RESEARCH ARTICLE

Ecosystem type affects how Amazonian tree species invest in stem and twig wood

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Abstract

1. Wood density (WD) is a key functional trait for its importance in tree performance and in biomass calculations of forests. Yet, the variation of WD among different woody tree parts, how this varies across ecosystems, and how this influences estimates of forest carbon stocks remains little understood, particularly for diverse tropical forests such as the Amazon.

2. We assembled a dataset on stem and twig wood density from 119 tree species in three different Amazonian ecosystem types that differ considerably in soil nutrition and flooding: non-flooded forest (Terra Firme), white-water floodplain forest (Várzea) and black-water floodplain forest (Igapó) to investigate (i) variation of stem and twig wood density across ecosystems, (ii) the relationships between stem and twig wood density and how these relationships vary across ecosystems.

3. Wood density varied substantially across ecosystems. Várzea species showed lower mean WD for stems compared to Terra firme, while Igapó species showed higher WD for twigs compared to the other ecosystems. Twig and stem wood density were positively related ($R^2_{adj}=0.47$) with similarly increasing rates across ecosystems, although average WD values differed between Terra firme and Igapó. For any given twig density, stem density tends to be lower in floodplain environments but higher in Terra firme, a habitat-specific pattern of wood density variation within trees that may emerge from differences in the function of stem and twig wood for growth and survival in ecologically differentiated environments.

4. Our results show how ecosystem has strong impacts on how trees allocate resources to different woody tissues, suggesting contrasting ecological strategies linked to ecosystem constraints. Our results suggest that greater consideration of the variation of WD within trees and how these changes across ecosystems might lead to more accurate estimates of above-ground biomass in Amazonia.

KEYWORDS
Amazonian forests, ecological strategies, forest ecosystem types, functional traits, resource allocation, tropical trees, wood density

1 | INTRODUCTION

Wood density (WD) is a reliable proxy for plant life-history and hydraulic strategies, because it relates to growth rates, mechanical strength, resistance to herbivory, water transport and storage (Chave et al., 2009; Zanne et al., 2010). In addition, it is fundamental in calculations of biomass and therefore essential to understand forest dynamics, ecosystem services (de Souza et al., 2019), and their role as carbon sinks (Chave et al., 2005; Fearnside, 1997).

Wood density is a result of different arrangements between solid elements (i.e. cell wall, fibres) and space (i.e. lumen, vessels), reflecting plant allocation tradeoffs (Chave et al., 2009; Hacke et al., 2001; Ziemińska et al., 2013) that influence species performances and life history strategies (Iida et al., 2012; Jakovac et al., 2015; Poorter et al., 2010, 2019). Wood density, for example, is linked to growth rate, where low density wood is less costly to construct and allows for rapid growth, which is advantageous for occupying light gaps in environments with frequent disturbances. Wood density also plays a role in plant mechanical resistance, with higher-density woods more resistant to breaking (Chave et al., 2009) and therefore allowing for high survival against physical hazards (winds, storms) and long-life spans (Poorter et al., 2008; Swaine & Whitmore, 1988; Van Gelder et al., 2006; Worbes et al., 1992). There is also evidence that wood density influences plant-water relations, as denser woods are more resistant to cavitation, albeit less efficient in water transport (Cosme et al., 2017; Hacke et al., 2001). Wood density may also be related to pathogen resistance, with lighter wood more vulnerable to attacks (Augspurger et al., 2010; Romero & Bolker, 2008).

Stem wood density varies considerably across gradients and ecosystems in the tropics (Baker et al., 2004; Chave et al., 2005, 2009; Muller-Landau, 2004; Swenson & Enquist, 2007). For instance, along a soil fertility gradient in Amazonia, plot-to-plot variation in mean wood density varies from 0.2 to 1.0 g cm^{-3}, with higher values at nutrient-poor sites (Muller-Landau, 2004). In Amazonian floodplains, stem wood density is influenced by both soil nutrients and flooding. Generally, higher stem wood density is observed in nutrient-poor black-water floodplains (Igapó) than in nutrient-rich white-water floodplain (Várzea; Parolin & Ferreira, 1998; Schöngart et al., 2010), although some species can show opposite patterns in both ecosystems (Schöngart et al., 2005). Furthermore, a trend of increasing stem wood density occurs with higher flooding in late-successional várzea forests (Wittmann, Schöngart, Montero, et al., 2006). Despite several prevailing patterns of wood density along environmental gradients, wood density also varies considerably among co-occurring species (Muller-Landau, 2004).

Much of our knowledge on wood density is derived from stem wood, while information on twig wood density is scarce. Although stem and twig wood densities are expected to be correlated (Chave et al., 2009; Sarmiento et al., 2011) because they share a common biophysical regulation and hydraulic continuity (Anten & Schieving, 2010; Fortunel et al., 2014), they are also exposed to different environmental constraints and play different ecological functions (Fajardo, 2018; Gartner, 1995). Twigs are, in contrast to the stem, associated with crown architecture and therefore the tree's capacity to harvest light energy (Honda & Fisher, 1978; Poorter & Werger, 1999). How stem and twig woods differ in their functions with regard to water transport, pest/disease defence, resource storage and biomechanics remain underexplored. Understanding variation in twig wood density, its relationship to stem wood density and how both interact with the environment, is likely to reveal novel ecological insight that consideration of stem wood density alone cannot. For instance, understanding how wood density varies across plant parts and ecosystems can improve biomass estimates, which is particularly challenging in heterogeneous environments and species-rich tropical forests where monitoring carbon stocks remains a challenge. Although non-destructive branch sampling has been suggested for stem wood density estimates, very few studies have evaluated the strength of stem and twig wood density relationship (Sarmiento et al., 2011; Swenson & Enquist, 2008), and critical analysis of this question is still lacking.

Here, we assembled a large dataset including 119 tree species from three major Central Amazonian ecosystems with contrasting conditions in soil nutrition and flooding to investigate how wood density varies between stem and twig. By comparing the wood density of both twigs and stems of tree species from these ecosystems, we addressed the following questions and hypotheses:

1. Are there differences in the average stem and twig wood density among tree species of three major Amazonian ecosystems (Terra firme, white-water and black-water floodplain forests)? We expect higher average wood density in species growing in nutrient-poor ecosystems because they will invest in conservative strategies (Reich, 2014), and in species inhabiting non-flooded ecosystems because lower seasonality leads to slow growth more evenly distributed throughout the year (Bredin, Hawes, et al., 2020).
2. How close is the relationship between stem and twig wood density among species? Does this relationship differ across ecosystems? We expect that stem and twig wood density among species will be strongly correlated because of the continuity in biophysical and hydraulic characteristics along the whole plant, and conservation of the same life history strategy. Alternatively, the differences in environmental pressures on stems and twigs will select for different functions among woody plant parts, leading to predictable variation between twig and stem WD linked to differences in nutrient availability and flooding of ecosystems.

2 | MATERIALS AND METHODS

2.1 | Amazonian ecosystems

We used data from three Amazonian ecosystem types located in different sites in Central Amazonia (Figure 1): non-flooded forests (Terra firme, Ducke Reserve and Uatumã Sustainable Developments Reserve-SDR), seasonally flooded white-water forests (Várzea;
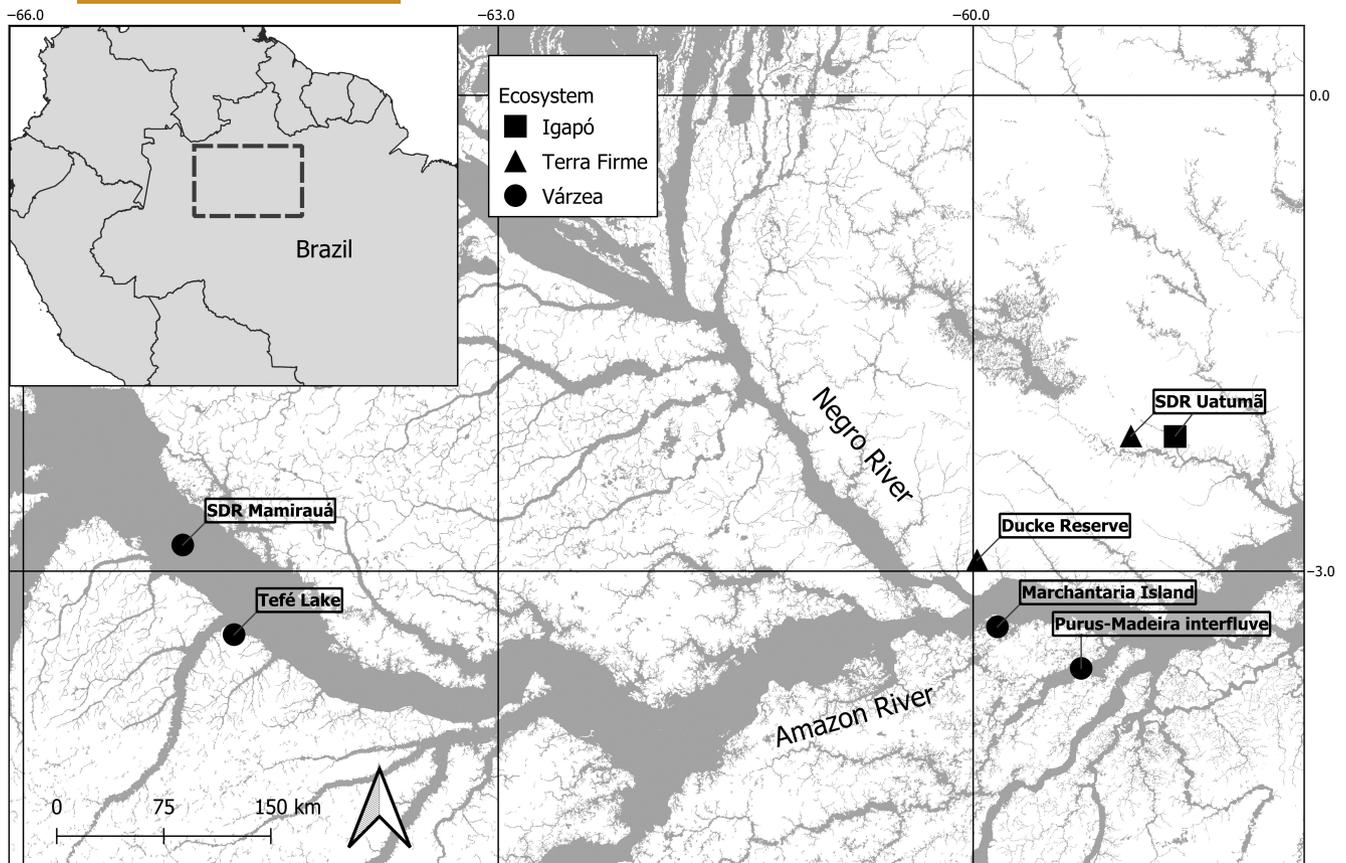
FIGURE 1 Map of Central Amazon with the seven study sites (Ducke Reserve, Uatumã Sustainable Developments Reserve-SDR, Mamirauá SDR, Marchantaria Island, Tefé Lake, and Purus-Madeira interfluve) indicated by triangles (Terra firme forest), dots (white-water floodplain forest 'Várzea'), and square (black-water floodplain forest 'Igapó').

Mamirauá Sustainable Developments Reserve-SDR, Purus-Madeira interfluve, Tefé Lake and Marchantaria Island/Lower Solimões River), and seasonally flooded black-water forests (Igapó, Uatumã SDR). Central Amazonia has a typical hot and humid tropical climate with mean annual temperature of 26.6°C and mean annual precipitation of 2100 mm/year (Fittkau, 1971). Soils are mainly derived from tertiary rocks and sediments that are heavily leached and low in mineral nutrients (Irion, 1978).

Terra firme forests refers to vegetation not subjected to annual floods. The relief varies from valleys, lower riparian areas with sandy and generally less fertile soils that can be briefly waterlogged in localized areas during the rainy season, to plateaus at relatively higher elevations with clayey soils generally more fertile (IBGE, 2012; Schietti et al., 2014; Tomasella et al., 2008). In contrast, seasonally flooded forests (floodplain forests) are subjected to long-lasting annual flood pulses (Junk et al., 1989). These floodplains are divided into two major types based on the hydro-chemical characteristics of the rivers that inundate them, the Várzeas and Igapós. Várzea forests occur along the Amazonian white-water rivers carrying large amounts of sediments originating from Andes or pre-Andean regions. These forests are highly fertile and show high turnover dynamics (Junk et al., 2011; Sioli, 1956). The Igapó forests extend along the black- and clear water rivers that originate from the Guyana and

Central Brazilian Shields and carry small amounts of sediments. Black-water floodplains show a slow stem turnover dynamic due to the low soil fertility and prolonged annual floods (Junk et al., 2015).

2.2 | Dataset

Wood density of twigs and stems was estimated following standard protocols. A twig was collected by a professional climber with a pole clipper from terminal sun-exposed branches in each tree. The samples had a diameter ranging from 1 to 2 cm and all bark was removed. A core of the stem was obtained at 1.30 m off the ground with increment borers (inner diameter 5 mm, length 500 mm, Haglöf, Sweden). Fresh volume (cm^3) of collected twigs and stem cores were measured using the water displacement method (Archimedes method, Cornelissen et al., 2003), subsequently, twigs and stems were dried at 103°C for 72 h and the dry mass (g) was measured with an analytical scale (accuracy = 0.001 g). The wood density was calculated as the ratio of oven-dry wood over green volume ($g\,cm^{-3}$; Chave et al., 2005; Swenson & Enquist, 2008).

In order to maximize the number of species, we collated data of twig and stem WD taken directly by us as well as from additional sources. Terra firme stem and twig WD were obtained from

published data (Cosme et al., 2017; Rezende, 2020), and both stem and twig WD were obtained from the same tree individuals. For Igapó, twig WD was obtained by us (Mori et al., 2021) and stem wood was obtained by us and from published data (Neves, 2018). Consequently, 27% of twig and stem samples belong to the same individual (Appendix S2). Twig samples of white-water (Várzea) were collected by us (Mori et al., 2021), while stem WD of Várzea species were obtained from published data of Várzea, selecting WD measurements from the Mamirauá SDR whenever available, or nearby Várzea in the same Central Amazonian region, to minimize possible variations resulting from different environmental conditions outside our focal region (Cintra et al., 2013; Da Fonseca Junior et al., 2009; Leoni et al., 2011; Martius, 1992; Parolin & Ferreira, 1998; Schöngart, 2003; Wittmann, Schöngart, Parolin, et al., 2006; Worbes, 1994).

Our dataset contains 119 species distributed in Igapó (30 species), Várzea (55 species) and Terra firme (34 species). We leveraged approximately 580 individuals for twig samples (295 in Igapó, 240 in Várzea and ~58 in Terra firme), and 1198 individuals for stem samples (223 in Igapó, 917 in Várzea and ~58 in Terra firme). For analysis, we used the average twig and stem wood density values of tree species. Additionally, we used the specific leaf area-SLA (leaf area over dry mass, $cm^2 \, g^{-1}$), and tree structural attributes (height, diameter, and basal area) available for a subset of our dataset to show differences in tree characteristics among ecosystems. For SLA, sun-exposed leaves were sampled for each tree, the fresh leaves (petiole excluded) were scanned with a portable scanner (HP 200) and leaf area was calculated with the ImageJ software (cm^2). Subsequently, leaves were dried at 65°C during 72h and dry mass was obtained with an analytical balance. Data taken directly by us were carried out under collecting permits 015/2016-DEMUC/SEMA (Department of Climate Change and Management of Protected Areas of Secretary of Amazonas State for the Environment) and SISBIO 52109-1 (Chico Mendes Institute for Biodiversity Conservation, ICMBio). Detailed information of all study sites and of the dataset is provided in the Supporting information (see Appendices S1 and S2).

2.3 | Data analysis

Wood density data were normally distributed, and the structural attributes were log-transformed to correct for deviations from normality. First, we compared stem and twig wood density values (WD) across ecosystems by testing for mean differences using analysis of variance (ANOVA) with post-hoc Tukey test (Gotelli & Elison, 2010) and ecosystem type as a factor. Stem and twig WD may vary in different ways among ecosystems, therefore, we examined how ecosystem affected the relationship between stem and twig WD of species in three different ways. First, we examined whether stem WD is higher, equal or lower than twig WD by calculating the stem:twig ratios of species among ecosystems and tested for mean differences in stem: twig ratios between ecosystem using ANOVA. Second, we used ordinary least squares models to regress twig WD on stem WD with ecosystem

included as either additive or an interactive factor. An interactive model would suggest that ecosystem-level effects are contingent on wood density, whereas an additive model would suggest that stem: twig relationships are consistent across the variation in wood density.

We also tested the robustness of our results to both spatial and phylogenetic autocorrelations by comparison to models that better accounted for the spatial structure (sites within ecosystems) and ecosystem-level differences in forest composition (phylogeny). To test for spatial effect, we ran a linear mixed model using wood density and ecosystem as fixed effects and site as a random effect and calculated the marginal and conditional r squared. Marginal r^2 indicates the proportion of variance explained by the fixed effects relative to overall variance, while conditional r^2 indicates the variation explained by both fixed and random effects (Zuur et al., 2009). To control for phylogenetic relationships, we duplicated ordinary least squares models, using a phylogenetic regression with the *phylolm* function of the phylolm R package (Tung Ho & Ané, 2014). We reconstructed phylogenetic relationships among the 119 species using Phylocom v.4.2 (Webb & Donoghue, 2005) based on the Neves et al. (2020) phylogeny of Amazonian angiosperms and used Brownian Motion (BM) and Orntein-Uhleck (OU) evolutionary models. We checked the model summaries and compared their Akaike information criterion (AIC) values. Additionally, we compared differences of tree attributes between ecosystem and tested its correlation with stem and twig WD to describe tree specific characteristics for each ecosystem. Finally, we repeated phylogenetic best fitted models and correlation analysis with a subset of our dataset excluding species with no intraspecific variability. The analysis showed equal results; therefore, we discuss the results based on the complete dataset that provides greater representativeness of species per ecosystem (Table S7). All statistical analyses were performed in R version 4.0.2 (R Core Team, 2021).

Research statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Species	Ecosystem	30 species of black-water floodplain forest (Igapó), 55 species of white-water floodplain forest (Várzea), 34 species of Terra firme forest

3 | RESULTS

3.1 | Wood density of stems and twigs of trees in Amazonian forests

Wood density varied considerably across ecosystems; more than three-fold in stems (0.26–0.95 g cm^{-3}) and more than two-fold in twigs (0.35–0.97 g cm^{-3}; Table 1). We detected mean differences in stem WD among ecosystems (One-way ANOVA, $F=5.60$, $p=0.004$;

Table 1), with Terra firme tree species between ~11% and 15% more dense than Igapó and Várzea species, respectively. A Tukey posthoc test, however, only supported statistical differences between the Terra firme-Várzea comparison ($p = 0.004$). Twig WD also differed among ecosystems ($F = 12.06$, $p < 0.001$; Table 1), with Igapó species ~15% and 18% more dense than Terra firme and Várzea, respectively, with Tukey posthoc tests supporting statistical differences between Igapó-Terra firme and Igapó-Várzea comparisons ($p < 0.001$).

We detected mean differences between stem and twig wood density in all ecosystems ($F = 10.66$, $p < 0.001$). In Terra firme, most species had twigs with lower wood density than stems (stem: twig WD ratio >1, Figure 2), with stems ~7% denser than twigs. Interestingly, the floodplain species showed an opposite pattern, with denser twigs than corresponding stems (stem: twig ratio <1). In Igapó, twigs were ~20% denser than stems, and in Várzea, twigs were ~6% denser than stems.

3.2 | Relationships of stem and twig wood density at the ecosystem level

The density of stem and twigs were positively correlated in all ecosystems (Figure 3), and the twig WD and ecosystem explained 47% of variation in stem WD (Table 2). Ecosystem was supported as an additive factor, indicating that for a given value of twig WD, mean differences in stem WD exist among ecosystems, but that slopes of the relationships between twig and stem WD did not differ among ecosystems. Specifically, Igapó had the highest twig WD for a given value of stem WD, and Terra firme the lowest. Phylogenetic models were consistent with non-phylogenetic models and linear mixed models, meaning that compositional differences among ecosystems and within ecosystem variation (site) are not explaining observed differences (Figure 3; Appendix S1; Tables S3 and S4). The SLA correlated negatively to stem ($r = -0.20$ and $p = 0.005$) and twig WD ($r = -0.36$ and $p < 0.001$) indicating a relation of an increase in SLA

with a decrease in wood density. The structural attributes correlated negatively only with twig wood density, indicating that larger trees have lower twig WD (Appendix S1; Table S6; Figure S2).

4 | DISCUSSION

We found that stem and twig wood density vary significantly across Amazonian ecosystems, with lower stem density in Várzea trees and higher twig density in Igapó trees. Twig and stem WD were positively correlated independent of ecosystem type, with differences in average wood density values between Terra firme and Igapó. There are two contrasting patterns across ecosystems where trees with soft-wooded stems tend to have higher twig density, and hard-wooded stems tend to have lower twig density; this pattern was most prominent in Igapó species, suggesting different strategies of resource allocation on woody parts depending on the ecosystem.

4.1 | Wood density across Amazonian ecosystems

We expected that wood density of stems and twigs would change across ecosystems as a response to different selection pressures across gradients of soil fertility and flooding (Chave et al., 2009; Hacke et al., 2001; Hietz et al., 2017; Poorter et al., 2010). Indeed, stems were generally softer in Várzea species than Terra firme species, whereas twigs were generally denser in Igapó species. Várzea's average lower stem WD compared to Terra firme may reflect the higher turnover rates and higher presence of pioneer species in this ecosystem (Parolin et al., 2002), such as *Pseudobombax munguba* ($0.26\,\text{g cm}^{-3}$) and *Ceiba pentandra* ($0.31\,\text{g cm}^{-3}$), and other fast-growth strategists common in Várzea (Mori et al., 2019, 2021).

Igapó and Terra firme species had, on average, medium-hard wooded stems ($0.6–0.8\,\text{g cm}^{-3}$). Igapó forests are known to have slow growth rates because they grow under both nutrient-poor

TABLE 1 Average values of stem and twig wood density (WD), analysis of variance (One-way ANOVA), and post-hoc Tukey test based on 119 tree species occurring in different Amazonian ecosystems: black-water 'Igapó' floodplain forest, white-water 'Várzea' floodplain forest and Terra firme forests.

Attribute	Ecosystem (n)	WD (g cm^{-3}) Mean-SD	Minimum–maximum	Tukey test	F-statistic	p-value
Stem WD					5.60	**0.005**
	Igapó (30)	0.64 ± 0.12	0.37–0.87	Terra firme|Igapó		0.508
	Várzea (55)	0.59 ± 0.15	0.26–0.85	Várzea|Igapó		0.142
	Terra firme (34)	0.70 ± 0.15	0.34–0.95	Várzea|Terra firme		**0.004**
Twig WD					12.06	**<0.001**
	Igapó (30)	0.77 ± 0.10	0.58–0.97	Terra firme|Igapó		**0.001**
	Várzea (55)	0.63 ± 0.13	0.35–0.91	Várzea|Igapó		**<0.001**
	Terra firme (34)	0.65 ± 0.09	0.45–0.81	Várzea|Terra firme		0.797

Note: The columns indicate mean stem and twig WD ± standard deviation (SD), minimum (min) and maximum (max) values (g cm^{-3}), Tukey-test, F-statistic and significance (p-value). The bold vaues indicate significance is equal or below 0.05.
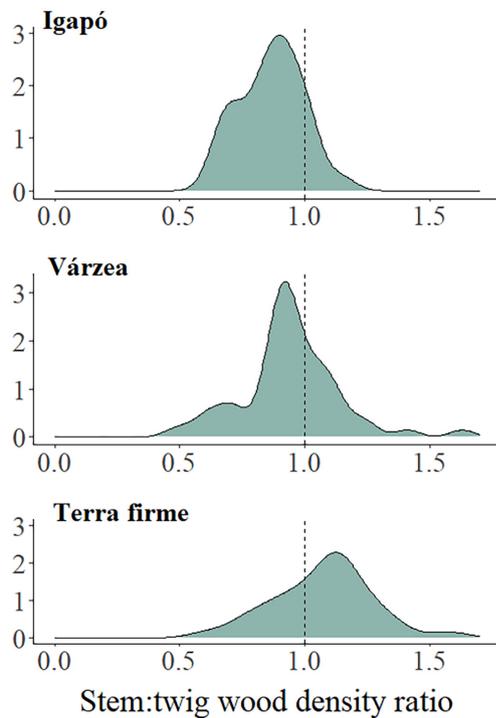
FIGURE 2 Kernel density distribution of stem:twig WD ratio in different Amazonian ecosystems: black-water 'Igapó' floodplain forest, white-water 'Várzea' floodplain forest and Terra firme forest tree species. The stem:twig WD indicates if stem WD is higher than twig WD (>1), equal (1), or lower (<1); the dashed line indicates the stem:twig WD ratio equal to 1.
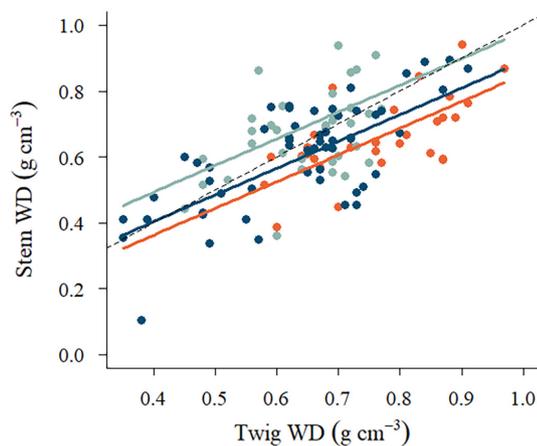

FIGURE 3 Phylogenetic regression of stem and twig wood density (WD, $g\,cm^{-3}$) of 119 tree species of Central Amazonian ecosystems: black-water 'Igapó' floodplain forest, white-water 'Várzea' floodplain forest and Terra firme forests fitting an Ornstein Uhlenbeck model. The solid lines represent the phylogenetic linear regression additive models of Igapó (orange), Várzea (dark blue) and Terra firme (light blue) species (Adjusted $R^2 = 0.47$); the dashed line indicates equal stem and twig wood density.

soils and longer periods of flooding compared to Várzea forests (Da Fonseca Junior et al., 2009; Junk et al., 2015; Schöngart et al., 2005), and species are generally more resource-conservative,

building persistent tissues and harder woods (Mori et al., 2021; Parolin & Ferreira, 1998). Terra firme species may have an average higher wood density for mechanical stability because they do not experience high flooding that can limit growth, resulting in generally taller canopies than seasonally flooded forests (Hawes et al., 2012). Hard wood also correlates with lower cavitation risk (Hacke et al., 2001), which can be advantageous during the dry season; for the Igapó species because the predominantly sandy soils reduce water availability and superficial root mats reduce water access (Latrubesse & Franzinelli, 2005; Meyer et al., 2010), and for Terra firme species due to limited access to water depending on the distance to the groundwater (Cosme et al., 2017; Costa et al., 2022).

4.2 | Different investments in stem and twig wood across Amazonian trees and ecosystems

Several studies have previously demonstrated correlations between stem and twig wood density (Sarmiento et al., 2011; Swenson & Enquist, 2008), and our results are in general agreement with these (Figure 3). However, we additionally show considerable ecosystem-level variation in stem and twig WD relationships, indicating possible functional specialization in woody plant parts (Figure 2).

A leading hypothesis explaining changes in WD from stem to twigs is that trees during growth have a greater need for mechanical support at their base, leading to higher WD in the stem relative to twigs (Dória et al., 2019; Fajardo, 2018; Gartner, 1995). However, our results showed that other patterns are also common, and that species often allocate resources quite differently depending on the ecosystem they grow in as well as the density of their wood. In particular, we found that trees with lower stem WD tended to have higher corresponding twig density, a pattern especially prevalent in floodplains, and particularly in Igapó trees (Figure 2). But why would trees with soft-wooded stems tend to have twigs with higher wood density? Here we bring up some possible explanations related to life-history, biomechanics and resource-use strategies.

Wood density is related to multiple functions of plants and anatomic arrangements, but it especially increases with a higher proportion of fibre that confers strength and avoids cavitation risk (Hacke et al., 2001). Wood density is also strongly correlated to the wood carbon content (Elias & Potvin, 2003), which can be separated into structural (increasing resistance) or non-structural components (storage; Larjavaara & Muller-Landau, 2010). Compared to floodplains, the taller Terra firme trees (Appendix S1; Figure S2) may have generally higher investment in stem than twig WD to maintain plant stability and protect against cavitation during the dry season, while lower-density twigs may allow fast-growth or increase local water storage to supply leaves. In flooded forests, lower WD stems may reflect reduced need for mechanical strength (Niklas, 1993; Niklas & Spatz, 2010) due to shorter floodplain canopies and a greater need for increased storage of water and non-structural carbohydrates to maintain water balance and anaerobic metabolism during prolonged flood periods (Parolin, 2012). Investigating

TABLE 2 Phylogenetic regression of stem wood density (WD, g cm^{-3}) in relation to twig WD and ecosystem type (black-water 'Igapó' floodplain forest, white-water 'Várzea' floodplain forest and Terra-firme forests) of 119 tree species for Ornstein-Uhlenbeck (OU) evolutionary model.

Predictors	Model 1				Model 2			
	Estimates	SE	t	p	Estimates	SE	t	p
Intercept	0.04	0.07	0.55	0.581	0.22	0.14	1.57	0.120
Twig WD	0.81	0.09	9.47	**<0.001**	0.57	0.18	3.08	**0.003**
Terra firme	0.13	0.03	4.52	**<0.001**	−0.22	0.19	−1.15	0.251
Várzea	0.41	0.03	1.52	0.131	−0.10	0.16	−0.64	0.522
WDtw|Terra firme					0.48	0.27	0.27	0.078
WDtw|Várzea					0.18	0.21	0.21	0.395
R^2/R^2 adjusted	0.49/0.47				0.44/0.41			
AIC	−182.26				−183.91			
alpha	0.254				0.025			

Note: The columns indicate the predictors, coefficient estimates, standard error, *t*-statistic, *p*-value, R^2, adjusted R^2, Akaike criterion information value (AIC) and alpha for additive (Model 1) and interactive (Model 2) models. The bold vaues indicate significance is equal or below 0.05.

the anatomical arrangements of stems and twigs should be the next step to understand the mechanisms that are involved in these variations, especially when related to the storage of water, carbohydrates or sugars, which might be particularly important in nutrient-poor environments subjected to flooding.

For the flooded nutrient-poor Igapó forests, particularly high-density twigs may additionally be important for sustaining longer-lived leaves, as in resource-poor environments the maintenance of relatively more expensive, but better-protected leaves for longer periods of time may be more cost-efficient than replacing cheaper leaves. Specific leaf area is an indicator of leaf longevity (Poorter et al., 2009), the negative correlation of twig WD with SLA and structural attributes indicates a possible coordination between conservative/long-lived leaves (lower SLA) and reduced growth (lower tree height and diameter) with hard-wooded twigs (Appendix S1; Figure S2; Table S6), but further investigations including leaf longevity and forest dynamics data are necessary to confirm this hypothesis.

To our knowledge, this is the first study to considered changes in stem and twig density in contrasting Amazonian ecosystems. While we acknowledge that some wood density values of our dataset do not belong to the same individual and that this may have contributed to some of the observed variation in wood density, we attempted to minimize its influence by carefully screening for species specific wood density measurements from nearby locations with similar abiotic conditions, which should minimize site-specific variation in WD (Bredin, Peres, & Haugaasen, 2020; Muller-Landau, 2004). Despite this weakness, the dataset we have assembled is an important first look into WD variation across species and ecosystem in one of the most diverse tropical forests worldwide. We showed that species allocate their resources differently in regard to woody tissues depending on ecosystem type, giving rise to divergent plant strategies. Additionally, we also showed that the correlation between stem and twig wood density in Igapó is weaker than previously reported

(Swenson & Enquist, 2008), indicating that twig WD is not good predictor for stem WD and may not be accurate for biomass calculation for all ecosystems. As the above-ground biomass of stands is estimated as a function of tree density, individual tree size and the wood density (Chave et al., 2005, 2014), the higher differences in wood density values between stem and their correspondent twigs would lead to considerable differences in biomass estimates that would invariably be extrapolated over larger spatial scales. Not incorporating twig wood density in these calculations could be leading to over- and/or underestimates of the overall biomass in the mosaic of ecosystems composing the Amazon biome.

5 | CONCLUSIONS

There is a high variation in wood density in stems and twigs across Amazonian ecosystems, with generally low-wooded stems in Várzea compared to Terra firme, and hard-wooded twigs in Igapó compared to Terra firme and Várzea. Stem density increases with twig density independent of ecosystem, but the proportion of investments in stem and twig wood changes between species of Terra firme and flooded Várzea/Igapó forests, potentially reflecting specialization of woody plant parts depending on the availability of resources and on abiotic stresses. We suggest that branches/twigs should be considered to more accurately estimate above-ground biomass in the Amazon.

AUTHOR CONTRIBUTIONS
GBM, MTFP, JS and JuS planned and designed the study. GBM and MR collected the data and performed laboratory analysis. GBM analysed the data with the contribution of JS, JuS and JEH. GBM led the writing of the manuscript with contribution of MTFP, JS, JuS, FW, JEH and LP. All authors contributed critically to the drafts and gave final approval.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from: https://doi.org/10.5194/bg-10-7759-2013, (Cintra et al., 2013); https://doi.org/10.1111/nph.14508 (Cosme et al., 2017); https://doi.org/10.1007/s00468-008-0261-4 (Da Fonseca Junior et al., 2009); https://doi.org/10.1016/j.foreco.2010.09.025 (Leoni et al., 2011); https://doi.org/10.1007/BF02615357 (Martius, 1992); https://doi.org/10.1007/s11258-020-01110-4 (Mori et al., 2021), https://doi.org/10.1080/03680770.1995.11900891 (Parolin & Ferreira, 1998); Rezende, 2020; Schöngart, 2003; https://doi.org/10.1163/22941932-90000153 (Wittmann, Schöngart, Parolin, et al., 2006); Worbes, 1994.

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SUPPORTING INFORMATION

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

Table S1: Soil chemical and physical characteristics of the study sites.

Table S2: Analysis of variance of stem wood density (WD), twig WD, stem:twig WD ratio, specific leaf area (SLA) and structural attributes (stem diameter, height, basal area) between ecosystems.

Table S3: Least squared models of stem wood density (WD) in relation to twig WD and ecosystem type.

Table S4: Linear mixed models of stem wood density (WD) in relation to twig WD and ecosystem type.

Table S5: Phylogenetic regression of stem wood density (WD) in relation to twig WD and ecosystems.

Table S6: Pearson correlation between stem/twig wood density (WD) with structural attributes (stem diameter, height, basal area) and specific leaf area (SLA).

Table S7: Phylogenetic regression of stem wood density (WD) in relation to twig WD and ecosystem type (black-water 'Igapó' floodplain forest, white-water 'Várzea' floodplain forest and Terra-firme forests) of subset data.

Table S8: Pearson correlation between stem / twig wood density (WD) with SLA and structural attributes of subset data.

Figure S1: Boxplots of stem and twig wood density values, SLA and with structural attributes (stem diameter, height, basal area) across ecosystems.

Figure S2: Correlations of stem and twig wood density (WD) with SLA and structural attributes.

Appendix S1: Detailed description of the study sites.

Appendix S2: Dataset of the study.