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Local scale carbon stock measurements, including deep soil layers, in a terra firme forest in northwestern Amazon

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Research Article

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Abstract

Most studies aiming to quantify carbon stocks in tropical forests have focused on aboveground biomass, omitting carbon in soils and woody debris. Here, we quantified carbon stocks in soils up to 3 m depth, woody debris, and aboveground and belowground tree biomass for the 25-ha Amacayacu Forests Dynamics plot in the northwestern Amazon. Including soils to 3 m depth, total carbon stocks averaged 358.9 ± 24.2 Mg C ha^{-1}, of which soils contributed 53%, biomass 44.2%, and woody debris 2.7%. When only including soils to 0.5 m depth, carbon stocks diminished to 222.1 Mg C ha^{-1} and biomass became the largest contributor. Among 1-ha subplots, total carbon stocks were correlated with soil carbon stocks at $\geq$0.5 m depth, belowground biomass of all trees, and aboveground biomass of trees $\geq$60 cm DBH. Our results support the assumption of biomass as the likely largest carbon source associated with land use change in northwestern Amazonia. However, mining and erosion following land use change could also promote a significant release of carbon from soil, the largest carbon stock. To improve the global carbon balance, we need to better quantify total carbon stocks and dynamics in tropical forests beyond aboveground biomass.

Introduction

Tropical forests account for two-thirds of total terrestrial biomass carbon stocks (Pan *et al.* 2013), which makes this ecosystem of critical importance for the future trajectory of the global carbon cycle (Houghton *et al.* 2015; Hubau *et al.* 2020; Spawn *et al.* 2020). Many studies at local and regional scales have sought to quantify tropical forest carbon stocks, with most focusing on the contribution of tree aboveground biomass (Araujo *et al.* 2023; Avitabile *et al.* 2016; Saatchi *et al.* 2007). However, carbon stocks in soils and woody debris (Wdebris) of tropical forests are also substantial (Anderson-Teixeira *et al.* 2016; Doetterl *et al.* 2015; Duque *et al.* 2017a; Gora *et al.* 2019; Phillips *et al.* 2019a). Improving our understanding of the amount of carbon stored in tropical forests in forest compartments other than aboveground biomass will help better inform global carbon cycle models (Anderson-Teixeira *et al.* 2021) and will enable improved assessments of the extent to which forest conservation could ameliorate ongoing climate and atmospheric change (Powers *et al.* 2011). Quantifying and understanding the amount of carbon stored in all major forest compartments (Anderson-Teixeira *et al.* 2016; Navarrete *et al.* 2016; Sierra *et al.* 2007) and their change with deforestation and forest degradation is critical to fully account for anthropogenic greenhouse gas emissions due to land use change (Grace *et al.* 2014).

In mature tropical forests, the proportion of carbon stored in different compartments (i.e., soils, necromass, and aboveground biomass) varies among studies and regions (Anderson-Teixeira *et al.* 2021). The relative contribution of each compartment to total forest carbon stocks of course depends on soil sampling depth, but differences persist even when measurements are made to the same depth. In three Amazon forests, Malhi *et al.* (2009) mean values range between 143 and 209 Mg C ha^{-1} for aboveground biomass, between 10.5 and 43.9 Mg C ha^{-1} for coarse Wdebris, and between 121 and 180 Mg C ha^{-1} for soils to 3-m depth. In Singapore, Ngo *et al.* (2013) reported around 169, 111, and 16 Mg C ha^{-1} in the aboveground biomass, soils, and coarse Wdebris, respectively. Along an elevational gradient in the Colombian Andes, where total carbon stocks varied between 102.9 and 342.2 Mg C ha^{-1}, soils to 1-m depth contributed 50.4% (range 22.6–82.2%) on average, aboveground biomass 40.7% (13.5–62.1%), and Wdebris 8.9% (4.3–18.1%) (Phillips *et al.* 2019a). Most studies assessing soil carbon stocks, however, have focused on the first 20–30 cm, providing limited information about total soil carbon stocks (Araujo *et al.* 2023).

In this study, based on an intensive survey of carbon stocks carried out in the 25-ha Amacayacu Forest Dynamics Plot in terra firme forest of the Amazon (Davies *et al.* 2021), we quantify carbon stocks in soils up to 3 m depth, fallen and standing Wdebris, and live shrubs and trees ≥1 cm in diameter at breast height (DBH). Specifically, we asked (1) at the plot scale (25 ha), what is the relative contribution of soils, Wdebris, and aboveground and belowground tree biomass to total carbon stocks? (2) What are the contributions of different soil depths, Wdebris size classes, and tree size classes to these carbon stocks? And (3) how do these carbon stocks covary among 1-ha plots (within the 25-ha plot), and what are the implications for the potential to explain total or individual carbon stock components based on any of the other carbon stocks? Our study is in line with the Intergovernmental Panel on Climate Change (Eggleston *et al.* 2006) definition of carbon reservoirs in forest ecosystems, which includes aboveground biomass, roots, soil organic matter, and coarse and fine necromass (Wdebris). Thus, this study contributes to our knowledge of the potential effect of Amazon forest conversion on the global carbon cycle, and therefore, on ongoing climate change.

Methods

Study site

This study was carried out at the 25-ha Amacayacu Forest Dynamics Plot (AFDP), located in Amacayacu National Natural Park in the southern part of the Colombian Amazon (3°48′33.02″ South and 70°16′04.29″ West). The plot is part of the Forest Global Earth Observatory (ForestGEO; Davies et al. 2021), a network that comprises >75 forest plots worldwide established following standard protocols (Condit 1998). The AFDP is located in highly diverse Amazon Terra Firme Forest and harbours around 1200 tree and shrub species in 25 ha (Duque *et al.* 2017b; Zuleta *et al.* 2020). The plot is located on tertiary sediments of the Pebas formation, which due to its Andean origin is considered a relatively fertile soil in comparison with other tertiary-originated soils, such as those derived from the Guiana Shield (Hoorn 1994). The soils have been classified as part of the group of Acrisols (Lips and Duivenvoorden 2001), which are characteristic of relatively young sediments, such as those with Andean origin (Quesada *et al.* 2011). The mean annual temperature (MAT) is 25.8 °C, the mean annual precipitation is 3216 mm with no months with <100 mm and the mean relative humidity is ~86%.

Soil carbon stocks

To assess soil organic carbon stocks and their spatial variation, we divided the plot into 25 square1-ha subplots (Figure 1). In the centre of each 100 × 100 m subplot, we took soil samples at 0–10 cm, 10–20 cm, 20–50 cm, 50–100 cm, 100–150 cm, 150–200 cm, 200–250 cm, and 250–300 cm, or until the auger encountered bedrock if soil depth was less than 300 cm. We subsampled this soil profile to assess soil bulk density (SBD; in gr cm^{-3}). In the centres of each of the corner of 20 m × 20 m quadrats located in the centre of each 1-ha subplot, we took soil samples at 0–10 cm, 10–20 cm, 20–50 cm, and 50–100 cm. Finally, in the centres of the 20 × 20 m quadrat on the side of each 1-ha subplot, we took soil samples at 0–10 cm and 10–20 cm depth. Thus, in each 1-ha subplot there were nine samples of 0–10 cm, nine of 10–20 cm, five of 20–50 cm, five of 50–100 cm, and one each of 100–150 cm, 150–200 cm, 200–250 cm, and 250–300 cm (if we did not encounter the bedrock earlier) (see Figure S1). Within each 1-ha subplot, all samples taken at the same depth were mixed to calculate soil organic carbon concentrations (SOC; %), and soil carbon stocks (SCS; in Mg C ha^{-1}). Soil samples were packed in zipper plastic bags and transported to the Smithsonian Tropical Research Institute Soils Laboratory in Panama. Once there, soil samples were dried in an oven at 100 °C until they reached a constant weight, weighed, crushed, and sieved (2 mm) to remove all the stones; then, they were weighed again. SBD of each sample was quantified using the dry weight of the sample (in g), free from stones, and the volume of the steel ring (in cm^3). SOC was assessed by employing an Elemental Analyser. SCS for each hectare and soil depth class was calculated as the product of the SBD, SOC, and the depth of the horizon from which the sample was taken. We analysed how SBD, SOC, and SCS varied with soil depth. Uncertainties in soil carbon stocks were quantified as the 95% confidence intervals (CI) of the means over the 25 1-ha subplots.

Wdebris carbon stocks

Carbon stocks in Wdebris were calculated as the sum of the dry mass stored in fallen coarse Wdebris (FCWD), fallen fine Wdebris (FFWD), and standing coarse Wdebris (SCWD), multiplied by a factor of 0.456 (Martin *et al.* 2018). Line-transect methods were used to census both fine and coarse fallen Wdebris. FCWD, defined as pieces with a diameter (D, in cm) ≥20 cm, were censused in 10 parallel transects of 500 m (5000 m in total) divided into sections of 20 m each. FFWD, defined as pieces with a diameter between 2 and 20 cm, were censused in the first 2 m of each 20-m transect section. To assess carbon stocks (Mg) of fallen coarse and standing coarse Wdebris at the 1-ha scale (100 m × 100 m), we used two 100 m long transects in each one of the 25 100 × 100 m subplots (Figure 1). SCWD was censused in 100 0.16-ha subplots of 40 m × 40 m (Figure 1). To assess SCWD at the 1-ha scale, we combined data from the four 0.16-ha subplots within each 100 m × 100 m subplot (Figure 1). Technical details for the calculation of the amount of carbon stored in Wdebris followed Larjavaara & Muller-Landau (2011) and can be found in the supporting information (Methods S1; Figure S2). For both fallen and standing Wdebris, we quantified uncertainty as the 95% confidence intervals (CI) of the means over the resulting 25 1-ha values.

Biomass carbon stocks

To assess the aboveground biomass (AGB) and belowground biomass (BGB) we used the third census of trees with diameter at breast height (DBH; measured at 1.3 m height) ≥1 cm carried out in the 25-ha AFDP between July 2019 and May 2022. In this census, which was interrupted by the pandemic, 119,151 shrubs, trees, palms, and tree ferns with DBH ≥1 cm were mapped, tagged, measured, and collected for species identification following the standardized methods for long-term tropical forest dynamics plots (Condit 1998). Voucher specimens were deposited and identified in the Colombian Amazonian Herbarium (COAH) of the Instituto Amazónico de Investigaciones Científicas SINCHI. Wood density (WD) data for each species were assigned using the BIOMASS library for R (Rejou-Machain *et al.* 2017). When species-level WD values were not available, we used genus- or family-level averages.

All tree diameters measured at a height of 1.4 m or higher were corrected to equivalent diameters at 1.3 m using the taper equation proposed by Cushman *et al.* (2021); the taper-corrected values are hereafter simply referred to as DBH. Individual tree AGB (in kg dry mass) in each census was estimated with the BIOMASS library for

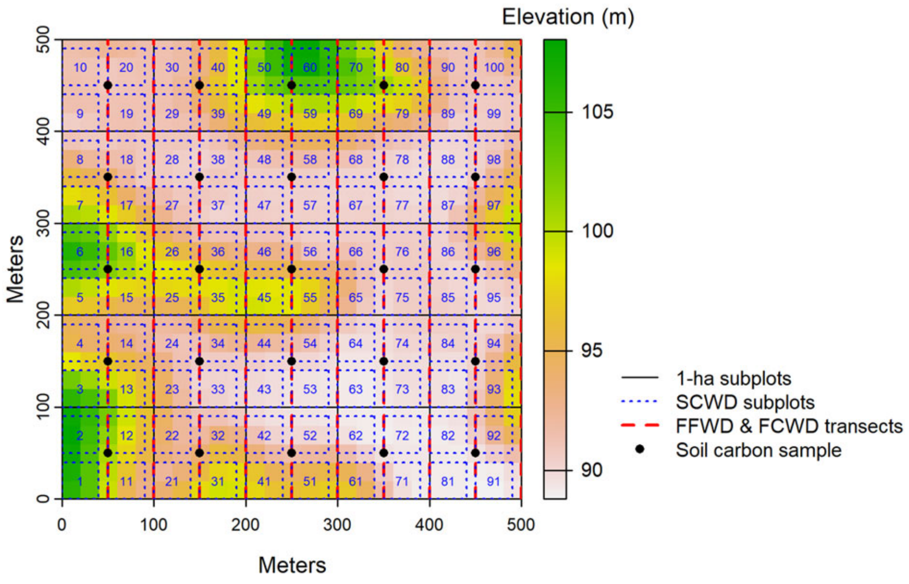

Figure 1. Map of the 25-ha Amacayacu forest dynamics plot and the sampling design for forest carbon stocks. Solid black lines show the boundaries of 25 1-ha subplots for which we separately assessed carbon stocks. Black points show the centres of the 1-ha subplots, which is where soil carbon was sampled to the greatest depths. Fine dashed blue lines show 100 0.16 ha subplots in which we assessed standing coarse woody debris (SCWD). Red dashed lines indicate the 10 transects of 500 m each employed to assess fallen fine (FFWD) and fallen coarse woody debris (FCWD). Biomass carbon stocks were calculated from census data for all shrubs, trees, palms, and tree ferns with DBH ≥1 cm in the 25-ha plot. Colours indicate the elevation at 5-m vertical resolution.

R (Rejou-Machain et al., 2017) using the general model developed by Chave *et al.* (2014):

$$\mathrm{AGB} = 0.0673(\mathrm{WD} \times \mathrm{DBH}^2 \times H)^{0.976},$$

where H is tree height (m), WD is wood density (gr cm^{-3}), and DBH is diameter at breast height (cm). We estimated the heights of all trees using a local height-diameter allometry fitted to data for 9112 trees whose heights were measured with the sine method using a Vertex 5 Hypsometer (Larjavaara and Muller-Landau 2013). The best model to estimate H from DBH was selected using the modelHD function in the BIOMASS library. The selected model was Weibull:

$$H = 34.695\left(1 - \exp\left(-\left(\frac{\mathrm{DBH}}{27.625}\right)^{0.877}\right)\right),$$

where H is in m and DBH is in cm (Figure S3). The belowground biomass (BGB, in kg dry mass) of each tree was estimated using the allometric equation proposed by Sierra *et al.* (2007):

$$\mathrm{BGB} = 0.01694 \times \mathrm{DBH}^{2.693},$$

where DBH is in cm. The total biomass (BIOM, in kg) of each tree was calculated as BIOM = AGB + BGB.

At the 1-ha scale, total biomass was assessed as the sum of the AGB + BGB of each rooted tree in each 100 m × 100 m subplot. The carbon stored in AGB (AGC), BGB (BGC), and total biomass (BIOM) was calculated by multiplying the dry mass by 0.456 (Martin *et al.* 2018). We calculated AGC, BGC, and total biomass by DBH classes (1–10 cm, 10–20 cm, 30–40 cm, 40–50 cm, 50–60 cm, and ≥60 cm). For consistency with our treatment of uncertainty for soil and Wdebris, we quantified uncertainty in biomass carbon as the 95% CI of the means over the 25 1-ha subplots. (Confidence intervals for AGB and AGC estimated by propagating errors from wood density and tree height, and allometry using the AGBmonteCarlo in the BIOMASS package were very similar to those calculated from means over 1-ha subplots.)

Spatial covariation of carbon stocks

Total carbon stocks (Ctot; Mg C ha^{-1}) were calculated as the sum of total soil carbon stocks up to 3 m depth (SCS; Mg C ha^{-1}), total biomass (BIOM; Mg C ha^{-1}), and total Wdebris (Mg C ha^{-1}). To assess the covariation across 1-ha plots between total carbon stocks (Ctot) and individual carbon compartments (SCS, BIOM, and Wdebris, and subsets of these), we calculated the Pearson correlation coefficient (r) of the log-transformed values. Finally, we analysed the correlations of the log-transformed total biomass (BIOM) with AGC, BGC, and biomass in different DBH size classes (specifically, 1–10 cm DBH, 10–20 cm DBH, 20–30 cm DBH, 30–40 cm DBH, 50–60 cm DBH, and DBH ≥60 cm).

All analyses were conducted using R 4.3.0 (R Core Team 2023).

Results

Carbon stocks

Soil bulk density (SBD) ranged between 0.61 gr cm^{-3} and 1.62 gr cm^{-3} and increased with depth (Figure 2A). Soil organic carbon concentrations (SOC) ranged between 0.227% and 3.105% and decreased with depth (Figure 2B). Total soil carbon stock (SCS) to 3 m depth was 193.4 ± 23.25 Mg C ha^{-1} (mean ± CI over 1-ha subplots). When we divided the soil profile into layers of 50 cm each, we found SCS was significantly higher in the most superficial one (0–50 cm) than in the 50–100 and 150–200 cm layers, but not than in the 100–150 cm layer (Figure 2C). Estimated total soil carbon stocks increased non-linearly with the depth included from 56.5 ± 4.3 Mg C ha^{-1} for 0–50 cm to 97.4 ± 8.1 Mg C ha^{-1} for 0–1 m, and 185.2 ± 19.6 Mg C ha $^{-1}$ for 0–2 m depth, before tending to asymptote to 3 m (Figure 3A).

The total carbon stored in Wdebris was 9.5 ± 4.0 Mg C ha^{-1}. Overall, the FFWD represented 35.1 ± 15.1%, FCWD represented 48.4 ± 13.2%, and SCWD represented 19.5 ± 7.0% of Wdebris (Figure 3B). The total carbon stored in biomass (BIOM) was 156.1 ± 8.2 Mg C ha^{-1}. Of this, AGC constituted 79.5 ± 0.39%, while the BGC accounted for 20.5 ± 0.39% (Figure 3C). The biomass stored in shrubs and small trees with DBH < 10 cm contributed 5.79 ± 0.35%, while trees with DBH ≥ 60 cm contributed 17.59 ± 1.13% of

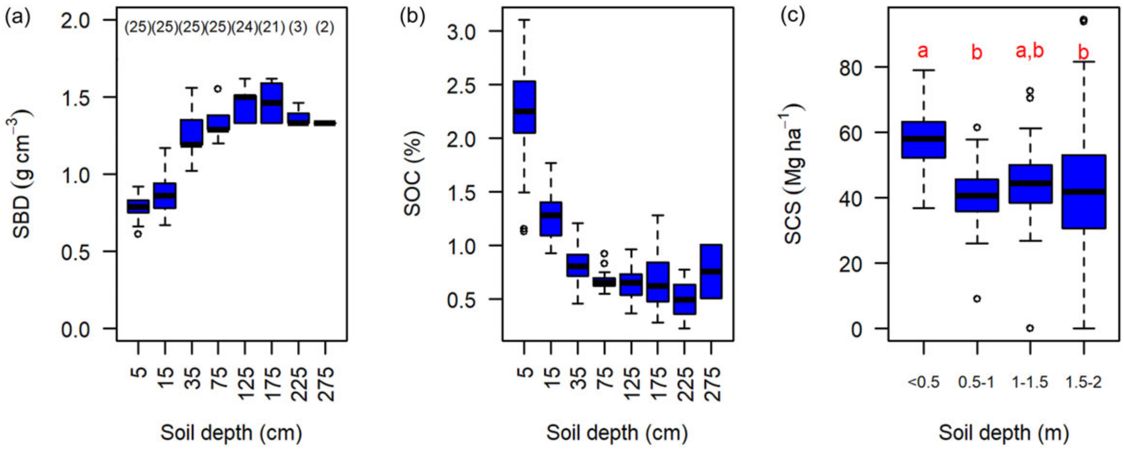

Figure 2. Variation with soil depth in (A) soil bulk density (SBD; g cm^{-3}), (B) soil organic carbon concentration (SOC; %), and (C) soil carbon stocks (SCS; Mg C ha^{-1}). Box plots show variation among 1-ha subplots within the 25-ha plot (Figure 1); the ends of the boxes indicate the 25th and 75th percentiles, the whiskers extend to the most extreme values that do not exceed 1.5 times the interquartile range, and open points show values beyond those extremes. Values within parenthesis in panel A represent the number of hectares with data at each corresponding soil depth. Different letters in panel C (in red) represent soil layers with significant differences in SCS.

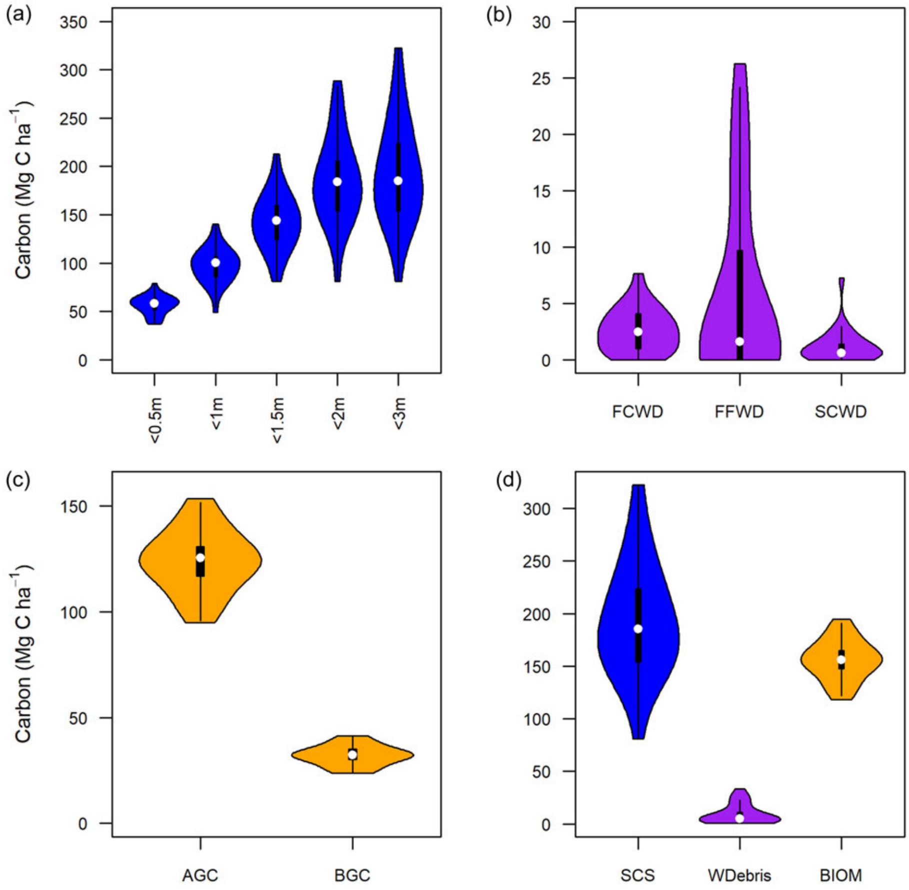

Figure 3. Variation in carbon stocks (Mg C ha^{-1}) at the 1-ha scale in different forest compartments in the 25-ha Amacayacu Forest Dynamics Plot. (a) Soil carbon stocks at different depths up to 3 m depth. (b): Woody debris carbon stocks in fallen fine (FFWD), fallen coarse (FCWD), and standing coarse woody debris (SCWD). (c) Biomass carbon stocks in the aboveground (AGC) and belowground biomass (BGB). (d): Total carbon stocks in soils (SCS), woody debris (WDebris), and total biomass (BIOM).

the total biomass. Among the DBH 10 cm DBH size classes examined, the 30–40 cm size class had the highest carbon stocks, but it was not significantly different from the 20–30 cm, 40–50 cm, and ≥60 cm DBH size classes (Figure 4).

The estimated near-total carbon stock (Ctot) in this Terra firme Amazon Forest was 358.9 ± 24.2 Mg C ha^{-1}. Total soil carbon stocks represented 53.1 ± 3.6%, biomass represented 44.2 ± 3.2%, and Wdebris represented 2.7 ± 1.1% of Ctot (Figure 3D; Table S1).

Covariation of carbon stocks

Across 1-ha plots, total carbon stocks (Ctot) were significantly correlated with total soil carbon stocks, but not with Wdebris or total biomass. In general, soil carbon stocks were significantly correlated with Ctot when including soil carbon to at least 50 cm depth. Ctot was also significantly correlated with the BGC of all trees and with the AGC of trees ≥60 cm DBH. The total biomass (Mg C ha^{-1}) was also significantly explained by the AGC of large

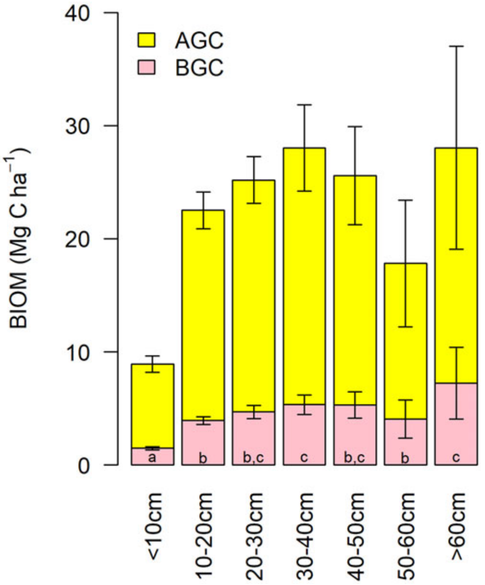

Figure 4. Distribution of the total biomass carbon stocks (BIOM; Mg ha^{-1}) across size classes defined by diameter at breast height (DBH). AGC: Aboveground carbon stocks. BGC: belowground carbon stocks. Size classes with the same letter are not significantly different ($p \geq 0.05$) in biomass carbon stocks (according to Tukey's Honest Significant test). Whiskers show the standard deviation of variation among 1-ha plots for both belowground (pink) and aboveground (yellow).

trees (DBH $\geq$ 50 cm) (Figure 5). Total biomass was not significantly related to soil carbon stocks to any soil depth (results not shown).

Discussion

Our study adds to a growing body of studies considering assessments of tropical forest carbon stocks beyond aboveground biomass (Araujo *et al.* 2023). In the Amacayacu Forest Dynamics Plot (AFDP), soils accounted for more than half (i.e., 53%) of the total carbon stocks when sampling soils to 3 m depth. The amount of carbon stored in the total biomass was three times larger than that found in the first 50 cm of soils, which is in line with other studies in Amazon forests (Malhi *et al.* 2009). Although the most superficial soil layer has the highest probability to be the most affected soil carbon pool in case of forest conversion to pastures or croplands (Veldkamp *et al.* 2020), our study emphasizes the importance of the larger deeper soil carbon stock, and of protecting this stock from loss due to the proliferation of illegal mining (Nunes *et al.* 2022) and illegal rudimentary infrastructure in northwestern Amazonia.

Carbon stocks in different forest compartments of the Amacayacu Forest Dynamics Plot

Soil carbon stocks can be seen as a 'mystery box' in carbon studies of tropical forests. The 193.4 ± 23.3 Mg C ha^{-1} found in our study shows that local variation of soil carbon stocks can resemble the regional variation reported in different Amazon forests (Malhi *et al.* 2009 and references therein; Quesada *et al.* 2020). Soil variation in the 25 ha plot was largely determined by soil depth, which would be expected to be associated with the spatial variation of soil denudation and the subsequent topographic variation found in this tertiary sedimentary plain (Zuleta *et al.* 2020). However, according to a one-way ANOVA, carried out after assigning a topographic unit (ridges, slopes, and valleys) according to Zuleta *et al.* (2017) to each one of the 25 20 m ×20 m quadrat centred in each 1-ha plot (doing that at the 1-ha scale is not feasible), there were no significant differences in total soil carbon stocks ($F = 0.237$, $p = 0.79$). The same happened when we tried at different soil depths (<20 cm, <50 cm, and <100 cm). Although we must acknowledge a relatively small sampling size to be conclusive in this regard, our data shows a very high variability within topographic units or habitats (Figure S4) that does not mirror the expected variation of the aboveground biomass at the 20 × 20 m quadrat scale (Zuleta *et al.* 2017).

Our findings disagree with the widespread idea that most of the carbon stored in soils is found in the first 30–50 cm (Quesada *et al.* 2020). In the AFDP, the silty-clayed nature of Acrisol soils, derived from Andean sediments (Hoorn 1994), also accumulates in depth (100–150 cm depth) a portion of carbon similar to that accumulated in the most superficial layer (Figure 2). This pattern of high carbon accumulation at deeper soil layers differs from that observed in sandy shield-derived soils of Amazon lowlands (Lips and Duivenvoorden 1996, 2001) as well as from soils of Andean highlands sampled to 1-m depth (Phillips *et al.* 2019a), where the most superficial soil layers override the amount of soil carbon stored through the soil profile. Although carbon reservoirs at deep soil layers have a lower probability of being depleted by deforestation alone, they could become an important source of CO_2 when subject to intensive land use change and extractive activities, such as mining, which affect the subsoil of tropical forests (Alvarez-Berríos and Aide 2015; Veldkamp *et al.* 2020).

Coarse Wdebris is also an important carbon pool in tropical forests (Baker *et al.* 2007; Baker and Chao 2011; Duque *et al.* 2017a; Gora *et al.* 2019). In the AFDP, the approximate proportions of fallen and standing coarse Wdebris, 80% and 20% respectively, were very similar to those reported in other tropical forests (e.g., Gora *et al.* 2019). The mean value of 9.5 ± 4.0 Mg C ha^{-1} found in Wdebris represented only 2.7 ± 1.1% of the total carbon stocks and was similar in size to the 10.5 Mg C ha^{-1} reported in a plot in Manaus (Chambers *et al.* 2000), which was in turn the lowest value for coarse Wdebris reported in a compilation of studies carried out in the Amazon basin (Malhi *et al.* 2009). Nevertheless, due to the high uncertainty in our estimates of carbon stocks in coarse Wdebris (the coefficient of variation is almost 100%), the observed values are not significantly different from those reported in other assessments of coarse Wdebris carried out in mature forests of the Colombian Amazon (16.9 ± 3.4 Mg C ha^{-1}; Navarrete *et al.* 2016). The wide confidence intervals for Wdebris reflect a very high sampling error within 1-ha plots given the small sample sizes applied using the transect method (Harmon *et al.* 1995) in tropical forests (Gora *et al.* 2019). To obtain a more reliable and accurate estimate of this carbon pool in this Amazon Forest, we would need to significantly enlarge our sample.

The total amount of carbon stored in both belowground and aboveground biomass reported in our study (156.1 ± 8.2 Mg C ha^{-1}) equals 342.3 ± 18.1 Mg ha^{-1} of biomass. Most of the forest biomass was concentrated in intermediate size classes (10–60 cm), a structural pattern typical of wet-warm climates and forests with a long tree-growing season (Piponiot *et al.* 2022). This highlights the importance of considering intermediate size trees too, not just large trees (e.g., DBH $\geq$ 60 cm), even if large trees are a dominant component of the biomass in many forests worldwide (Lutz *et al.* 2018; Slik *et al.* 2013). At our site, large trees with DBH$\geq$ 60 cm accounted for less than 18% of total

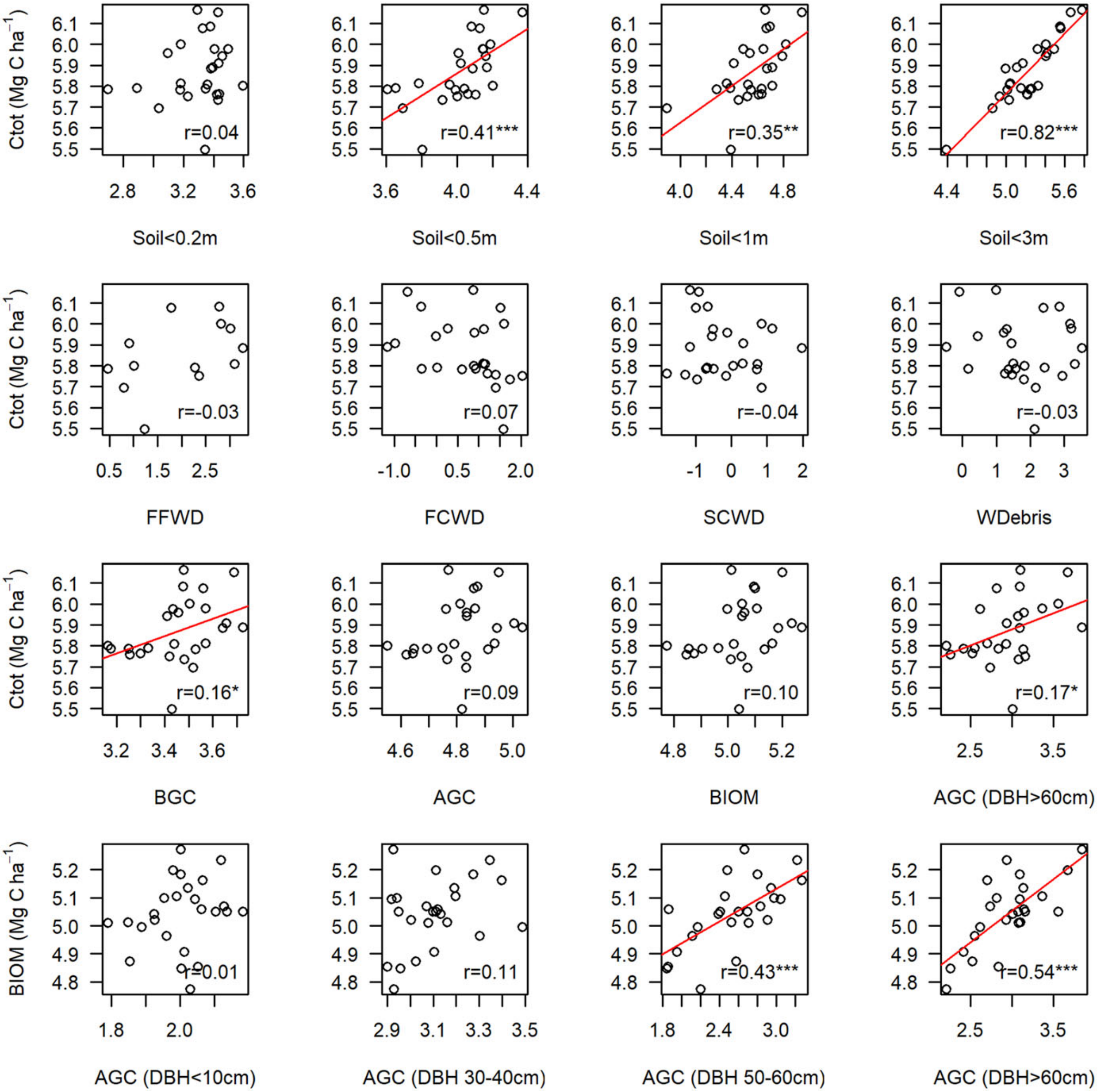

Figure 5. Relationships of total forest carbon stocks with forest stocks in particular components, and interrelationships among stocks in components, across the 25 1-ha subplots within the Amacayacu Forest Dynamics Plot. All variables are log-transformed for analysis. Pearson's correlation coefficients are shown for all relationships; linear regression lines (red) are shown when correlation coefficients are significant ($p \leq 0.05$). Abbreviations are defined in the methods. In all cases, the units are log Mg C ha^{-1}. In the panel's row at the bottom, we omitted the non-significant correlation between BIOM and the AGC size classes 10–20 cm DBH and 20–30 cm DBH for graphical purposes.

biomass. Nonetheless, spatial variation in biomass in these large trees was a good predictor of spatial variation in total biomass.

In the AFDP, the aboveground biomass (AGB), the most common currency employed to refer to carbon stocks in tropical forests, was 271.9 ± 13.9 Mg ha^{-1} (DBH $\geq$ 1 cm), which is almost identical to the AGB reported in Yasuni (Valencia *et al.* 2009). The high similarity between these two forests located in the northwestern Amazon is consistent with the expected influence of soil fertility and rainfall (Phillips *et al.* 2004) as drivers of patterns of carbon stocks in these very diverse forests (Duque *et al.* 2017b). However, the use of different AGB allometric equations in Yasuni (Chave *et al.* 2005; without including tree height) and Amacayacu (Chave *et al.* 2014; including tree height) hampers comparisons of C stocks. Although measuring tree height in wet tropical forests is challenging due to the difficulty of visualizing the tallest part of the crown from the ground (Duque *et al.* 2017a), its inclusion in AGB allometric models increases accuracy, even as it tends to result in lower estimated AGB values (Phillips *et al.* 2016). In the AFDP, the use of Chave *et al.* (2014) equation without tree height (e.g., Piponiot *et al.* 2022; Zuleta *et al.* 2017), results in estimated average AGB of 298.4 ± 15.9 Mg ha^{-1}, a value 9.7 ± 0.5% higher than that estimated above using the local H:DBH allometry.

In the AFDP, the belowground biomass estimated from a tree-by-tree assessment based on DBH (Sierra *et al.* 2007) results in a belowground:aboveground ratio of 0.26:1, which is higher than the 0.21:1 root:shoot ratio applied by Malhi *et al.* (2009) in central Amazon forests. If we had used an equation for belowground biomass developed in Africa (Kachamba *et al.* 2016) instead of the one developed by Sierra *et al.* (2007) in the tropical Andes, the estimated belowground:aboveground ratio would have increased to 0.40:1. The refinement and understanding of the belowground biomass variability needs more field studies to better understand local and regional variations of this specific carbon pool in tropical forests (Waring and Powers 2017) as well as to calibrate and evaluate future assessments based on remote-sensing products.

Pattern of covariation of carbon pools in the Amacayacu Forest Dynamics Plot

The use of expansion factors, which can be defined as a multiplication factor that enables estimation of the biomass of a whole tree or a specific structural compartment from a particular metric or portion of the tree, has been a common practice popularized by the IPCC (Eggleston *et al.* 2006). In the AFDP, near-total carbon stocks were correlated most strongly with soil carbon stocks and were not correlated with biomass carbon stocks or Wdebris carbon stocks. Soil carbon stocks to 50 cm or more were good predictors of total carbon stocks across 1-ha subplots. This is consistent with the findings that estimated soil carbon stocks varied more among hectares than biomass carbon stocks, and that soils and biomass contributed similar proportions to total stocks (Figure 3D). Interestingly, the substantial variation in soil carbon stocks in this area is not associated with systematic variation in topography (Zuleta *et al.* 2020).

The more limited variation in biomass reflects the relative homogeneity of forest structure in this area; the variation that is present is uncorrelated with the amount of C soil stocks at the 1-ha scale. This finding is in line with the similarity in aboveground biomass reported in different studies across the northwestern Amazon (Phillips *et al.* 2009). Although we found a significant correlation between the AGB of large trees (DBH $\geq$ 60 cm) and total carbon stocks, ($r = 0.17^*$) across 1-ha plots, we do not know whether such a relationship holds more broadly. An expanded analysis of the correlations among different forest carbon pools within and among other tropical forests could yield new insights into patterns and predictors of forest carbon stock variation, and thereby improve understanding of the consequences of forest loss and degradation for global carbon budgets.

Conclusions and future directions

This study contributes to the evidence that Amazon tropical forests are an important carbon reservoir, one that must be protected not only to avoid the destruction of a magnificent ecosystem but also to avoid its becoming a major source of greenhouse gases to the atmosphere. Most obviously, deforestation results in the loss of biomass carbon stocks, and associated releases of greenhouse gases (Cabrera *et al.* 2020). Since the AFDP soils represent the largest carbon stock when we sampled to 3 m depth, our findings warn about the proliferation of illegal mining and the development of infrastructure that can promote the release of the huge carbon reservoirs stored in deep soils. Analyses of land use change impacts do not take into account the potential for substantial emissions due to soil carbon losses.

Overall, we still have much to do to improve our estimates of carbon stocks in tropical forests. To improve the global carbon balance and the accounting of greenhouse gas emissions we need to better understand carbon stocks and dynamics in tropical forests beyond aboveground biomass. Estimates of biomass carbon stocks remain highly uncertain, based on generalized allometric equations that fail to capture extensive local variation. We need more allometric data and better allometric models for both aboveground and belowground biomass, but especially for the latter, which remains very poorly known. Collection of biomass harvest data to inform such equations is expensive, logistically demanding, and destructive. We need to take advantage of new technologies, such as LiDAR, that have the potential for nondestructive yet precise estimates of tree biomass (Spawn *et al.* 2020). We also need more measurements of carbon stored in deep soils to quantify this important carbon stock and a better understanding of its fate under land use change.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0266467424000270.

Data availability statement. The data employed to run the analyses at the 1-ha scale are available at the Smithsonian DataOne portal (https://smithsonian.dataone.org/portals/tropical; doi:10.60635/C3D59S).

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Competing interests. The authors declare none.

Ethical statement. None.

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