert *et al.* 2008). A general allometric scaling model for crowded tree-dominated assemblages (Niklas, Midgley & Enquist 2003a) predicts that total stand biomass (TB) scales as the $-1/3$ exponent of stem density ($TB = N^{-1/3}$). These negative relationships with stem density imply that greater biomass stocks should be found in forests with fewer stems and larger individuals (Midgley 2001) and that the most of the stand biomass should be in larger individuals.

Various studies have found that large trees (those with diameter at breast height (dbh) > 70 cm) comprise the largest component of biomass in forests. Nearly half of the stand biomass can be attributed to large individuals in mixed-conifer forests in North America (Lutz *et al.* 2012) and in tropical forests in Asia (Paoli, Curran & Slik 2008) and Africa (Slik *et al.* 2013). In Neotropical forests, a large but variable (14–45%) proportion of stand biomass is attributed to trees with dbh > 70 cm (Brown *et al.* 1995; Clark & Clark 1996; Brown, Schroeder & Birdsey 1997; Chave, Riéra & Dubois 2001; Chave *et al.* 2003; Slik *et al.* 2013).

One explanation for the variable contribution of large trees to stand biomass across forests may be disturbance (gap opening) regimes. Frequent disturbances may prevent self-thinning and the development of large-statured high-biomass stands. By causing density-independent mortality, disturbance may alter the densities of individuals relative to expectations of thinning theory and prevent individuals from reaching larger diameters (Niklas, Midgley & Rand 2003b). We hypothesize that if the disturbance regime is more important than resource limitation, the relationship between stand biomass and number of stems will strongly deviate from the self-thinning rule and trees will not fill all the canopy space. In this case, we expect stand biomass to increase with the density of stems and increasing space filling in the canopy, in contrast to the negative relationship predicted by the self-thinning rule. Furthermore, if disturbance has a propensity to impact larger trees, as in the case of prolonged droughts (Phillips *et al.* 2010), or if disturbance is frequent, stand biomass may be concentrated in small- to mid-sized stems because large individuals should be rare.

In the Amazon basin, there is an east-west gradient of forest dynamics and structure that has been attributed to natural-disturbance gradients, such as soil conditions initiating endogenous disturbance (Phillips *et al.* 2004; Quesada *et al.* 2012) and windstorms causing exogenous disturbances, such as blowdowns of variable sizes (Espírito-Santo *et al.* 2010). Higher turnover rates (Phillips *et al.* 2004) and lower stand-biomass stocks were found in the more fertile but less physically structured soils in western Amazonia (Quesada *et al.* 2012), where there are also higher frequencies of storms (Nelson *et al.* 1994; Espírito-Santo *et al.* 2010). In contrast, the less dynamic and higher biomass forests were found in chemically poorer but physically well-structured soils in eastern Amazonia, where lower frequencies of storms were observed. According to these observations, forest-structure components related to biomass (density of stems and average individual mass) and stand biomass should vary in relation to the frequency of storms, soil physical restrictions and fertility gradients. Therefore, we expect that stand biomass should decrease and the density of stems should increase as disturbance increases. Patterns postulated to be related to disturbances are superimposed on patterns associated with seasonality (dry-season length) that should result in decreasing biomass where the climate is more seasonal (Malhi *et al.* 2006).

We investigated the relationships between stand structural variables, stand biomass, environmental gradients of

disturbance (storms and soil) and seasonality in 55 permanent plots along a 600 km transect, from near Manaus in central Amazonia to Humaitá on the central-southern frontier of the Amazon forest. This transect along the Purus–Madeira interfluvial region is topographically relatively homogeneous, but covers gradients in seasonality, frequency of storms, and soil physical structure and fertility. Dissecting biomass into its components (density of stems and mean individual mass) and over size classes allowed us to evaluate mechanisms for environmental controls over forest structure and biomass.

Materials and methods

STUDY AREA

The study was conducted in 55 1 ha plots along a 600 km transect in the Purus–Madeira interfluvium, south of the Amazon River in central Amazonia (Fig. 1). The plots were distributed in 11 research sites along the BR-319 highway, a road that has been impassable for regular traffic since 1988 (Fearnside & de Alencastro Graça 2006). In each site, five plots were regularly distributed along a 5 km trail and the plots were 1 km apart. Plots were established at least 1 km from the road to avoid secondary forests. The Purus–Madeira interfluvial region has a relatively recent geological origin with unstable sediments from Late Pleistocene or Early Holocene and predominantly flat topography (Sombroek 2000). Elevation above sea level varies from 27 to 80 m along the transect (shuttle radar topography data). This region is part of the Amazon basin ‘loamy plains’ (Sombroek 2000), a landform covering around 11% of the Amazon basin, including the low interfluvial areas of Rio Negro–Amazonas and Juruá–Purus–Madeira and the Beni area of north-eastern Bolivia.

Soils are mainly Gleysols and Plinthosols with poor drainage, and the predominant texture is silt to fine sand (Sombroek 2000). Large

areas are waterlogged during the rainy season, and many of the small streams dry out during the dry season. The water-table is shallow, within 7 m of the surface throughout the year in most of the region but some areas stay with a short column of flooding (~50 cm) when the water-table reaches the highest levels (J. Schiatti, unpubl. data). The mean annual precipitation varied from 2000 to 2400 mm, with a number of consecutive months with less than a 100 mm of rainfall (a threshold generally considered an indicator of the dry season) ranging from 1 month in the north of the transect to 4 months per year in the south (Sombroek 2001). The vegetation is classified as lowland dense rain forest in the north and lowland open rain forest dominated by palms in the south (BRASIL 1974).

VEGETATION DATA

Diameter at breast height of 29 984 stems including trees and palms was measured in the 55 plots. The plots had a 250 m central transect that follows the terrain elevation to minimize variation in soil characteristics and water-table depth within plots. We followed a hierarchical system to measure the trees and palms along the 250 m plot central line (Magnusson *et al.* 2005). All stems with dbh $\geq$ 30 cm were measured in 1 ha (250 $\times$ 40 m), stems with dbh $\geq$ 10 cm were measured in a subplot of 0.5 ha (250 $\times$ 20 m) and stems with dbh $\geq$ 1 cm were measured in subplot of 0.025 ha (250 $\times$ 1 m).

Above-ground wood biomass of individual trees was calculated based on diameter (D), height (H) and wood specific gravity (ρ_w). We used eqn (1) for moist-forest stands from Chave *et al.* (2005) with parameters adjusted by Feldpausch *et al.* (2012).

$$\text{Tree biomass} = \exp(-2.9205 + 0.9894 \times \ln(D^2 \rho_w H)) \quad \text{eqn 1}$$

Tree height was estimated using D–H allometric equations adjusted for each of the 11 research sites along the transect (see Appendix S1 in Supporting Information). The diameter and height of 1481 trees

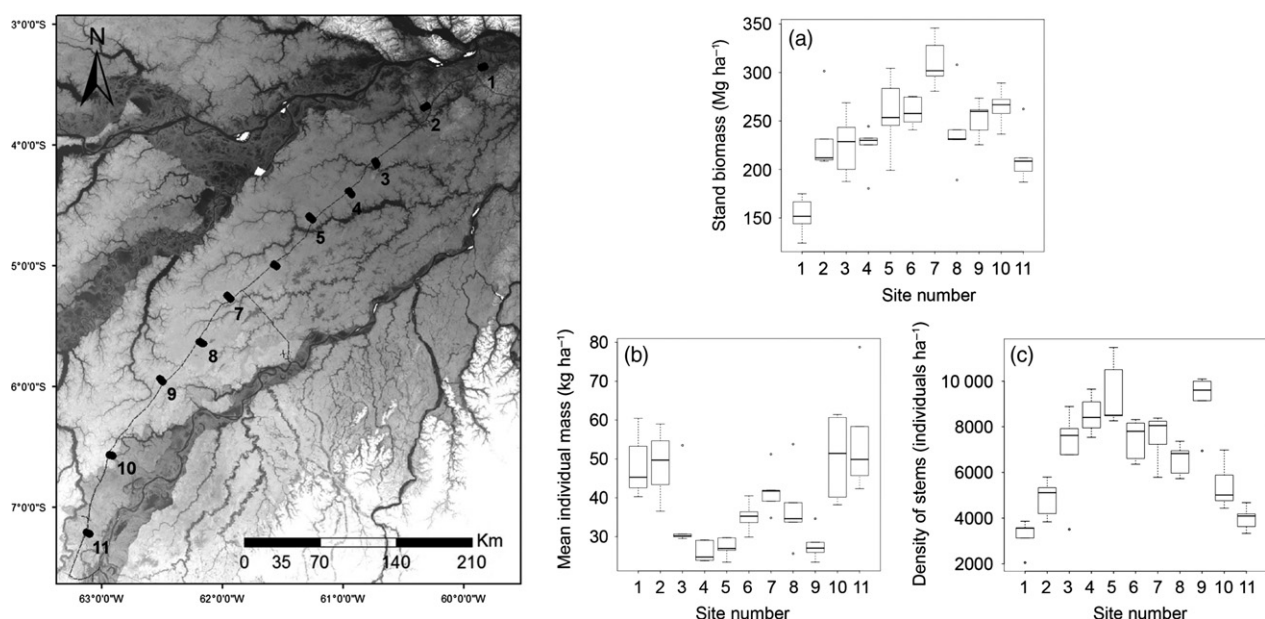


Fig. 1. Map of the study area showing the 600 km transect along the interfluvium between the Purus and Madeira Rivers in central Amazonia. Eleven research sites (1–11) are located along the transect. Each site has five 1-ha plots where trees were measured. Box plots show the variation in (a) stand biomass, (b) mean individual mass and (c) density of stems along the transect. Stand biomass and density of stems show higher values in the central region of the interfluvium and lower values in the northern and south-western extremes. The mean individual mass shows an opposite pattern.

(on average 135 trees per site) were measured in different diameter classes. Heights were estimated by a single observer (D. Martins) using a Vertex hypsometer (Vertex Laser VL400 Ultrasonic-Laser Hypsometer III, Haglöf of Sweden). We used a power model to fit the H - D allometric equations and compared the errors of our H - D locally adjusted equations with other H - D allometries already published such as the ones for western and central-eastern Amazonia from Feldpausch *et al.* (2012) and for central Amazonia dense forest, southern Amazonia open forest and south-western Amazonia dense forest from Nogueira *et al.* (2008) (see Figure S1).

Wood specific gravity was obtained from the global wood-density data base (Chave *et al.* 2009; Zanne *et al.* 2009) for 22 plots where plant species identification was available. In the other 33 plots, we estimated the average wood specific gravity of the plot by extracting core samples from the trunk of 20 canopy trees (dbh $\geq$ 30 cm) randomly selected along the plot. Wood specific gravity was estimated by the dry weight per fresh volume of the cores. Individual wood specific gravity values were attributed to trees using (i) wood specific gravity values from sampled cores in this study, (ii) mean species value, (iii) mean genus or (iv) mean family value from the global wood-density data base or (v) the mean value per plot based on the 20 individuals sampled in this study.

Palm biomass was estimated using the family-level biomass allometric eqn (2) based on diameter (Goodman *et al.* 2013).

$$\text{Palm biomass} = \exp(-3.3488 + 2.7483 \times \ln(\text{dbh})) \quad \text{eqn 2}$$

The number of stems and individual biomass (of trees and palms) was summed in the subplots and then expressed as the density of stems and the stand above-ground wood biomass (hereafter called stand biomass) per plot at the 1 ha basis. The average individual mass was calculated by dividing the stand biomass per plot by the density of stems.

ENVIRONMENTAL GRADIENTS

Seasonality was calculated based on daily precipitation data interpolated from a network of rain gauges in the region for the period from 1973 to 2011 (CPTEC/INPE). Dry-season length was indexed by the mean number of months per year with precipitation < 100 mm for the 38-year period.

The frequency of storms was indexed by the number of days per year with precipitation ≥ 20 mm (data from Espírito-Santo *et al.* 2010), which is strongly correlated with the occurrence of blowdowns in the Brazilian Amazon (Espírito-Santo *et al.* 2010). Previous work also showed congruence between the spatial distributions of blowdowns and high frequency of storms in the Brazilian Amazon at the end of the 1980s (Nelson *et al.* 1994), suggesting the frequency of storms (given by days per year with precipitation ≥ 20 mm) can be a good proxy for the occurrence of windstorm disturbances. To estimate the frequency of storms, daily precipitation in 1999 was integrated from NOAA (National Oceanic and Atmospheric Administration) satellite images with 4 km resolution and 10.7 mm band from NOAA satellite 8 (see Espírito-Santo *et al.* 2010 for details).

As proxies of soil fertility, we assessed the sum of individual extractable bases (Ca^{2+} , K^+ , Mg^{2+}), that is the sum of bases, and the available phosphorus (extracted with Mehlich-1) (EMBRAPA 2011) in topsoil samples. Phosphorus has been identified as the most important nutrient for biomass production in Amazonian forests (Quesada *et al.* 2012). Soil phosphorus and the individual extractable bases

were determined in a compound sample derived from 6 subsamples from the first 30 cm depth of soil collected along the central line in each of the 55 plots.

Soil physical restrictions were scored based on effective soil depth, a qualitative structural index, anoxic conditions and topography following Quesada *et al.* (2010). The scores for soil physical limitations are semi-quantitative. Summing the scores of all soil-constraint categories, we calculated the index Π_1 of soil physical limitations, which can vary from 0 to 16 (Quesada *et al.* 2010). Higher scores denote more limited soil conditions for plants. The soil physical classification was made based on soil effective depth, soil structure and anoxic conditions (depth of soil saturation) (see Table S2); all determined in 2-m-deep pits dug in each research site and in soil-profile samples from all plots (Martins *et al.* 2014).

DATA ANALYSES

To evaluate the extent of self-thinning relationships in the Purus-Madeira interfluvial region, we investigated the direction of the relationships between the average individual mass per plot or stand biomass with the density of stems by simple linear regressions. All variables were $\log_{10}$ -transformed. We also investigated the importance of size classes to stand-biomass accumulation by determining the diametric classes at which half of the stand biomass, starting from the smallest individuals, was accumulated at the plot scale and, the percentage of the stand biomass accumulated in large trees (dbh ≥ 70 cm). For the first analysis, we first calculated biomass in 1-cm-diameter bins (Table S6).

To investigate the variation in forest-structure components and stand biomass along seasonality and natural-disturbance gradients, we used linear mixed-effect models (LMM) of the density of stems, mean individual mass and stand biomass against dry-season length, frequency of storms, soil fertility (available P and sum of bases) and soil physical restrictions (fixed effects). The density of stems and the average individual mass were $\log_{10}$ -transformed. Site was included in the model as a random effect to account for the nested design (plots within sites) (Zuur *et al.* 2009).

Analyses were undertaken for minimum diameters of 1 and 10 cm. Results for all individuals above 1 cm dbh are presented in the manuscript. Plot-level data below and above 10 cm diameter and LMM results for dbh ≥ 10 cm are given in the Supporting Information (see Tables S3, S4, S5 and Fig. S2). All analyses were undertaken in R 3.1.1. (R Core Team 2013). LMM analyses were conducted with the package lme4 (Bates, Maechler & Bolker 2013), and the marginal and conditional LMM R^2 were calculated using the package MuMIn (Bartón 2014).

Results

Stand biomass in the Purus-Madeira interfluvial ranged from 124 to 346 Mg ha^{-1} (mean = 239 Mg ha^{-1}). The number of individuals per ha varied from 2051 to 11 475 considering all individuals with dbh ≥ 1 cm (Table 1) and from 450 to 1088 considering individuals with dbh ≥ 10 cm (see Table S3 for plot-level data with dbh ≥ 10 cm). Stand biomass was higher in the central area of the interfluvial and lower in the north-eastern and south-western extremes. A similar spatial pattern was found for the density of stems and an opposite trend for the average individual mass, with higher average individual mass in forests at the extremes of

the transect and lower average individual mass in the central area of the transect (Fig. 1)

FOREST-STRUCTURE COMPONENTS AND STAND BIOMASS

There was a negative relationship between the mean individual mass and the density of stems, supporting self-thinning expectations for resource-limited forests (Fig. 2a and Fig. S2a for $\text{dbh} \geq 10$ cm). However, higher stand biomass was found in forests with more densely packed stems (Fig. 2b and Fig. S2b for $\text{dbh} \geq 10$ cm), suggesting additional mechanisms, such as disturbance, might play a role in stand-biomass accumulation in the region. On average, half of the stand biomass was accumulated in relatively small individuals with diameters up to 27 cm. The dbh threshold of 50% biomass accumulation ranged from 19 to 53 cm in individual plots (Fig. 3), but in 70% of the plots more than half of the biomass was accumulated in individuals with diameters up to 27 cm (Fig. 4). Large individuals were rare in the forests along the Purus–Madeira interfluvium. The maximum diameter found in the plots varied from 48.4 cm to 184.9 cm (mean = 83 cm), and on average, there were 1.8 trees with $\text{dbh} > 70$ cm per ha (ranging from 0 to 11 trees ha^{-1}). These large trees ($\text{dbh} \geq 70$ cm) accounted on average for only 5.4% of stand biomass.

ENVIRONMENTAL-GRADIENT EFFECTS

Three plots (sites 2, 3 and 8, plots TN_4500, TS_2500 and TS_1500, respectively) were very different from the others in the combination between stand structure, biomass and the environmental characteristics. Two of these plots were along stream margins. Site 3 TS_2500 eventually got flooded during the rainy season (however not characterizing a floodplain forest which presents predictable flood pulse), and Site 2 TN_4500 is not subject to flooding but located in a different soil formation (comprising the headwaters of a white-water lake), with relatively high contents of available P and high stocks of biomass (differing from the regional pattern). Site 8 TS_1500 had notable abundance of a banana-like monocot (*Phenakospermum guyanensis*). If considered in the analyses, the leverage of these putative outlier plots would greatly change the slope, but not the direction, of the curve masking relationships with stand biomass and creating spurious relationships with the density of stems and mean individual mass (see partial regressions in Fig. 5). Therefore, we excluded these plots from the linear mixed-model analyses; however, they are presented in the partial-regression graphs on Fig. 5 and in Table S4.

No relationship was found between stand biomass and dry-season length or frequency of storms (Table 2). However, forest structure changed along these gradients. Forests in areas with longer dry season had lower density of stems and higher mean individual mass, whereas forests with higher frequency of storms had higher density of stems and lower mean individual mass.

Soils with more available P showed lower stand biomass and a trend of decreasing density of stems ($P = 0.054$), although no trend was detected for mean individual mass. Soils with higher sum of bases tended to have lower mean individual mass and also lower stand biomass ($P = 0.07$). No relationship was found between the density of stems and the sum of bases in the soil (Fig. 5). Soils with more physical restrictions had lower mean individual mass and no trends in the density of stems or stand biomass (Fig. 5). All results of the linear mixed-effect models with a minimum diameter of 10 cm are presented in Table S4.

Discussion

Large trees are rare along the Purus–Madeira interfluvium in central-southern Amazonia, they contribute relatively little to stand biomass and most of the stand biomass is in small- to mid-sized diameter classes. Forests with higher stand biomass are the ones with higher density of stems, contrary to the expectation for resource-limited forests (Westoby 1984; Luysaert *et al.* 2008). These results suggest that disturbance regimes may play a major role in regional variation of above-ground biomass and total carbon stocks. Another prediction of self-thinning theory did hold up, however. Mean individual mass scaled with stem density according to an inverse power law with a $-2/3$ scaling exponent. Thus, the resource limitation and density-dependent mortality dynamics associated with self thinning also appear to affect biomass and forest structure. A mosaic of different stages of recovery from disturbances may explain the relationships between stand biomass, individual mass and the density of stems. Future work should seek to reconcile these patterns with additional research into the mechanisms of size-structured dynamics and a broader-scale variation in forest biomass.

RELATIONSHIPS BETWEEN STAND-BIOMASS DISTRIBUTION AND FOREST-STRUCTURE COMPONENTS

Static size distributions used here may reflect disturbance regimes (Brown, Schroeder & Birdsey 1997; Williams, Hill & Ryan 2013) and give insights into phenomena driving forest structure (Niklas, Midgley & Rand 2003b). In most plots in the Purus–Madeira interfluvium, half of the stand biomass occurs in trees with $\text{dbh} < 27$ cm and only around 5% occurs in large trees (> 70 cm dbh). Although we have not monitored vegetation dynamics in the study area, a low proportion of biomass in large trees is considered a structural indicator of past disturbance and a present recovery stage in tropical forests (Brown & Lugo 1992; Brown, Schroeder & Birdsey 1997). These findings suggest that forests along Purus–Madeira interfluvium may be experiencing regimes of frequent disturbances, since these can cause higher mortality in large trees or prevent trees reaching large diameters (Coomes *et al.* 2003; Niklas, Midgley & Rand 2003b). However, future work will need to consider additional factors that may control maximum tree size.

Table 1. Forest-structure properties and stand biomass considering all stems with dbh ≥ 1 cm and environmental variables of 55 plots located along the Purus–Madeira interfluvium, in central-southern Amazonia (DSL – dry-season length; Π_1 – soil physical index)

Site	Plot id	Stems ha ⁻¹	Mean individual mass (kg)	Stand basal area (m ²)	Stand biomass (Mg ha ⁻¹)	DSL (months year ⁻¹)	Frequency of storms (days year ⁻¹)	Soil available P (mg kg ⁻¹)	Sum of bases (cmolc kg ⁻¹)	Π_1
1	TN_0500	3861	45	25.3	175	3.1	35	6.33	0.25	10
1	TN_1500	3562	43	22.9	152	3.1	37	6.36	0.32	10
1	TN_2500	2051	60	19.0	124	3.1	35	6.38	0.15	10
1	TN_3500	3129	53	25.4	167	3.1	35	4.33	0.38	10
1	TN_4500	3573	40	20.8	144	3.1	35	3.30	0.49	10
2	TN_0500	4197	50	28.1	209	3.0	42	1.79	0.22	8
2	TN_1500	5796	37	28.6	212	3.0	42	2.09	0.30	10
2	TN_2500	3837	55	25.4	210	3.0	42	2.47	0.11	8
2	TN_3500	5331	43	26.4	231	3.0	42	1.22	0.13	8
2	TN_4500	5112	59	33.1	301	3.0	42	4.80	0.10	8
3	TN_4500	7920	31	32.0	243	2.4	57	1.43	0.24	6
3	TS_0500	7621	30	28.0	229	2.4	58	1.01	0.18	7
3	TS_1500	8889	30	32.0	269	2.4	58	2.13	0.19	6
3	TS_2500	3505	54	22.0	188	2.4	58	4.70	0.27	10
3	TS_3500	6773	30	27.4	200	2.4	57	1.75	0.14	7
4	TN_(-)0500	7533	24	28.6	180	2.1	52	2.52	0.19	8
4	TN_0500	9091	25	33.4	225	2.1	52	1.05	0.24	8
4	TN_1500	7950	29	32.4	232	2.1	52	1.89	0.15	7
4	TN_2500	8408	29	35.1	244	2.1	52	2.81	0.15	6
4	TN_3500	9651	24	33.8	230	2.1	52	1.97	0.15	6
5	TN_(-)0500	8478	23	28.0	199	2.0	53	2.05	0.26	8
5	TN_0500	8257	30	37.2	245	2.0	53	2.38	0.10	11
5	TN_1500	8507	30	34.9	253	2.0	53	1.58	0.19	8
5	TN_2500	10506	27	37.3	284	2.0	53	3.19	0.15	8
5	TN_3500	11475	27	38.9	304	2.0	53	1.76	0.15	8
6	TN_(-)0500	6359	41	34.8	258	2.1	60	2.02	0.20	4
6	TN_0500	8160	34	34.5	275	2.1	60	1.88	0.09	4
6	TN_1500	6609	36	29.7	241	2.1	60	2.31	0.09	5
6	TN_2500	7801	35	35.9	275	2.1	58	0.78	0.13	8
6	TN_3500	8312	30	35.2	249	2.1	58	2.23	0.26	9
7	TS_0500	5788	51	30.9	296	2.5	47	0.83	0.11	6
7	TS_1500	7227	42	31.8	302	2.5	47	0.82	0.22	9
7	TS_2500	8240	42	34.2	346	2.5	53	0.69	0.11	5
7	TS_3500	8052	35	33.7	281	2.5	53	1.14	0.09	6
7	TS_4500	8379	39	35.8	328	2.5	54	1.14	0.10	10
8	TS_0500	5725	54	33.5	308	3.3	54	0.95	0.14	4
8	TS_1500	7365	26	27.2	189	3.3	54	0.95	0.09	4
8	TS_2500	6948	35	31.6	241	3.3	54	1.46	0.15	4
8	TS_3500	5970	39	29.5	231	3.3	54	2.61	0.14	5
8	TS_4500	6828	34	33.5	231	3.3	54	2.03	0.15	7
9	TS_0500	6945	35	32.5	241	3.4	57	2.49	0.16	9
9	TS_1500	9149	29	31.6	262	3.4	57	0.67	0.16	8
9	TS_2500	9609	23	30.9	225	3.4	57	0.86	0.15	9
9	TS_3500	9997	26	32.8	260	3.4	57	1.79	0.13	9
9	TS_4500	10096	27	31.4	274	3.4	57	0.65	0.20	7
10	TS_0500	6980	38	32.3	267	3.5	58	2.05	0.21	4
10	TS_1500	4766	61	32.5	289	3.5	58	0.83	0.12	4
10	TS_2500	5882	40	27.8	236	3.5	58	1.71	0.10	2
10	TS_3500	4432	61	28.4	272	3.5	58	2.21	0.10	2
10	TS_4500	5011	51	30.6	258	3.5	58	1.52	0.10	2
11	TN_0500	4676	42	28.0	198	3.9	50	2.18	0.13	7
11	TN_1500	3330	79	29.8	262	3.9	50	2.26	0.14	7
11	TN_2500	4180	50	26.8	208	3.9	50	2.79	0.09	10
11	TN_3500	3631	58	27.8	212	3.9	50	3.94	0.18	10
11	TN_4500	4090	46	24.6	187	3.9	50	2.25	0.12	9

Gap formation by mortality of large trees increases light and space availability and initiates a stage of understorey recovery in which competitive thinning is reduced due to the

decrease in stem density (Brokaw 1985; Clark 1992). Later in the regeneration process, the density of stems increases and density-dependent mortality becomes more important.

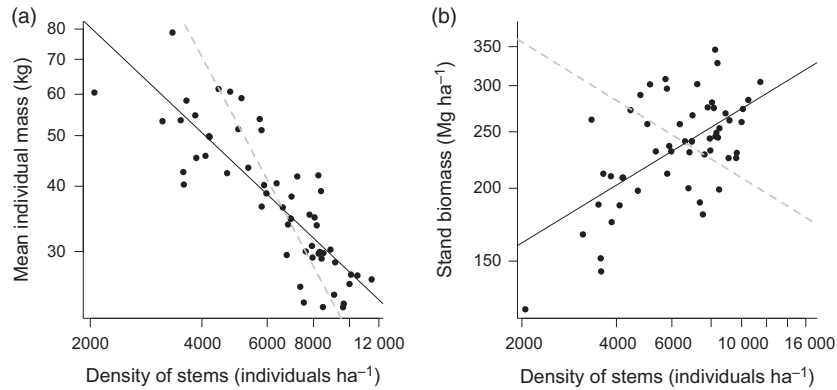


Fig. 2. Relationships between (a) mean individual mass (B_i) and density of stems (N) ($r^2 = 0.70$, scaling factor, $b = -0.67$); and (b) stand biomass (SB) and the density of stems ($r^2 = 0.36$, scaling factor, $b = 0.33$) for individuals with $\text{dbh} \geq 1$ cm in 55 1-ha plots in central-southern Amazonia. Variables were $\log_{10}$ -transformed and both relationships were significant ($P < 0.001$). The individual mass relationship agrees with self-thinning theory, while the relationship between total stand biomass and density does not. The negative relationships predicted by self-thinning are shown by the grey dashed lines, which are predicted by the process of density-dependent mortality, in which $B_i \sim N^{-4/3}$ and $SB \sim N^{-1/3}$.

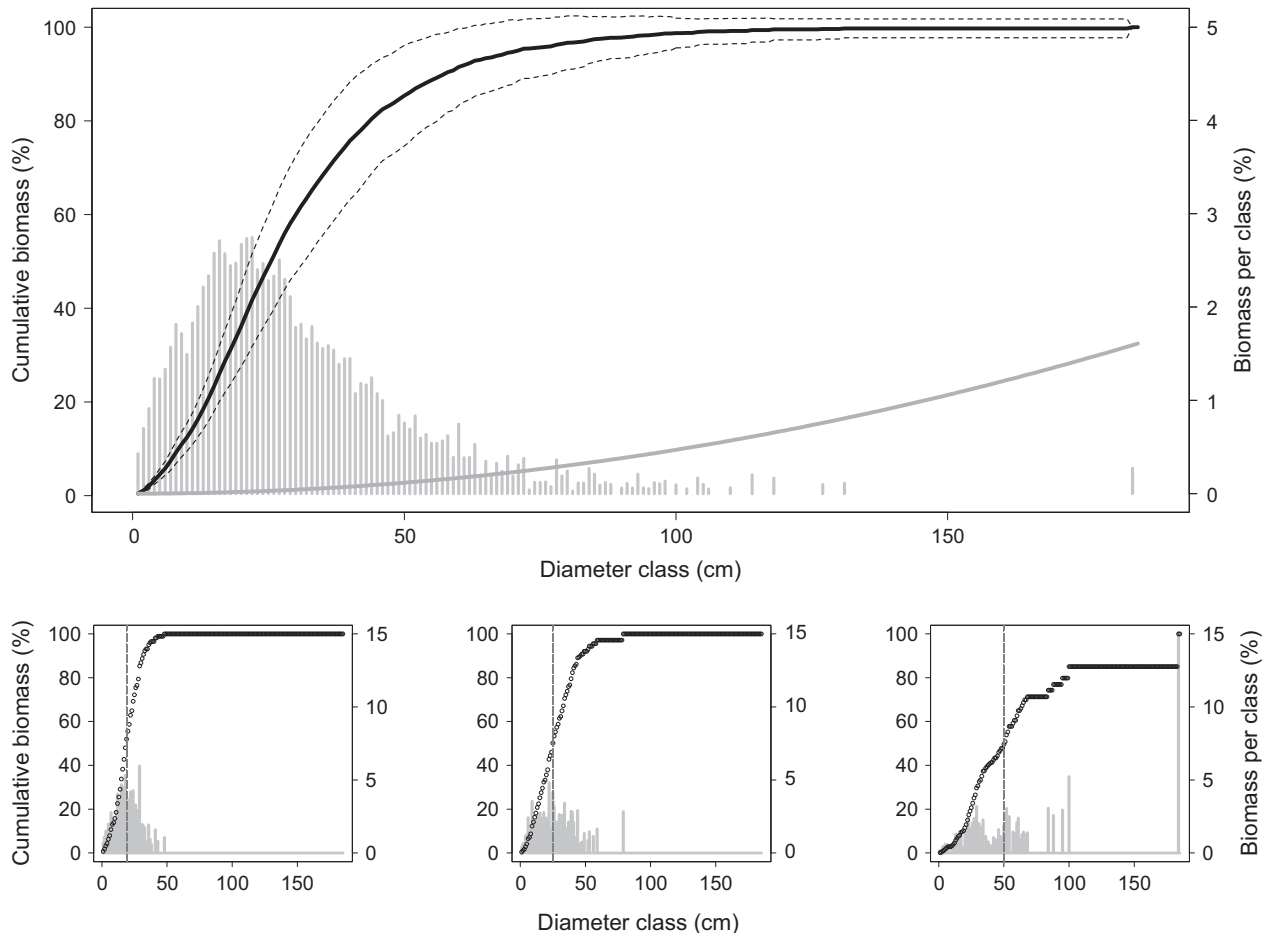


Fig. 3. Cumulative proportions of stand biomass in 1-cm size classes over all 55 1-ha plots along the Purus–Madeira interfluvium, in central-southern Amazonia (upper). The lower graphs show data for three plots, exemplifying the extremes (19–50 cm) and mean diameter value (26 cm) at 50% stand biomass accumulation (dashed lines). Grey bars show the biomass per 1-cm DBH interval, and the black circles show the cumulative biomass curve. The grey line in the upper graph shows the self-thinning prediction of biomass accumulation among size classes.

If disturbances are frequent, the positive relationship between stand biomass and density of individuals found across space in the forests of the Purus–Madeira interfluvium could be a

result of recovering states from past perturbations in the canopy. Based on current patterns of stand biomass, stems density and mean biomass relationships, there appears to be a

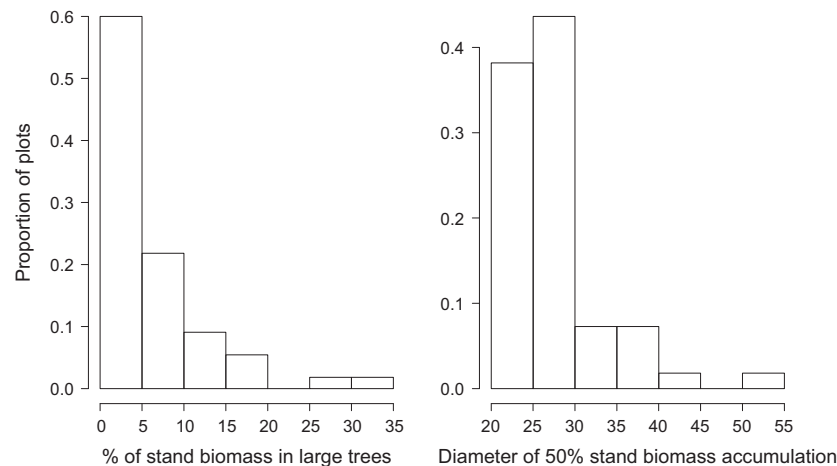


Fig. 4. Left – Density histograms showing that 60% of the plots in the Purus–Madeira interfluvial area hold < 5% of the stand biomass in large trees (dbh $\geq$ 70 cm). Right – In approximately 80% of the plots, half of the stand biomass was in trees with diameter at breast height < 27 cm.

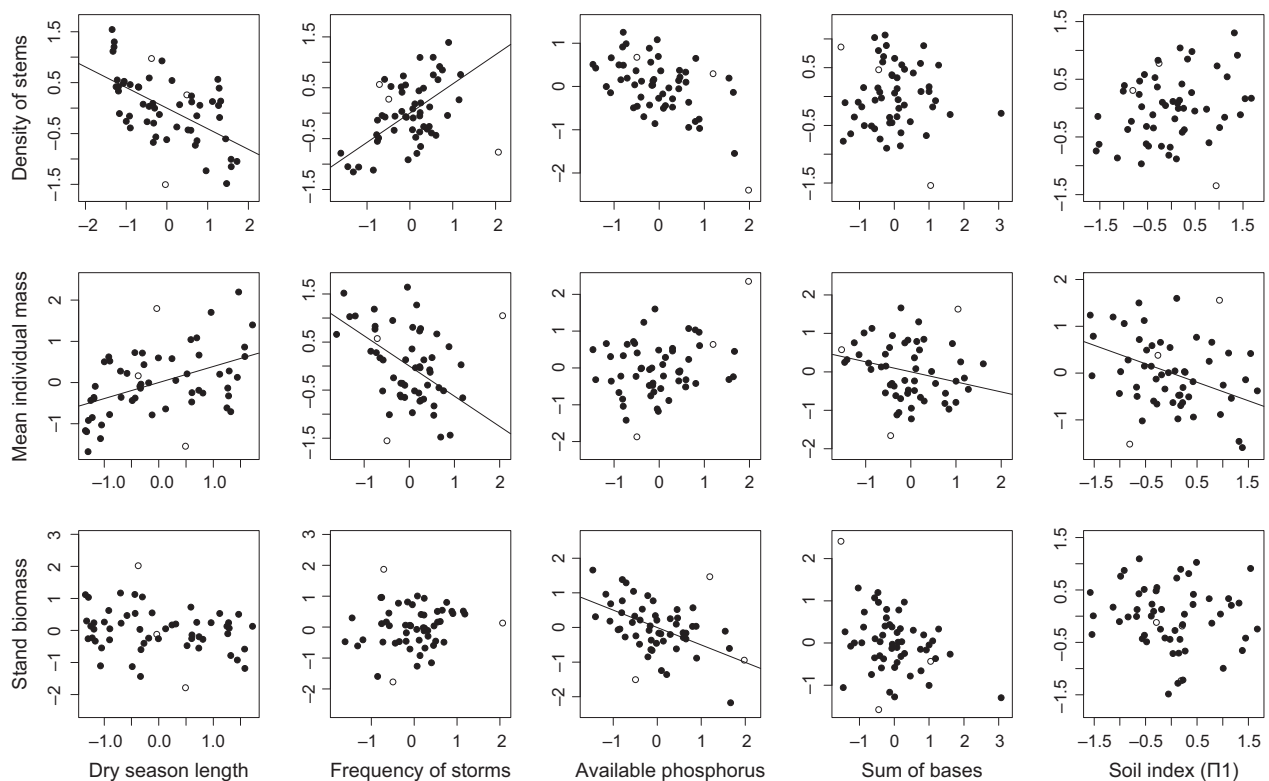


Fig. 5. Partial regressions derived from multiple regressions investigating the effects of dry-season length, frequency of storms, soil-available phosphorus, sum of bases and soil-physical-restriction index (soil index Π_1) on the (upper) density of stems ($R^2_{\text{marginal}} = 0.68$), (centre) individual mass ($R^2_{\text{marginal}} = 0.49$) and (bottom) stand biomass ($R^2_{\text{marginal}} = 0.57$) in forests along the Purus–Madeira interfluvial, in central-southern Amazonia. Fitted lines indicate fixed-effect probabilities < 0.05 in the linear mixed-model analyses excluding outliers (open circles, see the main text for more details).

balance between biomass accumulation driven by density-dependent and disturbance-initiated mortality in which resource limitation does not offset biomass accumulation from recovery states in these forests.

The negative relationship between stand biomass and the density of stems was also not found in other tropical forests in Africa (Lewis *et al.* 2013) and Borneo (Slik *et al.* 2010).

Lewis *et al.* (2013) and Slik *et al.* (2010) considered only stems with diameter $\geq$ 10 cm and actually, they found no relationship between these variables and not a positive relationship like we observed in central-southern Amazonia. Our results show that small stems can have a large contribution to stand biomass and that excluding 1- to 10-cm-diameter stems can weaken the relationship between stand biomass and the

Table 2. Results of the linear mixed-effect models (LMM) for the density of stems, average individual mass and stand biomass of individuals with dbh ≥ 1 cm as functions of dry-season length, frequency of storms, available phosphorus (available P), sum of bases and the index of soil physical restrictions, Π_1 (Quesada *et al.* 2010), (all fixed effects). Site was considered a random effect in all models. Marginal R^2 (R^2_{marg}) values are for the models adjusted only considering fixed effects, and the conditional R^2 (R^2_{cond}) corresponds to the full model, including the random effect. The relative contribution of predictors is given by the standardized coefficients of the LMMs. Probability for each predictor is shown in parentheses. Standardized coefficients in bold have $P < 0.05$.

Dependent variables	R^2		Relative contribution of predictors				
	R^2_{marg}	R^2_{cond}	Dry-season length	Frequency of storms	Available P	Sum of bases	Soil physical restrictions (Π_1)
Density of stems	0.73	0.85	−0.41 (0.007)	0.63 (< 0.001)	−0.19 (0.054)	0.12 (0.136)	0.15 (0.104)
Individual mass	0.56	0.74	0.45 (0.013)	−0.60 (0.003)	0.01 (0.907)	−0.22 (0.027)	−0.28 (0.023)
Stand biomass	0.64	0.69	−0.12 (0.298)	0.22 (0.154)	−0.44 (< 0.001)	−0.18 (0.071)	−0.09 (0.414)

density of stems. Therefore, different patterns of stand biomass and stem density relationship could be an artefact of not including 1- to 10-cm-diameter stems in the analyses. Alternatively, different patterns among tropical forest structure may be explained by other mechanisms such as dissimilar frequency of disturbance regimes acting on these forests, as suggested by Lewis *et al.* (2013).

SEASONALITY AND NATURAL DISTURBANCES

Dry-season length is considered a constraint for biomass accumulation (Chave *et al.* 2004; Malhi *et al.* 2006). We found strong and opposite effects of dry-season length on stand structural components but no relationship with stand biomass. Forests in sites with longer dry seasons along the Purus–Madeira interfluvium (4 months per year) had lower densities of stems and higher mean individual mass. Previous studies have also shown higher density of stems in less seasonal forests (Ter Steege *et al.* 2003; Phillips *et al.* 2004; Vieira *et al.* 2004; Slik *et al.* 2010), although these studies considered only trees with a minimum diameter of 10 cm. This can be linked to higher germination and recruitment of new individuals in wet-season conditions (Lieberman & Li 1992). The opposite trend in mean individual mass with dry-season length may be essentially a self-thinning result of the variation in the density of stems, or an indication that wet-season conditions could be unfavourable for tree growth in this region. The hypoxic and anoxic conditions caused by poor soil-water drainage (Sombroek 2000) and the shallow water-table in the Purus–Madeira interfluvium (Fan & Miguez-Macho 2010) are also associated with lower photosynthetically active radiation during the rainy season (Saleska *et al.* 2003; Brando *et al.* 2010). Despite the relatively strong effects of dry-season length on stand structural components, no significant relationship between stand biomass and seasonality was found. It is likely that opposite effects of stem density and mean individual biomass counterbalanced each other, resulting in an insignificant overall effect of dry-season length on stand biomass.

Forests with more frequent storms displayed greater density of stems and had lower mean individual mass. The higher density of stems is expected in more recently disturbed forests

as a response to gap formation in the canopy and increased resource availability (Brokaw 1985; Denslow 1995). The lower mean mass of individuals in forests experiencing more frequent storms could be a result of higher mortality rates associated with wind disturbances preventing trees reaching larger sizes. The susceptibility of stems to mortality due to windfalls in central Amazonia seems to be higher in mid- to large-sized trees (Marra *et al.* 2014), and the return time of these events can be ~100 year in the case of gaps less than 1 ha (Espírito-Santo *et al.* 2014). Gap formation regime with increased resource availability and higher tree mortality may explain changes in the forest size-structure along the storm frequency gradient, despite no significant change in stand biomass was detected along this gradient.

More fertile soils in the western Amazon usually support lower stand biomass than forests in the east of the basin on less-fertile soils (Baker *et al.* 2004; Mitchard *et al.* 2014). This large-scale pattern has been associated with higher versus lower turnover rates (Phillips *et al.* 2004), with more fertile soils being also more physically restrictive (Quesada *et al.* 2010) and supporting fast-growing species that invest less in mass structure and have lower wood density and lower maximum heights (Van Schaik & Mirmanto 1985; Baker *et al.* 2004; Quesada *et al.* 2012). In the Purus–Madeira interfluvium, soils with more available phosphorus had lower stand biomass in accordance with the pattern already described for the Amazon basin considering trees with a minimum diameter of 10 cm (Quesada *et al.* 2012). No tendency was found in the mean mass of individuals, but stand biomass was lower on soils with more available phosphorus, probably due to the trend of decrease in the density of stems with increase in soil phosphorus. Cintra *et al.* (2013) found higher woody biomass productivity based on tree ring analyses in more phosphorus-rich soils in the same study area. These results indicate that available phosphorus in this region is contributing to a higher biomass production in forests with lower stand biomass and more sparse stems. However, the influence of phosphorus on stand biomass remains controversial (Laurance *et al.* 1999; Paoli, Curran & Slik 2008; Baraloto *et al.* 2011) and the mechanisms explaining lower stand biomass and lower density of stems in more phosphorus-rich soils needs further investigation.

Stands on soils with higher sum of bases had lower mean individual mass and a tendency of lower stand biomass. Soils with higher sum of bases in Amazonia were found to support species with lower wood specific gravity (Quesada *et al.* 2012), and this could contribute to forests with lower mean individual mass and lower stand biomass. While forests with lower stand biomass on more fertile soils in terms of sum of bases showed lower mean individual mass, forests with lower stand biomass on soils with higher available phosphorus tend to be sparser.

In our study sites, the mean mass of individual trees decreases with soil physical restrictions (Π_1) although no changes in stand wood biomass were detected along this gradient. The lower stand-mean individual mass is expected for forests with small-sized trees due to the positive feedback caused by soil-initiated disturbances (Quesada *et al.* 2012). However, we hypothesize that mortality potentially caused by exogenous disturbances, such as windstorms, may be magnified by restrictive soil physical conditions in the region, with trees becoming more susceptible to uprooting in shallow soils that give low anchorage. Soil physical restrictions in the Purus–Madeira interfluvium seem to be associated mainly with high soil-water saturation (due to shallow water-table and poor soil drainage) and low soil depth. Besides having shorter trees (J. Schietti, unpubl. data) with lower individual mass, stands on these soils are also younger (Cintra *et al.* 2013), indicating that the disturbance regime in the region is limiting tree size and age.

Accumulation of stand biomass results from a multitude of effects operating at different spatial and time-scales. However, the effects of these on stand biomass in an area must act through density of stems and/or mean mass of individual trees and the balance of these two components defines most of the variation in stand biomass. Even though stand biomass varied little along some environmental gradients, forest structure changed along the same gradients. The effects of environmental gradients on these stand-structure components are variable, with clearer influences of dry-season length and the frequency of storms than soil properties on stand-structure components. It is also not known how these relationships will respond to future perturbations, such as climate change or human exploitation of the forest. Future studies of the determinants of plot-level biomass in tropical forests should investigate the individual components of biomass, and perhaps even additional decomposition to contributions of height, diameter and wood specific gravity. To improve our understanding and predictions of stand-biomass distribution, it will be necessary to investigate size-structure, including small size stems, and the effects of environmental gradients on all components of stand biomass.

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Data accessibility

All data used in this study are present in Table 1 and in the Supporting Information.

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Supporting Information

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

Table S1. Allometric constant (b), scaling exponent (a), coefficient of determination (r^2) and the number of measured trees for the Height–Diameter (H – D) allometric models adjusted for each of the 11 sites along the Purus-Madeira interfluvium in central Amazonia. H – D models were adjusted using power functions, $H = b * D^a$.

Table S2. Components of the soil physical restriction index from (Quesada *et al.* 2010). The summation of all components gives the Π_1 index.

Table S3. Forest-structure properties and stand biomass considering stems with $\text{dbh} \geq 1$ cm (≥ 1), $1 \text{ cm} \leq \text{dbh} < 10$ cm (1 – 10) and $\text{dbh} \geq 10$ cm (≥ 10) in 55 plots located along the Purus-Madeira interfluvium, in central-southern Amazonia.

Table S4. Results of linear mixed-effect models (LMM) for the density of stems, average individual mass and stand biomass of individuals with $\text{dbh} \geq 1$ cm and ≥ 10 cm as functions of dry-season length, frequency of storms, available phosphorus (available P), sum of bases and the index of soil physical restrictions (Π_1 – Quesada *et al.* 2010), (fixed effects). Site was considered a random effect in all models. Marginal R^2 (R^2_{marg}) values are for the models adjusted only considering fixed effects and the conditional R^2 (R^2_{cond}) corresponds to the full model, including the random effect. The relative contribution of predictors is given by the standardized coefficients of the LMMs. Probability for each predictor is shown in parentheses. Standardized coefficients in bold have $P < 0.05$. The three outliers excluded in the analyses presented in the manuscript are showed here in both diameter limit of inclusion.

Figure S1. Errors in tree height estimation ($\text{height}_{\text{estimated}} - \text{height}_{\text{predicted}}$) according to H – D site-adjusted equations of this study (a) (Table S1) and five other H – D equations: Weibull models for Western Amazonian forests ($H = 46.263(1 - \exp(-0.0876 \text{ dbh}^{0.6072}))$) (b) and for Central-Eastern Amazonia ($H = 48.131(1 - \exp(-0.0375 \text{ dbh}^{0.8228}))$) (c) from Feldpausch *et al.* (2012), and H – D Power models for Central Amazonia Dense Forest ($\text{Log}(H) = 0.625 + 0.538 * \log(\text{dbh})$) (c), Southern Amazonia Open Forest ($\text{Log}(H) = 0.564 + 0.558 * \text{Log}(\text{dbh})$) (d), and for Southwestern Amazonia Dense Forests ($\text{Log}(H) = 0.494 + 0.576 * \text{Log}(\text{dbh})$) (e) from Nogueira *et al.* (2008). Each colour represents one of the eleven sites along the Purus-Madeira interfluvium.

Figure S2. Relationships between (a) mean individual mass, B_i , and density of stems, N , ($r^2 = 0.38$, scaling factor, $b = -0.73$); and (b) stand biomass, SB , and the density of stems ($r^2 = 0.08$, scaling factor, $b = 0.27$) for individuals with $\text{dbh} \geq 10$ cm in 55 1-ha plots in central-southern Amazonia. Variables were log 10-transformed and both relationships were significant ($P < 0.001$ and $P = 0.04$ respectively). The individual mass relationship agrees with self-thinning theory, while the relationship between total stand biomass and density does not; self-thinning predicts a negative relationship. The grey dashed lines show the predictions according to the process of density dependent mortality by self-thinning, which predicts that $B_i \sim N^{-4/3}$ and $SB \sim N^{-1/3}$.

Table S5. Results of the linear regression analyses between mean individual mass, density of stems and stand biomass considering all 55 plots (with both minimum diameter of inclusion, 1 and 10 cm) and only the 22 plots with species identification of individuals with diameter ≥ 10 cm. Variables were log 10-transformed.

Table S6. Supplementary data.