

Palm live aboveground biomass in the riparian zones of a forest in Central Amazonia

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Abstract

Aboveground biomass estimates in the Amazon region remain uncertain, partly due to extrapolations based mainly on samples collected in upland terrains of *terra-firme* forests. Most biomass estimates were focused on dicotyledonous trees or included other plant groups as a category of trees. Palms dominate areas that represent 20% of the Brazilian Amazon. However, their contribution to biomass estimates and the variation within riparian zones remain poorly documented. We estimated the biomass of palms larger than 1-cm diameter at breast height (1.3 m aboveground) in riparian plots ($n = 40$); investigated the potential bias caused by the use of dicotyledonous- or family-rather than species-level equations for biomass estimation; compared palm biomass between riparian and non-riparian plots ($n = 72$); and evaluated the effects of soil, topography, and stream characteristics in riparian plots on palm biomass. Mean palm biomass in riparian zones estimated with species-level equations (27.50 ± 12.94 Mg/ha, range: 3.32–63.27 Mg/ha) was three times greater than biomass estimated with a family-level equation (9.04 ± 4.29 Mg/ha, range: 1.51–21.25 Mg/ha) and was greater than mean biomass estimated with a pantropical equation (20.46 ± 9.29 Mg/ha, range: 3.67–47.99 Mg/ha). Mean palm biomass in riparian zones was four times greater than in non-riparian zones. Palm biomass was high in flatter areas with poorly drained soils, but lower around streams with higher discharge. Inclusion of palms can contribute to reducing the uncertainties in biomass estimates in Amazonian forests. Recognition of the importance of riparian zones may improve conservation policies.

Abstract in Portuguese is available with online material.

KEYWORDS

Allometric equations, Amazon rainforest, Arecaceae, Brazil, environmental heterogeneity, shallow water table forests

1 | INTRODUCTION

Palms (Arecaceae) are emblematic and conspicuous components of the tropical rainforest. In Amazonian forests, six of the ten most common tree species in forest inventories are palms (ter Steege

et al., 2013). Myriad animals feed on palm fruits and indigenous and rural communities rely on palms for food security and household constructions (Henderson, 2002; Zambrana et al., 2007). The importance of palms as providers of a variety of products (i.e., fruits, fibers, oil, and wood) that secure the well-being of Amazonian inhabitants

has been widely recognized (Cámara-Leret et al., 2014; Zambrana et al., 2007). However, the role of palms in ecosystem services related to climate regulation through carbon stocks (i.e., aboveground biomass) has been little recognized.

The overlooked role of palms in the carbon cycle could be attributed to the fact that most forest-monitoring programs prioritized a widespread forest type in the Amazon called “*terra-firme*” (Luize et al., 2018). *Terra-firme* forests are not affected by seasonally inundations from large rivers, such as “várzea” and “igapo” forest types (Bredin et al., 2020), but waterlogged areas appear in low topographic positions frequently besides small streams (Costa et al., 2022). Teams establishing sampling plots have often avoided areas near streams (e.g., Laurance et al., 1999), where arborescent palms are commonly abundant (for some exceptions see Castilho et al., 2006, Draper et al., 2014, Zelarayán et al., 2015 and Toledo et al., 2017).

Palms were frequently excluded or analyzed as dicotyledonous trees in aboveground-biomass (AGB) estimates (e.g., Baker et al., 2004; Laurance et al., 1999) due to the lack of palm-family or species-level allometric equations at the time of those studies. Dicotyledonous trees and palms have structural and functional differences. For instance, wood density in palms is generally lower than in trees (Chave et al., 2009; Zanne et al., 2009); trees can increase the number of branches and hence crown size (Chave et al., 2005), but crown size is fixed in palms that rarely show aerial branches (Tomlinson, 2006). Furthermore, despite some palm species exhibiting secondary thickening due to the presence of a meristem band (e.g., *Attalea geraensis*, *Butia paraguayensis* and *Syagrus petraea*; Botânico & Angyalossy, 2013), the diameter–height relationship in most palm species is weak (Goodman et al., 2013). For those reasons, tree allometric equations are not appropriate for estimation of palm biomass.

Riparian zones are regularly influenced by inundation and extend from stream edges to the edges of upland communities (Décamps et al., 2009). In Central Amazonian *terra-firme* forests, most riparian zones are the lowest extreme of the topographic gradient (Ribeiro et al., 1999). These areas have distinctive plant–species composition (Drucker et al., 2008; Guedes et al., 2022; Pansini et al., 2016; Schietti et al., 2014) and provide multiple ecosystem services (Dybala et al., 2019). Vegetation in riparian zones contributes to carbon sequestration (Zelarayán et al., 2015), not only as AGB but also in soils with potential for long-term carbon storage (Sutfin et al., 2016). Variation in plant composition within riparian ecosystems is related to changes in hydrologic regime, soil-moisture conditions, and terrain surface features (Sutfin et al., 2016).

The stressful environment in riparian zones due to flooding events influences plant growth and mortality–recruitment dynamics, allowing the dominance of plants adapted to poorly structured soils, such as palms (Emilio et al., 2014), that are common under waterlogged conditions, and consequently modulate AGB stocks. Palm vascular anatomy and root structure differ from trees (Tomlinson, 2006), which make them more resistant to embolism than trees (Aparecido et al., 2015). These adaptations could explain the greater abundance of arborescent palms in riparian zones.

Palm AGB varies greatly at the landscape scale (~1–10% of the AGB per hectare) in Amazonian *terra-firme* forests, and this variation is related to soil properties, with higher palm AGB on poorly drained sandy soils, and where the water table is closer to the surface (Castilho et al., 2006; Emilio et al., 2014; Muscarella et al., 2020; Toledo et al., 2017). Areas over shallow water tables (<5 m-depth) cover about 52.4% of the Amazon *terra-firme* forests and are mostly confined to the margins of streams in the eastern, northern, and southern portions of the Amazon (Costa et al., 2022). Hence, the inclusion of palms could influence AGB estimates, especially where palms dominate forest (Goodman et al., 2013; Muscarella et al., 2020), such as in the riparian zones.

Palm AGB estimates vary depending on the availability and selection of allometric equations. Equations developed for dicotyledonous trees perform poorly for palms and could induce AGB overestimation, if compared with family-level AGB estimates (e.g., Muscarella et al., 2020). The AGB estimates using family-level equations are potentially more accurate than those based on equations for dicotyledonous trees, especially when the equations include height, but can underestimate AGB when compared to species-level AGB estimates (Goodman et al., 2013). Diameter and height allometry vary among palm species (Avalos et al., 2019), so pooling different palm species in an equation affects AGB estimates.

In this study, we aim to (a) investigate the contribution of palms to forest AGB at the landscape scale (64 km²), adding 40 1-hectare plots established in riparian zones (riparian plots) adjacent to first to third-order streams to a previous set of 72 1-ha plots (non-riparian plots) in a forest in central Amazonia; (b) evaluate the potential bias caused using dicotyledonous or family-level rather than species-level equations for palm AGB; (c) compare palm AGB between riparian and non-riparian plots; and (d) quantify the effects of environmental characteristics (soil texture and nutrients, terrain slope, and stream discharge) on the spatial variation in palm AGB estimates within riparian zones.

2 | METHODS

2.1 | Study area and sampling design

The study was conducted in Reserva Florestal Adolpho Ducke (RFAD), on the outskirts of Manaus city, Amazonas State, Brazil (02°55' S, 59°58' W) (Figure 1). The reserve covers 10 km² of *terra-firme* tropical rain forest, with a 30–37-m-high closed canopy (Guillaumet, 1987; Ribeiro et al., 1999). Between 1966 and 2016 the mean annual rainfall at the RFAD was 2572 ± 351 mm. The driest month was August with a mean rainfall of 98.8 ± 49.1 mm and a mean temperature of 26 ± 1°C. The wettest month was April, with a mean rainfall of 331.4 ± 88.8 mm and a mean temperature of 25.2 ± 0.9°C (Esteban et al., 2021). The dominant soil type is clayey yellow latosol on higher areas, transitioning to sandy hydromorphic podzols in the riparian areas of valley bottoms (Chauvel et al., 1987). The valley bottoms (hereafter, riparian zones) are areas with shallow water table and soils almost

permanently waterlogged, especially during the rainy season (Schietti et al., 2014).

The RFAD covers two major drainage basins (western and eastern) separated by a central ridge (Jorge et al., 2016); however, the stream network can be divided into five sub-basins (Rodrigues

et al., 2010). Streams vary from first to third order and the reserve is not subject to flooding by large rivers (Schietti et al., 2014). The streams in the eastern basin flow into the tributaries of the Amazon River and those in the western basin flow into tributaries of the Negro River (Castilho et al., 2006). Riparian zones are subject to

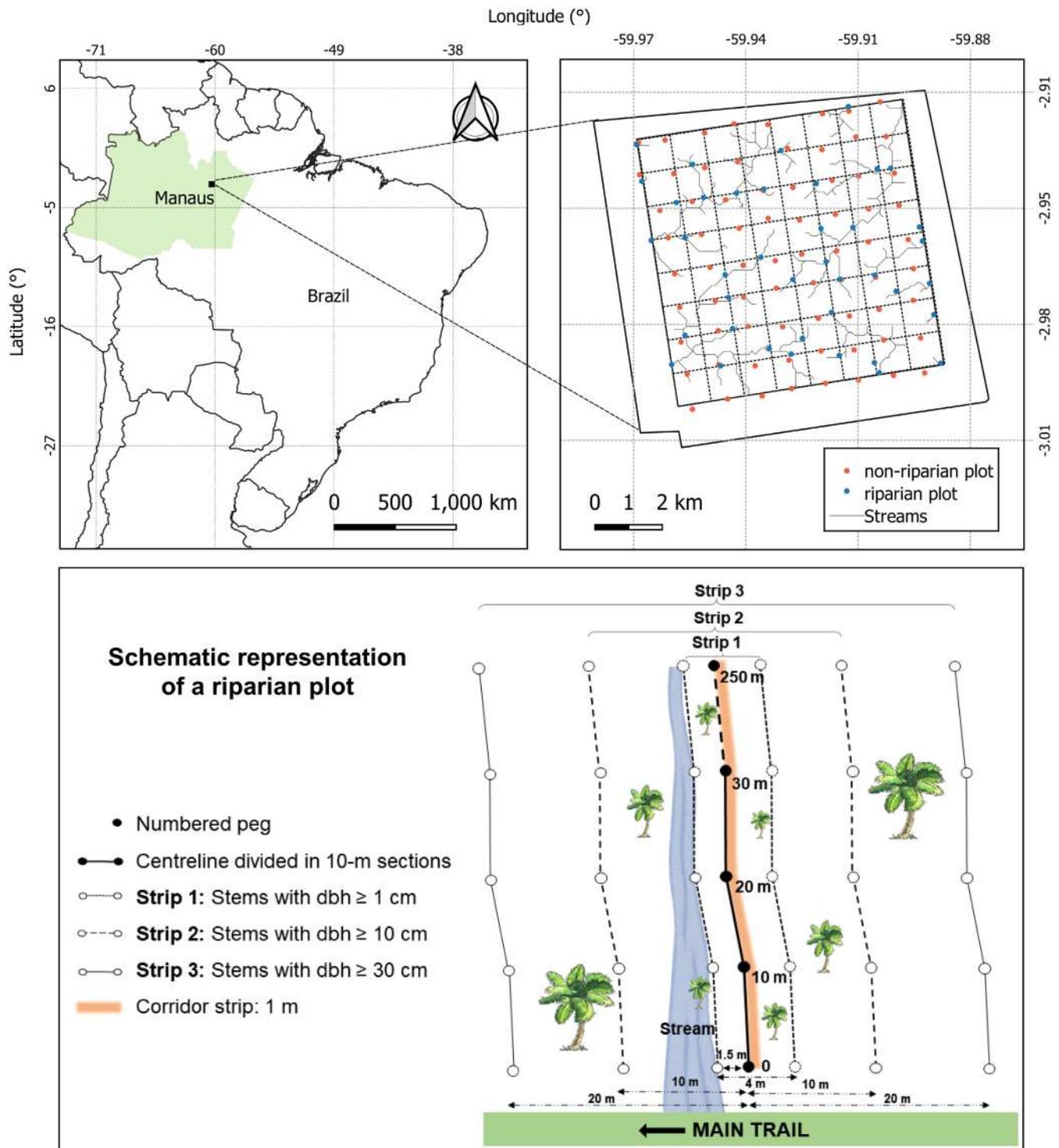


FIGURE 1 Map showing the study area located in the Amazonas state, Brazil, and the grid system in Reserva Florestal Adolpho Ducke (RFAD) with 72 non-riparian plots (orange filled circles) and 40 riparian plots (blue filled circles); black lines represent streams. The bottom design is a schematic representation of a riparian plot and the hierarchical sampling of palms within each plot. Geographic coordinate system, datum WGS84.

flooding after heavy rain events, resulting in frequent waterlogging that lasts for hours after rain stops (Jorge et al., 2016). These conditions promote distinct plant-assemblage composition (Drucker et al., 2008; Schiatti et al., 2014). The canopy in riparian zones reaches 25–30 m high in RFAD, and is composed of arborescent palms (e.g., *Oenocarpus bataua* and *Euterpe precatoria*), dicotyledonous trees (e.g., *Chrysophyllum sanguinolentum*; *Eperua duckeana* and *Pourouma ovata*; Toledo et al., 2017), and a dense understory composed of herbs and stemless palms (Ribeiro et al., 1999).

We sampled 40 riparian plots uniformly distributed across the western and eastern basins within a 64-km² trail system throughout RFAD. Plots followed the RAPELD system, a spatially standardized sampling method for use in long-term ecological research, which allows unbiased comparisons among sampling sites (Magnusson et al., 2005). Riparian plots have a centerline that runs ≥ 1.5 m from stream margins divided in 25 10-m linear segments (see Figure 1). More information can be found at https://ppbio.inpa.gov.br/en/Riparian_Plots.

2.2 | Vegetation data

We sampled palms in riparian plots following the methods for sampling trees and palms in non-riparian plots (for details see Castilho et al., 2006). These plots follow the topographic contours to minimize within-plot variation in vegetation (Magnusson et al., 2005), and cover the classes (plateau, slope, and valley) most used to classify topography in the RFAD (Ribeiro et al., 1999). We used a hierarchical design in which diameter at breast height (dbh) was used to define sampling areas (Castilho et al., 2006) as follows: stems with dbh ≥ 30 cm were sampled within ~ 1 hectare (ha) (250 \times 40 m); stems with 10 cm \leq dbh < 30 cm were sampled within ~ 0.5 ha (250 \times 20 m); and stems with 1 cm \leq dbh < 10 cm were sampled in a subplot of ~ 0.1 ha (250 \times 4 m) (see Figure 1). RAPELD plots vary subtly in area, but for comparison with a previous study in non-riparian plots that used the approximate plot sizes (Castilho et al., 2006), we used the same methodology.

Palm individuals were identified and measured in 40 riparian plots. The dbh was measured to the nearest 1 mm at 1.3 m above ground level. Stem height (H_{stem}) was estimated visually in 40 plots by an observer. The visual estimates were calibrated against clinometer measurements in four plots. The relationship between visual estimated height (H_{VE}) and measured height (H) was $H = 0.92 \times H_{\text{VE}} + 1.83$ ($N = 183$, $r^2 = 0.79$), with H_{VE} ranging from 3.4 to 21.5 m (see Figure S1; Notes S1). Palm species were identified in the field by a trained parataxonomist and by checking a field guide to the flora of Reserva Ducke (Ribeiro et al., 1999).

2.3 | Biomass equations

We used two allometric equations and a set of species-level equations to estimate AGB in riparian zones (Table S1). Biomass estimates using species-level equations are represented as AGB_{Sp} . To

investigate potential bias due to use of biomass equations for dicotyledonous trees to estimate palm AGB, we used the geographical-based pantropical equation (Chave et al., 2014). This equation is based on dbh, wood density (g/cm^3) and an environmental factor and is implemented in the BIOMASS package (Réjou-Méchain et al., 2017). Wood density was assigned to each species based on the finest taxonomy available in the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009). The environmental factor (E) is a measure of environmental stress estimated from the plot coordinates that account for variation in the height-diameter relationship when total height of individuals is not available. Biomass estimates using the pantropical equation are represented as AGB_{p} .

We used one of the family-level equations for Amazonian palms developed by Goodman et al. (2013) (Table S1). This equation is based on dbh, H_{stem} and dry-mass fraction (dmf). Mean stem dmf for each genus is available in Goodman et al. (2013) and the overall mean (0.37) was used for other genera. As one of our goals was to estimate palm AGB more accurately, we used a set of species-level equations (Goodman et al., 2013). For species without a specific equation, we used the equation for species from the same genus or the family-level equation. Biomass estimates with this equation are represented as AGB_{F1} .

We compared palm AGB between riparian ($n = 40$; present study) and non-riparian plots ($n = 72$; data from Castilho et al., 2006). As palm height was not measured in that study, we applied the family-level equations of Goodman et al. (2013) that are based on dbh and dmf (Table S1). Biomass estimates with this equation are represented as AGB_{F2} .

2.4 | Environmental data

Hydrological conditions in riparian zones were represented by the stream discharge (m^3/s). We used previously collected data on the width, depth, and flow velocity of streams adjacent to each riparian plot. The measurements were collected every 50 m at 6 points distributed along the stream (Jorge et al., 2016). The width (m) of the stream was measured using a tape measure stretched from one bank to the other, perpendicular to the stream course. Stream depth (m) was measured at nine regular intervals across the stream along a transect perpendicular to the stream bank. Water velocity (m/s) was estimated by launching a silicon ball in the current in the middle of the stream and recording the time for it to move 1 m (Jorge et al., 2016). Stream discharge was calculated as the product of the stream cross-sectional area (width \times mean depth) multiplied by water velocity. Stream-discharge values at the six points were averaged to obtain a single discharge value per plot.

Soil samples were collected in riparian plots at six points, each 50 m along the centerline to 10-cm depth. The six soil samples per plot were bulked into a single composite sample and cleaned of roots, air-dried, and sieved before laboratory analyses (Jorge et al., 2016).

Samples were analyzed in the Thematic Laboratory of soils and plants at INPA following standard methods (EMBRAPA, 2009) and are briefly summarized in Notes S2.

We represent topography as slope that was measured perpendicular to the main axis of the plot with a clinometer every 50 m (six in total), and the mean slope of each plot was used in the analyses. A summary of the environmental data is available in the Table S2.

2.5 | Data analyses

We calculated percent differences between AGB estimates using species-level equations and AGB estimates using family-level and pantropical equations. To compare AGB in riparian and non-riparian plots we used the non-parametric Wilcoxon rank sum test. Additionally, we reported the effect size to provide a quantitative measure of the magnitude of our results. We used the effect size of Pearson r correlation for the Wilcoxon rank sum test.

We used a correlation matrix in a Principal Component Analyses (PCA) to describe soil gradients, including 12 chemical-physical soil attributes summarized in two axes. To investigate the influence of soil, hydrological and topographic gradients on palm AGB in riparian zones, we used a generalized linear mixed model (GLMM), assuming a Gamma distribution for AGB and including sub-basin as a random effect in the model to control spatial autocorrelation between plots nested in the same sub-basin. Our model did not show multicollinearity problems as all variables showed variance inflation factor (VIF) < 1.51.

All analyses were conducted in R version 3.6.3 (R Core Team, 2022). We used the “coin” package for the Wilcoxon test (Hothorn et al., 2008). The GLMM model was built using the “lme4” package (Bates et al., 2015). For calculation of VIFs, we used the “car” package (Fox & Weisberg, 2019), to graphically display plots depicting partial residuals, we use the “visreg” package (Breheny & Burchett, 2017), and to calculate the marginal and conditional R^2 (R^2_m ; R^2_c) (Nakagawa & Schielzeth, 2013) of the model we used the “performance” package (Lüdtke et al., 2020).

3 | RESULTS

3.1 | Environmental gradients

Mean slope was $5.27 \pm 3.92^\circ$, ranging from 0.42 to 14.58° ; and mean stream discharge was $0.088 \pm 0.102 \text{ m}^3/\text{s}$, ranging from 0.004 to $0.425 \text{ m}^3/\text{s}$ (Table S2). The PCA analyses revealed two main soil gradients in riparian zones. Axis 1 captured 41.9% of the total variation in the data and was correlated with Ca^{2+} , Mg^{2+} , Al^{3+} , K^+ , P , Mn^{2+} , Zn^{2+} , and pH , which reflects the main gradients of soil fertility. Axis 2 accounted for 20.2% of the variation and was highly correlated with sand and silt contents (and to a lesser degree with Na^+ and Fe^{2+}), reflecting the textural gradient in riparian soils. Since soil properties

and topography are related in RFAD (Castilho et al., 2006), we tested for possible correlation and none of the soil variables was highly correlated with slope ($r < 0.355$ in all cases; Table S3).

3.2 | Palm species and density in riparian plots

We recorded 2379 stems (before strip extrapolation) distributed in 12 genera and 15 species in riparian plots, with *Oenocarpus bataua* and *Euterpe precatoria* being the most abundant species (Table 1).

The class containing palm with <10 cm dbh had the highest density (99.75 stems/ha), but represented, on average, less than 6.5% of the AGB per plot (with every type of equation). Palm density in the class with dbh between 10 and 30 cm (98.40 stems/ha) represented the greatest portion of AGB per plot (93%). Stems with dbh > 30 cm occurred in low density (0.30 stems/ha) and represented less than 1.3% of AGB per plot (Table S4).

3.3 | Comparisons among AGB-estimation equations

Across the 40 riparian plots, palm AGB estimates varied depending on the selection of allometric equations. Based on species-level equations (AGB_{Sp}), palms contributed from 3.32 to 63.27 Mg/ha, with a mean of $27.5 \pm 12.94 \text{ Mg/ha}$. The mean AGB estimated with the family-level equation (AGB_{F1}) was $9.04 \pm 4.29 \text{ Mg/ha}$, and the values range from 1.51 to 21.25 Mg/ha. Using the pantropical equation (AGB_{p}), mean biomass was $20.46 \pm 9.29 \text{ Mg/ha}$, ranging

TABLE 1 Abundance and relative abundance of palm species registered in 40 riparian plots in Reserva Florestal Adolpho Ducke, Manaus, Amazonas, Brazil.

Species	Abundance (stems)	Relative abundance (%)
<i>Oenocarpus bataua</i>	1660	69.78
<i>Euterpe precatoria</i>	302	12.69
<i>Socratea exorrhiza</i>	144	6.05
<i>Bactris acanthocarpoides</i>	73	3.07
<i>Astrocaryum gynacantum</i>	60	2.52
<i>Bactris maraja</i>	53	2.23
<i>Iriartella setigera</i>	28	1.18
<i>Hyospathe elegans</i>	20	0.84
<i>Mauritia flexuosa</i>	17	0.71
<i>Geonoma maxima</i>	8	0.34
<i>Mauritiella aculeata</i>	6	0.25
<i>Oenocarpus minor</i>	4	0.17
<i>Syagrus inajai</i>	2	0.08
<i>Attalea maripa</i>	1	0.04
<i>Oenocarpus bacaba</i>	1	0.04

from 3.67 to 47.99 Mg/ha. Palm AGB_{Sp} was on average 204% and 34% greater than AGB_{F1} and AGB_p , respectively (Figure 2).

3.4 | Palm AGB in non-riparian vs. riparian plots

Mean palm AGB_{F2} in non-riparian plots (2.39 ± 4.15 Mg/ha, range: 0.06–26.38 Mg/ha) was 78% lower than in riparian plots (10.97 ± 4.97 Mg/ha, range: 2.13–26.41 Mg/ha) (Figure 3). The Wilcoxon rank sum test showed that AGB_{F2} in non-riparian plots was significantly lower than in riparian plots ($Z = -7.58$, $p < .005$, effect size Pearson r correlation = 0.72). Median AGB_{F2} was 1.02 and 9.97 in non-riparian and riparian plots, respectively. Although non-riparian plots were not designed to uniformly sample riparian environments, some of them were located partially in valley bottoms ($n = 19$) and categorized as “bottomland plots” according to the topographical classification of Costa et al. (2009). Nevertheless, when we used the same test excluding those plots, we obtained similar results ($Z = -8.07$, $p < .005$, effect size Pearson r correlation = 0.84). Likewise, palm AGB_{F2} estimated in bottomland plots was significantly lower than in riparian plots ($Z = -3.37$, $p < .005$, effect size Pearson r correlation = 0.44).

3.5 | Influence of environmental variables on riparian-palm AGB

The regression model including soil, hydrological, and topographical gradients as predictor variables and sub-basin as a random

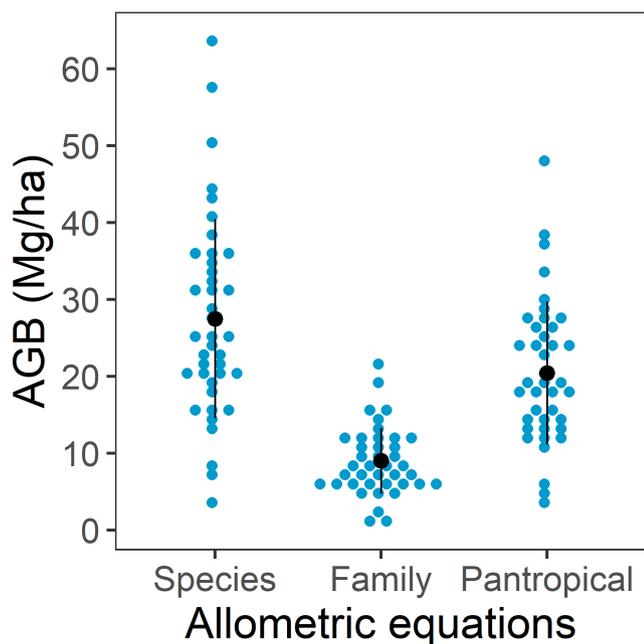


FIGURE 2 Dot histogram of palm AGB in 40 riparian plots estimated with pantropical, family-level, and species-level equations. Standard deviation bars and mean values are represented in black for each AGB-estimation equation.

effect, explained about 31% of the palm AGB variation among riparian zones plots. Fixed effects explained 19% of the AGB variation (Figure 4; Table 2). Soil properties did not contribute significantly to the model. AGB had a negative relationship with slope, with higher palm AGB in flatter riparian zones. AGB was negatively affected by stream discharge, indicating that higher palm AGB is associated with banks of smaller streams. Applying the following transformation: $[\exp(\text{coefficient})-1] \times 100$, we found that for each increase of one degree in slope, AGB decreases by 4%, and for each increase in stream discharge (m^3/s), AGB decreases by about 61%. As stream discharge varied from 0.004 to $0.425 m^3/s$ (Table S2), the differences between the lowest and highest discharges in our samples would have resulted in a difference of about 262% in AGB.

4 | DISCUSSION

4.1 | Effects of allometric equations on palm AGB estimates

Goodman's palm equations and Chave's pantropical equations are valid in the range of 4–50 cm and 5–156 cm, respectively. As we applied these equations for smaller palm sizes ($dbh < 5$ cm), this may result in potential errors caused by extrapolating allometric models beyond their valid dbh range (Chave et al., 2004). However, palms in dbh class < 5 cm represented, on average, less than 0.81 Mg/ha (4.33%) when using any of the three groups of allometric equations.

In riparian plots, AGB_{Sp} estimates were 204% greater than AGB_{F1} . Species- and family-level equations developed by Goodman et al. (2013) were used on the same sample, that included 9 palm-tree species and 136 individuals, so the large differences are likely to be related to the relative abundance of each species in the plots. While species-level equations can slightly overestimate AGB, family-level equations tend to underestimate AGB for some species such as *O. bataua* (Goodman et al., 2013), that represented the major palm component in our study

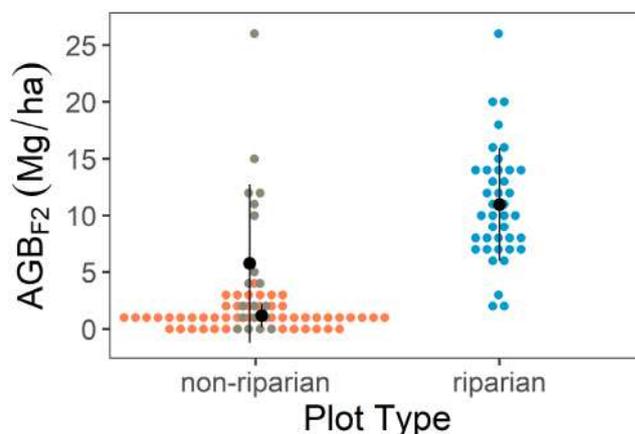


FIGURE 3 Dot histogram of palm AGB_{F2} in 72 non-riparian plots, which include 19 bottomland plots (gray points), and 40 riparian plots. Standard deviation bars and mean values are represented in black for each type of plot.

FIGURE 4 Partial regressions derived from the multiple regression model showing the relationships between palm AGB_{Sp} and (a) stream discharge (m^3/s), and (b) Slope ($^\circ$). Partial regressions have the same units as the original variables but the variables on the X-axis are centered around the means of the original variables.

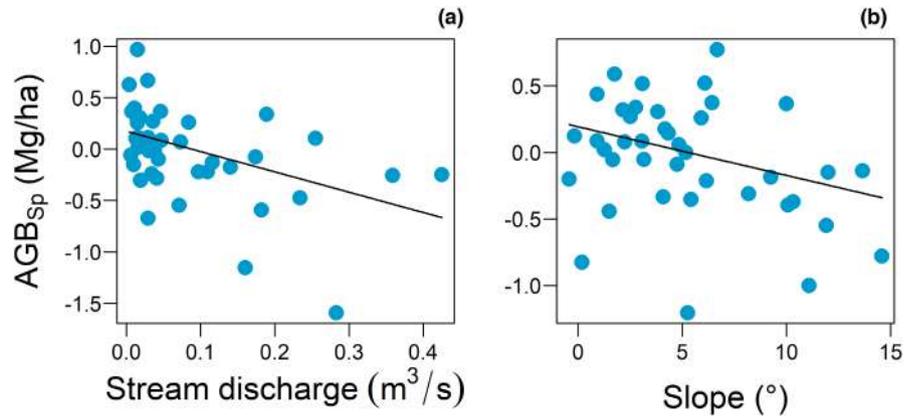


TABLE 2 Summary of multiple-mixed-regression analyses examining the effects of environmental variables on palm AGB_{Sp} in riparian plots.

Fixed effects	Estimate	SE	p
Intercept	3.60313	0.18894	<.001
Stream discharge	-1.97427	0.79016	.0125
Slope	-0.0365	0.01852	.0487
PC1	-0.01972	0.03228	.5412
PC2	0.03773	0.07133	.5968
Random effect	Variance	R^2_c	R^2_m
Residual	0.02868	0.31	0.19
sub-basin	0.1566		
$N_{sub-basin}$	5		
Observations	40		

Note: Marginal R^2 (variance explained by fixed effects; R^2_m), conditional R^2 (variance explained by the fixed effects + random effect; R^2_c).

Abbreviation: SE, standard error.

area. Additionally, diameter and stem-height allometric relationships vary intra- and interspecifically (see Figure S2), so it is expected that biomass estimates-based species-level equations will be more accurate than biomass estimates based on family-level equations. We used family- and species-level equations developed from Western Amazonian samples, but palm species vary in allometry in response to geographic position and forest strata (Avalos et al., 2019). Therefore, there may be some bias when these equations are applied on plots located in Central Amazon forests, despite the two locations having similar species composition (e.g., predominance of *O. bataua*, *E. precatória*, *M. flexuosa*, and *S. exhorrida*).

AGB_{Sp} estimates were 34% greater than AGB_p estimates. Allometric equations for trees estimate AGB based on dbh and perform relatively poorly at estimating palm AGB because diameter and height are not usually related in palms (Goodman et al., 2013; Muscarella et al., 2020). Palms grow taller with proportionally smaller diameters than dicotyledonous trees (Avalos et al., 2019), so AGB of tall palm individuals with small diameters could be underestimated by the pantropical equation (Goodman et al., 2013). Chave's pantropical equation was based on a dataset of 2410 harvested trees.

The authors cautioned that it should only be used for broadleaf tree species and different equations should be used for palms and other taxa (Chave et al., 2005).

General allometric equations used for dicotyledonous trees (and some palm family-level equations) commonly use palm total height as one of the equation components. Although total height is a good estimator of palm AGB (Goodman et al., 2013), measurements of total height in the field can be subjective, because individuals of some species (e.g., *O. bataua*) have a large portion of total height in their elongated crowns. Stem-height measurements in datasets are important to improve the accuracy of palm AGB estimates. We estimated stem height visually and calibrated our estimates, but more precise methods (e.g., using laser hypsometers, LiDAR airborne systems) are needed for future assessments, especially in palm AGB-dynamics research.

4.2 | Palm AGB contribution across riparian and non-riparian plots

Palm AGB_{F2} in riparian plots was on average 10.97 Mg/ha and was four times higher than AGB_{F2} in non-riparian plots. Mean palm AGB_{F2} in non-riparian plots was 2.39 Mg/ha and represented less than 1% of total AGB in these plots. However, palms are conspicuous components in some forest types, such as riparian zones. Although 19 non-riparian RAPELD plots did not follow a design for sampling riparian environments, they included portions of riparian zones. The AGB in those plots was on average 16.65 Mg/ha, lower than the mean value of palm AGB found in riparian plots. Conventional square plots would underestimate mean palm AGB in the riparian zone even more. Therefore, sampling riparian environments using standardized protocols can improve the understanding of how palm AGB is distributed at the landscape scale.

Areas where arborescent palms dominate do not occur only near streams. Large, low-lying valleys and terrain depressions could be relatively farther from stream margins, but closer to the water table and in consequence be subject to waterlogging and poor-drainage conditions (Schietti et al., 2014). To improve palm AGB estimates it is necessary to know where each taxon is abundant. Recent remote-sensing advances combining satellite and airborne images with field

data may help reduce uncertainties in palm AGB estimates (e.g., Tagle Casapia et al., 2019; Wagner et al., 2020).

4.3 | Variation in palm AGB within riparian zones

Topography and hydrological characteristics explained 19% of palm AGB variation among riparian plots in our study area. Palm AGB decreased on steep slopes, and this may be related to palm root systems. Most palm species do not develop extensive roots but have roots with high resistance to water pressures (Tomlinson, 2006). Although this may confer a competitive advantage in poorly drained and shallow-water-table soils (Emilio et al., 2014), palm root systems are less suitable to sustain mechanical stability on steep slopes, with the exception of stilted-rooted palm species (e.g., Iriarteoid palms; Henderson, 1990).

Moreover, topography drives water availability, so it is expected that palms on steep slopes would have less access to water and nutrients (Schietti et al., 2014). In contrast, the distribution of *Iriartea deltoidea*, the most abundant palm species in a forest in Ecuador, was not related to topography (Valencia et al., 2004). Species with stilt roots, such as *I. deltoidea*, maintain stability under diverse slope conditions (Avalos et al., 2005). Likewise, the density of arborescent palms (>10 m tall) in a forest of Costa Rica peaks on steep slopes, probably because treefall gaps may favor palm recruitment (Clark et al., 1995).

The RFAD is not affected by the flooding regimes of large rivers, but local rainstorms change stream discharge rapidly in riparian zones (Drucker et al., 2008). Although palms in Amazonian forests tend to occur in waterlogged environments, extreme flooding events affect some processes, such as seed germination, establishment, survivorship, and recruitment of plants, which may explain the lower abundance of palms near larger streams (Eiserhardt et al., 2011; Svenning, 2001). For example, *E. precatoria* seeds do not germinate under anoxic conditions (Gonçalves et al., 2010) and germinated seeds of *S. exorrhiza* had high mortality rates during the flooded period (Pacheco, 2001). Although flooding has strong effects on the distribution of palms, it remains unclear if those effects are more related to the anoxic conditions or other indirect factors typical of flooded environments, such as low vegetation structure and high light availability (Eiserhardt et al., 2011).

Soil properties are associated with topography in Central Amazonia (Chauvel et al., 1987), and in a large dataset of plots, they explained 55% of AGB variation, with higher palm AGB on sandy soils (Castilho et al., 2006). We included soil properties in our analyses, but they were not associated with palm AGB variation among riparian plots. Soil physical characteristics in riparian plots varied little (sand percentage: 59%–94%) in comparison with the variation over the entire reserve, where sand percentage ranges from 8–98% (Castilho et al., 2006). This may explain why we detected no association with soil physical properties. Soil fertility has been associated with palm-assembly composition at local scales within lowland rainforest in western Amazon (Vormisto

et al., 2000). However, we did not detect an association between soil chemical properties and palm AGB. Soil nutrient content in central Amazonia varies subtly and there is only a weak relationship between tree (including palms) AGB and nutrients in RFAD (Castilho et al., 2006).

Much of the variation in palm AGB in riparian plots remains unexplained. Riparian areas are heterogeneous environments, with different gradients of water retention, light incidence, and flooding patterns (Drucker et al., 2008; Pazin et al., 2006). Those effects are assumed to influence palm composition and, therefore, palm AGB (Toledo et al., 2017). However, changes in composition are more evident for understory than for arborescent palms (Costa et al., 2009). Variation in dominant species between riparian zones may be related to dispersal limitation (Costa et al., 2009) and complex interactions between palms and dispersers (Eiserhardt et al., 2011).

Historical human impacts may also play a role in the distribution of dominant palm species at landscape and local scales (Eiserhardt et al., 2011). *O. bataua* was the most abundant palm species in our sample. This species depends on natural or anthropogenic gaps for recruitment of adults (Guarín et al., 2014). There is evidence that pre-Colombian societies affected the distribution and abundance of useful plants, such as *O. bataua* (Levis et al., 2017). Thus, it is possible that human past disturbances have contributed to the high biomass of *O. bataua* and present biomass variation between riparian plots. Moreover, changes in palm distribution at the landscape scale can result from recent harvesting by residents (e.g., Clark et al., 1995). The southern edge of the RFAD has had close contact with suburbs since the early 2000s and palms and their fruits are harvested in plots near the edge (C. Castilho, unpublished).

4.4 | Conclusions and future directions

Our study shows that stratifying studies of palm biomass and including covariables, such as stream discharge, can reduce uncertainty in biomass estimates. However, more effort is needed to collect palm stem-height data in the field and develop allometric equations for more species (Goodman et al., 2013; Muscarella et al., 2020). Moreover, to reduce the AGB-estimation uncertainties in the Amazon region, we need to include samples from riparian zones, where arborescent palms are abundant components. Additionally, stemless palms can be very abundant (Higashikawa et al., 2019) and it is not known whether their AGB varies among habitats. Recent studies are recognizing the need to consider all forest strata to understand regional patterns in Amazonia (e.g., Draper et al., 2021). Thus, including stemless palms, which occupy the understory strata of the forest, may improve the understanding of the role of palms in the carbon cycle (Castilho et al., 2006).

Palms in areas with shallow water tables, such as riparian zones, are more resistant to drought and can compensate for biomass loss in forests affected by moisture deficits (Sousa et al., 2020). However, riparian zones are subject to anthropogenic pressures, which could change stream discharge patterns and biomass stocks. Current

Brazilian conservation law protects only a 30-m-wide riparian buffer around small streams. Some studies have shown the importance of adjusting the width of riparian-protected buffers to protect flora and fauna distinctive assemblages (Bueno et al., 2012; Drucker et al., 2008; Pereira et al., 2019). Our study indicates that there is no absolute distance appropriate for palms as the width of the riparian zone is associated with water-table depth. However, since carbon stocks in palm biomass in riparian zones provide a relevant ecological service, these areas require more nuanced conservation policies in areas subject to anthropogenic degradation.

AUTHOR CONTRIBUTION STATEMENT

Lourdes Falen contributed to conceptualization, methodology, project administration, investigation, data curation, formal analysis, writing—original draft, writing—review and editing, and visualization. **Mariane Guedes** contributed to investigation, project administration, and writing—review and editing. **Carolina V. de Castilho, Francisco M. Bezerra, and Rafael F. Jorge** contributed to investigation and writing—review and editing. **William E. Magnusson** contributed to conceptualization, methodology, formal analysis, resources, writing—original draft, writing—review and editing, supervision, and funding acquisition. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in PPBio repository at <https://search.dataone.org/view/PPBioAmOc.676.3>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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