Soil and Biomass Carbon Storage is Much Higher in Central American than Andean Montane Forests

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Abstract. Tropical montane forests (TMF) play a key role in the global carbon (C) cycle and by sequestering large amounts of above and belowground carbon. Elevation gradients in TMF have helped reveal the influence of environmental factors on C stocks. Few studies have evaluated the influence of elevation and soil nutrient availability on C stocks in the context of heterogeneous patches of ectomycorrhizal (EM) and non-EM forests in the Neotropics, especially in the mountains. We estimated aboveground biomass (AGB), coarse wood debris (CWD), and soil C based on field inventories in ten 1-ha plots along an elevational gradient from 880 to 2920 m a.s.l varying in relative abundance of EM-trees in western Panama. Trees $\geq$ 10 cm diameter at breast height (DBH) and CWD $\geq$ 10 cm diameter were measured to calculate biomass and necromass. Soil C to 1 m depth was estimated. Furthermore, climate and edaphic characteristics were described for each plot to evaluate the influence on these variables on each C pool. AGB, downed CWD and soil C were strongly positively correlated with elevation. We found exceptionally high AGB, up to 574.3 Mg ha^{-1}, and soil C, up to 577.9 Mg ha^{-1} at higher elevations. After controlling for elevation, neither nutrient availability nor EM-dominance had an effect on AGB or soil C. Nonetheless, high AGB at high elevations was attributed to the presence of *Quercus* species. We found previous LiDAR-derived estimates for our site substantially underestimated the aboveground carbon (AGC) present in the plots which were between two and six times lower than our field-based estimates. Remarkably high soil C at high elevations might be a consequence of reduced decomposition rates associated with lower temperature, or geological history, where repeated volcanic eruptions buried surface soil organic layers. Our results highlight large regional uncertainty in C pool estimates in Neotropical montane forests, with potentially large underestimates for Central American C stocks.

1 Introduction

Tropical forests store ~40-55% of the total carbon (C) in terrestrial ecosystems (Pan et al., 2011; Meister et al., 2012; Pan et al., 2013), and therefore play a key role in the global C cycle and climate regulation (Malhi and Grace, 2000; Keenan and Williams, 2018; Mitchard, 2018). This carbon is sequestered in several pools, consisting of live biomass, necromass (i.e. coarse woody debris or litter), and soil. Estimating of the size of each pool is critical to evaluating uncertainty in future global C budget predictions. While it is well known that climate and edaphic processes influence C stocks (Moser et al., 2011; Clark et al., 2002; Girardin et al., 2010), mycorrhizal interactions have also been shown to have a significant impact on C cycling at the global scale (Phillips et al., 2013; Averill et al., 2014; Steidinger et al., 2019). Evaluating the effects of temperature, nutrient availability and tree mycorrhizal status on tropical forest C stocks is an important step in predicting future atmospheric CO_2 levels (Keenan and Williams, 2018).

Studies along elevational gradients in the tropics, especially in the Andes, have been shown to provide powerful natural experiments to understand how the environment directly and indirectly influences processes related to C cycling (Girardin et al., 2014; Malhi et al., 2017; Girardin et al., 2010; Nottingham et al., 2015a; Homeier and Leuschner, 2021). Factors such as temperature, cloud cover, precipitation, nutrient availability, and species composition change as elevation increases, affecting
45   aboveground biomass (AGB), woody debris and the soil C stock. For AGB, a meta-analysis found that AGB tends be higher at lower elevations (Muller-Landau et al. 2020). However, low values of AGB have also been found in the Amazon below 500 m a.s.l due to low fertility (Quesada et al., 2012). High temperatures in the lowlands are typically associated with fast plant growth rates; in the Amazon, studies have shown faster growth rate is associated with lower mean wood density (Malhi et al., 2004; Baker et al., 2004), suggesting low AGB. However, it is important to note that low wood density is not always associated with a
50   reduction in AGB (Phillips et al., 2019b). On the other hand, for soil C stocks, in upper montane forests, C can accumulate at low temperatures by decreasing microbial decomposition (Nottingham et al., 2015a).

While elevational gradients can help us understand how temperature influences ecosystem carbon stocks, additional potentially confounding factors vary with elevation. For instance, cloud cover varies from 57% at low elevations up to 98% at high elevations (Muller-Landau et al., 2020; Dalling et al., 2021) and precipitation can peak at middle or high elevations (Malhi
55   et al., 2010). In montane forests soil nutrient availability can vary over short geographic scales, associated with variation in parent material and substrate age (Prada et al., 2017). Soil nutrient availability affects forest productivity in the tropics, but its effect on AGB is less clear, showing a positive, negative, or no relationship (Muller-Landau et al., 2020). Furthermore, soil nutrient availability influences tree tissue nutrient content and therefore litter quality and potentially wood decomposition rate (Aerts and Chapin, 1999). Recalcitrant tissues with low nutrient concentrations decompose slowly and increase soil carbon
60   sequestration due to their long residence time in soil (De Deyn et al., 2008). However, there is also evidence that fast-decomposing labile tissues can remain in the soil as mineral-associated soil organic matter, and thus increase soil C (Cotrufo et al., 2013).

While environmental factors play a critical role in forest structure and function, plant mutualisms with microbes also strongly impact soil C storage. Ectomycorrhizas (EM) and arbuscular mycorrhizas (AM) are thought to influence C stocks via
65   effects on decomposition (De Deyn et al., 2008; Averill et al., 2014; Phillips et al., 2013). Studies have found that forest trees associated with EM fungi promote slow C cycling compared to trees associated with AM fungi (Soudzilovskaia et al., 2019; Phillips et al., 2013). In temperate forests this may be partly due to lower quality litter in EM trees than in AM trees, resulting in slower decomposition (Craig et al., 2018; Keller and Phillips, 2019). Additionally, the stratification of soil C storage with soil depth also appears to depend on mycorrhizal type; soil under EM trees stores more C in the surface layers while soil under AM
70   trees stores more carbon in deep layers (Craig et al., 2018).

In this study we estimated the size of three C pools: AGB, coarse wood debris (CWD), and soil C in ten 1-ha plots along an elevational gradient in western Panama and evaluated the influence of climate, edaphic and biotic factors on each pool. To our knowledge this is the first study in EM-associated forests that integrates both the effect of soil nutrient availability and elevation on C stocks in the Neotropics. Studies in western Panama provide new insights into the drivers of C storage because
75   unlike many Andean forests, the dominant ecological group shifts with elevation, from AM-dominated forests at low elevations to EM-dominated forests at high elevation. We hypothesized that i) a reduction in temperature with increasing elevation results in reduced growth rates, increased wood density and therefore reduced forest turnover rate and CWD, and potentially also AGB (if stand height also declines with elevation as in other neotropical forests (Girardin et al., 2010; Unger et al., 2012)); ii) decreasing nitrogen availability with elevation (Marrs et al., 1988; Homeier and Leuschner, 2021) would further favor trees with
80   conservative nutrient cycling strategies (i.e., high wood density and low nutrient concentration; Soong et al., 2020), also resulting

in lower canopy turnover rates and CWD. However, wood from low soil nutrient availability sites has lower nutrient concentrations (Heineman et al., 2016), resulting in slower decomposition, which may allow CWD and soil C to accumulate; iii) forests associated with EM-tree species have high overall C storage, EM-tree taxa that form monodominant stands in tropical forests have previously been associated with low nutrient soils (Hall et al., 2020), tend to have conservative nutrient cycling

85   strategies (Phillips et al., 2013) and have been associated with soils with higher C:N (Lin et al., 2017; Averill et al., 2014). Therefore, following our previous hypothesis, we expected the presence of EM-trees to increase AGB relative to those with and non-EM trees species at similar elevation. Additionally, if EM associations either reduce decomposition rates due to differences in litter quality or nutrient immobilization (McGuire et al., 2010; Read and Perez-Moreno, 2003), then we predicted higher accumulation of soil C in EM-dominated forests. Our ground sampling across forests with contrasting edaphic conditions and

90   species composition also allow us to compare C estimates for our sites with previously published data from other neotropical forests along elevation gradients.

In recent decades LiDAR technology has been used broadly to map aboveground carbon stocks at large scale (Saatchi et al., 2011; Zolkos et al., 2013; Carreiras et al., 2017). However, in complex terrains, such as montane tropical forests, LiDAR using low point densities can result in large AGB uncertainty (Leitold et al., 2014), while models of AGB need to specifically

95   represent montane forests structure (González-Jaramillo et al., 2018). We highlight this need by comparing the ground-derived estimates of AGB for our plots with an existing prediction of AGB derived from a combination of airborne Light Detection and Ranging (LiDAR) and more limited ground truthing datasets of Panama that did not account for structural and compositional variation between lowland and montane forests (Asner et al., 2013).

2 Materials and methods

100   ### 2.1 Study Site

The study was conducted in western Panama along an elevational gradient ranging from 880 to 2920 m a.s.l within the Fortuna Forest Reserve (Fortuna), the southern edge of the adjacent Palo Seco Forest Reserve (8˚45'N, 82˚13'W), and at Finca El Velo (8˚49"11'N, 82˚28"58'W), on the northeastern slope of Volcan Barú National Park (Barú) (Fig S1). The elevational gradient extends from super-humid premontane forests (700-1000 m a.s.l) and lower montane forest (1000-1500 m a.s.l) (Holdridge

105   1947) in Fortuna, to mid-elevation montane forests (1700-2000 m a.s.l) and upper montane cloud forests (>2000 m a.s.l) at Barú. At Fortuna, mean annual rainfall ranges between 4600 and 6300 mm (Prada et al., 2017; Dalling et al., 2021), while at 2300 m a.s.l at Barú, mean annual temperature is 14 ˚C and mean annual rainfall from 2019 to 2021 was 2260 mm. For this study, ten permanent 1-ha plots were used: six plots established at Fortuna in 2003 and four at Barú in 2015, where all trees with ≥ 5 cm diameter at breast height (DBH) were measured and identified to the lowest taxonomic level possible. When a species

110   identification was not determined a morphospecies was designated. In this study to facilitate comparisons with other published datasets only trees, palms and tree ferns ≥ 10 cm DBH were included in the analyses.

Across the elevational gradient, plots vary in relative abundances of different taxonomic and functional groups that are known to have important ecological roles in tropical forests, including trees associated with EM, N-fixers, and palms (Table 1). Trees were classified as EM (ectomycorrhizal) based on literature sources and root studies made at the field site (Corrales et al., 2018;

115   Soudzilovskaia et al., 2020; Averill et al., 2019; Corrales et al., 2016). Using the same references, trees that have been classified as forming associations with AM, ericoid mycorrhizas (e.g., *Vaccinium*), or as non-mycorrhizal trees (e.g., *Roupala*), as well as species for which the mycorrhizal type is unclear, were classified as non-EM taxa. N-fixing ability was classified following

(Huss-Daniel, 1997; Sprent, 2009). The contribution of these ecological groups (EM, N-fixers and palms) was calculated as their percentage of the total basal area of each plot.

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Table 1. Summary of characteristics of ten 1-ha plots along an elevational gradient in western Panama including trees >10 cm DBH. Percent of basal area of species that form ectomycorrhizal associations (EM), N-fixing, and palm taxa. FFR= Fortuna Forest Reserve, VBNP = Volcan Baru National Park.

Plot	Plot code	Site	Type of forest	Elevation (m a.s.l)	No. trees	No. stems*	Basal area (m²ha⁻¹)	% EM	% N-fix	% Palms
PaloSeco‡	PS	FFR	Mixed	880	630	646	31.2	2.4	17.4	2.3
AltoFrio§	AF	FFR	Mixed	1100	1019	1042	44.6	7.1	8.5	0.0
ChorroA†	CA	FFR	Palm-dominated[b]	1100	979	1002	32.6	9.2	0.4	41.7
HondaA†	HA	FFR	Mixed/EM-dominated[c]	1155	800	804	41.6	24.0	4.4	0.4
Samudio*	SAM	FFR	Mixed	1215	1049	1071	33.7	0.78	10.4	0.8
Hornito¤	HOR	FFR	Mixed	1330	681	694	55.2	2.2	2.2	0.0
Mirador Þ	MIR	VBNP	Mixed	1987	457	477	46.7	1.1	4.9	0.0
CasitaA Þ	CASA	VBNP	EM-dominated[a]	2248	646	686	50.5	74.1	0.4	0.0
Quetzal Þ	QUE	VBNP	EM-dominated[a]	2599	543	564	59.0	48.1	3.2	0.04
Copete Þ	COP	VBNP	EM-dominated[a]	2923	630	728	63.0	63.3	7.3	0.0

125 Geology: ‡ mafic volcanic; § undifferentiated volcanics; †rhyolite; * mafic/rhyolite; ¤ dacite; Þ Holocene lahar flow. Forest type: [a] *Quercus*-dominated; [b] *Colpothrinax aphanopetala*-dominated; [c] *Oreomunnea mexicana*-dominated *No. of stems used for the analyses includes multiple stems of individual trees

2.2 Soil sampling variables

Soil data are described in detail for the plot network in Fortuna (Dalling et al., 2021; Turner and Dalling, 2021). For this study,
130 soil data were used for six plots from Fortuna plots network collected in July 2008 or July 2010 (Prada et al., 2017) and from four Barú plots, collected in May 2016. Soil from each plot was analyzed for bulk density (BD), pH, resin extractable P (ResinP), extractable inorganic N (NH_4 and NO_3), extractable cations (Al, Ca, Fe, K, Mg, Zn), effective cation exchange capacity (ECEC), total exchangeable bases (TEB), and total N and P. Following the protocols described in Prada et al. (2017), soil samples were collected from the surface 0–10 cm of soil after removing the litter layer. Soil samples were collected in a regular grid within
135 each 1-ha plot (center of every other 20 x 20 m subplot) resulting in thirteen sampling locations for each plot.

2.3 Climate variables

To evaluate the climate regime across the elevational gradient we obtained data from the CHELSA database (http://chelsa-climate.org) at 30 arc-sec spatial resolution (Karger et al., 2017) for each plot. We obtained ten variables that have been shown to be important in determining forest structure: MAT (mean annual temperature), MATvar (mean temperature range), MATmax
140 (max temperature), MATmin (min temperature), TS (temperature seasonality), MAP (mean annual precipitation), MPdry (mean of driest month), MPwet (mean of wettest month), ISO (isothermality) and MDR (mean diurnal range) (Hofhansl et al., 2015; Schmitt et al., 2013). Additionally, we extracted the average climatic water deficit (WD) data from a global climate layer for the long-term at 2.5 arc-minute resolutions (http://chave.ups-tlse.fr/pantropical_allometry.htm). Climatic WD describes seasonal moisture limitation, with very negative WD values indicating strongly seasonally water-stressed sites.

2.4 Carbon stock calculations

2.4.1 Aboveground biomass and aboveground carbon

We used the BIOMASS R package to estimate AGB (Réjou-Méchain et al., 2017); functions in this section are all part of this package. For each plot, all stems ≥ 10 cm DBH (including multi-stemmed trees) were measured and identified to genus, species or morphospecies. The DBH used for the analyses was the value from the last re-census measured from Fortuna and Barú (2018 and 2015 respectively). We estimated the height of a subsample of 78 ± 11 trees from each plot using a triangulation approach, measuring the angle to the tree base, the angle to treetop and the distance to the tree. The angles were measured using a manual clinometer (PM5/360PC, Suunto, Finland). To estimate the height of each tree in each plot, we created a plot height-diameter model using the *log 1* equation in the function *modelHD()* (Fig. S2). *Log 1* was the best model for seven of the plots based on the AIC index compared to the other models proposed in Réjou-Méchain et al (2017). To estimate the wood density of each tree we measured the density of 117 species across all plots, with an average of eight individuals measured for each species. Wood volume in the field was quantified with the water displacement method (Chave, 2006). This dataset was incorporated into the function *getWoodDensity*(), assigning a density to each tree based on our field wood density, then the nearest species, genus or family measurement if the field data were missing. Trees without any identification (23% of the total trees) were assigned the average plot level measurement. To estimate the AGB of trees we used Chave et al. (2014) allometric Eq. (1):

$$AGB = 0.0673 * (\rho * H * D^2)^{0.976} \tag{1}$$

Where ρ is the wood density, H is the height, and D is the DBH of each tree. We used Avalos et al. (2022) allometric equation for Palms aboveground carbon Eq. (2):

$$AGC = \exp(-4.11+1.96*\ln(D)+0.8*\ln(H)) \tag{2}$$

In this case a factor of 2 was used to convert carbon stock to AGB, and a factor of 1.4 was applied to account for the bias introduced by log-transformation, as described by Avalos et al. (2022). Finally we used Beets et al. (2012) allometric equation for tree ferns aboveground carbon Eq. (3):

$$AGC = 0.0027*(D^2*H)^{1.19} \tag{3}$$

A factor of 2 was used to convert carbon stock to AGB following Beets et al. (2012).

To compare the distribution of AGB values between lowland and montane forests across the region we used 212 plots from twelve studies in the Neotropics, including ten plots from this study (Table S1). The distributions of AGB values among forest types and elevation classes were assessed by bootstrapping the AGB with 1000 resamples. Finally, we compared the AGC values obtained in this study, calculated using the same *AGBmonteCarlo*() function but applied to carbon values (Réjou-Méchain et al., 2017) with a carbon ratio of 47.1% (Thomas and Martin, 2012), to those derived from the high-resolution airborne LiDAR maps of Panama produced by Asner et al. (2013, 2021). LiDAR-derived estimates for our site locations were extracted using GPS coordinates and matched to the same 1-ha spatial resolution, ensuring a consistent comparison.

2.4.2 Downed coarse wood debris

To estimate the downed CWD (DCWD) we used a line-intersect sample method following Gora et al. (2019) and Larjavaara & Muller-Landau (2011). Downed CWD was defined as wood debris fallen to ground level that was ≥ 10 cm diameter and crossed the transect. For each plot, we measured DCWD along twenty-two transects of 0.1 km. For the PS plot (Table 1) we only conducted 10 transects given the difficulty of traversing this plot. Transects were oriented south to north and east to west every 10 m within and including the edge of the plot. For each piece of DCWD we used a large caliper to measure the diameter at the point the transect crossed the sample. Using a qualitative classification method, each sample was classified into three

decomposition categories 1) 'Hard', if the sample was hard to the touch, 2) 'Medium', if the sample was still somewhat solid but soft to the touch, 3) 'Soft', if the sample was visually rotten and collapsed easily. For each decomposition category and for each plot we took destructive samples consisting of a cross-section that was weighed, measured, and dried to estimate the necromass (Gora et al., 2019). With the destructive samples we used linear regressions to estimate the necromass of the samples, where the necromass was a function of diameter, decomposition category, and plot. All cross-section masses were corrected by the random angle correction factor (π/2), summed and divided by the transect length. For the final estimates of the DCWD we calculated the 95% confidence intervals by bootstrapping over unit samples (10 m; Gora et al., 2019).

2.4.3 Standing coarse wood debris

To estimate the standing CWD (SCWD) we used a plot approach following Gora et al. (2019) and Larjavaara & Muller-Landau (2011). Standing CWD was defined as dead trunks with a DBH ≥ 10 cm. We measured SCWD in five 20×20 m subplots, for a total of 0.2 ha area sampled in each plot. For each SCWD sample we measured the DBH, height (H), classified it in the same decomposition categories as the DCWD, and additionally classified it in two qualitative branch categories: 1) With branches, if the sample retained between 20-100% of branches, and 2) without branches, if the sample retained < 20% of branches.

We estimated the necromass of the standing dead wood in two ways. For standing dead wood with branches we used the BIOMASS package (Réjou-Méchain *et al*., 2017) using Eq. (1) in this study. In this case ρ was calculated using the DCWD destructive samples. Since the wood densities differed between DCWD decomposition categories ($F_{(2,326)}$ = 87.35, P = <0.001), wood density was calculated as the average of each decomposition category by plot. Height was the total height of the sample measured in the field. Necromass was calculated as 87.5% of the total original AGB estimated (Gora et al., 2019) using Eq. (1). For standing dead wood without branches we calculated the volume and density of each sample. We used a taper function to estimate the diameter at the top using the Kozak *et al*. (1969) equation in Cushman et al. (2014) and the volume was calculated as a truncated cone for samples ≥ 3 m high. For samples < 3 m high we calculated the volume as a cylinder. Densities were calculated in the same way as branched SCWD. We summed the necromass of all the samples in all categories and we divided by the total area to estimate the SCWD by plot. We calculated the 95% confidence intervals by bootstrapping over unit samples (20×20 m subplots; Gora et al., 2019).

2.4.4 Soil Carbon

To estimate the soil C stocks in each plot we collected mineral soil in four depth increments from 0 to 100 cm at a subset of five of the thirteen locations sampled for soil nutrients. For the Fortuna network plots the 50-100 cm depth soil C value was based on a single estimate from profile pits adjacent to the plots excavated to 1.5–2.0 m (Turner & Dalling, 2021). The 0–10 cm, 10–20 cm and 20–50 cm depth samples were taken with a 5 cm diameter core, and for 50–100 cm depth samples we used a 6.25 cm diameter corer. Total C stock in each depth was calculated as the product of the total C%, bulk density, and the increment of each depth. Total C% was determined by elemental analysis (Thermo Flash 1112 analyzer, Bremen, DE) and bulk density following Prada et al. (2017). The 95% confidence interval of the total C stock was calculated by bootstrapping over locations for each plot.

2.5 Data analysis

All environmental variables were standardized to a mean of zero and standard deviation of one to perform the analyses. All statistical analyses were conducted in R version 4.2.2 (R Core Team, 2022).

2.5.1 Plot characterization

To explore and visualize the variation of environmental variables among plots, soil and climate variables were analyzed separately with a principal component analysis (PCA).

2.5.2 Effect of soil and mycorrhizal type on trees' wood density

One-way ANOVA was used to evaluate differences among plots soil characteristics and trees wood density. We included mycorrhizal type as a fixed effect and species as random effect. *P*-values of the main effects were estimated using model simplification (Crawley, 2013).

2.5.3 Effect of environmental variables and mycorrhizal type on C stocks

To examine the relationship between environmental variables and mycorrhizal type across the different carbon pools we used a structural equation model (SEM) to partition the variance of responses. An *a priori* model was hypothesized based on our predictions and simple linear regressions between environmental variables and each carbon pool (Fig. S3, Table S3). A second set of PCA was performed excluding resin-extractable P, NH_4 and temperature variables since we were interested in those direct effects; the first PCA scores were then used as environmental and edaphic parameters in the SEM (Fig. S4 a, b). To correct for collinearity the model included the correlation between variables that are highly correlated ($r > 0.5$, Table S4). Representation of EM-associated trees was incorporated in the model as the percent of plot basal area represented by EM-tree species (Table 1). We then used SEM to evaluate the indirect and direct effect of each independent variable on each carbon pool, using the piecewiseSEM R package (Lefcheck, 2016). To discriminate between models, we followed the approach of Glassmire et al., (2020) for adding and dropping variables. Akaike's information criterion (AIC) was used to compare the alternative models. The best model was the most parsimonious; the fit of the best model was evaluated using Fisher's C statistic (Lefcheck, 2016). Lower values of Fisher's C value indicate smaller differences between the model and the data. Standing CWD was not included in the SEM analysis since it was not correlated with any of the abiotic or biotic factors or to the other carbon pools.

3 Results

3.1 Edaphic and climate variation

Edaphic characteristics were highly heterogenous across plots – NH_4 varied six-fold, NO_3 twelve-fold, and resin-extractable P varied 87-fold (Table S5). The first two axes of the first soil PCA (Fig. 1a) explained 68.9% of the variance in the edaphic variables among plots. In the first axis, two plots, MIR and AF were grouped together by variables associated with high fertility (i.e., cation exchange capacity (ECEC)). The Fortuna plots CA, HA, PS and SAM grouped together and were associated low pH and high Fe in the soil. The second axis described soil variation with elevation (Fig. 1a). The plots at the highest elevation are at the bottom of the figure and are associated with high values of resin P.

The first two axes of the climate PCA (Fig. 1b) explained 87.9% of the variance in the climate variables among plots. The first axis grouped plots by the sites Fortuna and Barú and shows the association between climate variation and elevation (Fig. 1b). The plots at the highest elevations are at the right of the figure and are associated with low mean annual temperatures (MAT) and high mean precipitation during the driest month (MPdry). The second axis groups together three plots, CA, HA, and PS, which are associated with high values of mean diurnal range (MDR). The plots HOR and AF group together related to high

mean precipitation during the wettest month (MPwet). Although there is high variation in seasonal water stress (WD) (Table S5), its contribution to climate variation was low (Fig. 1b).

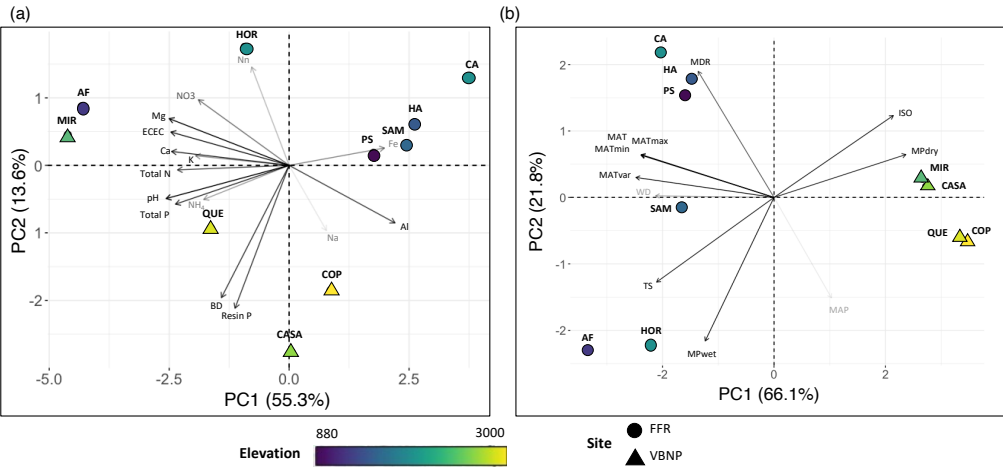



Figure 1. Principal component analysis (PCA) for (a) soil variables 0-10 cm depth, and (b) climate variables of ten 1-ha plots (Table 1) in an elevational gradient in Panama. Direction and length of vectors indicates the effect of the variable. Black arrows represent significant effects ($p<0.05$) and gray arrows non-significant effects. Color represents the elevation of the plot, and the symbols represent the site. BD = bulk density, ResinP = resin extractable P, ECEC = effective cation exchange capacity, TEB = total exchangeable bases, MAT = mean annual temperature), MATvar =mean temperature range, MATmax = max temperature, MATmin = min temperature, TS = temperature seasonality, MAP = mean annual precipitation, MPdry = mean of driest month, MPwet = mean of wettest month, ISO = isothermality, MDR = mean diurnal range, WD= water deficit, FFR= Fortuna Forest Reserve, VBNP=Volcan Baru National Park. Plot name codes are given in Table 1.

3.2 Total carbon stock estimates

Total carbon stocks for the ten plots ranged from 249.5 to 882.1 Mg ha^{-1} (Table S1, Fig. 2a). Aboveground carbon and soil C were the most important carbon pools, contributing 23–50% and 32.5–70.7%, respectively, of the total carbon budget of the forest (Fig. 2b). The contribution of CWD to the total carbon budget was highly variable, ranging from 3.8–44% between plots. For example, for QUE and HOR the plot total CWD was nearly 10 times smaller than AGC, while for HA the total CWD contribution was higher than AGC (Fig. 2b).

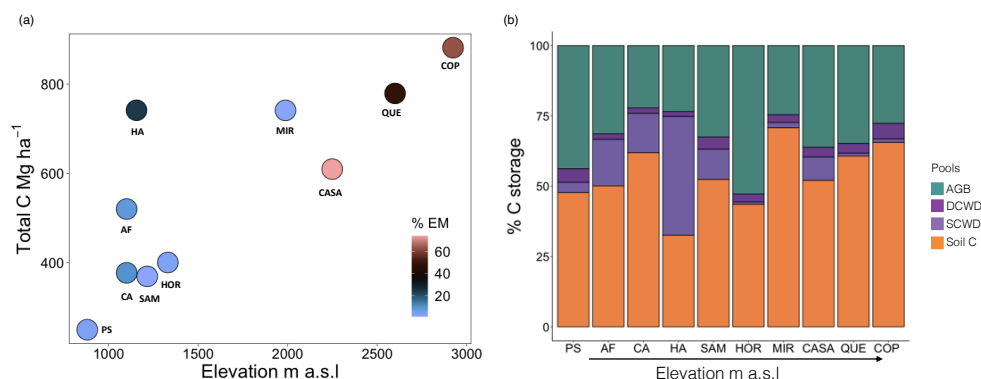



Figure 2. Total C stocks (a) and contribution (b) of the different pools to the total carbon stocks for ten 1-ha plots in an elevational gradient in western Panama. AGC = Aboveground carbon; DCWD= Downed coarse wood debris; SCWD = Standing coarse wood debris; % EM= percent of plot basal area occupied by EM trees.

3.2.1 *Aboveground Biomass*

To estimate the AGB, 7434 trees (from 91 plant families) and 780 tree heights were measured across all of the ten plots. Aboveground biomass varied three-fold among plots, ranging from 177.6 to 574.3 Mg ha^{-1} (Table S1). Different taxa contributed to AGB in different plots, with important contributors including Fagaceae (57.0-83.8%), Sapotaceae (22.1-38.8%) and Arecaceae (34.5%). In addition to taxon differences, contributions of ecological groups to AGB also differed across plots. EM-trees ranged from 0.98-83.8% of AGB across plots. EM-trees in the genus *Quercus* were the most important contributors to AGB at the highest elevation plots (57-83.8%), and at the HA plot, where EM-trees including *Oreomunnea mexicana* (Juglandaceae) accounted for 24% of basal area and 18.4% of the AGB. N-fixing trees accounted for 0.25-19.2% of the total AGB of the plots. Palms were the most important ecological group in the CA plot, accounting for 34.5 of AGB, whereas palms contributed < 1% of total AGB in the remaining plots. EM-trees had higher wood density compared to AM-trees ($F_{(1,259)}$= 15.32, d.f. = 1, $p < 0.001$) where mean wood density (g cm^3) for EM-trees was 0.71 ± 0.02 and for AM-trees 0.54 ± 0.008 (SE).

Combining data from this study and eleven published studies in Neotropical forests (Table S2) we found that variance in AGB for montane forests (1037-3537 m a.s.l) was exceptionally high, compared to lowland forests (41-1000 m a.s.l) (Fig. S5 a, b). We also found that LiDAR-estimated aboveground carbon (Asner 2013, 2021) and this study aboveground carbon exhibited a strong positive correlation (r = 0.83). However, the Mean Bias Error (MBE) of -112.52 Mg C ha^{-1} indicates that LiDAR systematically underestimated biomass compared to field measurements. LiDAR based values for AGC were reliant on conversion factors generated from ground-truthing lowland forests and were between two and six times lower than our field-based estimates (Fig. 3).

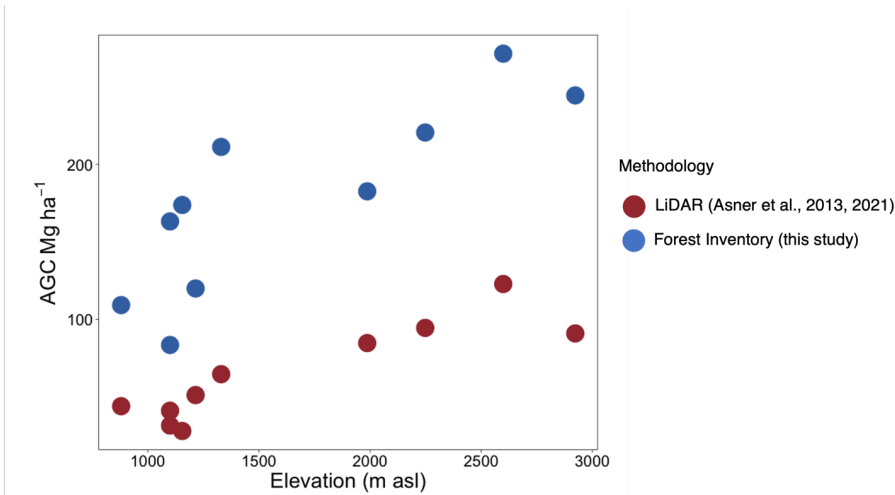



Figure 3. Variation in aboveground carbon (AGC) among ten 1-ha plots in western Panama using forest inventories (blue) and (red) airborne light detection and ranging (LiDAR) data.

3.2.2 Coarse wood debris

In total, 2037 samples of DCWD were found in 20.8 km of transect, and 232 samples of SCWD were measured in 0.2 ha per plot. For DCWD, we found that individual fallen trees were recorded twice on adjacent transects on only 23 occasions. Total CWD varied across plots, ranging from 14.75 to 326.51 Mg ha^{-1} (Table 2). Across plots there was no clear pattern in the contribution of DCWD and SCWD to the total CWD. For PS, HOR, MIR, QUE and COP dead wood was mainly stored in the form of DCWD, contributing 2.7-5.5% to the total carbon of the plot, while for AF, CA, SAM, CASA and HA, SCWD was the main CWD pool, contributing 8.2 to 42.2%.

3.2.3 Soil carbon

Total soil C calculated from 0-100 cm depth differed among plots, and was similar in magnitude and variance to AGB, ranging from 119.0 to 577.9 Mg ha^{-1} (Table 2). There were differences among plots ($F_{(9,181)}$ = 10.9, $p = < 0.001$) and depth categories ($F_{(3,181)}$= 31.5, $p = <0.001$). Plots at the highest elevation (1900 – 2923 m a.s.l) accumulated notably large amounts of carbon in the deeper soil layers (50-100 cm), ranging from 92.8 to 246.3 Mg ha^{-1} (Fig. S6). The percent of C in each depth relative to the total C% in each plot was not correlated with % EM, except in the 10-20 cm depth (Fig. S7). For this layer, percent of C was negatively correlated with the percent of basal area contributed by EM-trees (% EM; r2 = 0.36, p < 0.05,), however this effect was not significant after controlling for elevation.

3.2.4 Effect of elevation on abiotic and biotic factors, and carbon pools

Most climate variables were strongly correlated with elevation (Table S6); variables related to temperature (MAT, MATmax, MATmin and MATvar), water deficit and mean diurnal range were negatively correlated with elevation. Precipitation during the driest month was positively correlated with elevation. Among edaphic variables there was in general no correlation with

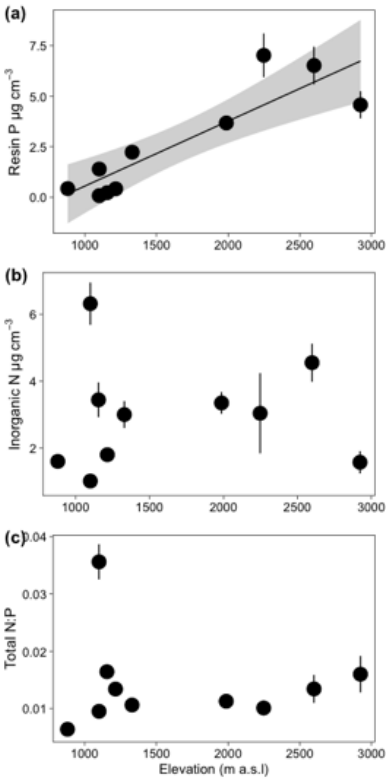
320 elevation (Table S6), including inorganic N and total N:P ratio (Fig. 4), however, resin P was strongly positively correlated with elevation (r = 0.88, $p < 0.001$, Fig. 4). Additionally, % EM was also highly positively correlated with elevation (r = 0.80, $p < 0.001$). Resin P and % EM were therefore also highly correlated with temperature (r = -0.89, $p < 0.001$ and r = -0.76, $p < 0.05$, respectively (Table S6).

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Figure 4. Relationship between elevation and soil parameters for ten 1-ha plots. Each point represents the plot mean (± 1 SE) of a) resin P, b) inorganic N and c) total N:P. The solid line indicates a significant relationship and the shaded area represents the 95% confidence interval.

330 Aboveground biomass and soil C showed a significant positive relationship with elevation ($r^2 = 0.73$ $p < 0.001$; $r^2 = 0.76$, $p < 0.001$, respectively, Fig. 5a,b). Total CWD was not correlated with elevation ($r^2 = -0.06$, $p = $ NS), even after removing plot HA, an outlier, ($r^2 = 0.001$, $p = $ NS). However, DCWD was positively correlated with elevation ($r^2 = 0.76$, $p < 0.001$, Fig. 5c). Low values of AGB, DCWD and soil C are significantly correlated with high values of variables related with temperature, while soil C decreased with increasing wood density ($r^2 = 0.76$, $p < 0.001$), however, this effect was not significant after

335 controlling for elevation.

Among the AGB components, elevation was correlated with basal area but not with wood density or canopy height (Fig. 5d-f). Basal area was positively correlated with elevation, more than doubling over the elevation range of the study ($r^2 = 0.65$, $p < 0.001$). The number of stems per plot tended to decrease with elevation, but was not significant ($r^2 = 0.18$, $p = $ NS).

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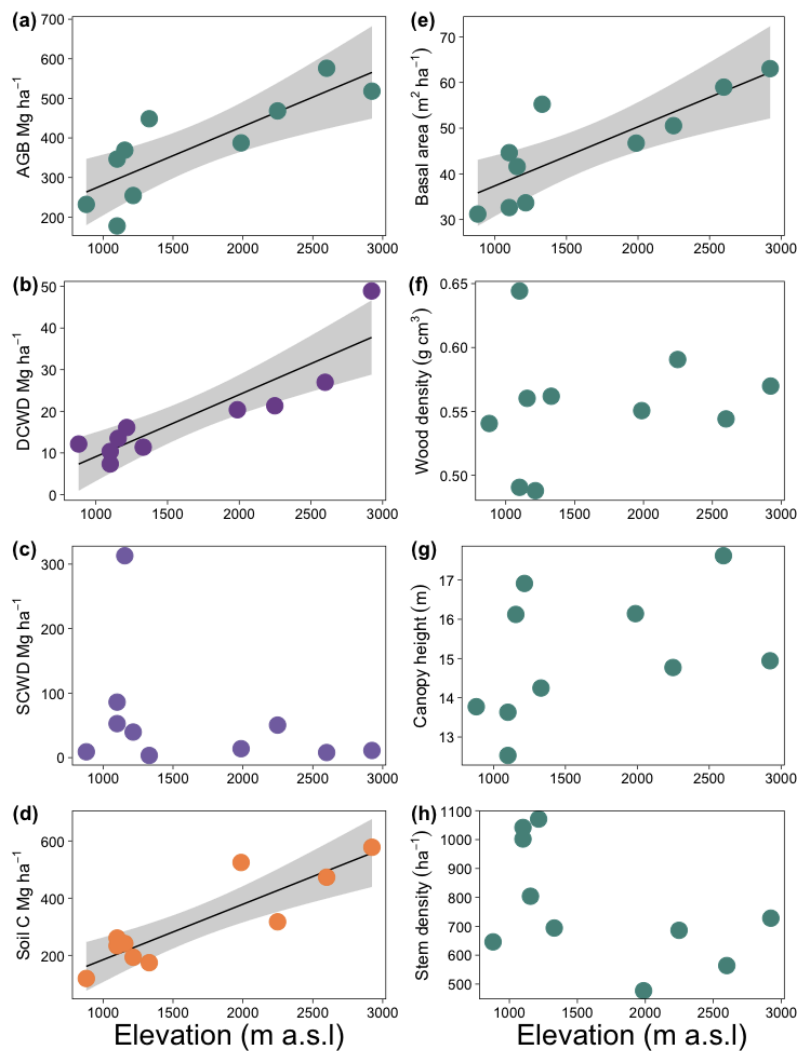
Figure 5. Effect of elevation on carbon pools (a – d) and aboveground biomass components (e – h) for ten 1ha plots in an elevational gradient in western Panama. Lines represent significant relationships and shaded areas represent the 95% confidence intervals. Each point is the mean value for each plot except for (e) that is the total basal area of the plot. AGB = Aboveground biomass; DCWD = Downed coarse wood debris; SCWD = Standing coarse wood debris.

345   From the structural equation model (SEM) that included soil, climate variables, AGB, DCWD, and soil C we found temperature was the variable that best predicted AGB and soil C, after controlling for soil and other climate parameters (Fig. 6). Temperature was significantly negatively correlated with AGB and soil C. NH_4 and % EM showed a significant correlation with DCWD. Downed CWD decreased significantly with high values of NH_4 and increased with high values of % EM. Additionally, % EM was significantly positively correlated with resin P. The effect of climate parameters other than temperature and soil

350   except $NH4$ and resin P (represented in the PCA axis, Fig. S4), did not have a significant effect on C pools. It is important to note that temperature, and consequently elevation, is highly correlated with resin P concentration (Fig. 4). This strong correlation complicates the disentangling of the specific contributions of temperature and resin P to the observed patterns—an issue that will be discussed further in a later section.

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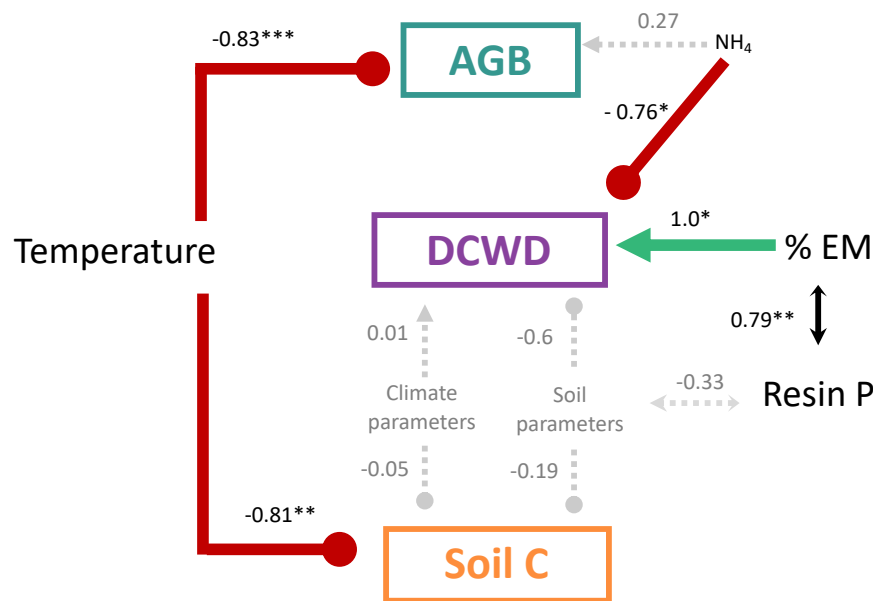
$C_{(18)} = 12.51$; p=0.82; AIC= 42.51

Figure 6. Structural equation model to evaluate the effect of environmental and edaphic variables on the different carbon pools in a montane forest. Soil and edaphic parameters are represented by the first axis of a PCA for each group of variables where resin P and NH_4 were not included. The best model was selected based on Akaike's information criterion (AIC) comparing

360   alternative models. Positive effects are in green and represented by arrows and negative effects in red with blunt-ended lines. Gray dashed arrows represent nonsignificant relationships. Lines with double arrows represent correlations between variables. Numbers are the standardized path coefficients. AGB = Aboveground biomass; DCWD = Downed coarse wood debris; % EM = percent of plot basal area occupied by EM trees.

4 Discussion

Exceptionally high carbon storage was observed along this elevational gradient in Panama. In contrast to most other published data from elevational gradients in TMFs, we found total carbon stocks were strongly *positively* correlated with elevation – a pattern associated with the dominance of the EM-tree genus *Quercus* at most of the high elevation plots. Although temperature showed a strong negative correlation with resin P, it was a stronger predictor of AGB and soil C. In contrast, we found resin P indirectly by the effect of % EM explained more variation in downed CWD (DCWD) stocks than temperature; DCWD accumulation was associated with increasing % EM and decreasing NH_4. Estimates of standing CWD (SCWD) were poorly constrained in this study, with exceptionally high values found in one site. We found high soil C was also associated with high elevation sites. We predicted soil C storage would be associated with EM-trees, however we found no effect of % EM on total soil C. The plot with patches dominated by the EM-tree *Oreomunnea mexicana* had intermediate values of soil C while high elevation plots at the Barú site both with and without EM-associated trees showed the highest values of soil C, possibly reflecting both reduced rates of decomposition, and volcanic activity that buried C rich surface soils beneath layers of volcanic ash in the past.

4.1 Carbon stocks of Panamanian montane forests in a regional and pantropical context

Values for AGB are highly variable across tropical forests. In Neotropical lowland forests, plot inventories of trees $\geq$ 10 cm DBH indicate that AGB ranges from 160.5 Mg ha^{-1} at La Selva, Costa Rica (Clark & Clark, 2000), 242.0 to 365.18 in the Área de Conservación Osa, Costa Rica (Hofhansl et al., 2020), 262 on Barro Colorado Island, Panama (Chave et al., 2003), and up to 397 ± 30 in the central Amazon of Brazil (Nascimento and Laurance, 2002). Previous studies along elevational gradients have shown no consistent pattern between elevation and AGB, either in the Neotropics (Fig. 7a), or in meta-analyses of Neotropical, African and SE Asian forests (Cuni-Sanchez et al. 2021). In contrast, our study showed a significant increase in AGB with elevation, reaching a maximum value just a few hundred meters beneath the tree line on Volcan Barú. Comparing this study with four other Neotropical elevational gradients indicates sites in Colombia (González-Caro et al., 2020), some sites in Ecuador (Homeier and Leuschner, 2021), and Panama (this study) share relatively high AGB at mid-elevations (1500-2000 m) compared to other sites in Ecuador (Moser et al., 2008; Homeier and Leuschner, 2021), Peru (Malhi et al., 2017), and Venezuela (Vilanova et al., 2018) (Fig. 7a). However, at high elevations AGB in our study was between three and seven times higher than AGB reported from these other gradients. Our Panama sites, however, do share high AGB with African montane forest plots spanning a similar elevation range. A recent meta-analysis of AGB for 226 African montane forest plots spanning a similar elevation range to our study found on average 326.75 Mg ha^{-1} (± 28.5 Mg ha^{-1} 95% CI; Cuni-Sanchez et al. 2021), a value that is similar to our Panama study sites (372.07 ± 39.7 Mg ha^{-1}), but also to Costa Rica lowland forest that can store up to 365 Mg ha^{-1} (Hofhansl et al., 2020)

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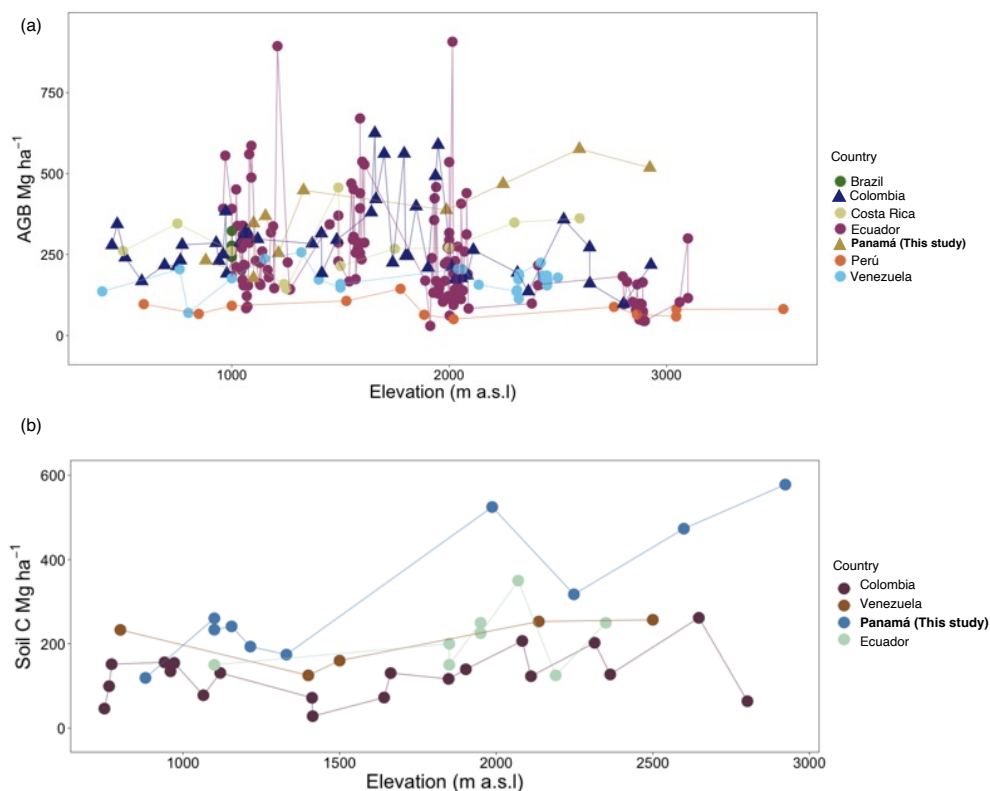
Figure 7. Comparison of above-ground biomass (a) and soil C (b) stocks among countries in the Neotropics from reports > 400 elevation. (a) Points represent AGB Mg ha⁻¹ in values for six countries plus the current study in Panamá; symbols indicate sites with reported EM dominated forests (triangle) or low tree EM presence (less than 10 % or absence) (circles). Studies were performed in Brazil (Alves et al., 2011), Colombia (González-Caro et al., 2020), Costa Rica (Clark et al., 2002, Hofhansl et al., 2020, Lieberman et al., 1996, Tanner et al., 2016), Ecuador (Homeier & Leuschner et al., 2021; Moser et al., 2008), Peru (Malhi et al., 2017), Venezuela (Delaney et al., 1997; Vilanova et al, 2018) (b) Points represent soil C Mg ha⁻¹ at 1 m depth for four countries. Studies were performed in Colombia (Phillips et al., 2019), Venezuela (Delaney et al., 1997) and Ecuador (Schrumpf et al., 2001).

High levels of uncertainty in the magnitude and drivers of AGB across forests (Muller-Landau et al., 2020; Sierra et al., 2007) presents considerable challenges for estimating AGC at large spatial scales. LiDAR provides a powerful tool that can be used to help estimate C stocks at high resolution across the globe (Réjou-Méchain et al., 2015; Asner et al., 2013). However, applying this approach requires adequate ground referencing to validate calculations. Asner et al. (2013) estimated and mapped aboveground carbon for the country of Panama using LiDAR. Although the map was validated with field data from different ecoregions of the country, no montane forest data were used. We found that the Asner et al. (2013) map consistently and substantially underestimated the AGC present in our plots (Fig. 3), with implications for the national carbon inventory, given the

large amount of montane forest cover in the country. These results highlight the need to include inventory data that incorporates elevation dependent changes in soils, climate and species composition that underpin elevational changes in AGB-canopy height relationships. Using LiDAR in combination with field measurements in montane forests in Ecuador (González-Jaramillo et al., 2018) highlights the importance of terrain features (e.g., ridges, depressions, and protection) in estimates of AGB. For example, ravines, a landscape attribute that is usually ignored at large scales, but can have high AGB. In lowland forests high C stocks can be found in ravine forest (163 Mg ha⁻¹) compare to nearby slopes and ridges (154 Mg ha⁻¹ and 136 Mg ha⁻¹, respectively) (Hofhansl et al., 2020).

As in previous studies, soil C stocks were highly variable in this study. However, unlike other Neotropical studies (Fig. 7b) we found the highest soil C stocks in the highest elevation plots, supporting our initial hypothesis of increases in soil C with elevation. At our highest elevation site, COP, soil C to 1 m depth (578 Mg ha⁻¹) was more than four times higher than comparable measurements in lowland forests in Panama (133 Mg ha⁻¹, Cusack et al., 2018). Similarly, in our study, the soil C stock was five times higher in lower montane forest (1500-2000 m a.s.l) and two times higher in upper montane forest (2000-3600 m a.s.l), compared to studies in Colombia (Phillips et al., 2019a), Ecuador (Schrumpf et al., 2001) and Venezuela (Delaney et al., 1997). Additionally, high levels of soil organic carbon can be found in the organic layer in montane forest ranging from 11.1 to 75.1 Mg ha⁻¹ in the Ecuadorian Andes (Moser et al., 2011).

Differences in methodologies and sample sizes across studies make comparisons of coarse wood debris difficult. Furthermore, variation in total CWD within and among plots in this study was exceptionally high. One plot, HA, exhibited exceptionally high SCWD biomass (313 Mg ha⁻¹), accompanied by large confidence intervals. This variability was attributed to the presence of two large standing dead oak trees, with some branches included in the subsamples. The presence of a few large standing dead trees can greatly skew estimates of SCWD (Gora et al. 2019), necessitating large sample sizes to capture the true mean pool size. Nonetheless, our study highlights the potential importance of CWD to the ecosystem C budget, and adequately constraining SCWD measurements to detect climate change effects on ecosystem carbon storage via elevated tree mortality rates.

Carbon in forests is also stored in pools not included in this study (root biomass and litter), which could contribute significantly to the total carbon stock. Roots biomass estimates are mostly from samples from tropical lowland forests, understating montane ecosystems (Iversen et al., 2021). Recent findings from old-growth montane forests in Africa, where AGC is very high (Cuni-Sanchez et al., 2021), show that tree roots can store up to 59.3 Mg C ha⁻¹ (Yaffar et al., 2023). Values of AGC of Cuni-Sanchez et al (2021) are similar to the ones we found in this study; assuming parity with African montane forests, inclusion of root biomass estimates in our system would increase the total C stock by nearly 9%. In Andean forests in Ecuador roots can store from 12.46 to 33.14 Mg C ha⁻¹. Additionally, at 2900 m elevation fine-roots store approximately 5.5 Mg C ha⁻¹ in *Quercus* forests in Costa Rica (Hertel et al., 2003), and 5.4 Mg C ha⁻¹ in the Ecuadorian Andes (Moser et all., 2011). Finally, in montane forests, litter production—including leaves, reproductive organs, twigs, and other components—can range from 2 to 5 Mg C ha⁻¹ y⁻¹ (Moser et al., 2011). This suggests that total C stocks in our plots could increase by up to approximately 1% per year when accounting for litter production.

4.2 Responses of carbon pools to environmental and biotic factors

4.2.1 Aboveground biomass

After controlling for elevation, we found no effect of soil fertility (measured as NH₄-N and resin P) on AGB. Evaluating the effects of nutrient availability on AGB along elevational gradients is challenging as direct fertility effects may be masked by the strong correlations between elevation, and therefore temperature, and soil N and P. Neotropical forests have been reported to transition from being phosphorus-limited in lowland areas (Wright, 2019; Vitousek, 1984; Condit et al., 2013) to nitrogen-

limited in montane regions (Wright, 2019; Vitousek, 1984; Tanner et al., 1998) influencing plant functioning and therefore forest productivity. In this study, we found that resin P was highly correlated with elevation, consistent with another elevational

485 gradient in Peru (Nottingham et al., 2015a) and indicating P is not a limiting factor in this montane system. Although there is more P available in montane systems, this does not always result in higher productivity. For instance, in an elevational gradient in Ecuador, forest productivity was influenced not by P or N alone, but by a combination of soil fertility factors, which can outweigh the effects of elevation. (Homeier and Leuschner, 2021). With respect to AGB, responses to soil nutrient availability are highly inconsistent among studies (Muller-Landau et al., 2020). For example, in lowland tropical forests in the Guiana Shield

490 (Soong et al., 2020) AGB did not respond to soil P, whereas more broadly across the Amazon basin low AGB was found to be associated with high soil P (Quesada et al., 2012). At the same time, decreasing temperatures could have multiple effects altering AGB. Decreasing temperature can reduce growth rates and is associated with increased wood density (Muller-Landau, 2004; Chave et al., 2009), which may increase AGB, however it was not the case in our study. Alternatively lower temperatures are also associated with reduced stand height in other tropical forests, reducing AGB (Wilcke et al., 2008). Here we found there is a

495 positive relationship between elevation and AGB, despite wood density and canopy height not being correlated with elevation; showing basal area was the variable driving the AGB pattern. A positive relationship between elevation and basal area has been seen in other tropical forests (Unger et al., 2012; Lieberman et al., 1996; Clark et al., 2015), and in some cases a peak is attributed to the presence of *Quercus* spp (Muñoz Mazón et al., 2020), a genus associated with high wood densities (Cavender-Bares, 2019).

500 While EM tree species had higher wood densities compared to AM trees, and made a large contribution to AGB, the observed positive relationship between elevation and AGB was not dependent on wood density (i.e., the pattern remained if all species were given the same wood density value). In tropical forests in Colombia and Indonesia, relatively high AGB in highland forests is associated with a significant contribution of families such as Fagaceae and Podocarpaceae (Peña et al., 2018; Culmsee et al., 2010; González-Caro et al., 2020). Recent studies have shown that the evolutionary history of tree communities can

505 contribute to tropical forest structure, with phylogenetic signal detected in AGB (de Aguiar-Campos et al., 2021; González-Caro et al., 2020). In Colombia, AGB at intermediate elevation (1800-2200 m a.s.l), is associated with a high proportion of temperate-affiliated species (González-Caro et al. 2020). Among the most important of these is the genus *Quercus* (González-Caro et al., 2020; Peña et al., 2018). This aligns with our results, where *Quercus* was the largest contributor to AGB in three of the four highest elevation plots. *Quercus*, and related EM genera in the Fagaceae appear to be well adapted to the cool conditions of

510 tropical high elevation forests in SE Asia, Central America, and the northern Colombia, where individuals reach large sizes and high wood densities (Corrales et al. 2018, Cavender-Bares, 2019). However, while we found in this study that there was a strong positive correlation between elevation and the percent of basal area contributed by EM trees, the effect of % EM on AGB was no longer significant after accounting for elevation. Notably, at the Barú site, the MIR plot had an AGB value comparable to *Quercus*-dominated plots despite very low % EM basal area (1% versus 48-74% in other Barú plots; Table 1). We propose that

515 non-EM trees (e.g., *Magnolia*, *Cornus*, *Cedrela*, *Cinnamomum*), which have wood densities ranging from 0.45 to 0.68, may require similar architectural and wood density traits to coexist with oak species, whose wood densities range from 0.68 to 0.81. These results, therefore, contrast with AGB patterns at a smaller spatial scale in a 50 ha plot in a temperate forest in China, where AGB was positively associated with the proportion of EM-basal area in the stand (Mao et al., 2019).

Nonetheless, high AGC for 226 African montane forest plots (Cuni-Sanchez et al. 2021) is also achieved in the absence

520 of EM-tree species (Fagaceae and Juglandaceae are absent from African mountains). The authors concluded that high montane forest carbon storage in Africa (70% higher than previous estimates for Neotropical forests) could reflect unique structural characteristics of African montane forests resulting from the presence of large herbivores (elephants), or a low frequency of large

525 disturbances (cyclones and landslides). A third potential explanation, where high AGB is associated with the presence of conifers (Podocarpaceae) was not supported by the data (Cuni-Sanchez et al. 2021). However, the same meta-analysis showed that SE Asian montane forests appear to have similar AGC to African forests. In conclusion, our results now suggest that rather than African forests having anomalously high carbon storage, central Andean forests may instead have anomalously low carbon storage.

530 **4.2.2 Coarse woody debris**

Coarse woody debris in tropical forests is a critical component of the C cycle, with highly variable distributions in space and time, rendering it hard to study (Iwashita et al., 2013; Gora et al., 2019). The amount of CWD in the forest can depend on wood quality, climate and stand turnover rates (Chambers et al., 2001, 2000). Here we found that the responses of CWD to environmental and biotic factors differed between CWD pools — downed CWD and standing CWD. Total CWD and SCWD

535 were not correlated with elevation. After controlling for elevation, we found resin P, and NH_4 were negatively correlated with DCWD, and % EM positively correlated with DCWD. Previous studies in the Fortuna site have shown that wood from trees associated with low nutrient soils had higher wood density and lower wood nutrient concentrations than those of higher nutrient soils (Heineman et al., 2016). Although climate can be the best predictor of decomposition in Neotropical forests (Cusack et al., 2009), litter quality is also important (Zhang et al., 2008). Low litter N and P concentration is associated with slow

540 decomposition (Zhang et al., 2008), which may account for the high accumulation of DCWD on the forest floor on this study. Additionally, in the Amazon, high wood density is associated with lower decomposition rates (Chambers et al., 2000). In this study, DCWD accumulation with increasing % EM may be explained by higher values of wood density in EM-trees species compared to AM-trees species, and potentially also lower soil N availability in EM-dominated forests (Lin et al., 2017; Phillips et al., 2013; Prada et al., 2022)

545 *4.2.3 Soil Carbon*

We found that temperature was the most important factor influencing soil C stocks. Soil C accumulated with increases in elevation, a pattern that has been reported previously for tropical montane forests (Kitayama and Aiba, 2002; de la Cruz-Amo et al., 2020; Schrumpf et al., 2011; Girardin et al., 2010; Moser et al., 2011). Continually cool temperatures at high elevation decrease microbial activity, which results in a decrease in decomposition rates and mineralization of soil organic matter

550 (Davidson and Janssens, 2006; Nottingham et al., 2015b). Following the Microbial Efficiency-Matrix Stabilization (MEMS) framework (Cotrufo et al., 2013), slow decomposition rates at high elevations suggest C in the soil would be present as particulate soil organic matter (POM), consistent with the large organic horizon observed at the Barú sites. However, in this study we also found elevation was highly positively correlated with resin P. This strong correlation makes it hard to unravel the true effect of both temperature and P on soil C stocks.

555 Additionally, in montane forests POM would be expected to increase in EM-forests (Craig et al, 2018). In this study, we cannot separate the effect of elevation and mycorrhizal association on POM accumulation. Increasing evidence also shows significantly higher soil C stock near the soil surface beneath EM-trees in both temperate and tropical forests (Averill et al., 2014; Craig et al., 2018; Lin et al., 2017; Steidinger et al., 2019), while greater soil C stock may occur at greater soil depths in AM-forest (Craig et al., 2018). Mechanisms explaining differences in soil C stock have been attributed to differences in the

560 enzymatic capacity of AM and EM species to mineralize organic matter, differences in litter quality, or in mycorrhizal carbon inputs (McGuire et al., 2010; Read and Perez-Moreno, 2003; Averill, 2016; Huang et al., 2022). In this study the effect of % EM on soil C may have been confounded by the correlation between % EM and elevation. Furthermore, recent work at a wider range

of sites at Fortuna has shown that contributions of EM to soil organic matter varies widely among watersheds and is dependent on soil pH (Seyfried et al., 2021). A clear example of how high soil C stocks are not necessarily dependent on the presence of

565   EM-trees is provided by the MIR plot— a mixed forest in which EM-trees accounted for only 1.1% of basal area and yet had one of the highest soil C stocks. An additional complication that affects numerous high elevation sites through Panama and Costa Rica is the impact of the eruptive history of a volcanically-active mountain chain. Deep volcanic ash deposits, dating to 7 million years are apparent at the HA, SAM and especially the CA plots at Fortuna (Wegner et al., 2011; Turner & Dalling, 2021), while soil pits at Barú show soil C layers that are overlain by much more recent deposits of volcanic ash. At least four eruptions of

570   Volcan Barú have occurred in the last 1600 years (Sherrod et al., 2008). The last episode, 500 years ago, may have included widespread tephra fallout, pyroclastic flows, and lahars across the area occupied by our plots (Sherrod et al., 2008). Volcanic eruptions result in the burial of the existing organic layer at the time of the event, and can result in the long-term persistence of significant quantities of soil organic carbon (Chaopricha and Marín-Spiotta, 2014). For example on Mt. Kilimanjaro, Tanzania, soil organic carbon below 1 m depth ranged from 117 to 627 Mg ha^{-1} in elevations from 2100 to 2800 m a.s.l (Zech, 2006). High

575   carbon content observed at higher elevations suggests that sampling down to 1 m could offer a more comprehensive understanding of nutrient dynamics and carbon stocks in mountainous ecosystems, especially where significant carbon storage occurs below 50 cm. Particulate soil organic matter is expected to be more vulnerable to disturbance than C that is as mineral-associated organic matter MAOM (Poeplau et al., 2018) in lowland forests. Volcanic eruptions may protect POM, increasing soil C accumulation in these montane forests.

580   *4.2.3 Role of tropical elevational gradients in global C stocks*

Our results from the Fortuna - Barú gradient highlight the significance of these forests in the global C cycle, as they sequester large amounts of C in tree biomass and in the soil. While tropical forests represent a large proportion of the terrestrial carbon sink (Spracklen & Righelato, 2014; Duque et al., 2021), the importance of the contribution of montane forests (Cuni-Sanchez et al., 2021) and of the temperate family Fagaceae has only been fully recognized more recently (Culmsee et al., 2010; González-

585   Caro et al., 2020; Peña et al., 2018). Nonetheless, factors explaining the dynamics and accumulation of C in the soil are still ambiguous. Large uncertainty in C pool estimates suggests that further research is needed to correctly estimate and evaluate C stocks in tropical montane forests.

Author contributions. CMP and JWD conceived the ideas; CMP, KH and MP carried out field data measurements; CP

590   contributed with model analyses; CMP and JWD performed the general data analysis and wrote the paper.

Competing interests. The authors declare that they have no conflict of interest.

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References

600   Aerts, R. and Chapin, F. S.: The Mineral Nutrition of Wild Plants Revisited: A Re-evaluation, Advances in Ecological Research,

30, 1–67, 1999.

de Aguiar-Campos, N., Coelho de Souza, F., Maia, V. A., Rezende, V. L., de Souza, C. R., de Paula, G. G. P., Santos, P. F., de Oliveira Menino, G. C., da Silva, W. B., and dos Santos, R. M.: Evolutionary constraints on tree size and above-ground biomass in tropical dry forests, Journal of Ecology, 109, 1690–1702, https://doi.org/10.1111/1365-2745.13589, 2021.

605 Asner, G. P., Mascaro, J., Anderson, C., Knapp, D. E., Martin, R. E., Kennedy-bowdoin, T., Breugel, M. Van, Davies, S., Hall, J. S., Muller-landau, H. C., Potvin, C., Sousa, W. P., Wright, J., and Bermingham, E.: High-fidelity national carbon mapping for resource management and REDD+, Carbon Balance and Management, 8, 1–14, https://doi.org/10.1186/1750-0680-8-7, 2013.

Asner, G. P., Mascaro, J., Anderson, C., Knapp, D. E., Martin, R. E., Kennedy-Bowdoin, T., Breugel, M. van, Davies, S., Hall, J. S., Muller-Landau, H. C., Potvin, C., Sousa, W., Wright, J., and Bermingham, E.: Global Airborne Observatory: Forest canopy

610 height and carbon stocks of Panama (Version 1.0) [Data set], Zenodo, https://doi.org/10.5281/zenodo.4624240, 2021.

Avalos, G., Cambronero, M., and Alvarez-Vergnani, C.: Allometric Models to Estimate Carbon Content in Arecaceae Based on Seven Species of Neotropical Palms, Frontiers in Forests and Global Change, 5, https://doi.org/10.3389/ffgc.2022.867912, 2022.

Averill, C.: Slowed decomposition in ectomycorrhizal ecosystems is independent of plant chemistry, Soil Biology and Biochemistry, 102, 52–54, https://doi.org/10.1016/j.soilbio.2016.08.003, 2016.

615 Averill, C., Turner, B. L., and Finzi, A. C.: Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage, Nature, 505, 543–545, https://doi.org/10.1038/nature12901, 2014.

Averill, C., Bhatnagar, J. M., Dietze, M. C., Pearse, W. D., and Kivlin, S. N.: Global imprint of mycorrhizal fungi on whole-plant nutrient economics, Proceedings of the National Academy of Sciences of the United States of America, 116, 23163–23168, https://doi.org/https://doi.org/10.1073/pnas.1906655116, 2019.

620 Baker, T. R., Phillips, O. L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T. J., Laurance, S. G., Laurance, W. F., Lewis, S. L., Lloyd, J., Monteagudo, A., Neill, D. A., Patino, S., Pitman, N. C. A., Silva, J. N. M., and Martínez, R. V.: Variation in wood density determines spatial patterns in Amazonian forest biomass, Global Change Biology, 10, 545–562, https://doi.org/10.1111/j.1365-2486.2004.00751.x, 2004.

Beets, P. N., Kimberley, M. O., Oliver, G. R., Pearce, S. H., Graham, J. D., and Brandon, A.: Allometric equations for estimating

625 carbon stocks in natural forest in New Zealand, Forests, 3, 818–839, https://doi.org/10.3390/f3030818, 2012.

Carreiras, J. M. B., Quegan, S., Le Toan, T., Ho Tong Minh, D., Saatchi, S. S., Carvalhais, N., Reichstein, M., and Scipal, K.: Coverage of high biomass forests by the ESA BIOMASS mission under defense restrictions, Remote Sensing of Environment, 196, 154–162, https://doi.org/10.1016/j.rse.2017.05.003, 2017.

Cavender-Bares, J.: Diversification, adaptation, and community assembly of the American oaks (Quercus), a model clade for

630 integrating ecology and evolution, New Phytologist, 221, 669–692, https://doi.org/10.1111/nph.15450, 2019.

Chambers, J. Q., Higuchi, N., Schimel, J. P., Ferreira, L. V, and Melack, J. M.: Decomposition and carbon cycling of dead trees in tropical forests of the central Amazon, Oecologia, 122, 380–388, https://doi.org/10.1007/s004420050044, 2000.

Chambers, J. Q., Schimel, J. P., and Nobre, A. D.: Respiration from coarse wood litter in central Amazon forests, Biogeochemistry, 52, 115–131, https://doi.org/10.1023/A:1006473530673, 2001.

635 Chaopricha, N. T. and Marín-Spiotta, E.: Soil burial contributes to deep soil organic carbon storage, Soil Biology and Biochemistry, 69, 251–264, https://doi.org/10.1016/j.soilbio.2013.11.011, 2014.

Chave, J.: Measuring wood density for tropical forest trees: a field manual for the CTFS sites., Lab. Toulouse: Evolution et Diversité Biologique, Université Paul Sabatier, 1–6 pp., 2006.

Chave, J., Condit, R., Lao, S., Caspersen, J. P., Foster, R. B., and Hubbell, S. P.: Spatial and temporal variation of biomass in a

640 tropical forest: Results from a large census plot in Panama, Journal of Ecology, 91, 240–252, https://doi.org/10.1046/j.1365-

2745.2003.00757.x, 2003.

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., and Zanne, A. E.: Towards a worldwide wood economics spectrum, Ecology Letters, 12, 351–366, https://doi.org/10.1111/j.1461-0248.2009.01285.x, 2009.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C., Duque, A., Eid, T., Fearnside, P.
645   M., Goodman, R. C., Henry, M., Martínez-Yrízar, A., Mugasha, W. A., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W.,
Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C. M., Saldarriaga, J. G., and Vieilledent,
G.: Improved allometric models to estimate the aboveground biomass of tropical trees, Global Change Biology, 20, 3177–3190,
https://doi.org/10.1111/gcb.12629, 2014.

Clark, D. B., Clark, D. A., Brown, S., Oberbauer, S. F., and Veldkamp, E.: Stocks and flows of coarse woody debris across a
650   tropical rain forest nutrient and topography gradient, Forest Ecology and Management, 164, 237–248,
https://doi.org/10.1016/S0378-1127(01)00597-7, 2002.

Clark, D. B., Hurtado, J., and Saatchi, S. S.: Tropical rain forest structure, tree growth and dynamics along a 2700-m elevational
transect in Costa Rica, PLoS ONE, 10, 1–18, https://doi.org/10.1371/journal.pone.0122905, 2015.

Condit, R., Engelbrecht, B. M. J., Pino, D., Pérez, R., and Turnera, B. L.: Species distributions in response to individual soil
655   nutrients and seasonal drought across a community of tropical trees, Proceedings of the National Academy of Sciences of the
United States of America, 110, 5064–5068, https://doi.org/10.1073/pnas.1218042110, 2013.

Corrales, A., Arnold, A. E., Ferrer, A., Turner, B. L., and Dalling, J. W.: Variation in ectomycorrhizal fungal communities
associated with Oreomunnea mexicana (Juglandaceae) in a Neotropical montane forest, Mycorrhiza, 26, 1–17,
https://doi.org/10.1007/s00572-015-0641-8, 2016.

660   Corrales, A., Henkel, T. W., and Smith, M. E.: Ectomycorrhizal associations in the tropics – biogeography, diversity patterns and
ecosystem roles, New Phytologist, 220, 1076–1091, https://doi.org/10.1111/nph.15151, 2018.

Cotrufo, M. F., Wallenstein, M. D., Boot, C. M., Denef, K., and Paul, E.: The Microbial Efficiency-Matrix Stabilization
(MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable
soil organic matter?, Global Change Biology, 19, 988–995, https://doi.org/10.1111/gcb.12113, 2013.

665   Craig, M. E., Turner, B. L., Liang, C., Clay, K., Johnson, D. J., and Phillips, R. P.: Tree mycorrhizal type predicts within-site
variability in the storage and distribution of soil organic matter, Global Change Biology, 24, 3317–3330,
https://doi.org/10.1111/gcb.14132, 2018.

Crawley, M. J.: The R Book, Wiley, Chichester, West Sussex, United Kingdom, 2013.

Culmsee, H., Leuschner, C., Moser, G., and Pitopang, R.: Forest aboveground biomass along an elevational transect in Sulawesi,
670   Indonesia, and the role of Fagaceae in tropical montane rain forests, Journal of Biogeography, 37, 960–974,
https://doi.org/10.1111/j.1365-2699.2009.02269.x, 2010.

Cuni-Sanchez, A., Sullivan, M., Platts, P., Lewis, S., Marchant, R., Imani, G., Hubau, W., Abiem, I., Adhikari, H., Albrecht, T.,
Altman, J., Amani, C., Aneseyee, A., Avitabile, V., Banin, L., Batumike, R., Bauters, M., Beeckman, H., Begne, S., Bennett, A.,
Bitariho, R., Boeckx, P., Bogaert, J., Bräuning, A., Bulonvu, F., Burgess, N., Calders, K., Chapman, C., Chapman, H.,
675   Comiskey, J., de Haulleville, T., Decuyper, M., DeVries, B., Dolezal, J., Droissart, V., Ewango, C., Feyera, S., Gebrekirstos, A.,
Gereau, R., Gilpin, M., Hakizimana, D., Hall, J., Hamilton, A., Hardy, O., Hart, T., Heiskanen, J., Hemp, A., Herold, M., Hiltner,
U., Horak, D., Kamdem, M., Kayijamahe, C., Kenfack, D., Kinyanjui, M., Klein, J., Lisingo, J., Lovett, J., Lung, M., Makana, J.,
Malhi, Y., Marshall, A., Martin, E., Mitchard, E., Morel, A., Mukendi, J., Muller, T., Nchu, F., Nyirambangutse, B., Okello, J.,
Peh, K., Pellikka, P., Phillips, O., Plumptre, A., Qie, L., Rovero, F., Sainge, M., Schmitt, C., Sedlacek, O., Ngute, A., Sheil, D.,
680   Sheleme, D., Simegn, T., Simo-Droissart, M., Sonké, B., Soromessa, T., Sunderland, T., Svoboda, M., Taedoumg, H., Taplin, J.,

Taylor, D., Thomas, S., Timberlake, J., Tuagben, D., Umunay, P., Uzabaho, E., Verbeeck, H., Vleminckx, J., Wallin, G., Wheeler, C., et al.: High aboveground carbon stock of African tropical montane forests, Nature, 596, 536–542, https://doi.org/10.1038/s41586-021-03728-4, 2021.

Cusack, D. F., Chou, W. W., Yang, W. H., Harmon, M. E., and Silver, W. L.: Controls on long-term root and leaf litter

685   decomposition in neotropical forests, Global Change Biology, 15, 1339–1355, https://doi.org/10.1111/j.1365-2486.2008.01781.x, 2009.

Cusack, D. F., Markesteijn, L., Condit, R., Lewis, O. T., and Turner, B. L.: Soil carbon stocks across tropical forests of Panama regulated by base cation effects on fine roots, Biogeochemistry, 137, 253–266, https://doi.org/10.1007/s10533-017-0416-8, 2018.

Cushman, K. C., Muller-Landau, H. C., Condit, R. S., and Hubbell, S. P.: Improving estimates of biomass change in buttressed

690   trees using tree taper models, Methods in Ecology and Evolution, 5, 573–582, https://doi.org/10.1111/2041-210X.12187, 2014.

Dalling, J. W., Prada, C. M., Heineman, K. D., Andersen, K. M., Morris, A., Pardo, J., Hollenbeck, E., Caballero, P., Espinosa, C., García, E., and Turner, B. L.: Introduction to the Fortuna Forest Reserve: Soil and Climate Effects on the Tree Communities of a Premontane Tropical Forest, in: Fortuna Forest Reserve, Panama. Interacting Effects of Climate and Soils on the Biota of a Wet Premontane Tropical Forest., edited by: Dalling, J. W. and Turner, B. L., Smithsonian Scholarly Press, Washington, D.C, 1–

695   28, 2021.

Davidson, E. A. and Janssens, I. A.: Temperature sensitivity of soil carbon decomposition and feedbacks to climate change, Nature, 440, 165–173, https://doi.org/10.1038/nature04514, 2006.

Delaney, M., Brown, S., Lugo, A. E., Torres-Lezama, A., and Quintero, N. B.: The distribution of organic carbon in major components of forests located in five life zones of Venezuela, Journal of Tropical Ecology, 13, 697–708,

700   https://doi.org/10.1017/S0266467400010877, 1997.

De Deyn, G. B., Cornelissen, J. H. C., and Bardgett, R. D.: Plant functional traits and soil carbon sequestration in contrasting biomes, Ecology Letters, 11, 516–531, https://doi.org/10.1111/j.1461-0248.2008.01164.x, 2008.

Duque, A., Peña, M. A., Cuesta, F., González-caro, S., Kennedy, P., Phillips, O. L., Calderón-loor, M., Blundo, C., Carilla, J., Cayola, L., Farfán-ríos, W., Fuentes, A., Grau, R., Homeier, J., Loza-rivera, M. I., Malhi, Y., Malizia, A., Malizia, L., Martínez-

705   villa, J. A., Myers, J. A., Osinaga-acosta, O., Peralvo, M., Pinto, E., and Saatchi, S.: Mature Andean forests as globally important carbon sinks and future carbon refuges, Nature Communications, 1–10, https://doi.org/10.1038/s41467-021-22459-8, 2021.

Girardin, Malhi, Y., Aragão, L. E. O. ., Mamani, M., Huaraca Huasco, W., Durand, L., Feeley, K. J., Rapp, J., Silva-Espejo, J. E., Silman, M., Salinas, N., and Whittaker, R. J.: Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes, Global Change Biology, 16, 3176–3192, https://doi.org/10.1111/j.1365-

710   2486.2010.02235.x, 2010.

Girardin, Farfan-Rios, W., Garcia, K., Feeley, K. J., Jørgensen, P. M., Murakami, A. A., Cayola Pérez, L., Seidel, R., Paniagua, N., Fuentes Claros, A. F., Maldonado, C., Silman, M., Salinas, N., Reynel, C., Neill, D. A., Serrano, M., Caballero, C. J., La Torre Cuadros, M. de los A., Macía, M. J., Killeen, T. J., and Malhi, Y.: Spatial patterns of above-ground structure, biomass and composition in a network of six Andean elevation transects, Plant Ecology and Diversity, 7, 161–171,

715   https://doi.org/10.1080/17550874.2013.820806, 2014.

Glassmire, A. E., Zehr, L. N., and Wetzel, W. C.: Disentangling dimensions of phytochemical diversity: alpha and beta have contrasting effects on an insect herbivore, Ecology, 101, 1–12, https://doi.org/10.1002/ecy.3158, 2020.

González-Caro, S., Duque, Á., Feeley, K. J., Cabrera, E., Phillips, J., Ramirez, S., and Yepes, A.: The legacy of biogeographic history on the composition and structure of Andean forests, Ecology, 101, 1–11, https://doi.org/10.1002/ecy.3131, 2020.

720   González-Jaramillo, V., Fries, A., Zeilinger, J., Homeier, J., Paladines-Benitez, J., and Bendix, J.: Estimation of above ground

biomass in a tropical mountain forest in southern Ecuador using airborne LiDAR data, Remote Sensing, 10, https://doi.org/10.3390/rs10050660, 2018.

Gora, E. M., Kneale, R. C., Larjavaara, M., and Muller-Landau, H. C.: Dead Wood Necromass in a Moist Tropical Forest: Stocks, Fluxes, and Spatiotemporal Variability, Ecosystems, 22, 1189–1205, https://doi.org/10.1007/s10021-019-00341-5, 2019.

725 Hall, J. S., Harris, D. J., Saltonstall, K., Medjibe, V. de P., Ashton, M. S., and Turner, B. L.: Resource acquisition strategies facilitate Gilbertiodendron dewevrei monodominance in African lowland forests, Journal of Ecology, 108, 433–448, https://doi.org/10.1111/1365-2745.13278, 2020.

Heineman, K. D., Turner, B. L., and Dalling, J. W.: Variation in wood nutrients along a tropical soil fertility gradient, The New phytologist, 211, 440–454, https://doi.org/10.1111/nph.13904, 2016.

730 Hertel, D., Leuschner, C., and Hölscher, D.: Size and Structure of Fine Root Systems in Old-growth and Secondary Tropical Montane Forests (Costa Rica)1, Biotropica, 35, 143, https://doi.org/10.1646/02022, 2003.

Hofhansl, F., Schnecker, J., Singer, G., and Wanek, W.: New insights into mechanisms driving carbon allocation in tropical forests, New Phytologist, 205, 137–146, https://doi.org/10.1111/nph.13007, 2015.

Hofhansl, F., Chacón-Madrigal, E., Fuchslueger, L., Jenking, D., Morera-Beita, A., Plutzar, C., Silla, F., Andersen, K. M.,

735 Buchs, D. M., Dullinger, S., Fiedler, K., Franklin, O., Hietz, P., Huber, W., Quesada, C. A., Rammig, A., Schrodt, F., Vincent, A. G., Weissenhofer, A., and Wanek, W.: Climatic and edaphic controls over tropical forest diversity and vegetation carbon storage, Scientific Reports, 10, 1–11, https://doi.org/10.1038/s41598-020-61868-5, 2020.

Homeier, J. and Leuschner, C.: Factors controlling the productivity of tropical Andean forests: Climate and soil are more important than tree diversity, Biogeosciences, 18, 1525–1541, https://doi.org/10.5194/bg-18-1525-2021, 2021.

740 Huang, W., van Bodegom, P. M., Declerck, S., Heinonsalo, J., Cosme, M., Viskari, T., Liski, J., and Soudzilovskaia, N. A.: Mycelium chemistry differs markedly between ectomycorrhizal and arbuscular mycorrhizal fungi, Communications Biology, 5, 1–8, https://doi.org/10.1038/s42003-022-03341-9, 2022.

Huss-Daniel, K.: Tansley Review No. 93.. Actinorhizal symbioses and their N2 fixation, New Phytologist, 136, 375–405, https://doi.org/10.1046/j.1469-8137.1997.00755.x, 1997.

745 Iversen, C. M., Powell, A. S., McCormack, M. L., Blackwood, C. B., Freschet, G. T., Kattge, J., Roumet, C., Stover, D. B., Soudzilovskaia, N. A., Valverde-Barrantes, O. J., van Bodegom, P. M., and Violle, C.: Fine-Root Ecology Database (FRED): A Global Collection of Root Trait Data with Coincident Site, Vegetation, Edaphic, and Climactic Data, Version 3, Oak Ridge National Laboratory, TES SFA, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A., 2021.

Iwashita, D. K., Litton, C. M., and Giardina, C. P.: Coarse woody debris carbon storage across a mean annual temperature

750 gradient in tropical montane wet forest, Forest Ecology and Management, 291, 336–343, https://doi.org/10.1016/j.foreco.2012.11.043, 2013.

Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., and Kessler, M.: Climatologies at high resolution for the earth's land surface areas, Scientific Data, 4, 1–20, https://doi.org/10.1038/sdata.2017.122, 2017.

755 Keenan, T. F. and Williams, C. A.: The Terrestrial Carbon Sink, Annual Review of Environment and Resources, 43, 219–243, https://doi.org/10.1146/annurev-environ-102017-030204, 2018.

Keller, A. B. and Phillips, R. P.: Leaf litter decay rates differ between mycorrhizal groups in temperate, but not tropical, forests, New Phytologist, 222, 556–564, https://doi.org/10.1111/nph.15524, 2019.

Kitayama, K. and Aiba, S. I.: Ecosystem Structure and Productivity of Tropical Rain Forests along Altitudinal Gradients with

760 Contrasting Soil Phosphorus Pools on Mount Kinabalu , Borneo, Journal of Ecology, 90, 37–51, 2002.

de la Cruz-Amo, L., Bañares-de-Dios, G., Cala, V., Granzow-de la Cerda, Í., Espinosa, C. I., Ledo, A., Salinas, N., Macía, M. J., and Cayuela, L.: Trade-Offs Among Aboveground, Belowground, and Soil Organic Carbon Stocks Along Altitudinal Gradients in Andean Tropical Montane Forests, Frontiers in Plant Science, 11, 1–11, https://doi.org/10.3389/fpls.2020.00106, 2020.

765 Larjavaara, M. and Muller-Landau, H. C.: Cross-section mass: An improved basis for woody debris necromass inventory, Silva Fennica, 45, 291–296, https://doi.org/10.14214/sf.119, 2011.

Lefcheck, J. S.: piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics, Methods in Ecology and Evolution, 7, 573–579, https://doi.org/10.1111/2041-210X.12512, 2016.

Leitold, V., Michael Keller, Douglas C Morton, Bruce D Cook, and Yosio E Shimabukuro: Airborne lidar-based estimates of tropical forest structure in complex terrain: Opportunities and trade-offs for REDD+, Carbon Balance and Management, 10, 770 https://doi.org/10.1186/s13021-015-0013-x, 2014.

Lieberman, D., Lieberman, M., Peralta, R., and Hartshorn, G. S.: Tropical Forest Structure and Composition on a Large-Scale Altitudinal Gradient in Costa Rica, The Journal of Ecology, 84, 137, https://doi.org/10.2307/2261350, 1996.

Lin, G., McCormack, M. L., Ma, C., and Guo, D.: Similar below-ground carbon cycling dynamics but contrasting modes of nitrogen cycling between arbuscular mycorrhizal and ectomycorrhizal forests, New Phytologist, 213, 1440–1451, 775 https://doi.org/10.1111/nph.14206, 2017.

Malhi, Y. and Grace, J.: Tropical forests and atmospheric carbon dioxide, Trends in Ecology and Evolution, 15, 332–337, https://doi.org/10.1016/S0169-5347(00)01906-6, 2000.

Malhi, Y., Baker, T. R., Phillips, O. L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C. I., Di Fiore, A., Higuchi, N., Killeen, T. J., Laurance, S. G., Laurance, W. F., Lewis, S. L., Montoya, L. M. M., Monteagudo, A., Neill, D. A., Vargas, P. 780 N., Patino, S., Pitman, N. C. A., Quesada, C. A., Salomao, R., Silva, J. N. M., Lezama, A. T., Martínez, R. V., Terborgh, J., Vinceti, B., and Lloyd, J.: The above-ground coarse wood productivity of 104 Neotropical forest plots, Global Change Biology, 10, 563–591, https://doi.org/10.1111/j.1529-8817.2003.00778.x, 2004.

Malhi, Y., Silman, M., Salinas, N., Bush, M., Meir, P., and Saatchi, S.: Introduction: Elevation gradients in the tropics: Laboratories for ecosystem ecology and global change research, Global Change Biology, 16, 3171–3175, 785 https://doi.org/10.1111/j.1365-2486.2010.02323.x, 2010.

Malhi, Y., Girardin, C. A. J., Goldsmith, G. R., Doughty, C. E., Salinas, N., Metcalfe, D. B., Huaraca Huasco, W., Silva-Espejo, J. E., del Aguila-Pasquell, J., Farfán Amézquita, F., Aragão, L. E. O. C., Guerrieri, R., Ishida, F. Y., Bahar, N. H. A., Farfan-Rios, W., Phillips, O. L., Meir, P., and Silman, M.: The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective, New Phytologist, 214, 1019–1032, https://doi.org/10.1111/nph.14189, 2017.

790 Mao, Z., Corrales, A., Zhu, K., Yuan, Z., Lin, F., Ye, J., Hao, Z., and Wang, X.: Tree mycorrhizal associations mediate soil fertility effects on forest community structure in a temperate forest, New Phytologist, 223, 475–486, https://doi.org/10.1111/nph.15742, 2019.

Marrs, R. H., Proctor, J., Heaney, A., and Mountford, M. D.: Changes in Soil Nitrogen-Mineralization and Nitrification Along an Altitudinal Transect in Tropical Rain Forest in Costa Rica, Journal of Ecology, 76, 466–482, https://doi.org/10.2307/2260606, 795 1988.

McGuire, K. L., Zak, D. R., Edwards, I. P., Blackwood, C. B., and Upchurch, R.: Slowed decomposition is biotically mediated in an ectomycorrhizal, tropical rain forest, Oecologia, 164, 785–795, https://doi.org/10.1007/s00442-010-1686-1, 2010.

Meister, K., Ashton, M. S., Craven, D., and Heather, G.: Carbon Dynamics of Tropical Forests, in: Managing Forest Carbon in a Changing Climate, edited by: MarkS.Ashton, MaryL.Tyrrell, DeborahSpalding, and BradfordGentry, Springer Science+Business 800 Media B.V. Family, 1–414, https://doi.org/10.1007/978-94-007-2232-3_4, 2012.

Mitchard, E. T. A.: The tropical forest carbon cycle and climate change, Nature, 559, 527–534, https://doi.org/10.1038/s41586-018-0300-2, 2018.

Moser, Leuschner, C., Hertel, D., Graefe, S., Soethe, N., and Iost, S.: Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): The role of the belowground compartment, Global Change Biology, 17, 2211–2226,

805   https://doi.org/10.1111/j.1365-2486.2010.02367.x, 2011.

Moser, G., Röderstein, M., Soethe, N., Hertel, D., and Leuschner, C.: Altitudinal Changes in Stand Structure and Biomass Allocation of Tropical Mountain Forests in Relation to Microclimate and Soil Chemistry, 229–242, https://doi.org/10.1007/978-3-540-73526-7_22, 2008.

Muller-Landau, H.: Interspecific and Inter-site Variation in Wood Specific Gravity of Tropical Trees, Biotropica, 36, 20–32,

810   2004.

Muller-landau, H. C., Cushman, K. C., Arroyo, E. E., Martinez Cano, I., Anderson-Teixeira, K. J., and Backiel, B.: Patterns and mechanisms of spatial variation in tropical forest productivity, woody residence time, and biomass, New Phytologist, https://doi.org/10.1111/nph.17084, 2020.

Muñoz Mazón, M., Klanderud, K., Finegan, B., Veintimilla, D., Bermeo, D., Murrieta, E., Delgado, D., and Sheil, D.: How

815   forest structure varies with elevation in old growth and secondary forest in Costa Rica, Forest Ecology and Management, 469, 118191, https://doi.org/10.1016/j.foreco.2020.118191, 2020.

Nascimento, H. E. M. and Laurance, W. F.: Total aboveground biomass in central Amazonian rainforests: A landscape-scale study, Forest Ecology and Management, 168, 311–321, https://doi.org/10.1016/S0378-1127(01)00749-6, 2002.

Nottingham, A. ., Whitaker, J., Turner, B. L., Salinas, N., Zimmermann, M., Malhi, Y., and Meir, P.: Climate Warming and Soil

820   Carbon in Tropical Forests: Insights from an Elevation Gradient in the Peruvian Andes, BioScience, 65, 906–921, https://doi.org/10.1093/biosci/biv109, 2015a.

Nottingham, A. T., Turner, B. L., Whitaker, J., Ostle, N. J., McNamara, N. P., Bardgett, R. D., Salinas, N., and Meir, P.: Soil microbial nutrient constraints along a tropical forest elevation gradient: A belowground test of a biogeochemical paradigm, Biogeosciences, 12, 6071–6083, https://doi.org/10.5194/bg-12-6071-2015, 2015b.

825   Pan, Y., Birdsey, R. A., Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. A., Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, A. D., Piao, S., Rautiainen, A., Sitch, S., and HayesYude, D.: A Large and Persistent Carbon Sink in the World's Forests, Science, 333, 4, 2011.

Pan, Y., Birdsey, R. A., Phillips, O. L., and Jackson, R. B.: The structure, distribution, and biomass of the world's forests, Annual Review of Ecology, Evolution, and Systematics, 44, 593–622, https://doi.org/10.1146/annurev-ecolsys-110512-135914,

830   2013.

Peña, M. A., Feeley, K. J., and Duque, A.: Effects of endogenous and exogenous processes on aboveground biomass stocks and dynamics in Andean forests, Plant Ecology, 219, 1481–1492, https://doi.org/10.1007/s11258-018-0895-2, 2018.

Phillips, J., Ramirez, S., Wayson, C., and Duque, A.: Differences in carbon stocks along an elevational gradient in tropical mountain forests of Colombia, Biotropica, 51, 490–499, https://doi.org/10.1111/btp.12675, 2019a.

835   Phillips, O. L., Sullivan, M. J. P., Baker, T. R., Monteagudo Mendoza, A., Vargas, P. N., and Vásquez, R.: Species Matter: Wood Density Influences Tropical Forest Biomass at Multiple Scales, Surveys in Geophysics, 40, 913–935, https://doi.org/10.1007/s10712-019-09540-0, 2019b.

Phillips, R. P., Brzostek, E., and Midgley, M. G.: The mycorrhizal-associated nutrient economy: A new framework for predicting carbon-nutrient couplings in temperate forests, New Phytologist, 199, 41–51, https://doi.org/10.1111/nph.12221, 2013.

840   Poeplau, C., Don, A., Six, J., Kaiser, M., Benbi, D., Chenu, C., Cotrufo, M. F., Derrien, D., Gioacchini, P., Grand, S., Gregorich,

E., Griepentrog, M., Gunina, A., Haddix, M., Kuzyakov, Y., Kühnel, A., Macdonald, L. M., Soong, J., Trigalet, S., Vermeire, M.-L., Rovira, P., van Wesemael, B., Wiesmeier, M., Yeasmin, S., Yevdokimov, I., and Nieder, R.: Isolating organic carbon fractions with varying turnover rates in temperate agricultural soils – A comprehensive method comparison, Soil Biology and Biochemistry, 125, 10–26, https://doi.org/https://doi.org/10.1016/j.soilbio.2018.06.025, 2018.

845   Prada, C. M., Morris, A., Andersen, K. M., Turner, B. L., Caballero, P., and Dalling, J. W.: Soils and rainfall drive landscape-scale changes in the diversity and functional composition of tree communities in premontane tropical forest, Journal of Vegetation Science, 28, 859–870, https://doi.org/10.1111/jvs.12540, 2017.

Prada, C. M., Turner, B. L., and Dalling, J. W.: Growth responses of ectomycorrhizal and arbuscular mycorrhizal seedlings to low soil nitrogen availability in a tropical montane forest, Functional Ecology, 36, 107–119, https://doi.org/10.1111/1365-

850   2435.13901, 2022.

Quesada, C. A., Phillips, O. L., Schwarz, M., Czimczik, C. I., Baker, T. R., Patiño, S., Fyllas, N. M., Hodnett, M. G., Herrera, R., Almeida, S., Alvarez Dávila, E., Arneth, A., Arroyo, L., Chao, K. J., Dezzeo, N., Erwin, T., Di Fiore, A., Higuchi, N., Honorio Coronado, E., Jimenez, E. M., Killeen, T., Lezama, A. T., Lloyd, G., Löpez-González, G., Luizão, F. J., Malhi, Y., Monteagudo, A., Neill, D. A., Núñez Vargas, P., Paiva, R., Peacock, J., Peñuela, M. C., Peña Cruz, A., Pitman, N., Priante Filho, N., Prieto,

855   A., Ramírez, H., Rudas, A., Salomão, R., Santos, A. J. B., Schmerler, J., Silva, N., Silveira, M., Vásquez, R., Vieira, I., Terborgh, J., and Lloyd, J.: Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate, Biogeosciences, 9, 2203–2246, https://doi.org/10.5194/bg-9-2203-2012, 2012.

R Core Team: R: A language and environment for statistical computing, Vienna, Austria. https://www.r-project.org/., 2022.

Read, D. J. and Perez-Moreno, J.: Mycorrhizas and nutrient cycling in ecosystems - A journey towards relevance?, New

860   Phytologist, 157, 475–492, https://doi.org/10.1046/j.1469-8137.2003.00704.x, 2003.

Réjou-Méchain, M., Tymen, B., Blanc, L., Fauset, S., Feldpausch, T. R., Monteagudo, A., Phillips, O. L., Richard, H., and Chave, J.: Using repeated small-footprint LiDAR acquisitions to infer spatial and temporal variations of a high-biomass Neotropical forest, Remote Sensing of Environment, 169, 93–101, https://doi.org/10.1016/j.rse.2015.08.001, 2015.

Réjou-Méchain, M., Tanguy, A., Piponiot, C., Chave, J., and Hérault, B.: Biomass: an R Package for Estimating Above-Ground

865   Biomass and Its Uncertainty in Tropical Forests, Methods in Ecology and Evolution, 8, 1163–1167, https://doi.org/10.1111/2041-210X.12753, 2017.

Saatchi, S. S., Harris, N. L., Brown, S., Lefsky, M., Mitchard, E. T. A., Salas, W., Zutta, B. R., Buermann, W., Lewis, S. L., Hagen, S., Petrova, S., White, L., Silman, M., and Morel, A.: Benchmark map of forest carbon stocks in tropical regions across three continents, Proceedings of the National Academy of Sciences of the United States of America, 108, 9899–9904,

870   https://doi.org/10.1073/pnas.1019576108, 2011.

Schmitt, C. B., Senbeta, F., Woldemariam, T., Rudner, M., and Denich, M.: Importance of regional climates for plant species distribution patterns in moist Afromontane forest, Journal of Vegetation Science, 24, 553–568, https://doi.org/10.1111/j.1654-1103.2012.01477.x, 2013.

Schrumpf, M., Guggenberger, G., Schubert, C., Valarezo, C., and Zech, W.: Tropical montane rain forest soils: development and

875   nutrient status along an altitudinal gradient in the south Ecuadorian Andes., Die Erde, 132, 43–59, 2001.

Schrumpf, M., Schulze, E. D., Kaiser, K., and Schumacher, J.: How accurately can soil organic carbon stocks and stock changes be quantified by soil inventories?, Biogeosciences, 8, 1193–1212, https://doi.org/10.5194/bg-8-1193-2011, 2011.

Seyfried, G. S., Canham, C. D., Dalling, J. W., and Yang, W. H.: The effects of tree-mycorrhizal type on soil organic matter properties from neighborhood to watershed scales, Soil Biology and Biochemistry, 161, 108385,

880   https://doi.org/10.1016/j.soilbio.2021.108385, 2021.

Sherrod, D. R., Vallance, J. W., Tapia Espinosa, A., and McGeehin, J. P.: Volcan Baru: Eruptive History and Volcano-Hazards Assessment, Open-File Report, 1–33 pp., https://doi.org/110.3133/ofr20071401, 2008.

Sierra, C. A., del Valle, J. I., Orrego, S. A., Moreno, F. H., Harmon, M. E., Zapata, M., Colorado, G. J., Herrera, M. A., Lara, W., Restrepo, D. E., Berrouet, L. M., Loaiza, L. M., and Benjumea, J. F.: Total carbon stocks in a tropical forest landscape of the
885 Porce region, Colombia, Forest Ecology and Management, 243, 299–309, https://doi.org/10.1016/j.foreco.2007.03.026, 2007.

Soong, J. L., Janssens, I. A., Grau, O., Margalef, O., Stahl, C., Van Langenhove, L., Urbina, I., Chave, J., Dourdain, A., Ferry, B., Freycon, V., Herault, B., Sardans, J., Peñuelas, J., and Verbruggen, E.: Soil properties explain tree growth and mortality, but not biomass, across phosphorus-depleted tropical forests, Scientific Reports, 10, 1–13, https://doi.org/10.1038/s41598-020-58913-8, 2020.

890 Soudzilovskaia, N. A., van Bodegom, P. M., Terrer, C., Zelfde, M. van't, McCallum, I., McCormack, M. ., Fisher, J. B., Brundrett, M. C., de Sá, N. C., and Tedersoo, L.: Global mycorrhizal plant distribution linked to terrestrial carbon stocks, Nature Communications, 10, 1–10, https://doi.org/10.1038/s41467-019-13019-2, 2019.

Soudzilovskaia, N. A., Vaessen, S., Barcelo, M., He, J., Rahimlou, S., Abarenkov, K., Brundrett, M. C., Gomes, S. I. F., Merckx, V., and Tedersoo, L.: FungalRoot: global online database of plant mycorrhizal associations, New Phytologist, 227, 955–966,
895 https://doi.org/10.1111/nph.16569, 2020.

Spracklen, D. V. and Righelato, R.: Tropical montane forests are a larger than expected global carbon store, Biogeosciences, 11, 2741–2754, https://doi.org/10.5194/bg-11-2741-2014, 2014.

Sprent, J. I.: Legume Nodulation: A Global Perspective, Wiley, Germany, 105–156 pp., 2009.

Steidinger, B. S., Crowther, T. W., Liang, J., Van Nuland, M. E., Werner, G. D. A., Reich, P. B., Nabuurs, G., de-Miguel, S.,
900 Zhou, M., Picard, N., Herault, B., Zhao, X., Zhang, C., Routh, D., Peay, K. G., Abegg, M., Adou Yao, C. Y., Alberti, G., Almeyda Zambrano, A., Alvarez-Davila, E., Alvarez-Loayza, P., Alves, L. F., Ammer, C., Antón-Fernández, C., Araujo-Murakami, A., Arroyo, L., Avitabile, V., Aymard, G., Baker, T., Bałazy, R., Banki, O., Barroso, J., Bastian, M., Bastin, J. F., Birigazzi, L., Birnbaum, P., Bitariho, R., Boeckx, P., Bongers, F., Bouriaud, O., Brancalion, P. H. S., Brandl, S., Brearley, F. Q., Brienen, R., Broadbent, E., Bruelheide, H., Bussotti, F., Cazzolla Gatti, R., Cesar, R., Cesljar, G., Chazdon, R., Chen, H. Y.
905 H., Chisholm, C., Cienciala, E., Clark, C. J., Clark, D., Colletta, G., Condit, R., Coomes, D., Cornejo Valverde, F., Corral-Rivas, J. J., Crim, P., Cumming, J., Dayanandan, S., de Gasper, A. L., Decuyper, M., Derroire, G., DeVries, B., Djordjevic, I., Iêda, A., Dourdain, A., Obiang, N. L. E., Enquist, B., Eyre, T., Fandohan, A. B., Fayle, T. M., Feldpausch, T. R., Finér, L., Fischer, M., Fletcher, C., Fridman, J., Frizzera, L., Gamarra, J. G. P., Gianelle, D., Glick, H. B., Harris, D., Hector, A., Hemp, A., Hengeveld, G., Herbohn, J., Herold, M., Hillers, A., Honorio Coronado, E. N., Huber, M., Hui, C., Cho, H., Ibanez, T., Jung, I., Imai, N., et
910 al.: Climatic controls of decomposition drive the global biogeography of forest-tree symbioses, Nature, 569, 404–408, https://doi.org/10.1038/s41586-019-1128-0, 2019.

Tanner, E. V. J., Vitousek, P. M., and Cuevas, E.: Experimental Investigation of Nutrient Limitation of Forest Growth on Wet Tropical Mountains, Ecological Society of America, 79, 10–22, https://doi.org/10.1890/0012-9658(1998)079[0010:EIONLO]2.0.CO;2, 1998.

915 Thomas, S. C. and Martin, A. R.: Carbon content of tree tissues: A synthesis, Forests, 3, 332–352, https://doi.org/10.3390/f3020332, 2012.

Turner, B. L. and Dalling, J. W.: Soils of the Fortuna Forest Reserve, in: Fortuna Forest Reserve, Panama. Interacting Effects of Climate and Soils on the Biota of a Wet Premontane Tropical Forest., edited by: Dalling, J. W. and Turner, B. L., Smithsonian Scholarly Press, Washington, D.C, 47–135, 2021.

920 Unger, M., Homeier, J., and Leuschner, C.: Effects of soil chemistry on tropical forest biomass and productivity at different

elevations in the equatorial Andes, Oecologia, 170, 263–274, https://doi.org/10.1007/s00442-012-2295-y, 2012.

Vilanova, E., Ramírez-Angulo, H., Torres-Lezama, A., Aymard, G., Gámez, L., Durán, C., Hernández, L., Herrera, R., van der Heijden, G., Phillips, O. L., and Ettl, G. J.: Environmental drivers of forest structure and stem turnover across Venezuelan tropical forests, PLoS ONE, 13, 1–27, https://doi.org/10.1371/journal.pone.0198489, 2018.

925   Vitousek, P. M.: Litterfall, nutrient cycling, and nutrient limitation in tropical forests, Ecology, 65, 285–298, 1984.

Wegner, W., Wörner, G., Harmon, R. S., and Jicha, B. R.: Magmatic history and evolution of the Central American Land Bridge in Panama since Cretaceous times, Bulletin of the Geological Society of America, 123, 703–724, https://doi.org/10.1130/B30109.1, 2011.

Wilcke, W., Oelmann, Y., Schmitt, A., Valarezo, C., Zech, W., and Homeier, J.: Soil properties and tree growth along an

930   altitudinal transect in Ecuadorian tropical montane forest, Journal of Plant Nutrition and Soil Science, 171, 220–230, https://doi.org/10.1002/jpln.200625210, 2008.

Wright, S. J.: Plant responses to nutrient addition experiments conducted in tropical forests, Ecological Monographs, 89, 1–18, https://doi.org/10.1002/ecm.1382, 2019.

Yaffar, D., Addo-Danso, S. D., Powers, J. S., and Meier, I. C.: Fundamental but underrepresented: root carbon stocks in African

935   montane forests, Frontiers in Forests and Global Change, 6, 1–4, https://doi.org/10.3389/ffgc.2023.1273996, 2023.

Zech, M.: Evidence for Late Pleistocene climate changes from buried soils on the southern slopes of Mt. Kilimanjaro, Tanzania, Palaeogeography, Palaeoclimatology, Palaeoecology, 242, 303–312, https://doi.org/10.1016/j.palaeo.2006.06.008, 2006.

Zhang, D., Hui, D., Luo, Y., and Zhou, G.: Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors, Journal of Plant Ecology, 1, 85–93, https://doi.org/10.1093/jpe/rtn002, 2008.

940   Zolkos, S. G., Goetz, S. J., and Dubayah, R.: A meta-analysis of terrestrial aboveground biomass estimation using lidar remote sensing, Remote Sensing of Environment, 128, 289–298, https://doi.org/10.1016/j.rse.2012.10.017, 2013.