



Forest type affects the capacity of Amazonian tree species to store carbon as woody biomass



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ABSTRACT

For tropical tree species, wood density can vary greatly both within and between species depending on environmental conditions. In Amazonian seasonally flooded forests, yearly flood pulses influence tree growth and floodplain trees have developed specialised strategies to cope with prolonged submersion during flooding. We therefore hypothesised that seasonal floods significantly affect the capacity of trees to store carbon as woody biomass per unit volume and that forest hydrology would be an important factor in determining above-ground woody biomass and carbon stocks across the Amazon Basin. To test these hypotheses, we collected and analysed wood cores from 44 species occurring in both seasonally flooded (*várzea*) forests and adjacent unflooded (*terra firme*) forests along the Juruá River, western Brazilian Amazon. We used wood specific gravity (WSG) as a proxy of woody biomass and carbon. We compared WSG values within species, genera and families and found higher WSG in unflooded forest trees compared to their conspecifics in seasonally flooded *várzea*. Moreover, the effect of forest type on WSG was strongest at the family level and weakest at the species level. We further assessed the implications of WSG accuracy on above-ground woody tree biomass and found significant differences in AGBW as a function of WSG. Again, the differences became greater with lower taxonomic specificity, but also increased with lower site-specificity and greater tree dimensions. In conclusion, habitat specific WSG is important to quantify and map the spatial distribution of above-ground woody biomass and carbon in Amazonian forests.

1. Introduction

Amazonia represents the largest remaining tract of intact forests and the most species-rich biome on Earth. Forest areas of the Amazon Basin cover approximately 5 million km² and contains more than 10,000 tree species (ter Steege et al., 2019). Of these, 8,049 species have been taxonomically verified and are represented by voucher specimens in herbaria (ter Steege et al., 2019). However, this forest domain is not homogenous and contains several different forest types. Upland, or unflooded, forests occur above the flood level of rivers and lakes. Generically, unflooded forests are referred to as terra firme forests, but based on soil properties and vegetation cover, terra firme forests may be classed into several types (Prance and Gardens, 1985; Salovaara et al., 2004; Shepard et al., 2001). Some examples include savanna forests on nutrient poor white sand soils, liana forests on mineral-rich soils, and interfluvial upland forests dominated by palms or different tree species (Murça Pires, 1984; Prance and Gardens, 1985). In addition, dry season length, topography and the underlying geology and forest dynamics

seem to be main drivers of terra firme compositional, structural and functional diversification (Baker et al., 2004; Higgins et al., 2015; Salovaara et al., 2004; ter Steege et al., 2006; Terborgh and Andresen, 1998). Such changes may be gradual and give rise to several types of transitional forests. Among these, one less well documented forest type is the unflooded paleo-*várzea* that occurs on old *várzea* sediments, which are no longer under direct influence of seasonal floods. Similarly, floodplain forests that occur on floodplains along rivers and lakes may be categorised based on the properties of floodwaters, the frequency and duration of floods, soil properties, and their plant communities (Junk et al., 2011b).

The largest categories of floodplain forests include igapó forests inundated by black-, or clear water, which are nutrient poor and rich in organic solutes. *Várzea* forests are inundated by white-waters, which carry high amounts of suspended, nutrient-rich sediments. Seasonally inundated paleo-*várzeas* constitute an intermediate floodplain type that was once flooded by white-waters but are now inundated by black or clear water (Assis et al., 2015a; Junk et al., 2011b, 2011a). Of these, the

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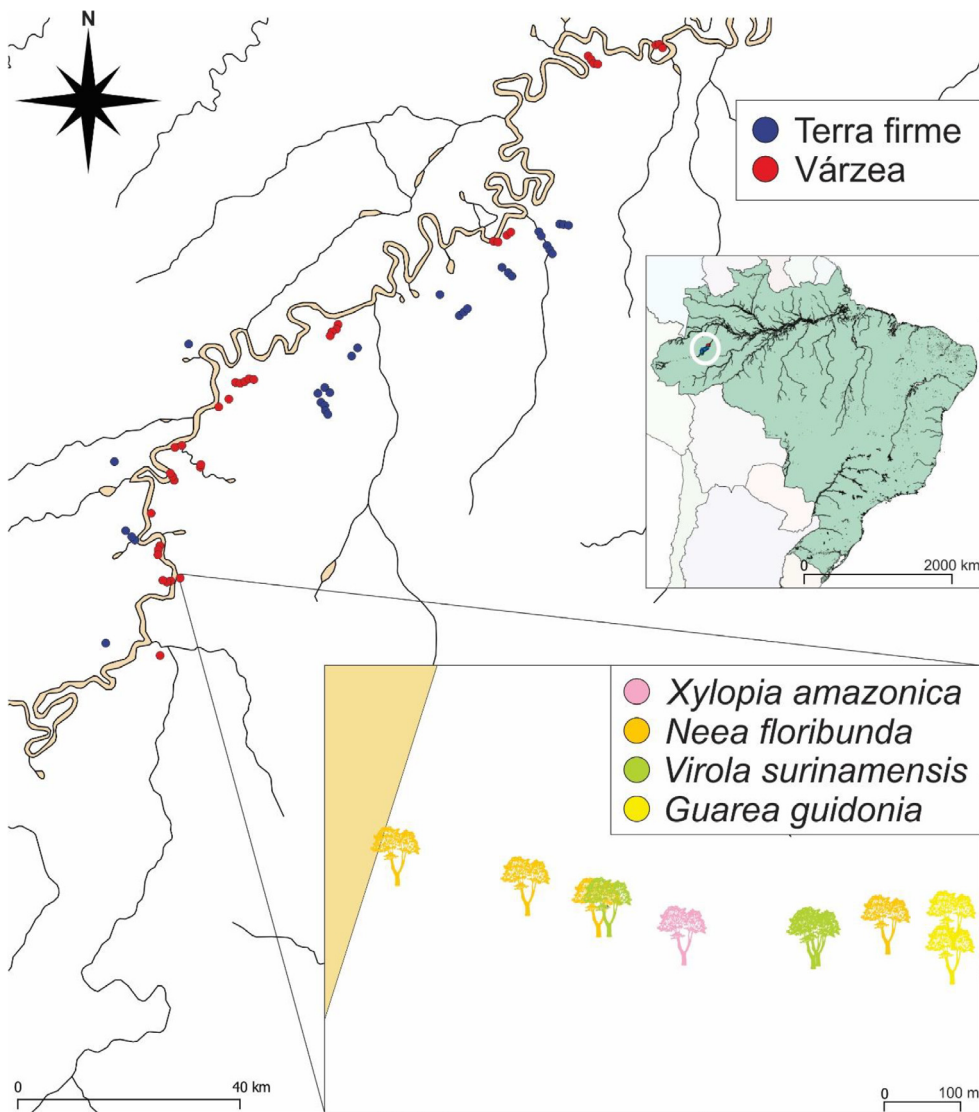


Fig. 1. Map showing the study area in western Brazilian Amazonia (indicated by the white circle in the inset map) and localities of sample trees in terra firme (blue) and várzea (red) along 150 km of the Jurua River (in beige). Smaller rivers and lakes are shown as black lines and in beige, respectively. The bottom-right submap shows the spatial distribution of 10 individual sample trees belonging to four species in one locality. The shortest distance between individual trees at this locality was 7 m. The map was generated in QGIS v.3.12.2 using background maps from the GADM database (Development, 2020; GADM database, 2015). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

várzea floodplains are the most extensive. They cover around 530,000 km², at least 270,000 km² of which are colonized by forests (Hess et al., 2015, 2003).

Previous studies exploring the ecology, succession and colonization of floodplain forests have found that the annual flood is a major driver of forest composition and structure (Arias et al., 2016; Assis et al., 2015b; Junk et al., 2011a; Targhetta et al., 2015; Wittmann et al., 2013, 2006a). Consequently, there is a clear zonation of tree communities along the hydro-topographic and successional gradients, with highly specialised wetland tree species occurring where flooding is most prolonged (e.g. Wittmann et al., 2006a). Additionally, seasonally inundated várzea forests tend to feature lower statured trees and a larger number of species typically representing light-wooded genera compared to their unflooded forest counterparts (e.g. Myster, 2016; Parolin, 2002; Wittmann et al., 2006b). Hydroperiod may thus drive variation in biomass by influencing tree dimensions, stem density and stand-level WSG in várzea forests, partly because of either succession or changed species composition along the flooding gradient. Due to these apparent differences in forest dynamics, forest structure and tree species composition, above-ground woody biomass (AGWB) is highly variable across the Amazon Basin (Phillips et al., 2019). Moreover, wood properties, such as wood density, fluctuate within species depending on growth conditions both within and among forests (Fearnside, 1997; Nogueira et al., 2008, 2005; Parolin, 2002; Wittmann et al., 2006b).

Although such variation has been documented for Amazonian trees, it is rarely incorporated into forest biomass estimates.

Here, we question to what extent WSG values from unflooded forests reflect the relationship between local tree species and AGWB in várzea floodplain forests, given that the seasonal flood pulse affects tree growth and floodplain trees have developed particular strategies to cope with prolonged below-ground anoxic conditions (Junk et al., 2010; Parolin, 2009, 2001). Indeed, we expect generalist species that straddle the boundary of both flooded and unflooded forest to exhibit differences in wood density across forest types. Consequently, we hypothesise that seasonal floods significantly affect the amount of carbon stored as woody biomass per unit volume in tree species occurring across flooded and unflooded forests, and that forest type is an important determinant of AGWB and carbon stocks beyond the level of species composition.

We therefore collected and analysed wood cores from 44 species occurring in both seasonally flooded várzea forests and adjacent terra firme forests in the central Jurua River basin. We use wood specific gravity (WSG) as a proxy of wood density to first answer the question (1) How does forest type influence the ability of trees to store carbon as woody biomass per unit volume across Amazonian flooded and unflooded forests? Next, we apply different WSG values to estimate above-ground tree woody biomass and ask (2) To what extent does accuracy in WSG affect above-ground woody biomass and carbon stock estimates at

the level of individual trees across Amazonian flooded and unflooded forests? We conclude by providing some recommendations on applying WSG values across várzea and terra firme forests to quantify and map the spatial distribution of AGWB and carbon stocks across the Amazonian forest macro-mosaic.

2. Methods

2.1. Study area

This study was conducted in the central Juruá River basin, western Brazilian Amazon. This is a region poorly represented by floristic inventories (Feeley, 2015). It includes areas within the Uacari Sustainable Development Reserve (RDS Uacari, 632,949 ha) and neighbouring forests located outside the reserve along 150 km of the Juruá River. The current work was performed in structurally intact seasonally flooded várzea forests (flooded for ca. 1–10 months annually; Hawes et al., 2012) and unflooded forests on paleo-várzea sediments since long abandoned by the Juruá River (Mesquita de Azevedo et al., 2010), located between 05°08'S, 67°01'W to 05°87'S, 67°88'W (Fig. 1). The terra firme forests of this study should thus be referred to as unflooded paleo-várzea forests. However, since unflooded paleo-várzea is not under the influence of seasonal floodwaters they are fundamentally different from, and must not be confused with, seasonally inundated paleo-várzea forests (cf. Assis et al., 2015a; Junk et al., 2011b, 2011a). For simplicity, the unflooded paleo-várzea forest is herein called terra firme.

The climate of the Juruá region is wet-tropical, with annual temperatures and rainfall averaging 27.1 °C and 3,679 mm, respectively (Hawes and Peres, 2016). The elevation within the study area ranged between 67 and 153 m above sea level (masl) for unflooded forests and 68–137 masl for várzea forests.

2.2. Wood specific gravity

The specific gravity of wood is the numerator of wood specific density and describes the relationship between the dry mass of wood at moisture content 0 and the volume of wood at its saturation point in relation to the density of water (Skogstad, 2009). It is thus a measure of the fraction of structural matter in wood (Williamson and Wiemann, 2010). As such, wood specific gravity (WSG) relates to both estimates of biomass and wood-bound carbon in woody vegetation (Chave et al., 2014, 2005; Fearnside, 1997). Whereas different wood gravity values are widely applied within the timber industry for different purposes, including calculating weights and evaluating wood quality for construction purposes (Skogstad, 2009), WSG is also an important functional trait in forest ecology studies that is central to tree life history, growth strategies and forest ecosystem services (cf. Parolin, 2002; Peres et al., 2016; Souza et al., 2018).

The most widely used wood gravity measure within forest ecological studies is wood basic gravity (WBG). WBG operates with green/fresh volumes of wood in relation to dry weights (Skogstad, 2009). It is therefore widely assumed that WBG better relates to the ecological properties of standing live trees than other wood gravities (Williamson and Wiemann, 2010). However, because WBG operates with green volumes, the moisture content of samples may vary (Simpson, 1993; Skogstad, 2009). A variation in intraspecific WBG across habitats may therefore not only reflect a difference in intrinsic abilities of trees to store carbon as woody biomass, but also the variation in water availability between habitats and among sites. Therefore, we use WSG whereby moisture content among samples is standardised at the water saturation point of the wood (Simpson, 1993; Skogstad, 2009).

2.2.1. Data acquisition

Between September 2016 and November 2017, we collected wood cores from 398 individuals belonging to 44 tree species occurring in

both seasonally flooded várzea forest and adjacent terra firme forest along the central reaches of the Juruá River (Table S1). We used a 5.15 mm Haglöf increment borer to sample trees with a diameter at breast height (DBH) of ≥ 10 cm. We extracted wood cores perpendicular to the bark at a height between 1 m and 1.3 m above ground. Where trees had buttressed roots, we extracted wood cores from above the buttress whenever possible. Cores were stored and transported in paper straws. To protect the cores from moisture and fungal attacks, samples were dried and kept with silica gel until they were analysed at the vegetation ecology lab at the National Institute for Amazon Research (INPA), Manaus.

2.2.2. Lab analysis

For this study, we only considered wood cores that covered at least 80% of the bole radius at breast height and included bark. To determine the WSG, wood cores were first saturated by submerging them in water for a minimum of 72 h. Depending on the length of the cores, we divided them into two or more segments. The segments were cut perpendicular to the bark and divided into the following sections; bark, 0–50 mm, 50 mm-pith (or middle based on the length of the radius at breast height), and beyond the middle. Where possible, heartwood and pith were visually determined, and the samples divided into further sub-segments to avoid an overrepresentation of heartwood and pith on the WSG values (Plourde et al., 2015). Saturated wood volume was measured by the water displacement method, using a fine needle to submerge the segments into a beaker of water placed on a scale with precision 0.01 g (Wiemann and Williamson, 2012). We used tap water kept at $24 \text{ }^{\circ}\text{C} \pm 0.6 \text{ }^{\circ}\text{C}$, equivalent to a density of approximately 0.9973 g/cm^3 . After recording the saturated wet volumes, we dried the wood cores at $107.5 \text{ }^{\circ}\text{C} \pm 2.5 \text{ }^{\circ}\text{C}$ for 72 h. This temperature is slightly higher than what is typically recommended ($101\text{--}105 \text{ }^{\circ}\text{C}$) (Williamson and Wiemann, 2010). Consequently, WSG measures presented here could be conservative as some volatile compounds may have evaporated (Nogueira et al., 2005). We recorded the dry weights of wood core segments using a scale with a precision of 0.01 g.

To calculate WSG values, we followed the method used by Muller-Landau (2004). In brief, we calculated a single weighted average value per tree based on the values for each segment weighted by the cross-sectional area of the trunk that the segments represented. For trees with replicate wood cores, we averaged the WSG based on the replicates.

2.3. Statistical analysis

To evaluate how WSG vary within tree species, genera and families across terra firme and várzea forests, we adapted the methods used by Mori et al. (2019). We calculated the mean WSG at breast height and associated standard deviation for each species, genus, and family. We paired these values across the two forest types at the level of taxonomic identity to visually inspect differences in WSG between forest types across taxonomic levels using strip plots (R package Lattice v.0.20–38, Sarkar, 2008), and boxplots (R package ggplot2 v.3.3.0, Wickham, 2016). To evaluate the influence of forest type on WSG, we used a linear mixed model for each taxonomic level with forest type as a fixed effect and taxonomic identity as a random effect (Zuur et al., 2013). For the following analyses we used the R packages lmerTest v.3.1–1 (Kuznetsova et al., 2017) and psycho v.0.4.0 (Makowski, 2018). For each taxonomic level, we compared a null model only considering taxonomic identity (R syntax: $\text{model}_0 = \text{WSG} \sim (1|\text{species/genus/family})$), to a model considering both forest type and taxonomic identity (R syntax: $\text{model}_1 = \text{WSG} \sim \text{Forest type} + (1|\text{species/genus/family})$). To see if models differed with the addition of forest type, we calculated a likelihood ratio by dividing the log-likelihood of the full model (model_1) by the log-likelihood of the null model (model_0). To assess the relative importance of forest type compared to the influence of taxonomic identity, we calculated the marginal and conditional R squares (mR^2 ; cR^2) of the full models (Makowski, 2018; Nakagawa and

Schielzeth, 2013). The mR^2 describes the relative influence of the fixed effect (Forest type) and the cR^2 describes the total explanatory power of both the fixed and random effect for each model (Forest type + taxonomic identity). Similar mR^2 and cR^2 values indicate a negligible influence of taxonomic identity on WSG.

To assess the influence of accuracy in WSG on above-ground woody biomass at the level of individual trees, we used the BIOMASS R package v.2.1.1 (Réjou-Méchain et al., 2017). We calculated the biomass of each tree at each taxonomic level using individual-specific WSG, habitat specific mean WSG, mean WSG from the other forest type (e.g. flooded for unflooded trees and vice versa), and the mean WSG for tropical South America from the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009). We inspected differences in AGBW estimates at each taxonomic level as a result of the different WSG methods visually through the ggplot function, R package ggplot2 v.3.3.0 (Wickham, 2016, 2009). We plotted the individual AGBW estimates against tree diameter (cm) and tree height (m) and fit linear models to the data through a smoother (Wickham, 2009). To evaluate the influence of accuracy in WSG on AGBW, we fit a linear mixed model with WSG as a fixed effect at each taxonomic level using the R package nlme v.3.1–142 (Pinheiro et al., 2019). Because above-ground woody biomass was estimated for the same individuals several times, we set individual as a random effect and assumed a linear autocorrelation within each individual (R syntax: $model_1 = AGBW \sim WSG, random = \sim 1 | individual, correlation = corLin(form = \sim WSG | individual)$). At each taxonomic level, we compared the full model to a null model including a fixed effect of 1 and the random effect (R syntax: $model_0 = AGBW \sim 1, random = \sim 1 | individual$) through the rcompanion package v.2.3.25 (Mangiafico, 2020). For each full model, we then ran a post-hoc Tukey-adjusted comparison applying the multcompView v.0.1–8 (Graves et al., 2019), lsmeans v.2.30–0 (Lenth, 2016), and multcomp v.1.4–13 (Hothorn et al., 2008) packages.

Following the example of Nogueira et al. (2005), we calculated the fractional difference in WSG across the two forest types, e.g. formula 1 (example formula for calculating the fractional difference in WSG using information from unflooded trees to predict the WSG of flooded trees): $\left(\frac{\sum \frac{WSG_{flooded}}{N} - \sum \frac{WSG_{unflooded}}{N}}{\sum \frac{WSG_{flooded}}{N}} \right)$, where N is the total number of observations within each group. In addition, we calculated the mean differences in kg / tree, formula 2b: $\left(\frac{\sum AGBW_{individual} - \sum AGBW_x}{N} \right) \times 1000$, the overall differences in Mg AGBW, formula 2a: $\frac{\sum AGBW_{individual} - \sum AGBW_x}{\sum AGBW_{individual}}$, and the differences in percent, formula 2c: $\frac{\sum AGBW_{individual} - \sum AGBW_x}{\sum AGBW_{individual}} \times 100$, for comparisons between AGBW estimates based on the individual WSG values and each of the other WSG methods. In formulas 2a–2c, $AGBW_{individual}$ is AGBW estimated using individual WSG, $AGBW_x$ is AGBW estimated using a different WSG method x , e.g. habitat specific mean WSG, and N is the total number of observations. Hence, we suggest correction levies for WSG values used in AGBW and carbon estimates across seasonally flooded and unflooded forests and show the potential influence that such corrections might have on AGBW estimates. All analyses were performed using the R platform, version 3.5.2 (R Environment R Core Team, 2018).

3. Results

Of the 44 tree species examined here (Table S1), only eight species had three or more individuals sampled in each forest type and are therefore retained in the subsequent analyses. A floristic inventory from the same region (YKB, unpubl. data) showed that the eight focal species represented approximately 3% and 8% of all individuals and 2% and 8% of the total basal area in terra firme and várzea, respectively. At genus level, 12 genera had a minimum sample of five individuals per forest type, and at family level, 14 families had a minimum of five individuals sampled per forest type (Table 1). The 12 genera represented

35% and 24% of all individuals (45% and 27% of the total basal area) and the 14 families represented 72% and 66% of all individuals (76% and 71% of the total basal area) in terra firme and várzea, respectively.

In general, within-species, within-genus and within-family WSG values were higher in terra firme forest compared to várzea. However, the trend was not unidirectional for all species/genera/families and for some the WSG was almost the same across forest types or higher in várzea. Nonetheless, forest type had a significant effect on overall mean WSG across all taxonomic levels (Fig. 2; Table 2). Moreover, the influence of forest type on WSG increased from species to family level. The influence of forest type on WSG was thus strongest at the family level and weakest at the species level (Table 3).

Comparisons of tree AGBW based on different WSG accuracy levels show that there are significant differences in AGBW as a function of WSG and that these differences become greater with lower taxonomic specificity (Table 4, Fig. 3). Differences among AGBW estimates also become greater with increased tree diameter and tree height. Thus, discrepancies among AGBW estimates are greatest for the largest trees (Fig. 3). When terra firme and várzea trees were analysed together, AGBW estimates based on global mean WSG were always significantly different from the AGBW based on individual WSG (Table 4, Fig. 3). Habitat specific WSG always resulted in AGBW estimates that were most similar to the reference values based on individual WSG (Table 4, Fig. 3).

4. Discussion

We found that várzea trees generally had lower WSG compared to their conspecifics in terra firme. At the genus and family levels, this trend became even clearer. Hence, forest type and hydrology clearly affect within-species, within-genera, and within-family WSG of Amazonian trees.

To our knowledge, this is the first study to investigate intraspecific wood gravity across Amazonian forest types with a focus on implications for above-ground woody biomass (AGBW) estimates. Whereas previous studies have demonstrated that shifts in species composition, abundance and tree dimensions across forest types are important determinants of AGBW and carbon stocks in the Amazon, our results imply that the influence of forest type on WSG is an important additional factor to consider in forest biomass estimates. In addition, by comparing AGBW based on different WSG accuracies at the level of individual trees, we found that greater taxonomic accuracy and greater habitat- and geographic specificity always result in better AGBW estimates (assuming that individual WSG best reflects true AGBW). Hence, we show that the difference in intraspecific wood gravity between unflooded and flooded forests result in an overestimation of woody biomass for várzea trees when WSG values from terra firme forests are used. Our results therefore support previous studies that found flooding to be an important determinant of WSG in floodplain trees, and that ignoring habitat-related variability in wood densities leads to large biases in woody biomass estimates (e.g. Phillips et al., 2019; Wittmann et al., 2006b). In fact, using WSG values derived from terra firme forest to predict AGBW in várzea trees or vice versa, even at the species-specific level, would lead to an estimation error of 5–11%. At higher taxonomic levels and for larger trees, the estimation errors become greater. Given the obvious influence that large trees have on the distribution of AGBW across tropical lowland forests (Ali et al., 2019; Slik et al., 2013), we may therefore expect that using habitat non-specific WSG to estimate and predict the distribution of forest biomass may have serious consequences for the mapping of AGBW.

The overlap in species composition between várzea and terra firme forests of the central Juruá may be as high as 44.5% (YKB, unpubl. data). It is likely that a similar overlap can be found elsewhere across Amazonia. Studies that rely on data from the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009) for biomass estimates in várzea forest, and those that attempt to provide AGBW estimates for

Table 1

Mean WSG at breast height and standard deviation (SD) per forest type and taxonomic level. Number of cores is the total number of individuals that were analysed to obtain WSG and SD values.

Taxonomic level	Scientific name	Unflooded			Flooded		
		No. cores	Mean WSG	SD	No. cores	Mean WSG	SD
Species	<i>Oxandra xylopioides</i> , Annonaceae	4	0.86	0.21	4	0.66	0.00
	<i>Symphonia globulifera</i> , Clusiaceae	4	0.59	0.04	3	0.58	0.03
	<i>Theobroma microcarpum</i> , Malvaceae	4	0.51	0.08	5	0.41	0.02
	<i>Carapa guianensis</i> , Meliaceae	5	0.58	0.03	15	0.58	0.07
	<i>Guarea guidonia</i> , Meliaceae	4	0.59	0.06	3	0.50	0.02
	<i>Virola calophylla</i> , Myristicaceae	8	0.43	0.03	19	0.44	0.09
	<i>Virola surinamensis</i> , Myristicaceae	4	0.45	0.04	16	0.42	0.24
Genus	<i>Leonia glycyarpa</i> , Violaceae	5	0.56	0.02	11	0.49	0.12
	<i>Guatteria</i> , Annonaceae	9	0.41	0.10	13	0.42	0.08
	<i>Licania</i> , Chrysobalanaceae	16	0.76	0.06	10	0.64	0.07
	<i>Hevea</i> , Euphorbiaceae	6	0.51	0.04	16	0.46	0.05
	<i>Eschweilera</i> , Lecythidaceae	42	0.71	0.08	43	0.63	0.06
	<i>Theobroma</i> , Malvaceae	12	0.55	0.06	16	0.40	0.04
	<i>Carapa</i> , Meliaceae	6	0.58	0.03	15	0.58	0.07
	<i>Guarea</i> , Meliaceae	7	0.62	0.06	7	0.54	0.04
	<i>Brosimum</i> , Moraceae	7	0.68	0.08	5	0.58	0.04
	<i>Virola</i> , Myristicaceae	22	0.46	0.06	43	0.41	0.16
	<i>Neea</i> , Nyctaginaceae	9	0.52	0.08	14	0.41	0.07
	<i>Pouteria</i> , Sapotaceae	5	0.68	0.09	33	0.61	0.08
	<i>Leonia</i> , Violaceae	5	0.56	0.02	14	0.48	0.11
Family	Annonaceae	17	0.54	0.22	90	0.44	0.10
	Chrysobalanaceae	18	0.76	0.06	10	0.64	0.07
	Clusiaceae	7	0.56	0.13	39	0.60	0.10
	Euphorbiaceae	19	0.58	0.08	47	0.43	0.09
	Lauraceae	8	0.63	0.10	20	0.50	0.10
	Lecythidaceae	49	0.70	0.09	64	0.59	0.09
	Leguminosae	17	0.63	0.12	85	0.56	0.14
	Malvaceae	21	0.52	0.12	54	0.37	0.07
	Meliaceae	15	0.62	0.08	23	0.56	0.07
	Moraceae	14	0.65	0.07	17	0.52	0.10
	Myristicaceae	40	0.54	0.11	45	0.41	0.15
	Nyctaginaceae	9	0.52	0.08	15	0.41	0.06
	Sapotaceae	15	0.61	0.08	57	0.60	0.08
	Violaceae	6	0.58	0.04	22	0.51	0.12

the basin as a whole, may thus carry a significant estimation error. This is because local WSG variation across habitat types is not appropriately accounted for. For our focal trees, for example, we found an estimation error of up to 30% when using Tropical South American mean WSG compared to individual WSG. This correspond well to findings from moist tropical Africa where Bastin et al. (2015), found up to 40% difference in tree AGBW while evaluating the effects of local WSG variations and global wood density data on tree AGBW. Conversely, at the species level, we find no difference in AGBW estimates based on global default WSG or species mean WSG for terra firme trees.

Within-species, within-genus, and within-family differences in WSG values were, however, not unidirectional across várzea and terra firme in this study. For some species, genera and families WSG was greater or similar in várzea trees compared to their terra firme conspecifics but WSG values were mostly higher in terra firme trees. Whether these directional differences in WSG are due to variation among species in their responses to soil nutrient availability or hydrological stressors across habitats cannot be determined from the current study. However, flooding arrests tree growth for part of the year, thereby likely stimulating rapid growth during the low-water season (approx. August to January), especially in seedlings and saplings (Wittmann et al., 2010). This growth may be further promoted by the high soil fertility on várzea floodplains. In addition, seasonal changes in water-level introduce elements of mechanical stress in floodplain habitats through the erosion of land and the deposition of alluvial sediments (Wittmann et al., 2010). In response, floodplain trees have developed special tissues and strategies to cope with the variable environmental stressors, which in turn may influence WSG (e.g. Parolin et al., 2002). Hence, we speculate that

high soil nutrient availability, rapid seasonal tree growth, and specialised tissues in várzea forest trees are likely to cause lower wood gravities compared to conspecifics in terra firme, particularly in early-successional species.

This would be consistent with Parolin (2002) and Wittmann et al. (2006b) who found increasing wood gravities from pith to bark in early successional tree species, but decreasing trends in late successional species. These findings are expected under the assumption that light-wooded trees are associated with fast growth rates (Bastin et al., 2015). In other words, floodplain trees and pioneer species invest in rapid growth during the establishment phase (=light heartwood), and later in structural stability (harder outer wood layer). Conversely, slower growth rates typical of late successional species and assumed investment in greater structural stability during the establishing phase of saplings, result in harder heartwood. However, the 35 floodplain species investigated by Parolin (2002) did not exhibit unidirectional radial changes in wood gravity. These intraspecific variations in both radial trends across different successional stages (cf. Parolin, 2002) and mean intraspecific WSG across habitats (cf. this study) may suggest intraspecific phenotypic plasticity in tree responses to different environmental stressors.

To predict tree survival rates under changing environmental conditions, we need information about how different species respond to abiotic and biotic stressors, and other sources of tree mortality (Yang et al., 2018). Hence, information about intraspecific adaptation in trees to varying environments could be used to predict changes in tree species composition and carbon stocks under, for example, changing climates and forest hydrology (Yang et al., 2018). However, to better

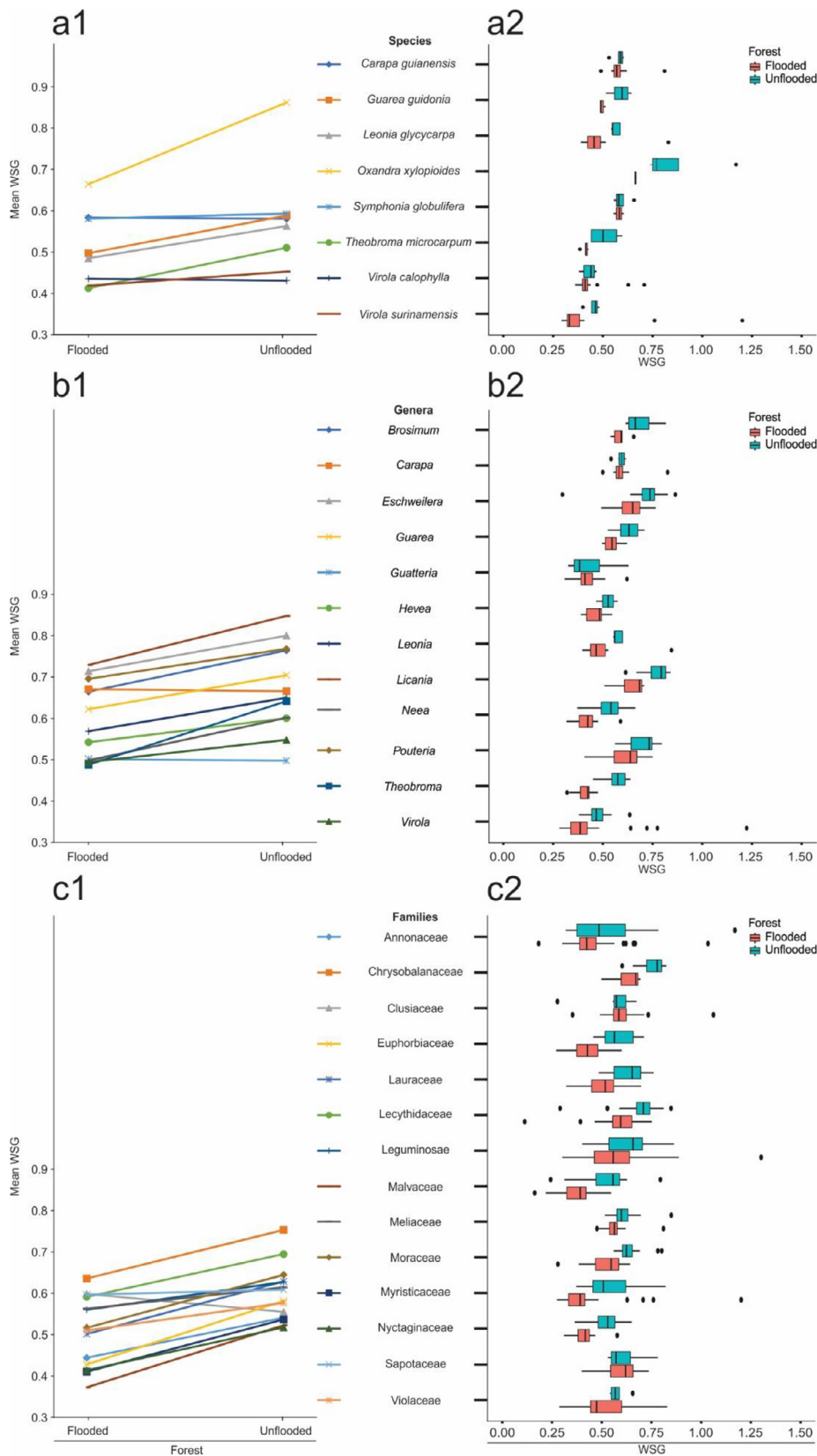


Fig. 2. Wood specific gravity (WSG) at breast height for (a) tree species, (b) genera, and (c) families occurring in both terra firme and várzea forests, with a) $n \geq 3$, b) $n \geq 5$, and c) $n \geq 5$ sampled individuals per forest type. Strip plots (a1-c1) show the intraspecific difference in mean WSG at breast height between flooded (várzea) and unflooded (terra firme) forests. Boxplots (a2-c2) show the intraspecific ranges in WSG within each forest type and taxonomic level. Colour-coded boxes represent the interquartile ranges. Thick black lines indicate median WSG per forest type; whiskers represent one and a half times the interquartile ranges, and solid dots represent outlier observations.

discern potential environmental thresholds in tree survivorship rates and map gradients of WSG change within species and tree communities among forest types on different soil types with varying water availability, we need more information about local WSG from different interfluvial regions and vegetation types across the Amazon and other

tropical forest regions.

5. Conclusions:

Reducing biases in AGBW estimates to better account for the spatial

Table 2

Variation in within-species, within-genus, and within-family WSG at breast height across seasonally flooded and unflooded forests. The columns indicate taxonomic level of analyses, β -coefficient, p-value, marginal R^2 (variance explained by the fixed effect, i.e. Forest type; r^2_m), conditional R^2 (variance explained by the fixed effect + random effect, i.e. Forest type + Taxonomic identity; r^2_c), and likelihood ratio (p-value indicates if models differ; ratio was calculated as $\text{model}_1 / \text{model}_0$, in R-syntax: $\text{WSG} \sim \text{Forest type} + (1| \text{Taxonomic identity}) / \text{WSG} \sim (1| \text{Taxonomic identity})$)).

Taxonomic level	WSG ~ Forest type + (1 Taxonomic identity)				likelihood	
	β -coefficient	p-value	r^2_m	r^2_c	ratio	p-value
Species	-0.050	< 0.05	0.023	0.434	1.031	< 0.05
Genus	-0.077	< 0.001	0.079	0.581	1.090	< 0.001
Family	-0.099	< 0.001	0.150	0.405	1.107	< 0.001

Table 3

Mean WSG at breast height and standard deviation (SD) per forest type (TF = terra firme, VZ = várzea) and taxonomic level for species with minimum three sampled individuals per forest type (Min. idvs.), genera and families with minimum five sampled individuals per forest type. Number of cores is the total number of individuals from which wood cores were analysed per forest type and taxonomic level. WSG adjustments describe the correction levy up (↑) or down (↓) in percent (%) across forest types (From → To) for WSG values from cores sampled at breast height.

Taxonomic level	Forest type	Min. idvs.	No. cores	Mean WSG	SD	From → To	WSG adjustment (%)	Up/Down
species	TF	3	38	0.56	0.14	uF → F	12.72	↓
species	VZ	3	76	0.49	0.15	F → uF	14.58	↑
genus	TF	5	146	0.61	0.13	uF → F	15.57	↓
genus	VZ	5	229	0.52	0.13	F → uF	18.45	↑
family	TF	5	255	0.61	0.13	uF → F	17.18	↓
family	VZ	5	588	0.51	0.13	F → uF	20.75	↑

Table 4

Differences in AGWB as a function of WSG accuracy. All comparisons use tree AGWB based on individual WSG as a reference value. “Other habitat” denotes WSG from várzea for terra firme trees and vice versa for várzea trees. “Global” WSG refers to Tropical South American mean values retrieved from the Global Wood Density Database (Chave et al., 2009; Zanne et al., 2009). Differences are reported as mean differences in kg per tree, in Mg for all trees combined, and in percent. Negative and positive values indicate overestimations and underestimations in AGWB, respectively.

WSG	Difference in AGWB for terra firme trees			Difference in AGWB for várzea trees			Overall Difference in AGWB		
	Kg/tree	Mg total	%	Kg/tree	Mg total	%	Kg/tree	Mg total	%
Habitat specific species mean	-1.7	-0.064	0	-13.5	-1.016	-4	-9.6	-1.080	-3
Other habitat species mean	17.4	0.643	5	-35.5	-2.665	-11	-18.1	-2.022	-5
Global default mean	-1.7	-0.062	0	-29.9	-2.242	-9	-20.6	-2.304	-6
Habitat specific genus mean	4.9	0.710	2	-1.8	-0.411	-1	0.8	0.300	0
Other habitat genus mean	37.8	5.446	12	-30.7	-6.973	-12	-4.1	-1.527	-1
Global genus mean	-80.6	-11.608	-25	-42.9	-9.747	-16	-57.6	-21.355	-20
Habitat specific family mean	-6.7	-1.691	-2	-0.9	-0.544	0	-2.7	-2.235	-1
Other habitat family mean	38.7	9.782	14	-41.3	-24.103	-17	-17.1	-14.322	-7
Global family mean	-16.8	-4.239	-6	-73.8	-43.110	-30	-56.6	-47.350	-22

distribution of wood bound carbon in Amazonian forests and subsequent monitoring are important goals in climate change science and forest ecology. In this study, we show that applying the same WSG values across forest types would lead to significantly biased AGWB and carbon estimates. Since tree species occurring in both terra firme and várzea forests appear to adapt to their local environments, the topography and seasonal floods may not merely determine where different tree species grow, but also how they express key functional traits, such as WSG. To reduce bias in the spatial representation of forest above-ground woody carbon within the Amazon Basin we require more detailed information on tree species composition and habitat specific WSG values. Where habitat specific WSG values are absent, we recommend adjustments of regional WSGs to the local forest type.

CRedit authorship contribution statement

Yennie K. Bredin: Conceptualization, Methodology, Project administration, Investigation, Data curation, Formal analysis, Resources, Writing - original draft, Writing - review & editing, Visualization.
Carlos A. Peres: Conceptualization, Funding acquisition, Methodology, Writing - review & editing, Supervision, Validation.
Torbjørn Haugaasen: Conceptualization, Funding acquisition, Methodology,

Writing - review & editing, Supervision, Validation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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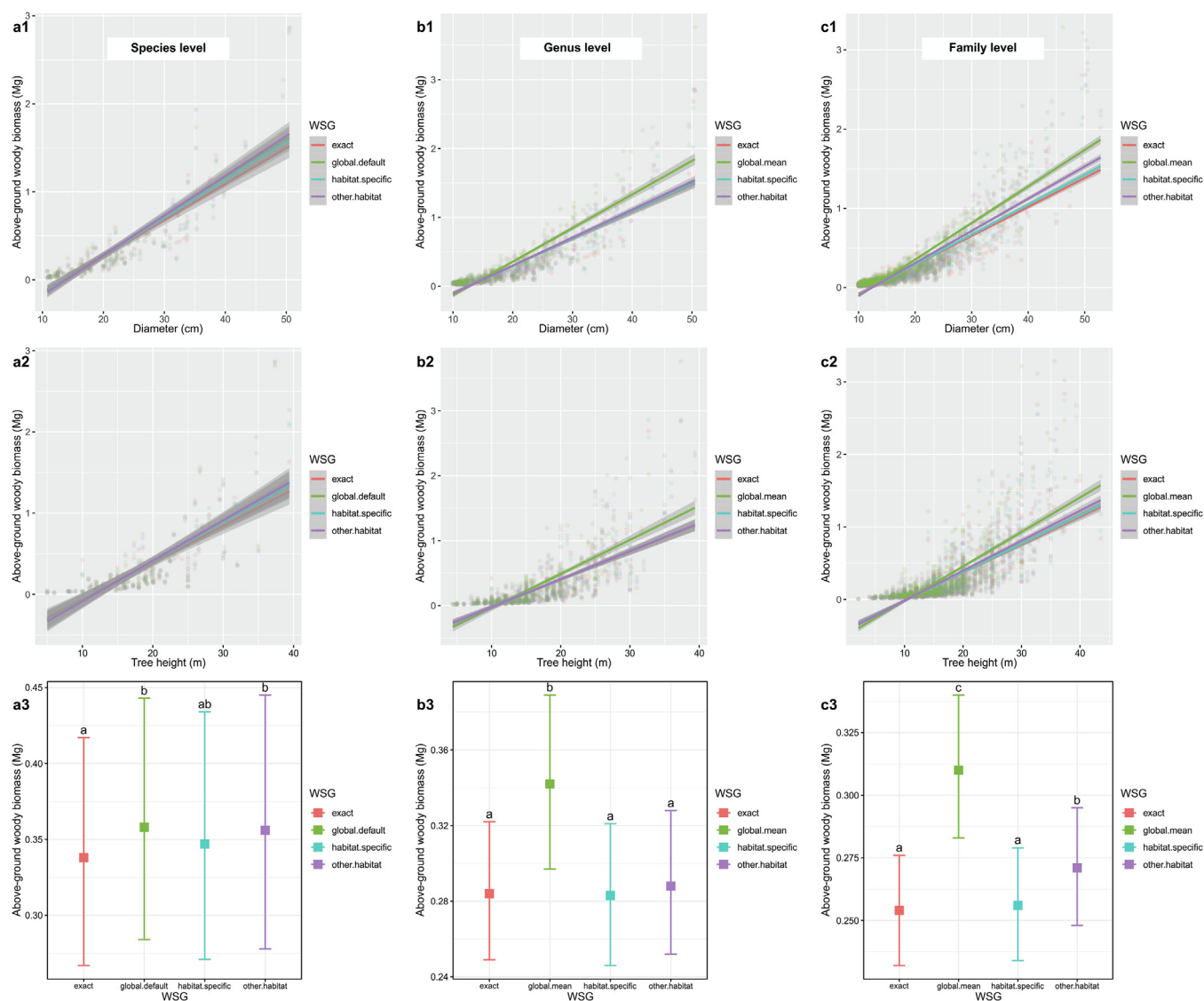


Fig. 3. Above-ground woody biomass (AGWB) calculated at the level of individual trees for a) species, b) genera, and c) families occurring in both terra firme and várzea forests, with a) $n \geq 3$, b) $n \geq 5$, and c) $n \geq 5$ sampled individuals per forest type. Scatter plots (a1–c1) show the trends of variability in tree AGWB in relation to tree diameter in centimetres (cm) as a function of WSG accuracy. Similarly scatter plots (a2–c2) show the trends of variability in tree AGWB in relation to tree height in meters (m) as a function of WSG accuracy. Trends were fit with linear models and show means as solid lines and associated confidence intervals in grey. Boxplots (a3–c3) show mean tree AGWB per accuracy-level as colour-coded boxes where whiskers represent one and a half times the interquartile ranges. Different lower-case letters above the whiskers indicate significant differences in tree AGWB as a function of WSG. Analyses were based on Tukey-adjusted comparisons of means. AGWB estimates were derived using WSG from individual tree cores (“exact”), habitat specific mean WSG (“habitat.specific”), mean WSG from flooded trees for terra firme individuals or vice versa (“other.habitat”) and Tropical South American mean WSG (“global.default” or “global.mean”). WSG set to “global.default” (plots a1–a3), were given as species mean WSG when available, otherwise as genus mean WSG. At the genus-, and family-levels “global.mean” WSG were assigned exclusively at the genus-level (b) or family-level (c).

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118297>.

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