



# Comparative analysis of nutrient concentrations in generalist and specialist tree species on clay and sandy soils in the Central Amazon

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## Abstract.

15 Tropical forest soils generally have low nutrient availability. Some species exhibit specialized behavior, occurring exclusively in a single soil type, while others are generalists, thriving across different soils and water table depths. This study assessed the influence of topographic variation on leaf and trunk macronutrient and carbon amounts of tree species occurring only in one topographic position and species occurring across topographic positions and their relationship with soil macronutrient and carbon stocks. We selected nine species occurring in different topographic positions: three plateau specialists, three valley  
20 specialists, and three generalists (with four replicates each, totalling 35 individuals), where leaf and trunk samples were collected from each individual, and soil samples for carbon and nutrient analysis and quantification. Leaf and trunk nutrient concentrations varied across specialist and generalist functional groups, with valley specialists showing the highest concentrations of leaf and trunk nutrients and carbon. Nutrient concentrations within generalists remained consistent across topographic positions, underscoring their adaptive strategy to sustain productivity across environments. The concentrations of  
25 certain trunk nutrients of plateau and valley specialists and generalists mirrored those found in leaves, albeit at lower relative concentrations. Trunk carbon concentrations did not vary significantly compared to leaves, suggesting that other biological or environmental factors influenced tree nutritional status. We found evidence of variations in plant carbon and nutrient



concentrations between generalist and specialist species inhabiting plateau and valley habitats in Central Amazonia, and a weak correlation between the stocks of some soil nutrients and leaf and trunk nutrient amounts.

30 **Keywords:** Biogeochemical cycles, tropical forest, Nutrient concentration on tropical species, carbon concentration, soil nutrients stock, macronutrients

## 1 Introduction

The Amazon rainforest supports abundant life despite considerable nutrient limitation on aged tropical forest soils. In general, Amazon soils are classified as acidic, low-fertility, nutrient-poor, and prone to leaching (Cleveland et al., 2011; Quesada et al., 2012), with scarcity of phosphorus (P) and other nutrients (Turner et al., 2018; Cunha et al., 2022). As a result, plant species in tropical regions such as the Amazon have developed multiple nutrient acquisition and recycling strategies such as fine-root P foraging, symbioses with arbuscular mycorrhizal fungi (AMF), organic acid exudation and acid phosphatase exudation (Cordeiro et al., 2020; Guilbeault-Mayers and Laliberté, 2024; Lugli et al., 2020; Reichert et al., 2022; Urbina et al., 2021; Vengavasi et al., 2021). The investment in fine roots, for example, is particularly notable in the central Amazon, where the species tend to have shallow root systems compared to other locations (e.g., eastern Amazon) due to well-distributed rainfall throughout the year (Spanner et al., 2022). Additionally, at a larger scale (e.g., Amazon basin) distinct soils types with different water table depths imposed by the topography create diverse environments with contrasting species composition and functional traits (Costa et al., 2023). Variations in soil properties, such as those found across clay-rich plateaus and sandy valleys in the Central Amazon, are key determinants of tree species distribution, as previously observed by other studies in other locations (John et al., 2007; Zuleta et al., 2020).

The primary reservoir of essential nutrients for the functioning of forest ecosystems lies within the soil (Nottingham et al., 2022; Vitousek and Sanford, 1986). However, due to the highly weathered soils of tropical ecosystems a great proportion of these nutrients in their readily available form are found in shallow soil layers and are associated with litterfall deposition and organic matter (Leff et al., 2012; Machado et al., 2016). A portion of these nutrients, available in organic matter as well as derived from parent rock sources, are stored in tree organs and tissues, playing a crucial role in the establishment and maintenance of tropical environments (Bauters et al., 2022). When a tree falls, dies and decomposes, nutrients in short-lived organs like leaves and fine roots are released quickly, whereas nutrients in long-lived woody tissues (branches, stems, twigs) are released more slowly (Martins et al., 2023; Summers, 1998). This difference in nutrient release interferes with their availability to the soil, where woody tissues generally contain higher total stock of certain nutrients, such as phosphorus (P) and nitrogen (N), compared to other plant components (Ferraz et al., 1997; Martins et al., 2023), serving as a long-term carbon



(C) reserve (Martin et al., 2018). Nonetheless, nutrient concentrations in wood and leaves exhibit substantial variation among forest species both locally (e.g. presence of N fixing species, species composition associated with topography, functional traits like wood density etc.) and globally (e.g., precipitation regimes, rock-derived nutrients etc.) (Heineman et al., 2016; Meerts, 2002), with the local drivers influencing the variations of nutrient concentrations remaining poorly understood.

60 Experiments with tree response to P nutrition have reported a strong relationship between the maximum electron transport rate ( $J_{\max}$ ) for both foliar N and P rates, with these relationships improved with the inclusion of wood density (Norby et al., 2017). In the tropics, wood density is widely recognized as a key factor in estimating biomass and an important ecological and forest dynamics trait (Chave et al., 2009). However, the relevance of wood density in models and species performance is still under debate (Larjavaara and Muller-Landau, 2010). Higher wood density, for example, results in less volume growth per  
65 unit of carbon allocation, where the construction and maintenance costs of resistant plant structures and biochemical defenses ultimately reduce resources available for plant growth and reproduction (Chave et al., 2006; Poorter et al., 2010). Also, high wood density species have higher survival rates due to biomechanical stability and hydraulic safety (Esquivel-Muelbert et al., 2020; Gray et al., 2019). On the other hand, low wood density species have higher mortality and decomposition rates compared to high wood density species (Chambers et al., 2000). Overall, the observations of high wood density species presenting slower  
70 growth and higher costs for wood production suggest the possibility of different nutrient acquisition strategies and nutrient storage in tissues and organs compared to low wood density species. In the Amazon, wood density and water storage are most strongly influenced by species identity, whilst others are primarily determined by environmental conditions (Lira-Martins et al., 2022). Therefore, understanding the variation in nutrient allocation in plant organs, such as leaves and trunk, among generalist and specialist species with diverse functional traits such as wood density in relation to soil nutrient stocks along a  
75 topographic gradient is essential to unravel the underlying biogeochemical mechanisms governing the functioning of Amazon forest ecosystems.

Despite a growing number of recent initiatives and studies in the Amazon, the current scarcity of information on nutrient stocks in the vegetation emphasizes the importance of quantifying nutrient compartments and quantities, such as P and N, in plant organs (trunk and leaves) and in the soil. This information can support the development of dynamic vegetation  
80 models with nutrient functionality, such as the Functionally Assembled Terrestrial Ecosystem Simulator (FATES) (Koven et al., 2020). Additionally, climate change can potentially impact forest productivity and function as well as the plant-environment interactions in the Amazon in the coming decades (Flores et al., 2024; Holm et al., 2023). The highly intricate and diverse environments and their links to species composition and different functional traits in the Amazon biome pose challenges in terms of determining which ecosystems and species will be more vulnerable to climate events such as El Niño-  
85 driven droughts. For example, it is well known that species occupying habitats with shallow water tables (e.g., valleys) are



more vulnerable to drought events than species from deep water tables (e.g., upland plateaus) due to differences in their hydraulic systems (Esteban et al., 2021). Nevertheless, our understanding of nutrient acquisition and strategies on these hyperdiverse forests and their links to topography is still limited (Rodrigues et al., 2024).

This study's objective was to evaluate the influence of topography on soil nutrient stocks and on the amount of leaf and trunk nutrients in 'generalist' and 'specialist' tree species in a *terra-firme* tropical forest in Central Amazon. Specifically, we aimed to determine whether (1) trunk and leaf C and nutrient concentrations vary between three functional groups: generalists, plateau specialists and valley specialists, (2) there is a relationship between wood density and nutrient and C concentrations in trunk, (3) and to assess whether the amounts of nutrients and C in tree species correlate with soil nutrient and C stocks. We hypothesized that (i) the nutrient and C concentrations of specialist species differ from those of generalist species, (ii) that wood density is a key factor explaining variation in trunk nutrient and C concentrations, and (iii) that the amounts of nutrients and C in the trunk of generalist and specialist species correlate with soil nutrient and C stocks.

## 2 Methods

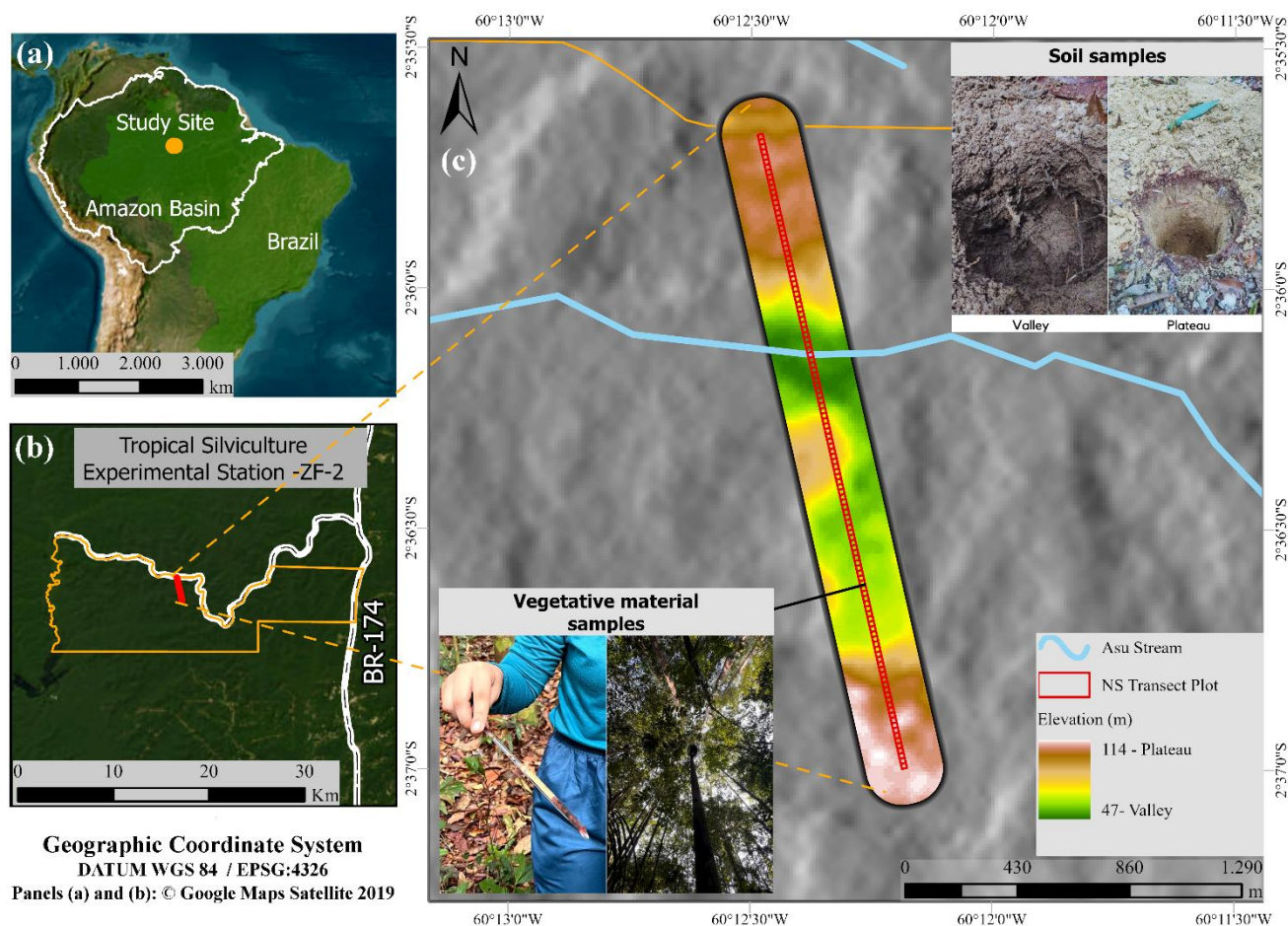
### 2.1 Study Area

The study was conducted along the North-South transect with 125 individual  $20 \times 20$  m permanent plots, which collectively span a 20-meter by 2,500-meter area, covering 5 hectares (Araujo et al., 2020). The North-South transect was installed in 1996 by the Jacaranda Project (a collaboration between INPA and Japan International Cooperation Agency, JICA) and is situated within the Cuieiras river basin, encompassing the territory of the Tropical Silviculture Experimental Station (commonly referred to as ZF-2,  $02^{\circ}35'55''$  S,  $60^{\circ}02'14''$  W), operated by the National Institute for Amazonian Research (E.E.S.T./INPA) (Fig. 1) (Araujo et al., 2020). The North-South transect plot was designed to representatively sample the dominant undulating topography of the region, which encompasses plateau, slope and valley positions and associated forest structural and functional differences (Piva et al., 2019). Forest censuses have been conducted since 1996, where all woody individuals with a diameter at breast height (DBH)  $\geq 10$  cm were measured (Da Silva et al., 2002).

Soil characteristics in the region have been previously described by (Ferraz et al., 1997). Soils in plateaus feature a more clayey texture and are classified as Yellow Latosol, while the shallower soils in the valleys have sandy texture, with a predominance of coarse sand, and are classified as hydromorphic spodosols. According to the white-sand vegetation classification in the Amazon described by (Demarchi et al., 2022), the valley forests at the study site can be classified as a mix of open forested campinarana (wetlands upon hydromorphic sand soils) and dense forested campinarana with the last one more comprehensive in terms of area at the NS transect (Fig. 1). The region has a predominantly tropical rainy climate, classified as *Amw* according to the Köppen classification. The average relative humidity at the study site is 72.8% on average, with a ranging



from a minimum of 69% to a maximum of 99%. The annual rainfall ranges from 1,900 to 2,400 mm (Alvares et al., 2013; Spanner et al., 2022). The rainy season typically extends from November to May, while the dry season spans from June to October. The average annual temperature stands at 26.7°C, with a peak of 31.2°C and a low of 23.5°C (Meng et al., 2022).



120 **Figure 1** North-South transect plot with an area of 5 ha (20 m × 2,500 m), located ~50 km north of Manaus, Brazil. Elevation data derived from SRTM images (courtesy of the U.S. Geological Survey; available at <https://earthexplorer.usgs.gov/>).

## 2.2 Species selection and categorization



In October 2022, we sampled a total of 35 trees whose functional group were categorized based on their position  
125 along the topographic gradient (Plateau/Valley). Our categorization was informed by prior studies conducted by (Carneiro,  
2004) and (Souza, 2011), which served as a foundation for our initial selection of sample species. We adopted the term  
"specialist" for species exclusively inhabiting one topographic position (i.e., plateau specialist and valley specialist), and  
"generalist" to those species distributed across the entire topographic gradient (Fig. S1 in the Supplementary Material). We  
selected three species exclusively found on the plateau (plateau specialists), three species exclusive to the lowlands or "valleys"  
130 (valley specialists), and three species that are present in both plateau and valley habitats (generalists), as further detailed in  
Table 1. We selected a total of nine sample species, each with four replicates, with the exception of the plateau specialist  
species *Croton lanjouwensis* Jabl., which had only three replicates due to the death of an individual (35 sample trees in total).  
The selected sample trees also encompass a range of diameter classes (Fig. S2 in the Supplementary Material).

In August 2022, prior to our sampling period, field assessments were conducted to further evaluate the status of the  
135 selected species. To verify their species identification, herbarium vouchers were taken for each individual, with the botanical  
identification conducted with botanical expert assistance. The plateau specialist species identified for this study are  
*Eschweilera tessmanii* (Lecythidaceae), *Ocotea percurrans* (Lauraceae), and *Croton lanjouwensis* Jabl. (Euphorbiaceae). The  
generalist species selected comprise *Brosimum rubescens* (Moraceae), *Scleronema micranthum* Ducke (Malvaceae), and  
*Protium hebetatum* (Burseraceae). The specialist valley species encompass *Micrandra siphonioides* (Euphorbiaceae), *Tapura*  
140 *lanceolata* (Dichapetalaceae), and *Brosimum utile* subsp. *ovatifolium* Ducke (Moraceae), as described by (Carneiro, 2004) and  
(Souza, 2011) (Fig. S3). In this study, N-fixing species, often associated with the Fabaceae family, were excluded from the  
species selection to mitigate potential confounding effects.

We also report the periodic annual increment (PAI) of each species. PAI is the mean annual increment per diameter  
at breast height (DBH) of a tree over a period of time (in this study from 2010 to 2022, 12 years) (Equation 1).





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$$PAI = \frac{\text{Current DBH size} - \text{Initial DBH size}}{\text{Current time} - \text{Initial time}} \quad (1)$$

**Table 1** Selected species along the North-South Transect. The table includes information on topographic position, functional group, family, species, number of individuals ( $n$ ), calculated basic wood density ( $\text{g}\cdot\text{cm}^{-3}$ ), and periodic annual increment (PAI).

Topographical position	Functional group	Species	Family	$n$	Wood density	PAI (cm)
Plateau	Plateau specialists	<i>Eschweilera tessmannii</i>	Lecythidaceae	4	0.7329	0.17
Plateau	Plateau specialists	<i>Ocotea percurrens</i>	Lauraceae	4	0.3878	0.30
Plateau	Plateau specialists	<i>Croton lanjouwensis</i>	Euphorbiaceae	3 <sup>a</sup>	0.3758	0.80
Plateau/Valley	Generalists	<i>Brosimum rubescens</i>	Moraceae	4	0.7051	0.11
Plateau/Valley	Generalists	<i>Scleronema micranthum</i>	Malvaceae	4	0.5307	0.16
Plateau/Valley	Generalists	<i>Protium hebetatum</i>	Burseraceae	4	0.5384	0.21
Valley	Valley specialists	<i>Micrandra siphonioides</i>	Euphorbiaceae	4	0.4524	0.20
Valley	Valley specialists	<i>Tapura lanceolata</i>	Dichapetalaceae	4	0.5700	0.08
Valley	Valley specialists	<i>Brosimum utile subsp. Ovatifolium</i>	Moraceae	4	0.4501	0.15

<sup>a</sup>Note: One individual of this species was found dead in the field and there is no other individual of the species within the boundaries of the plots in the North-South Transect.

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### 2.3 Leaf sample collection

For each of the 35 tree individuals, samples of sun-exposed canopy branches and twigs were collected with the assistance of a climber. Immediately after the branches were cut, fully expanded, healthy green (mature) leaves were selected,



placed in Ziploc® bags, and stored in a refrigerator at the field camp to reduce microbial activity. At the Forest Management  
155 Laboratory, the leaf samples were processed and then sent to the Soil and Plant Analysis Laboratory (LASP) of EMBRAPA-  
Amazônia Ocidental for carbon and nutrient quantification.

#### 2.4 Trunk woody material sample collection

Using the non-destructive method, we collected two samples of trunk woody material from each selected individual,  
160 totaling 70 samples. One wood sample was utilized to quantify nutrients in the trunk (sample 1), while the other was used to  
determine basic wood density (sample 2). Sample 1 was obtained by employing a 25 mm diameter drill attached to a drill press  
(Fig. S4), and inserted to a depth of approximately 7 cm (with each sample 1 being approximately 2.5 cm in diameter and 7  
cm in length). Sample 2 was acquired using a 5.15 mm diameter Pressler auger (Fig. S5) and used to determine basic wood  
density following the methodology described in section 2.7 *Physical analysis of wood samples*. All samples were collected at  
165 a height of approximately 1.10 meters from the ground.

Trunk samples were initially stored in liquid nitrogen for one week before being transported to the Forest Management  
Laboratory in Manaus. Upon arrival, all samples were weighed on a precision scale and oven dried at 65°C until a constant  
weight was achieved. The leaf samples collected for chemical analysis were stored in a refrigerator following the guidelines  
outlined in section Leaf sample collection. Later, they were transported to the Forest Management Laboratory for a 72-hour  
170 oven drying process at 65°C. Then, the leaf samples were ground using a knife mill and sent, along with the trunk samples, to  
the EMBRAPA Occidental chemical laboratory for C and nutrient concentration determination following EMBRAPA's  
established methodology. C was quantified using the Walkley-Black method, N through the Kjeldahl method, P with the  
molybdenum blue spectrophotometry method, and K, Ca, and Mg using atomic absorption spectrometry. For K a hollow  
cathode lamp was employed, while Ca and Mg required either a calcium-magnesium or individual arc discharge (or hollow  
175 cathode) lamp, with the addition of lanthanum or strontium to mitigate interference from phosphates and aluminum in  
determination of these two elements (Malavolta et al., 1997). For more information on the method used by EMBRAPA for  
nutrient quantification can be viewed at <https://doi.org/10.15486/ngt/2377278> (Gimenez et al., 2024) (protocols in Portuguese  
version).

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#### 2.5 Soil collection and determination of soil properties

Three soil cores (Fig. 2) were opened around each sample tree, about one meter apart, resulting in a total of 105 soil  
cores each 50-cm deep. Soil samples were collected at four depths: 0-5 cm, 5-10 cm, 10-30 cm and 30-50 cm. In each of the





185 three cores around each tree, one single sample was taken at each depth and combined with the others from each core to obtain  
a composite sample per depth per individual tree. This resulted in 140 soil samples (35 trees × 4 depths). Those samples were  
collected to quantify soil nutrient and C stocks around each sample tree. For the chemical analysis, the soil samples were air  
dried in the shade and sent for analysis to the Soil and Plant Analysis Laboratory (LASP) - EMBRAPA Amazônia Ocidental,  
where the analyses followed the EMBRAPA (1998) soil analysis protocol. Soil nutrient and carbon stocks (NCS) were  
calculated using the following equation:

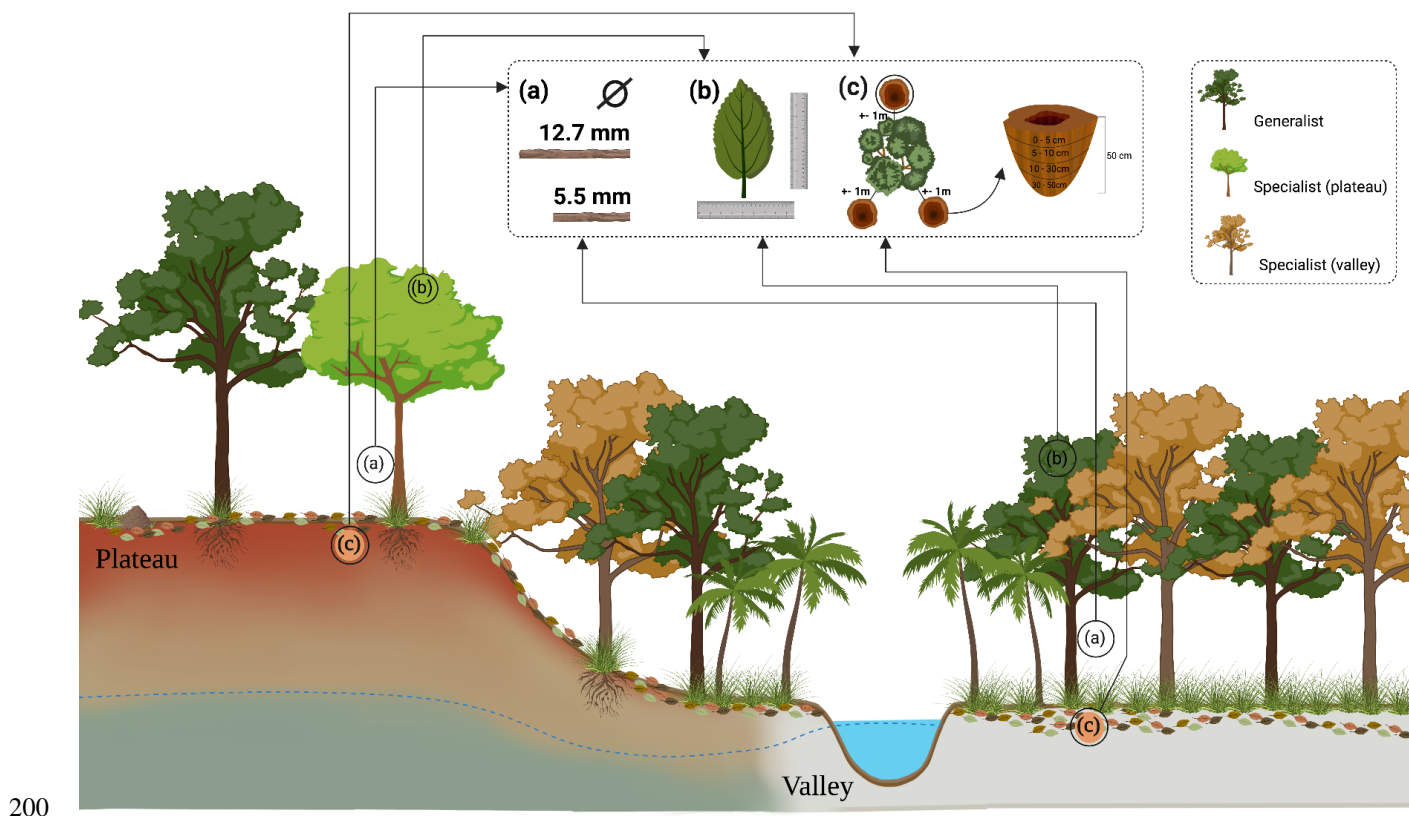
190 
$$NCS = \frac{C \times Ds \times E}{10} \quad (2)$$

where  $NCS$  = Soil nutrient and carbon stocks ( $Mg\ ha^{-1}$ ),  $C$  = nutrient concentration in the sampled soil layer ( $g\ kg^{-1}$ ),  $Ds$  = soil  
density ( $g\ cm^{-3}$ ),  $E$  = thickness of the soil layer considered (cm).

195 Soil density ( $Ds$ ) was determined using a volumetric ring of known volume to obtain an undeformed soil sample. The  
soil samples for density were taken to the Forest Management Laboratory (LMF), weighed on a precision scale to obtain their  
wet weight, dried in an oven at  $105 \pm 2^\circ C$  until they reached a constant mass to determine their dry weight. The difference  
between the wet weight and the dry weight was used to determine the soil moisture and, after this processing, the density was  
determined using the following equation:

$$Ds = \frac{m}{v} \quad (3)$$

where  $Ds$  = Soil density ( $g\ cm^{-3}$ ),  $m$  = Dry mass of soil (g),  $v$  = Internal volume of the ring ( $cm^3$ ).



200

**Figure 2** Field sampling scheme showing the (a) collection of trunk samples, (b) leaf samples and (c) the three soil collection points near each sample tree. The valley specialist species, plateau specialist's species, and generalist species are highlighted in the figure

205 **2.6 Quantification of carbon and nutrients in the leaf and trunk**

We estimated the amount (i.e., total weight) of carbon and nutrients in the leaf and trunk compartments of each sampled tree by first estimating the total tree biomass using an allometric model proposed by (Silva, 2007). The criteria of using the fresh weight (biomass) equation developed by (Silva, 2007) were based on the species composition used by (Silva, 2007) to fit the equations and estimate the coefficients. This was essentially done in the same study area (ZF-2, Manaus region), compared to other proposed equations which, while potentially more commonly used, were fitted for other regions of the Amazon forest with different floristic compositions and biomass (Nogueira et al., 2008).

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$$FW = a \times DBH^b \quad (4)$$

where  $FW$  = Tree biomass (total fresh weight in kg),  $DBH$  = Diameter at breast height (in cm),  $a = 2.7179$ ,  $b = 1.8774$

215 According to Silva (2007), in a mature forest of Manaus region leaf biomass represents approximately 3% of the total fresh biomass of a tree, while the trunk represents around 69% of the total fresh biomass. Based on this, we calculated the leaf fresh weight using the following equation:

$$LFW = FW \times 0.03 \quad (5)$$

where  $LFW$  = leaf fresh weight (kg),  $FW$  = tree biomass (total fresh weight in kg)

Similarly, the trunk fresh weight was calculated as:

220 
$$TFW = FW \times 0.69 \quad (6)$$

where  $TFW$  = Fresh weight of the trunk (kg),  $FW$  = Tree biomass (total fresh weight in kg)

(Silva, 2007) found that 59.7% of the fresh weight of the leaves is water, while 38.8% of the total weight of the trunk is water. Using this information, we calculated the dry weight of each compartment as following:

$$LDW = LFW \times 0.597 \quad (7)$$

225 where  $LDW$  = leaf dry weight (kg),  $LFW$  = leaf fresh weight (kg)

And the dry weight of the trunk (kg)

$$DWT = TFW \times 0.388 \quad (8)$$

where  $DWT$  = Dry weight of the trunk (kg),  $TFW$  = Trunk fresh weight (kg)

230 Therefore, the amounts of leaf C, N, P, K, Ca and Mg were calculated as follows: amount of leaf C and nutrients =  $LDW \times$  the concentration of each element in the leaf, where  $LDW$  is the leaf dry weight. Similarly, the amounts of trunk C, N, P, K, Ca and Mg in the trunk was calculated as: Amount of C and nutrients in the trunk =  $DWT \times$  concentration of each element in the trunk.  $DWT$  is dry weight in kilograms. These calculations allow us to estimate the amount of C and nutrients present in the leaf and trunk of the tree.

## 235 2.7 Physical analysis of wood samples

Basic wood density ( $\text{g cm}^{-3}$ ) was determined for each trunk sample taken with the increment borer, which was placed close to the point of where the  $DBH$  (diameter at breast height or 1.30 cm from ground level) measurement is taken. In the laboratory, the trunk samples were submerged in water for 20 days to obtain their saturated volume, then oven dried at  $105 \pm 2^\circ\text{C}$  until reaching a constant weight to determine the dry mass ( $\sim 0\%$  moisture).

240 
$$Db = \frac{m}{v} \quad (9)$$

where  $Db$  = basic wood density ( $\text{g cm}^{-3}$ ),  $m$  = dry mass of wood at  $105^\circ\text{C}$  (g),  $v$  = saturated volume of the sample ( $\text{cm}^3$ ).



## 2.8 Statistical analysis

All statistical analyses were carried out using R software version 4.2.3 for Windows (R Development Core Team, 2023). The data was tabulated using Excel software (Microsoft 365). Initially, the Shapiro Wilk test was applied to check the normality of each variable, leaf, wood and soil. In cases where the data did not follow a normal distribution, non-parametric statistics were used.

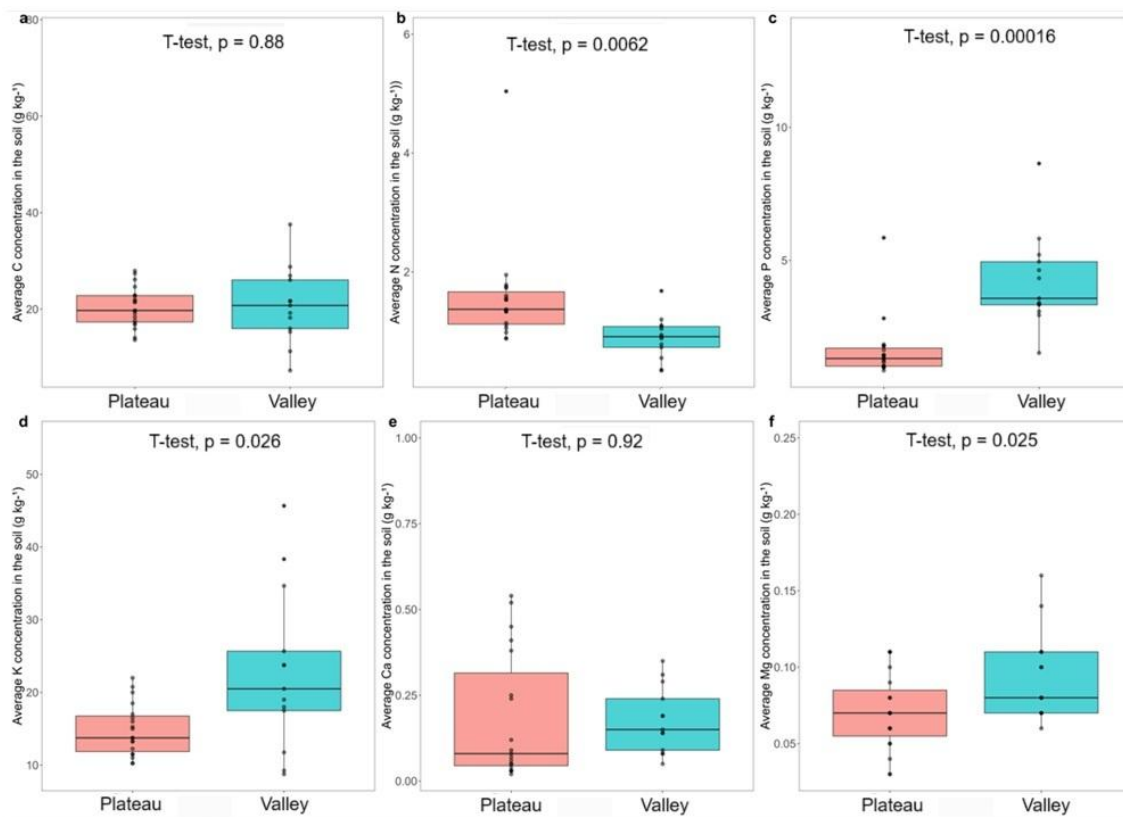
To test whether leaf and trunk nutrient and C concentrations differ between the generalist and specialist species, we performed an ANOVA when the data followed a normal distribution, and the Kruskal-Wallis test when the normality assumption was not met. Boxplots were constructed for each nutrient, grouped by classification (Generalists, Plateau Specialists, Valley Specialists).

Spearman's correlation was used to test the correlation between basic wood density and the concentration of nutrients and C in the trunk, and the correlation between the amount of nutrients in the leaf and trunk and the stocks of soil nutrients and C, in plateau areas and in valley habitats, at the 95% confidence level.

## 3 Results

### 3.1 Nutrients and carbon concentrations in soils of plateaus and valleys

The sandy valley soils presented significantly higher concentrations of P, K and Mg compared to plateau soils. On the other hand, the clayey plateau soils presented the highest concentrations of N. No significant difference in concentrations of C and Ca was found between both soil types (Fig. 3).

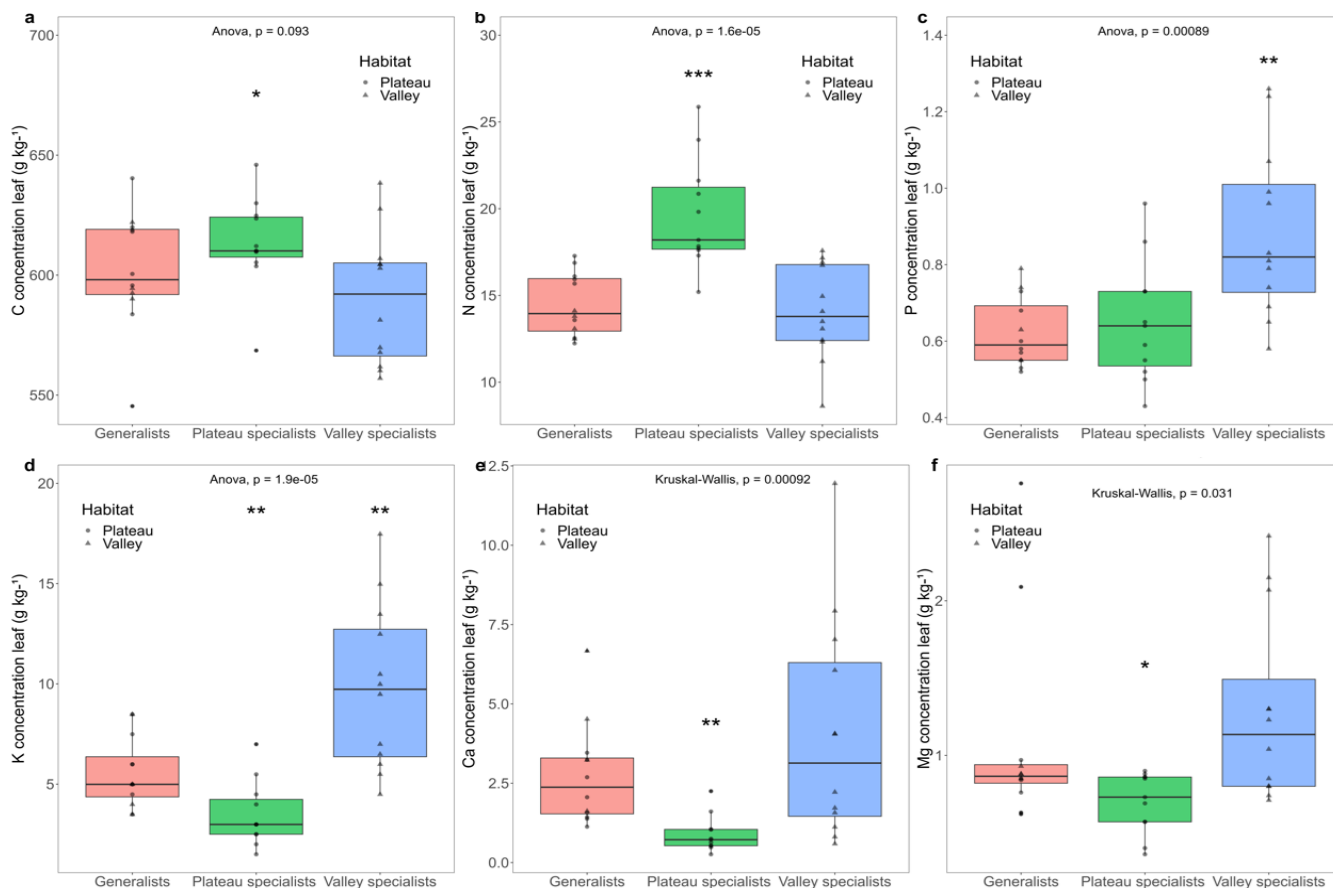


260 **Figure 3** Concentration of carbon and nutrients in the soils of plateaus and valleys

### 3.2 Leaf nutrient and carbon differences across plant functional types

We compared the average concentrations of leaf C and macronutrients of plateau specialists, valley specialists, and generalists (Fig. 3). We found significant differences in the concentrations of N ( $p < 0.001$ ), P ( $p < 0.001$ ), K ( $p < 0.001$ ), and Ca ( $p < 0.001$ ), suggesting a high level of confidence in the existence of differences among the functional groups. In the case of C ( $p = 0.092$ ) and Mg ( $p = 0.031$ ), there was no significant difference between functional groups. The ANOVA results are presented in the supplementary Tables 1 and 2.

The valley specialist functional group differed significantly by displaying notably higher concentrations of P at  $0.88 \pm 0.12$  g kg<sup>-1</sup> and K at  $9.56 \pm 2.08$  g kg<sup>-1</sup> in their leaves when compared to the other functional groups. Conversely, the plateau specialist species boasted the highest concentrations of C at  $613.09 \pm 10.99$  g kg<sup>-1</sup> and N at  $19.63 \pm 1.80$  g kg<sup>-1</sup>. The plateau specialist species also displayed the lowest concentrations of Ca at  $0.89 \pm 0.37$  g kg<sup>-1</sup> and Mg at  $0.70 \pm 0.12$  g kg<sup>-1</sup> (Table S3, Fig. S4)



**Figure 4** Boxplots showing the concentrations of leaf C and nutrients across the functional groups: valley specialists, plateau specialists and generalist species

### 275 3.3 Trunk nutrients and carbon across plant functional types

Similar to leaf analysis, we compared the average concentrations of C and macronutrients in the trunks to test whether generalist and specialist tree species differed significantly. We found significant differences in the concentrations of P ( $p = 0.0013$ ), K ( $p < 0.001$ ), Ca ( $p < 0.001$ ), and Mg ( $p = 0.003$ ) between functional groups (Fig. 5). Trunk N ( $p = 0.043$ ) was also

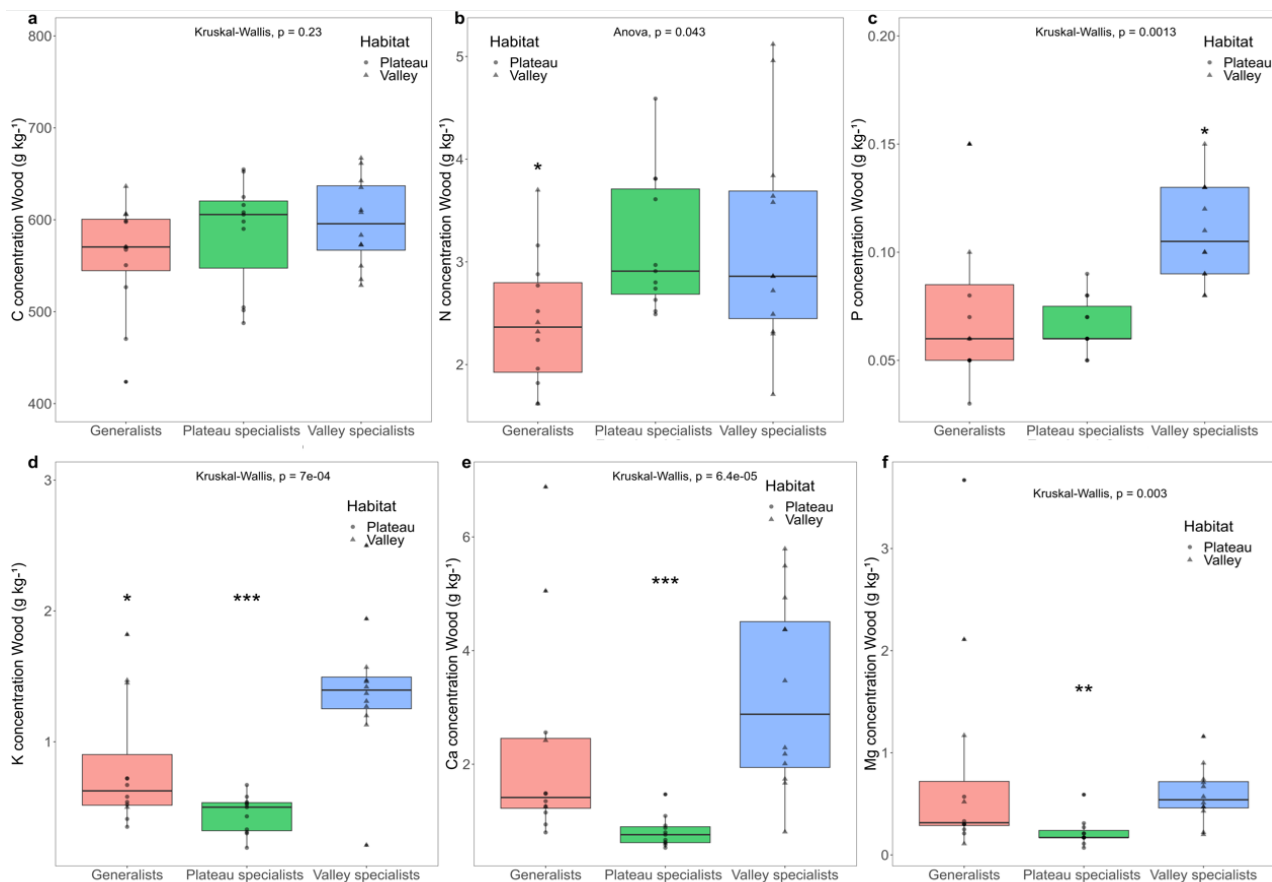




highly likely to differ, whereas trunk C ( $p = 0.23$ ) concentration did not show a significant difference among groups. The  
280 ANOVA results are presented in Supplementary Tables 4 and 5.

Among the three functional groups, valley specialists exhibited the highest concentration of P ( $0.11 \pm 0.01 \text{ g kg}^{-1}$ ) in  
the trunk. In contrast, the plateau specialists displayed the lowest concentrations of K at  $0.44 \pm 0.04 \text{ g kg}^{-1}$ , Ca at  $0.81 \pm 0.16$   
g  $\text{kg}^{-1}$ , and Mg at  $0.22 \pm 0.08 \text{ g kg}^{-1}$ . Notably, generalist species had the lowest N concentration at  $2.42 \pm 0.35 \text{ g kg}^{-1}$ . Regarding  
285 C concentration, it is probable that differences exist between the groups, with the highest and lowest concentrations observed  
in the valley specialists and generalists (Table S6 and Fig. 5).

The concentrations of certain trunk nutrients in plateau specialists, valley specialists, and generalists mirrored those  
found in the leaves, albeit with lower relative concentrations (Fig. 4, 5). However, trunk C concentrations did not exhibit  
significant variation compared to leaves.

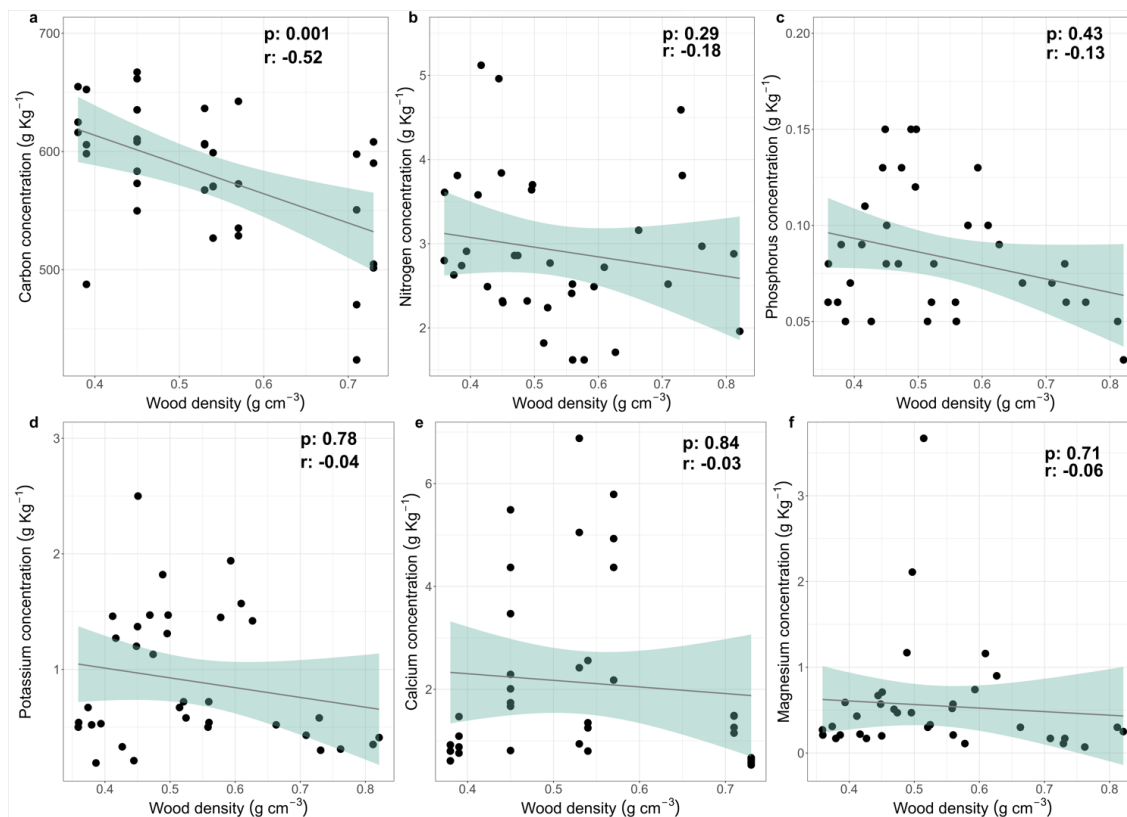


290 **Figure 5** Trunk carbon and nutrient concentrations of valley specialist, plateau specialist and generalist functional groups

### 3.4 Relationship between wood density and variation in nutrient and carbon concentrations in the trunk

We correlated the concentrations of nutrients and C in the trunk with basic wood density and found no correlation between wood density and the analyzed nutrients in the studied tree individuals (Fig. 6). These findings suggest that, within the group of species examined, there is no discernible association suggesting that wood nutrient concentration increases with wood density. However, for C, a moderate negative and statistically significant correlation was observed ( $r = -0.52$ ;  $p = 0.001$ ), suggesting that the highest concentrations of C were found in wood samples with lower wood densities.

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**Figure 6** Correlation between wood density (in  $\text{g cm}^{-3}$ ) and trunk carbon and nutrient concentrations (in  $\text{g kg}^{-1}$ )

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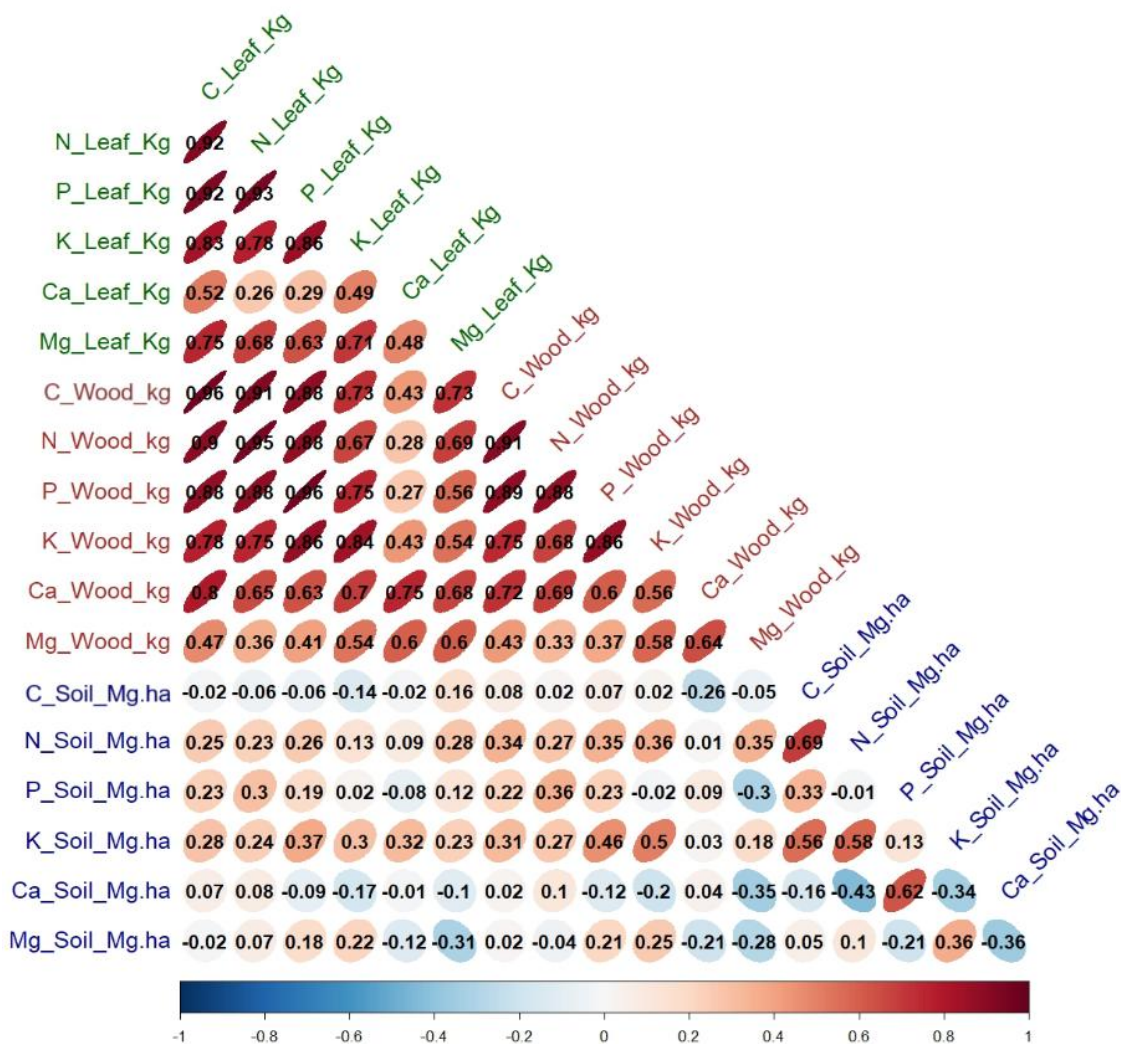
### 3.5 Relationship between nutrient and carbon concentrations in plant organs and soils

We found significant correlations between the C and nutrient amounts in the leaves and those in the trunk, suggesting a connection between the distribution of C and nutrients across different tree parts. However, fewer correlations were identified between the C and nutrient amount of the vegetation and their respective soil stocks. On the plateau, there were weak but positive correlations between soil K stocks and P, C, K, Ca, and Mg amounts. Additionally, correlations were observed between P and K amounts in the trunk. These findings suggest that soil K availability may influence the allocation of these nutrients to various parts of the trees. As these correlations were relatively weak, that other factors may also play a role in nutrient distribution.

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We found a strong positive correlation was observed between soil C and N stocks, indicating a significant relationship between the presence of C in the soil and N availability. Moreover, soil K stocks correlated positively with soil C and N stocks (Fig. 7).

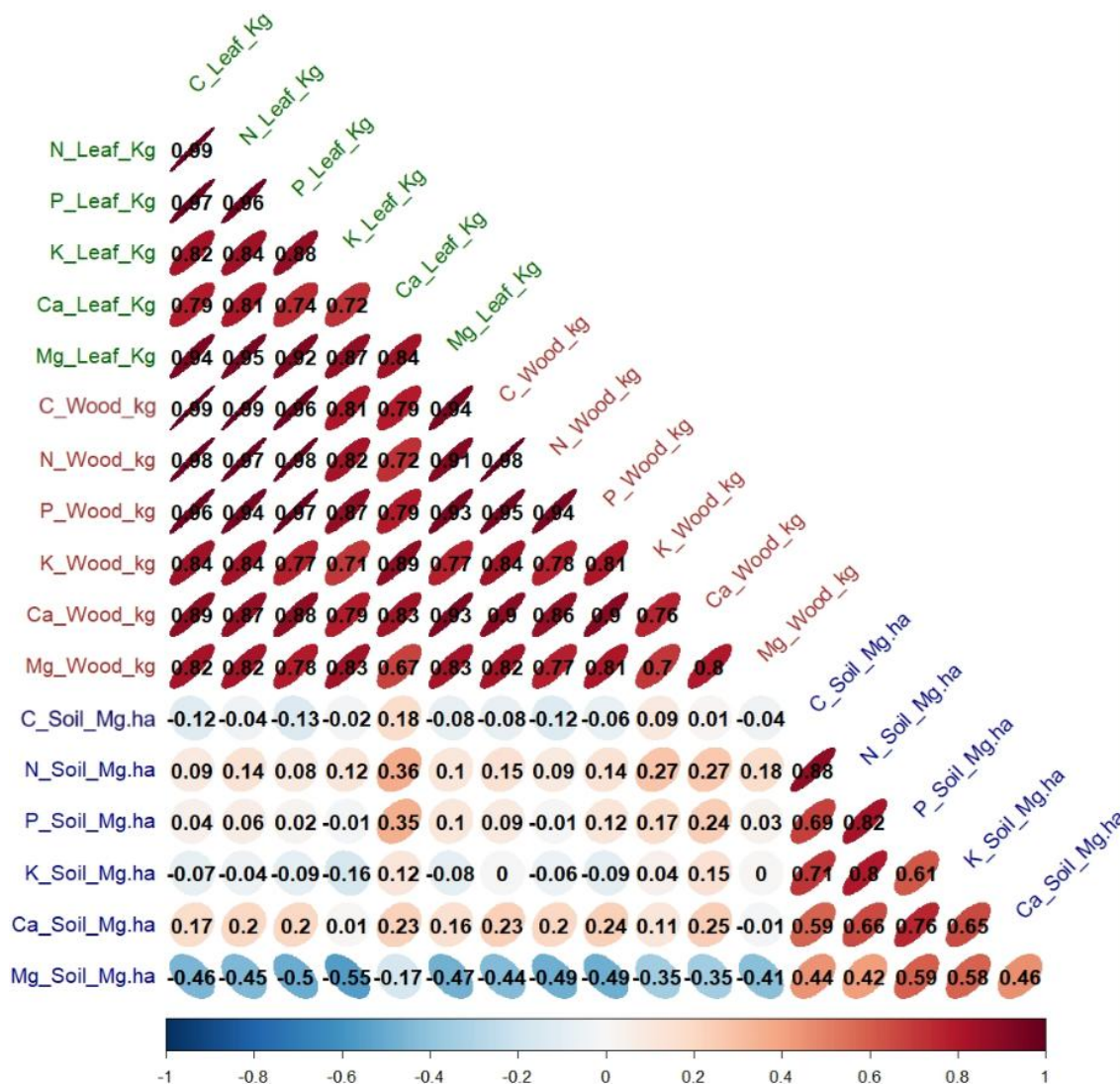


**Figure 7** Correlations between the amount of carbon and nutrients in the leaves and trunks and the stock of carbon and nutrients in the plateau soil up to a depth of 50 cm. The correlations were significant at the 95% significance level

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In valley soils, the soil C stock exhibited strong and positive correlations with soil P, N, and K stocks (Fig. 8). Furthermore, there was a positive correlation, although weak, between soil C and Mg stocks. These correlations underscore the connection between the presence of C in the soil and the availability of P, N, K, and Mg. Soil P stock also correlated with N, C, and K stocks, with a strong correlation observed with N ( $r = 0.82$ ).



**Figure 8** Correlations between the amount of carbon and nutrients in the leaf and trunk and the stock of carbon and nutrients in the valley's soil up to a depth of 50 cm. The correlations shown were significant at the 95% probability level



## 4 Discussion

### 325 4.1 Vegetation type, forest productivity, and topographic gradient

Nutrient dynamics in intact tropical ecosystems are highly intricate and influenced by various factors, including parent material, species composition, spatial context, canopy structure and topography. In ecosystems like the *terra-firme* forests of the Central Amazon it is well known the influence of topography (and its links to water table depth and soil texture variation) on forest productivity and biomass (de Castilho et al., 2006). Topography also influences species composition and divergent hydraulic functional traits such as specific leaf area and sapwood area (Cosme et al., 2017; Oliveira et al., 2019), litterfall decomposition (Powers et al., 2009), and nutrient dynamics (Broedel et al., 2017). In terms of nutrients dynamics, for example, the valleys tend to have greater nutrient fluxes in comparison to the upland plateaus due to the higher leaching rates, and large amount of macropores within the soil matrix that facilitate higher levels of percolation (Rodrigues et al., 2024). Corroborating with this, we found greater concentrations of P, K and Mg in valley soils compared to plateau soils (Fig. 3). However, higher nutrient concentrations in the valley are not reflected on higher aboveground biomass production, as the clay-rich substrates of upland plateaus show higher biomass (de Castilho et al., 2006).

In general, plateau and valley habitats differ in forest productivity and structure (Gonçalves et al., 2024). Excluding the biomass of palm species (which is higher in the valley than in the plateau), the sandy valley soils are characterized by lower forest productivity (de Castilho et al., 2006): forests on valleys (with shallow water table) had 18% less above-ground woody productivity and 23% less biomass stock than plateau forests (with a deeper water table) (Sousa et al., 2022). (Soong et al., 2020) in Guiana Shield revealed that tree growth rates in clayey soils were higher than in sandy soils due to greater prevalence of arbuscular mycorrhizal fungi (AMF). Another possible explanation for this contrasting productivity between plateau and valley habitats in the Amazon is the presence of shallow root systems due to the excess of water availability in valleys, which can affect the mechanical stability of trees and, consequently, tree height and growth rates (Ribeiro et al., 2016). The presence of shallow root systems in valleys can limit the nutrient access to deep layers of the soil, and may affect ecosystem productivity. Besides, valley species tend to invest in more efficient hydraulic systems compared to species from plateaus. Trees in plateaus have lower vessel area and vessel diameters compared to valleys, and could be another possible explanation for the differences in productivity between these two habitats due to trade-off differences (investment in hydraulic safety or efficiency for example)(Barros et al., 2019; Cosme et al., 2017). Another possible mechanism is that species growing on nutrient-poor plateau soils can present different nutrient acquisition strategies (Reichert et al., 2022). Based on the forest inventory dataset of the North-South transect, plateau specialists presented, on average, higher periodic annual increment (mean at 0.43 cm year<sup>-1</sup>, minimum *Eschweilera tessmannii* at 0.3 cm year<sup>-1</sup>; maximum *Croton Lanjouwensis* at 0.8 cm year<sup>-1</sup>) and the valley specialists





the lower periodic annual increment (mean at  $0.14 \text{ cm year}^{-1}$ , minimum *Tapura lanceolata* at  $0.08 \text{ cm year}^{-1}$ ; and maximum *Micrandra siphonioides* at  $0.2 \text{ cm year}^{-1}$ ) (Table 1). This lower periodic annual increment of the valley specialists corroborates  
355 with the assumption that sandy valley habitats are less productive than plateau habitats.

Similarly to differences in productivity between plateau and valley habitats, we observed that valley specialist species exhibited higher average concentrations of most analyzed leaf and trunk nutrients when compared to plateau specialist and generalist species. It is important to highlight that the predominant vegetation found in the valleys at the North-South transect plot have similarities with white-sand vegetation also known as campinarana, characterized by a dominance of few species,  
360 high endemism, and high presence of palm species (Demarchi et al., 2018). The observed pattern of higher trunk nutrients in the valley specialists aligns with (Heineman et al., 2016) findings, who noted that allocation of nutrients to wood, especially P, influences species distributions and nutrient dynamics in tropical forests.

One of the factors that could account for the higher concentration of nutrients in the valley specialist functional group was the greater presence of fine roots compared to generalists and plateau specialists, as observed by (Sampaio de Souza, 2016) (*dissertation in Portuguese*). (Sampaio de Souza, 2016) identified high fine root biomass, length, surface area, and turnover in valley species in the same study site, corroborating other studies that found a higher biomass of fine roots in areas with sandy soils (Jiménez et al., 2009; Noguchi et al., 2014; Silver et al., 2000). Depending on environmental conditions, plants have the capacity to modify their root architecture, encompassing root morphology, topology, distribution patterns, and forming associations with arbuscular mycorrhizal fungi to facilitate the uptake of specific and relatively scarce nutrients, such  
370 as P (Shen et al., 2011). Although no root morphology analysis was conducted in this study, we observed no significant differences in nutrient concentrations in leaves and trunks of generalist species across both topographic positions, with the exception of N concentration in leaves and P and K concentrations in trunks between valleys and plateaus (Fig. S7 and S8). This suggests that generalist species can maintain similar nutrient concentrations in their organs regardless of topographic position, implying that other adaptations may be at play. The limiting nutrient availability in the first 50 cm of soil on plateaus  
375 compared to valleys (Fig. 3) suggests that generalist species exhibit high nutrient use efficiency (Cuevas and Medina, 1986). This functional group, with tree species occurring in both plateau and valley habitats, is able to utilize nutrients more efficiently than valley specialists, in spite of relatively higher fertility in valley soils. The mechanisms underlying this efficiency should be further investigated.

#### 380 **4.2 Linking plant to soil nutrient concentrations along topographic positions**

At a local scale, topographic variation is a pivotal factor that significantly influences biogeochemical and ecological processes within a forest, given that climatic variables remain consistent (Cuevas and Medina, 1986; Davies et al., 2005).



Consequently, variations in topography, coupled with shifts in soil physicochemical factors in the Central Amazon, can modulate nutrient availability to plants, thereby affecting nutrient concentrations within plant organs tissues (Luizão et al., 2004). However, in this study, we observed weak correlations between soil nutrient stocks and nutrient amounts in leaves and trunks (Fig. 7 and Fig. 8). This weak correlation indicates that plant nutrient acquisition is dynamic and complex over time and space, making it difficult to establish direct correspondences of nutrient concentrations between soils and plant organs. One potential explanation for this weak correlation between the soil and plant organs is the influence of seasonality on nutrient fluxes through soil water percolation along topographic positions (Rodrigues et al., 2024) in addition to species-specific nutrient acquisition strategies (Bustamante et al., 2006). It is also important to consider whether the sampled soil adequately reflects the nutrient availability to the tree, either in terms of the spatial distribution of these nutrients or the ability of the extraction method used to capture the truly available nutrient pool.

At the community level, for example, species can present different nutrient acquisition strategies and symbioses such as with AMF, or using mining strategies like exudation of phosphomonoesterase enzymes (PMEs) and low-molecular weight organic acids (LMWOAs), and leaf P resorption, along different P gradients in the soil (Reichert et al., 2022). In addition to this active investment in nutrient acquisition, plants can also indirectly influence soil nutrients through litterfall deposition (Ye et al., 2022). This process is generally associated with leaf age and phenological stages of species which are complex over time, especially in tropical regions (Lopes et al., 2016; Nardoto et al., 2008). Consequently, the interplay of direct and indirect soil nutrient interactions makes it challenging to establish a simple, one-way cause-and-effect relationship between soil nutrients and nutrient levels in plants. This difficulty is maximized in hyperdiverse systems like the Amazon, which has an estimated 6,500 tree species (Cardoso et al., 2017), hundreds of species per hectare and approximately 600 individuals with  $DBH \geq 10$  cm at the ZF-2 site (based on the forest inventory of NS transect). Despite our method of having three soils cores of 60 cm depth around each sampled tree species (Fig. 2), these spots could have been influenced by other factors like the litterfall deposition of other species, such as N-fixing individuals, as well as different rates of microbiological activity due, for example, fallen branches and trunks with different decomposition rates. Future studies focusing on the coordination between nutrients in plants, litterfall, and soils could potentially address this complexity. This type of approach will help elucidate, for example, that foliar P allocation is species-specific and does not converge with habitat (Liu et al., 2023). Additionally, on a local scale, the possibility of different nutrient acquisition strategies between species inhabiting valleys and plateaus could be deeper investigated since on a larger scale, recent findings indicate that tropical tree ectomycorrhiza are distributed independently of soil nutrients (Medina-Vega et al., 2024).

In sandy valley soils, we found the highest concentrations of P, which was also highest in the leaf and trunks of valley specialists. These findings of elevated P concentrations in both wood and leaves, along with higher concentrations of other



nutrients in valley specialists, align with observations of (Bauters et al., 2022), who found that wood P, Ca, Mg, and K concentrations are often inter-correlated. This suggests that species with high wood P amount are also likely to store more Ca, Mg, and K in their wood. In our study, valley soils had higher concentrations of P, K, and Mg compared to plateau soils, which had significantly higher concentrations of N. It is important to note that our data were collected in October, typically coinciding with the peak of the dry season. Since nutrient dynamics in tropical forests are complex and intricate, water availability can potentially interfere in microbiological and decomposition rates. During the collection of soils, we observed higher humidity levels in the sandy soils from valleys, as well as an apparently higher organic matter amount. In coordination with the observed higher nutrient levels on the sandy valleys, the valley specialist species presented the higher concentrations of C, N, P, K, Ca, and Mg in tree trunks, as well as higher concentrations of P, K, Ca and Mg in the leaves. (Monteiro, 2005) (*thesis in Portuguese*) suggested that valleys have the highest nutrient input due to the higher decomposition of litterfall, which is influenced by seasonality. When comparing the results from (Monteiro, 2005) litter study with our findings, which analyzed nutrient concentrations in the living tissues of standing trees, it became apparent that the nutrient concentrations in the litterfall found by (Monteiro, 2005) mirror the nutrient concentrations in plant organs of valley specialists.

Opposite to the valleys, we found that clayey plateau soils had lower concentrations of P, as did the organs of plateau specialists (leaf and trunk). This mean that plateau specialists occurring in high-clay soils, which are relatively P-scarcer compared to valleys, can potentially present distinct cycling strategies such as AMF symbiosis and the exudation of PMEs and LMWOAs, to avoid P losses from the ecosystem (Reichert et al., 2022; Soong et al., 2020). Plateau specialists presented lower concentrations of almost all the nutrients in the trunks and leaves compared to the other functional groups, except for leaf N and C. This finding corroborates (Luizão et al., 2004) and (Nardoto et al., 2008), who also reported elevated leaf N concentrations in species occurring on plateau habitats, encompassing both legume and non-legume species. (Luizão et al., 2004) demonstrated that clayey soils, such as the yellow latosols in plateaus, exhibit higher N concentrations than sandy soils in valley habitats of the Central Amazon with limited net nitrate production capacity, which is a plant-available form of N (Vitousek and Matson, 1988). We found that the average trunk N concentration did not differ between plateau specialist and valley specialist species. However, average trunk N concentrations differed between generalist species and both specialist functional groups.

No significant differences were found in C concentrations between plateau and valley soils nor in the trunks among functional groups. However, we found a significant difference in leaf C concentration among functional groups. Leaf C concentration in plateau specialist species was statistically different from the other functional groups. This finding contrasted (Luizão et al., 2004), who found no significant differences in C concentrations in mature leaves of trees across the three topographic positions. One possible explanation could be that the authors worked with random species across a topographic



gradient without differentiating between the functional groups. In the context of our study, which analyzed distinct functional groups, it is evident that the generalist functional group displayed more consistent results, implying that species in this group are adaptable to both environments. This reinforces the need to understand the mechanisms inherent to these species, which likely possess more advanced adaptive strategies and may exhibit greater adaptability as they thrive in various environments. Our findings also underscore the intricate nature of nutrient cycling processes in tropical forest ecosystems and emphasize that litter production (an important exchange network between vegetation and soil) does not necessarily serve as a direct indicator of nutrient availability. Nutrient cycling in tropical forests predominantly occurs in the first soil layers where fine roots increase the degradation of structural compounds and nutrient release of the litter layer, facilitating nutrient reabsorption by plant roots (Martins et al., 2021). The decomposition of litter and other organic materials in conjunction with the internal reabsorption of nutrients by plants are an important process in tropical environments (Reed et al., 2012; Schreeg et al., 2013). In a coordination of different processes and species strategies, nutrients are reincorporated into vegetation, establishing a dynamic exchange between the soil and plant organs and tissues (Vitousek and Sanford, 1986). All these processes sustain forest productivity and health (Trumbore et al., 2015).

In Amazon forest topographic positions are a key component of hydraulic trait distribution and vulnerability to drought (Cosme et al., 2017; Zuleta et al., 2017). However, linking species distribution to soil nutrient concentrations along topographic positions is challenging due to the complexity of nutrient cycling and dynamics. Soil texture and nutrient availability appear to be crucial components of species distribution, although other local factors, such as water table depth, also play significant roles (Checa-Cordoba et al., 2024; Sousa et al., 2022). Recent findings indicate that soil nutrient availability is a critical variable in the distribution of plant traits (Guilbeault-Mayers et al., 2024). Nutrient acquisition requires resources, and the construction of plant biomass is limited by nutrient acquisition. In this context, maintenance respiration, construction, and turnover replacement costs of fine roots are significant factors that should be investigated (Knox et al., 2024). Future studies focusing on these aspects could help address gaps in our understanding of nutrient acquisition and cycling in tropical ecosystems like the Amazon forest.

### 4.3 Nutrient concentration and wood density

We also investigated the relationship between wood density and carbon and nutrient concentrations in the trunk. The woody tissues of trees have important functions, such as providing biomechanical support for the stems, conducting water and nutrients along the soil-plant-atmosphere continuum, and storing nutrients, carbohydrates, defensive secondary chemical compounds, lipids, and water (Chave et al., 2009). However, we observed weak correlations between the wood density spectrum and nutrient concentrations (Fig. 6). One possible explanation for this weak correlation is that other functional traits,



such as those linked to the leaf economics spectrum-which balances leaf construction costs against growth potential (Díaz et al., 2016)-could play major roles in nutrient concentrations. (Heineman et al., 2016), for example, hypothesized that wood  
475 nutrient concentrations were directly related to the investment of nutrients in storage reserves, positing that trunk nutrient concentrations would positively correlate with basic density. However, they found no support for this hypothesis, as the trunk nutrient concentrations did not increase with wood density. These authors noted a significant decrease in the average wood density of the species as phosphorus concentration increased. (Martin et al., 2014), in their study of N concentration in the trunk of tropical trees, identified a significant correlation between trunk N concentration and wood density.

480 Our results contrast those of (Martin et al., 2014), but corroborate (Heineman et al., 2016), as no nutrients were found to be positively correlated with wood density. Only C exhibited a significant negative correlation with wood density. Consequently, wood density was not directly linked to the trunk nutrient concentration. C concentration in trees, especially in the trunk, is linked to plant allocation of C to specific functions and life strategies. The initial hypothesis was that trees with high basic wood density would have increased trunk C concentrations as these trees typically exhibit slower growth rates,  
485 lower mortality rates, and greater resistance to xylophage attacks, among other traits associated with conservative species (Chave et al., 2009). However, these results did not confirm this initial hypothesis. One potential explanation is that the anatomical and chemical structures of wood regulate the trunk C concentration. Trees with high basic density may have low C amount, given that wood density is mainly associated with wood fiber traits (Ziemińska et al., 2013), as well as the density of vessels and vessel diameter. As a result, C may be allocated to structures other than lignin such as wood extractives, and in  
490 the conductive system (Venturas et al., 2017). The allocation of C to various wood structures reflects the life strategies of individuals in each environment. In the Amazon, environmental factors such as wind and light availability drive giant tree distribution and forest structure (Gorgens et al., 2021). For instance, higher C concentrations in extractives in the form of starches are linked to energy reserves, phenolic extractives may be related to the individual's defense mechanisms, and C allocated to cell walls is associated with mechanical structure and support. Consequently, further studies focusing on C  
495 allocation within wood structures and ultrastructures are essential to understand the functional ecology of specialist and generalist plants in varying environments.

## 5 Conclusions

500 Taken together, our findings provide robust evidence of consistent variations in C and nutrient concentrations among generalist and specialist species inhabiting the plateau and valley areas in the Central Amazon. Valley specialists exhibited the highest concentrations of C, and nutrients such as P, Ca, Mg, and K in both leaves and trunks. These results align with the



505 observations of (Bauters et al., 2022), which found that the concentrations of these nutrients are often inter-correlated, meaning that species with high wood P amount are also likely to store more Ca, Mg, and K in their wood. In contrast, the nutrient concentrations within the generalist group remained consistent across topographic classes (plateaus and valleys), underscoring their adaptive strategy to sustain productivity in both environments. The weak correlation observed between soil nutrient stocks and nutrient amount in leaves and trunks suggests that other factors, such as water table depth, in addition to soil nutrient availability, play a more significant role in shaping species distributions along Amazonian topographic gradients. Similar to the weak correlations of nutrient concentrations between soils and plant organs, no evidence was found between wood density and tree nutrient amount by this study. Despite, the woody tissues of trees perform important functions like biomechanical support and acting as a store for nutrients, carbohydrates, lipids and water, species specific nutrient acquisition strategies seem to play a major role than wood density. The observed disparities in species behavior in response to varying soil characteristics underscore the importance of distinguishing between functional plant types related to nutrients (generalists versus specialists). This distinction is vital for the accurate simulation of the carbon cycle in tropical forests throughout the 21st century using ecological models.

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### Authors Contributions

530 SC, BB and BOG led the conceptualization, collected the data and wrote the first draft. SC, BOG and MNVB led the data analysis. SC and BOG revised the first draft, led the writing on subsequent revisions, with significant input from B. Data from the field study was also collected by RCO. All authors had read and approved the final version of manuscript.





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### **Conflicts of Interest**

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

### 545 **Data Availability**

The data that support the findings of this study are openly available in the NGEE Tropics Data Collection at <https://doi.org/10.15486/ngt/2377278>, reference number NGT0213 (Gimenez et al., 2024).

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