Handwritten annotations:

General: - trunk → wood
- Conc. → contents
- Add soil description table to study area

- "trunk woody material" = wood
- stats? ANOVA ≠ post-hoc + just make lm in effect sizes

if not, correct using williamson a wiemann (2010)

- color in Fig 3, 4, 5 not necessary/meaningful

- pith to bark? ⇒ 2 reps per tree is better?

- basic WD: 20 days in water probably over-estimates fresh volume, so mention that usually conversion factors are applied sensu Vieilledent et al (2018)

- formatting in-text refs.

- why soil relations up to 50cm?

- acknowledge that you didn't look into nutrient avail. + pH!

- link between your functional groups and pioneer/sT/... ? ⇒ Env. context: land-use?

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.

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 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 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

(handwritten: soil Carbon → nutrient cycling)

1 Introduction

(handwritten: is it?)

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;
35   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
40   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
45   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
50   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)
55   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. —→ *local driven ~ species? unclear 60-62*

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

rephrase

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).

90   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

95   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

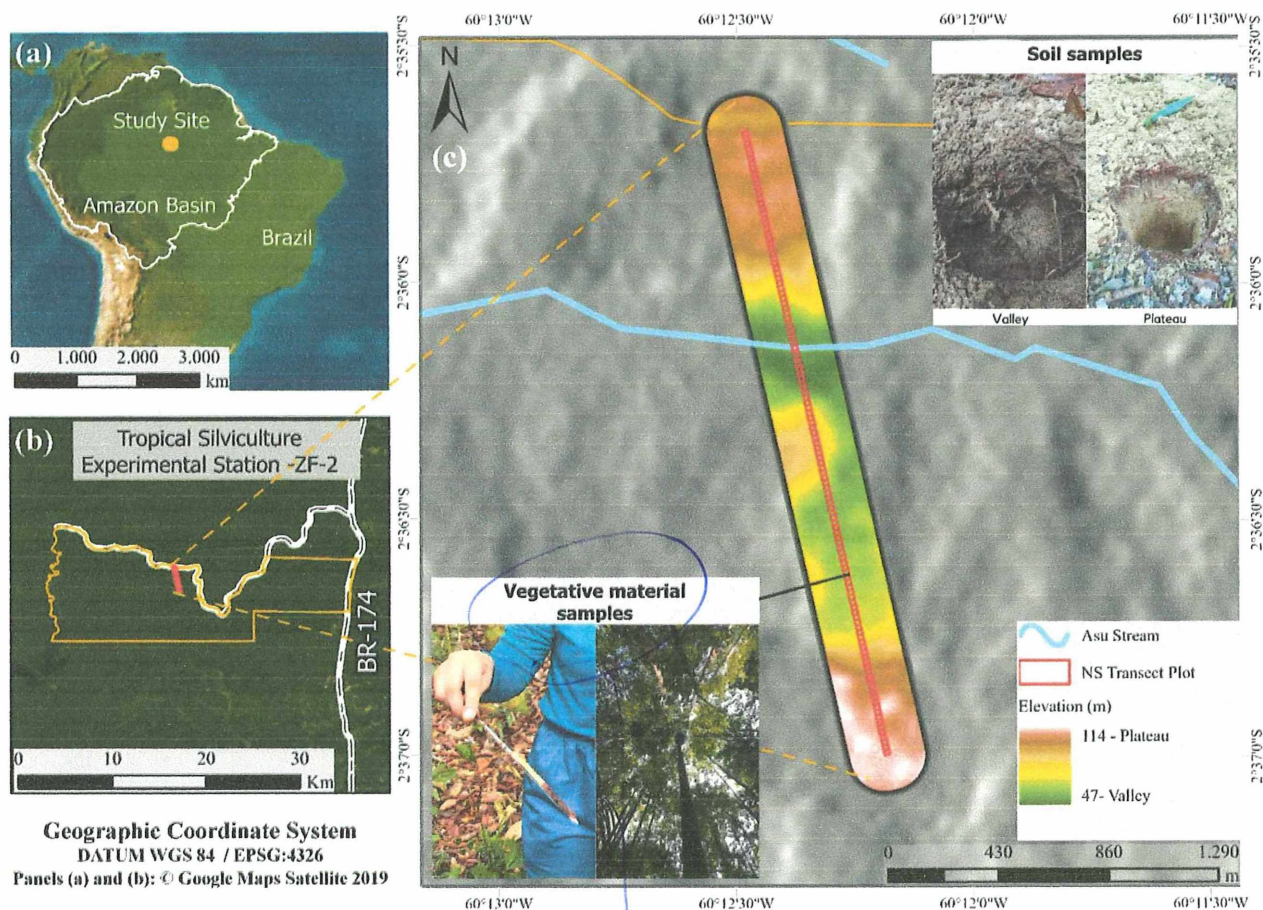
100   The study was conducted along the North-South transect with 125 individual 20 × 20 m permanent plots, which collectively span a 20-meter by 2,500-meter area, covering 5 hectares (Araujo et al., 2020). The North-South transect was installed in 1996 by the Jacaranda Project (a collaboration between 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°35'55" S, 60°02'14" W), operated by the National Institute for Amazonian Research

105   (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) ≥ 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
110   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

115   *Amw* according to the Köppen classification. The average relative humidity at the study site is 72.8% on average, with a ranging

daily range?
annual?

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/).

(a) =?(b) =?(c) = ?

2.2 Species selection and categorization

only in 1 spot it seems

[handwritten: → classification valid across Am. basin ?]

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,

[handwritten: formatting]

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

[handwritten: → how well distributed? Did they have a preference?]

"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"

(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

[handwritten: Add for all]

Eschweilera tessmanii (Lecythidaceae), *Ocotea percurrens* (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*

[handwritten: what is described?]

140 *lanceolata* (Dichapetalaceae), and *Brosimum utile* subsp. *ovatifolium* Ducke (Moraceae), as described by (Carneiro, 2004) and

[handwritten: formatting]

(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).

[handwritten: ok, but why? → feels a bit random]

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

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 (g.cm⁻³), and periodic annual increment (PAI).

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

[a]*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.

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).

180

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

three cores around each tree, one single sample was taken at each depth and combined with the others from each core to obtain

185   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

$$NCS = \frac{C \times Ds \times E}{10}$$ (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).

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

195   wet weight, dried in an oven at 105 ± 2°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:

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

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

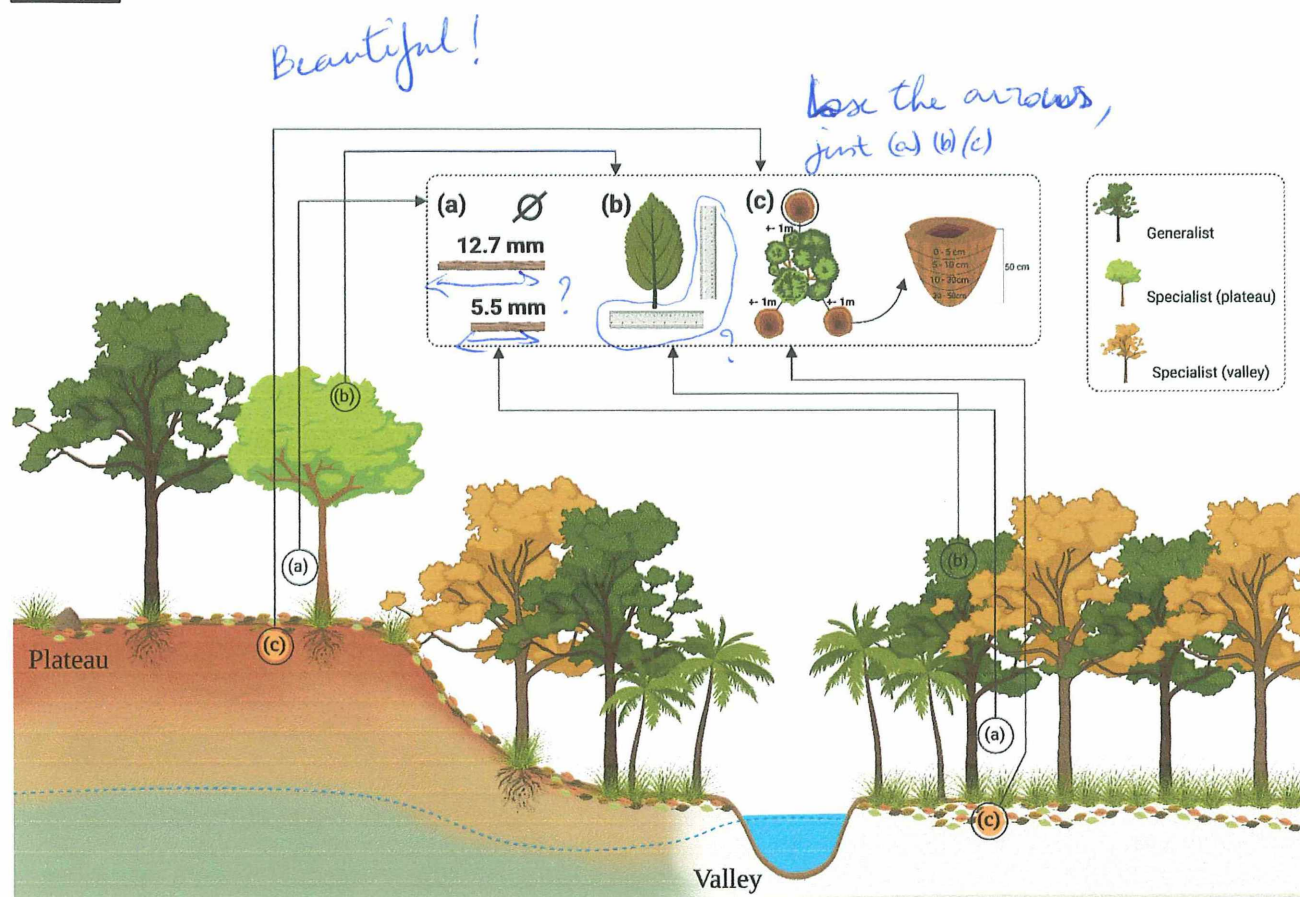



Figure 2 Field sampling scheme showing the (a) collection of trunk samples, (b) leaf samples and (c) the three soil collection points near each sample tree. The valley specialist species, plateau specialist's species, and generalist species are highlighted in the figure

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).

[handwritten: also roots ?]

$$FW = a \times DBH^b \tag{4}$$

where FW = Tree biomass (total fresh weight in kg), DBH = Diameter at breast height (in cm), a = 2.7179, b = 1.8774 *[handwritten: (Silva, 2007)?]*

According to Silva (2007), in a mature forest of Manaus region leaf biomass represents approximately 3% of the total

215 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: *[handwritten: → 100% - 3% - 69% = roots ?]*

$$LFW = FW \times 0.03 \tag{5}$$ *[handwritten: trivial]*

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

Similarly, the o trunk fresh weight was calculated as:

$$TFW = FW \times 0.69 \tag{6}$$ *[handwritten: trivial]*

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:

$$LDW = LFW \times 0.597 \tag{7}$$

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

And the dry weight of the trunk (kg)

$$DWT = TFW \times 0.388 \tag{8}$$

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

[handwritten right margin: For how many species was this evaluated]

Therefore, the amounts of leaf C, N, P, K, Ca and Mg were calculated as follows: amount of leaf C and nutrients =

230 LDW × 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 × 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 (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 ±

2°C until reaching a constant weight to determine the dry mass (~0% moisture). *[handwritten: ? Measured how? + 20 days ?]*

240

$$Db = \frac{m}{v} \tag{9}$$

[handwritten: water-]

where Db = basic wood density (g cm⁻³), m = dry mass of wood at 105°C (g), v = saturated volume of the sample (cm³).

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

245 normality of each variable, (leaf, wood and soil.) In cases where the data did not follow a normal distribution, non-parametric statistics were used. *being ?* *How did you compare ~~using~~ groups? between*

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).~~ *α = ?* *So what about t-test in Fig 3 ?*

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. *So you did a correlation test ?*

3 Results

255 ## 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).

[handwritten annotations: plot means as diamonds; y-axes labels bigger, to simpler; g C kg⁻¹, g Ca kg⁻¹; Why "average conc"?]

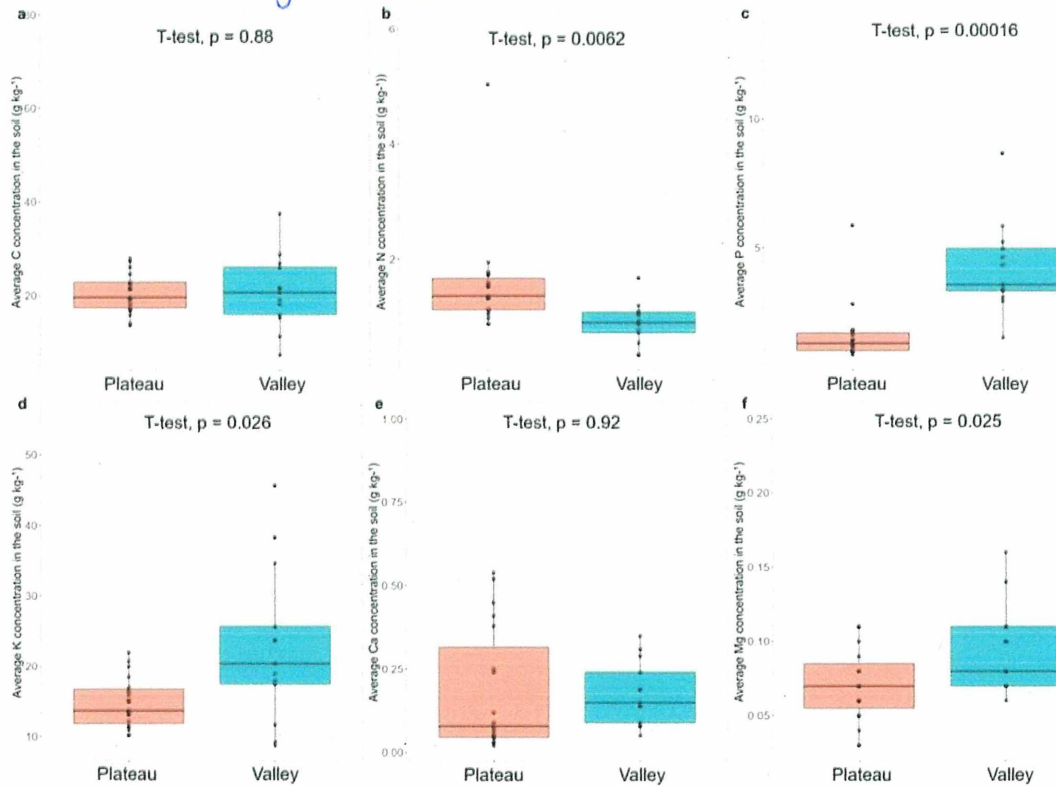



Figure 3 Concentration of carbon and nutrients in the soils of plateaus and valleys

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 ± 0.12 g kg⁻¹ and K at 9.56 ± 2.08 g kg⁻¹ in their leaves when compared to the other functional groups. Conversely, the plateau specialist species boasted the highest concentrations of C at 613.09 ± 10.99 g kg⁻¹ and N at 19.63 ± 1.80 g kg⁻¹. The plateau specialist species also displayed the lowest concentrations of Ca at 0.89 ± 0.37 g kg⁻¹ and Mg at 0.70 ± 0.12 g kg⁻¹ (Table S3, Fig. S4).

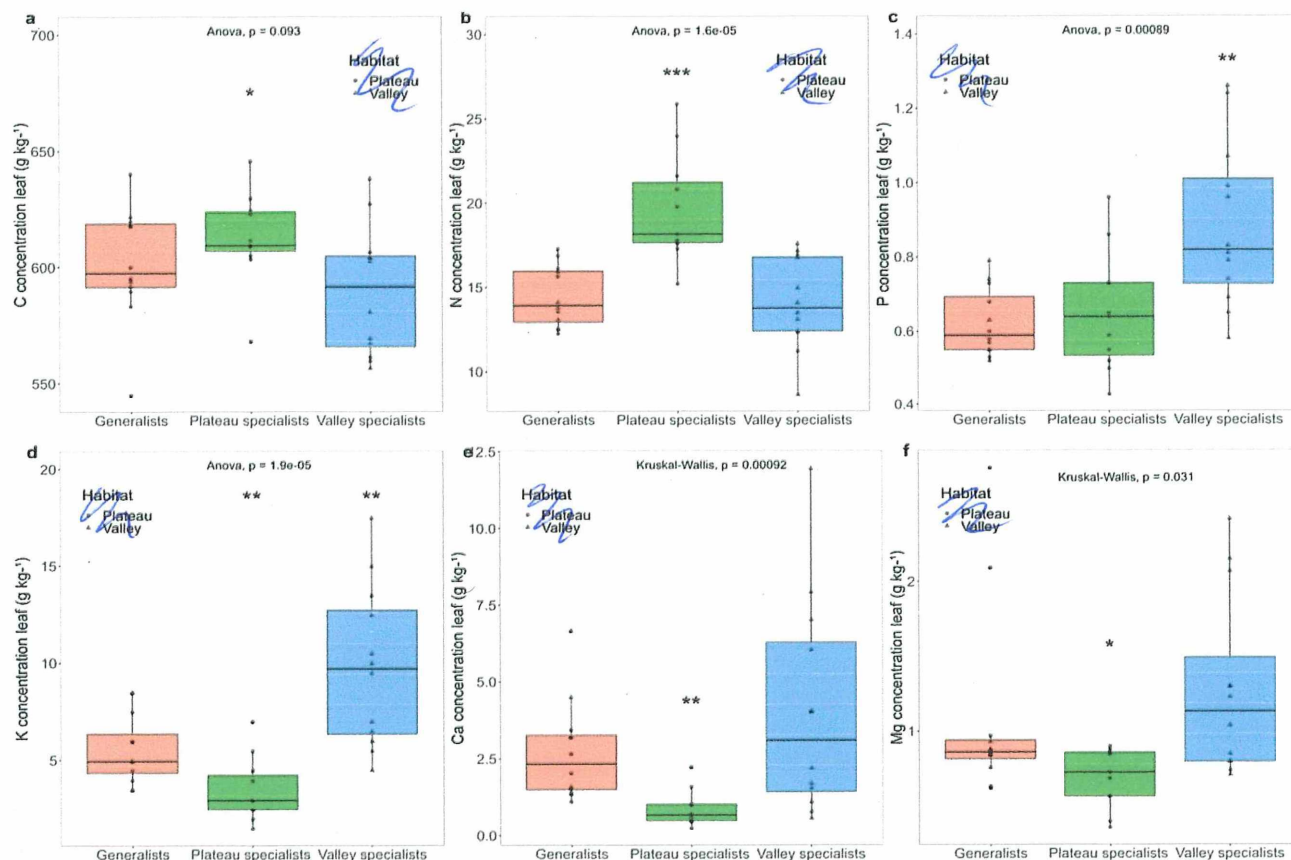



Figure 4 Boxplots showing the concentrations of leaf C and nutrients across the functional groups: valley specialists, plateau specialists and generalist species

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 ± 0.01 g kg⁻¹) in the trunk. In contrast, the plateau specialists displayed the lowest concentrations of K at 0.44 ± 0.04 g kg⁻¹, Ca at 0.81 ± 0.16 g kg⁻¹, and Mg at 0.22 ± 0.08 g kg⁻¹. Notably, generalist species had the lowest N concentration at 2.42 ± 0.35 g kg⁻¹. Regarding C concentration, it is probable that differences exist between the groups, with the highest and lowest concentrations observed

285   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.

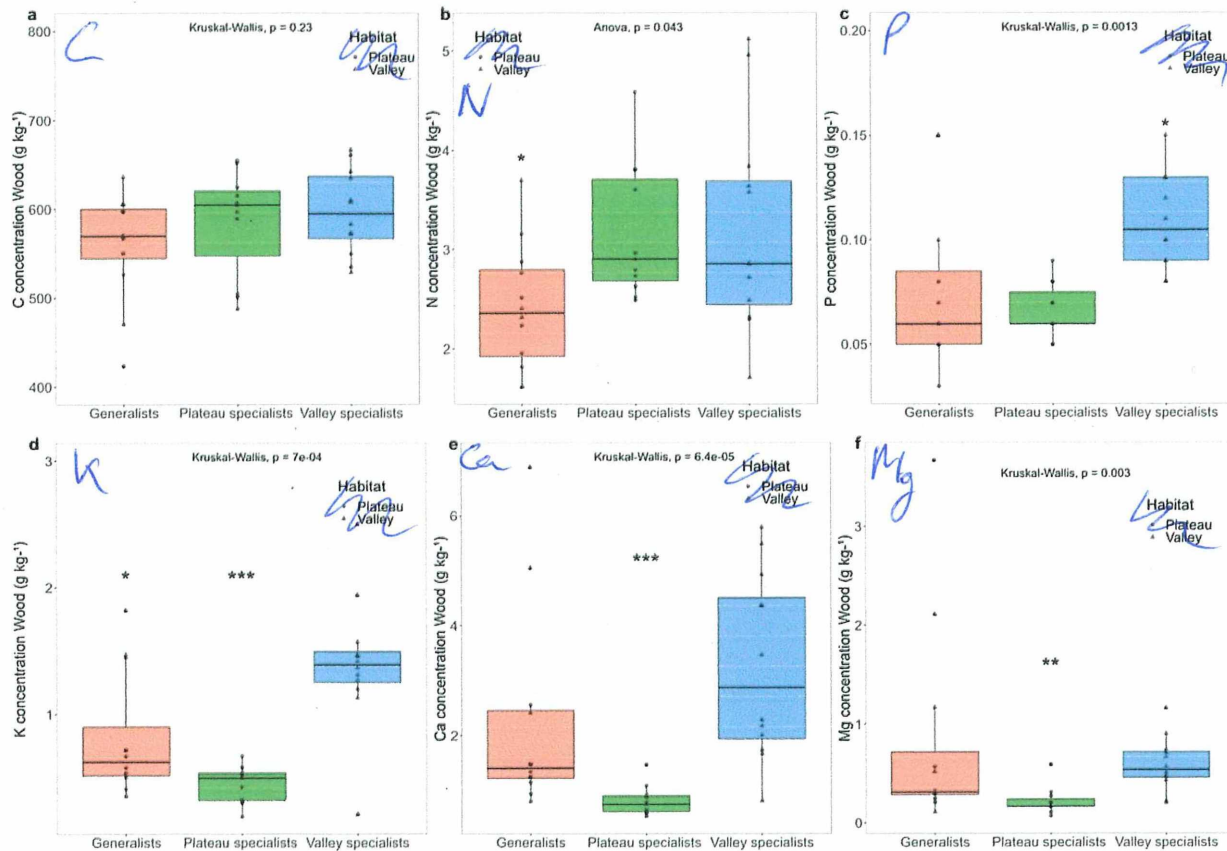



Figure 5 Trunk carbon and nutrient concentrations of valley specialist, plateau specialist and generalist functional groups *across species*

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

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.

what if you run the analyses per functional group?

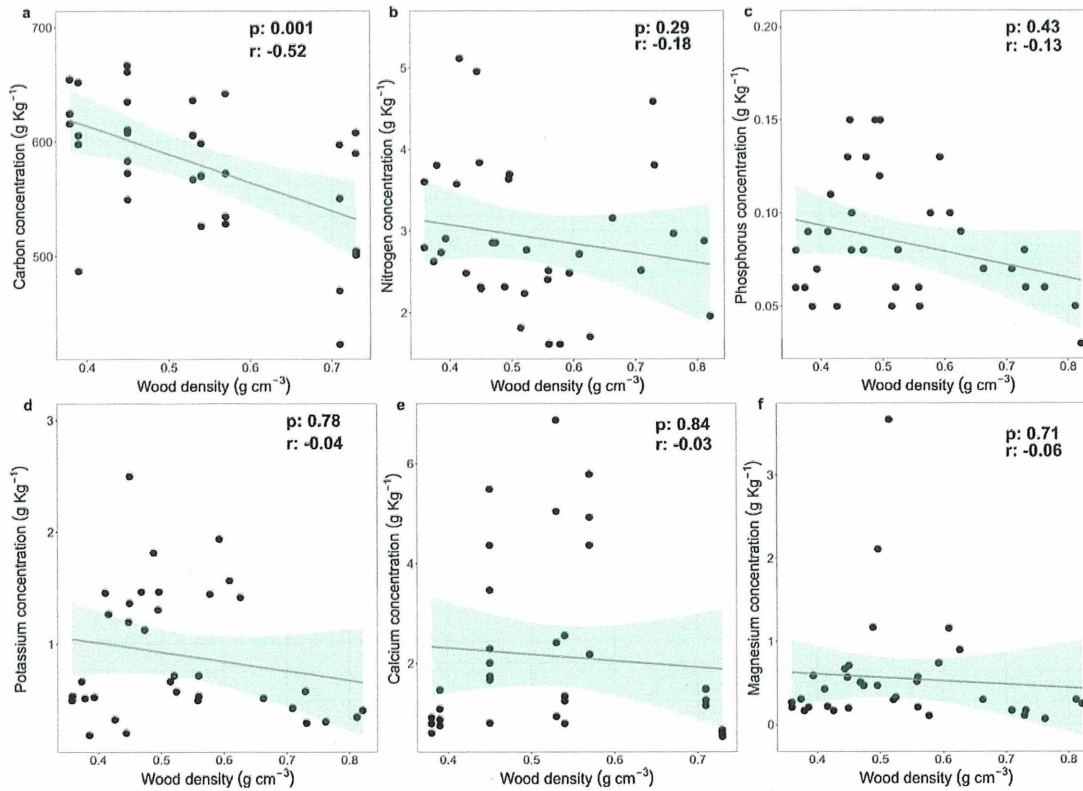



Figure 6 Correlation between wood density (in g cm^{-3}) and trunk carbon and nutrient concentrations (in g kg^{-1}).

what is shaded area?

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

> Make more clear that plateau vs valley 2 figures! phrasing

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.~~

Very limited

(fig. 7)

= discussion

300

305

[handwritten margin note: significance ↗ ≠ strong corr.!]

We found a strong positive correlation ~~was observed~~ between soil C and N stocks, indicating a significant relationship

310   between the presence of C in the soil and N availability. Moreover, soil K stocks correlated positively with soil C and N stocks

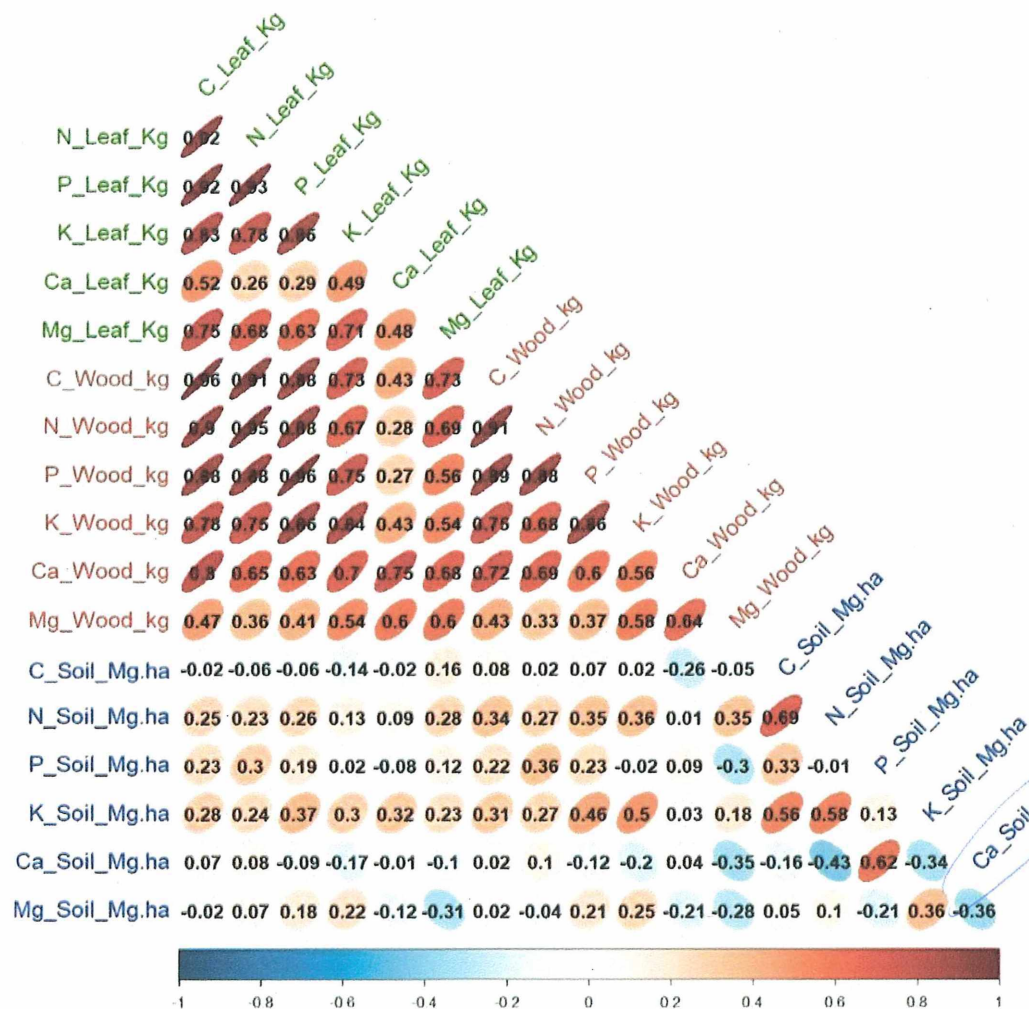
(Fig. 7).

[handwritten margin notes: improve names e.g. Ca_Soil_Mg.ha → Soil-Ca → units in caption]

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

[handwritten: all of them? + how was this tested?]

315

[handwritten: Color = ? better/red for ⊖ /green/blue for ⊕]

very limited

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.~~ *This is discussion* Soil P stock also correlated with N, C, and K stocks, with a strong correlation observed with N (r = 0.82).

Quite random which results are discussed

320

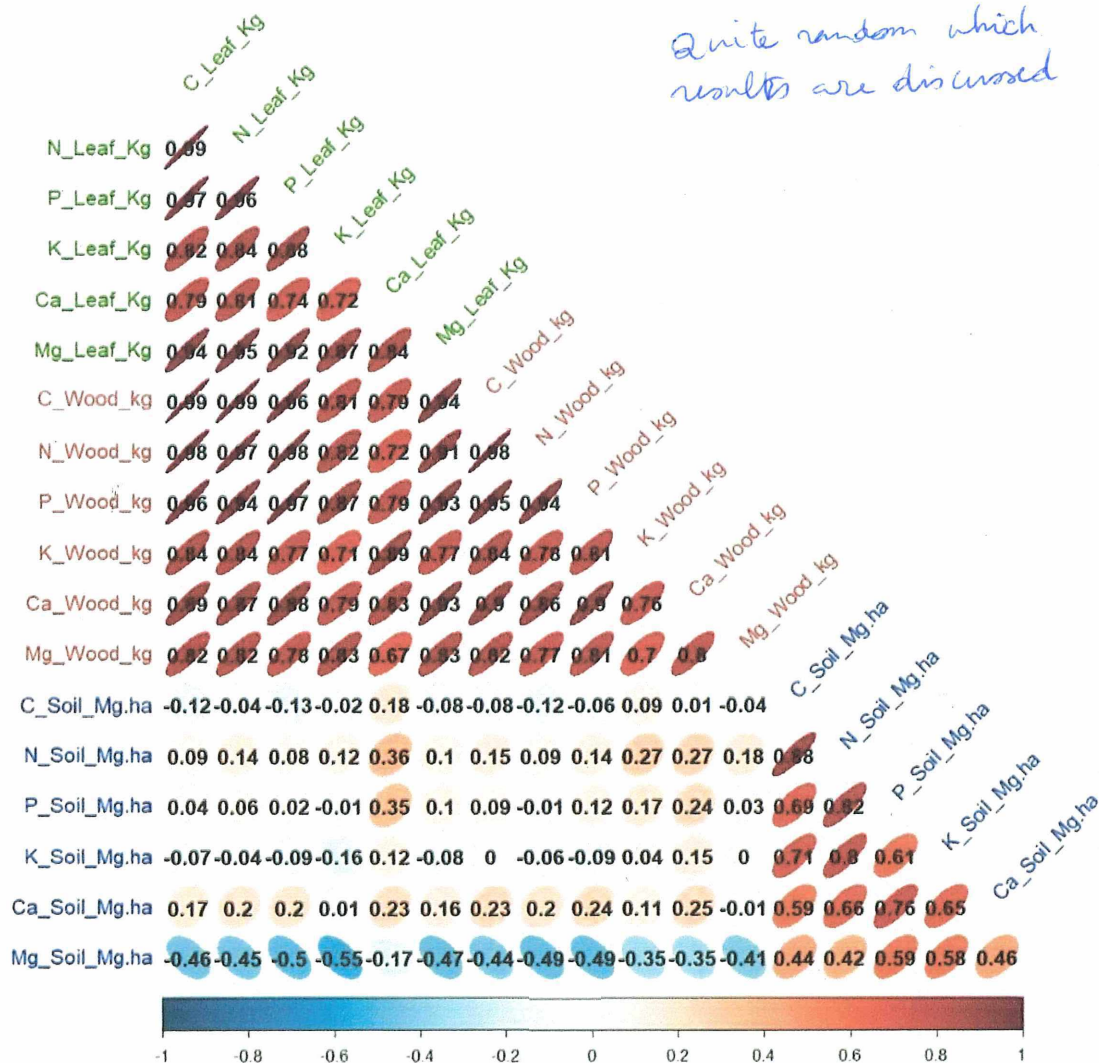



Figure 8 Correlations between the amount of carbon and nutrients in the leaf and trunk and the stock of carbon and nutrients in the valley's soil up to a depth of 50 cm. The correlations shown were significant at the 95% probability level.

= ?
+ all of them?
+ tested how?

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4 Discussion

[handwritten: Start with results and then move on to state-of-the-art?]

325 **4.1 Vegetation type, forest productivity, and topographic gradient** *[handwritten: → but "empty" subtitle]*

Nutrient dynamics in intact tropical ecosystems are highly intricate and influenced by various factors, including parent *[handwritten: soil]*
material, species composition, spatial context *[handwritten: vague]*, canopy structure and topography. In ecosystems like the *terra-firme* forests of
the Central Amazon it is well known the influence of topography *[handwritten: phrasing]* (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 *[handwritten: = ?]*

330 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 *[handwritten: = ? defined as?]* in comparison to the upland plateaus due to the higher leaching rates *[handwritten: why?]*, 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

335 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). *[handwritten: but C ≈, N ↓, Ca ≈ ...?]*

[handwritten left margin: Why? So is P not limiting here but N in?]

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): *[handwritten: why? refs?]* forests on valleys (with shallow water table) had 18% less above-ground woody

340 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

345 of shallow root systems in valleys can limit the nutrient access to deep layers of the soil, and may affect ecosystem productivity. *[handwritten: ** + ref?]*
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 *[handwritten: trivial]*

350 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^{-1},
minimum *Eschweilera tessmannii* at 0.3 cm year^{-1}; maximum *Croton Lanjouwensis* at 0.8 cm year^{-1}) and the valley specialists

[handwritten notes at bottom:]
✱ Not due to hydraulic / nutritional properties?
✱✱ But I can imagine valleys are a place where all erosion products from plateaus / hillsides accumulate? So also nutrients?
✱✱✱ But ~~...~~ valley species have "excess water" (line 343)?

[handwritten: ok but how does this relate to your results?]

the lower periodic annual increment (mean at 0.14 cm year⁻¹, minimum *Tapura lanceolata* at 0.08 cm year⁻¹; and maximum *Micrandra siphonioides* at 0.2 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 *[handwritten: why?]* 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. *[handwritten: Not very informative]* *[handwritten: specific root length or?]*

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,

365 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

5 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 *[handwritten: use]* nutrients more efficiently than valley specialists, in spite of relatively higher fertility in valley soils. The mechanisms underlying this efficiency should be further investigated. *[handwritten: So is it an issue of nutrient acquisition and availability or efficient cycling?]*

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).

[handwritten: What about soil Mg ?]

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.,

385   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. *[handwritten: ✷]* 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

390   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. *[handwritten margin: What's the message?]*

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

395   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

400   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 ≥ 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

405   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

[handwritten margin: ok, but you sampled until 50 cm → how did this relate?]

410   independently of soil nutrients (Medina-Vega et al., 2024). *[handwritten: You've only discussed arbuscular]*

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

[handwritten: ✷ Don't understand + why doesn't this simply mean that soil nutrient supply is simply sufficient? I.e. that nutrients are maybe not limiting]

being?

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,

415   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. *rephrase* In coordination with the observed

420   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*) *rates?*

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 *phrasing*

concentrations in the living tissues of standing trees, it became apparent that the nutrient concentrations in the litterfall found

425   by (Monteiro, 2005) mirror the nutrient concentrations in plant organs of valley specialists.

tissues
     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

430   concentrations of almost all the nutrients in the trunks and leaves compared to the other functional groups, except for leaf N *with*

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 *→ sandy or clayey?*

435   (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. (Fig. ...).   → generalist vs other OK all 3 different?

     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 *in wood C*

440   concentration in plateau specialist species was ~~statistically~~ different from the other functional groups. This finding contrasted *significantly higher/lower?*

(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

✳ So if you would combine the data in Fig. 7 & 8, you would see correlations w soil nutrient contents?

  ⇒ it would be more informative to make linear models of e.g. Foliar P ~ (functional type or position) ✳ soil P

    ⇒ This gives the interactive effects of the groups & soil.

✳✳ See general remarks; you haven't looked into availability

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

445 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

450 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~~

455 ~~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,

460 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

465 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~~

470 ~~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 *wood* 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. *REF.* 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~~ *our* 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

among or between?

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~~

- wood C ≈
- foliar C ↓ for valley!

+ N clearly lower for valley vs. plateau,
but ≈ valley & generalist

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

505 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

510 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

515 ecological models.

Acknowledgments

This research was supported as part of the Next Generation Ecosystem Experiments-Tropics (NGEE), funded by the U.S. Department of Energy, Office of Science, Office of Biological and Environmental Research under contract number DE-AC02-

520 05CH11231. Additional funding for this research was provided for the first author Sarah Camelo by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). Additional funding for this research was provided by INCT – Madeiras da Amazônia, Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) – Processo: 403839/2021-1 Chamada CNPq/MCTI/FNDCT Nº 18/2021 - Faixa A - Grupos Emergentes Universal 2021, and Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM). We are also thankful for the logistical and scientific support provided by the

525 Laboratório de Manejo Florestal (LMF) at the National Institute of Amazonian Research (INPA). We also thank Sidney "Matapi"and Manoel "Manel" for the support on the field campaigns, and Dr. Valdiek Menezes for the help on reviewing the Fig. 1 of the manuscript.

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.

535 **Funding**

This work is supported by the Next Generation Ecosystem Experiments-Tropics (NGEE-Tropics), as part of DOE's Terrestrial Ecosystem Science Program-Contract No. DE-AC02-05CH11231. The Brazil's National Council for Scientific and Technological Development (CNPq) and the Coordination for the Improvement of Higher Education Personnel (CAPES) provided additional funding for this research.

540

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).

References

550 Alvares, C. A., Stape, J. L., Sentelhas, P. C., Gonçalves, J. L. de M., and Sparovek, G.: Köppen's climate classification map for Brazil, Meteorol. zeitschrift, 22, 711–728, 2013.

Araujo, R. F., Chambers, J. Q., Celes, C. H. S., Muller-Landau, H. C., Santos, A. P. F. dos, Emmert, F., Ribeiro, G. H. P. M., Gimenez, B. O., Lima, A. J. N., Campos, M. A. A., and Higuchi, N.: Integrating high resolution drone imagery and forest inventory to distinguish canopy and understory trees and quantify their contributions to forest structure and dynamics, PLoS
555 One, 15, e0243079, 2020.

Barros, F. de V, Bittencourt, P. R. L., Brum, M., Restrepo-Coupe, N., Pereira, L., Teodoro, G. S., Saleska, S. R., Borma, L. S., Christoffersen, B. O., and Penha, D.: Hydraulic traits explain differential responses of Amazonian forests to the 2015 El Niño-induced drought, New Phytol., 223, 1253–1266, 2019.

Bauters, M., Grau, O., Doetterl, S., Heineman, K. D., Dalling, J. W., Prada, C. M., Griepentrog, M., Malhi, Y., Riutta, T., and
560 Scalon, M.: Tropical wood stores substantial amounts of nutrients, but we have limited understanding why, Biotropica, 54, 596–606, 2022.

Broedel, E., Tomasella, J., Cândido, L. A., and von Randow, C.: Deep soil water dynamics in an undisturbed primary forest in central Amazonia: Differences between normal years and the 2005 drought, Hydrol. Process., 31, 1749–1759, 2017.

565 Bustamante, M. M. C., Medina, E., Asner, G. P., Nardoto, G. B., and Garcia-Montiel, D. C.: Nitrogen cycling in tropical and temperate savannas, Biogeochemistry, 79, 209–237, 2006.

Cardoso, D., Särkinen, T., Alexander, S., Amorim, A. M., Bittrich, V., Celis, M., Daly, D. C., Fiaschi, P., Funk, V. A., and Giacomin, L. L.: Amazon plant diversity revealed by a taxonomically verified species list, Proc. Natl. Acad. Sci., 114, 10695–10700, 2017.

Carneiro, V.M.C.: Composição florística e análise estrutural da floresta primária de terra firme na bacia do rio Cuieiras
570 (master's thesis). Programa de Ciências de Florestas Tropicais. INPA, Manaus - AM. p. 77, 2004.

de Castilho, C. V, Magnusson, W. E., de Araújo, R. N. O., Luizao, R. C. C., Luizao, F. J., Lima, A. P., and Higuchi, N.: Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography, For. Ecol. Manage., 234, 85–96, 2006.

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

Chave, J., Muller-Landau, H. C., Baker, T. R., Easdale, T. A., Steege, H. ter, and Webb, C. O.: Regional and phylogenetic variation of wood density across 2456 neotropical tree species, Ecol. Appl., 16, 2356–2367, 2006.

Chave, J., Coomes, D., Jansen, S., Lewis, S. L., Swenson, N. G., and Zanne, A. E.: Towards a worldwide wood economics spectrum, Ecol. Lett., 12, 351–366, 2009.

580 Checa-Cordoba, E., Esteban, E. J. L., Emilio, T., Lira-Martins, D., Schietti, J., Pinto, J. P. V, Tomasella, J., and Costa, F. R. C.: Soil water regime and nutrient availability modulate fine root distribution and biomass allocation in amazon forests with shallow water tables, Plant Soil, 1–16, 2024.

Cordeiro, A. L., Norby, R. J., Andersen, K. M., Valverde-Barrantes, O., Fuchslueger, L., Oblitas, E., Hartley, I. P., Iversen, C. M., Gonçalves, N. B., and Takeshi, B.: Fine-root dynamics vary with soil depth and precipitation in a low-nutrient tropical
585 forest in the Central Amazonia, Plant-Environment Interact., 1, 3, 2020.

Cosme, L. H. M., Schietti, J., Costa, F. R. C., and Oliveira, R. S.: The importance of hydraulic architecture to the distribution patterns of trees in a central Amazonian forest, New Phytol., 215, 113–125, https://doi.org/10.1111/nph.14508, 2017.

Why only here?

Costa, F. R. C., Schietti, J., Stark, S. C., and Smith, M. N.: The other side of tropical forest drought: do shallow water table regions of Amazonia act as large-scale hydrological refugia from drought?, New Phytol., 237, 714–733, 2023.

590 Cuevas, E. and Medina, E.: Nutrient dynamics within Amazonian forest ecosystems: I. nutrient flux in fine litter fall and efficiency of nutrient utilization, Oecologia, 68, 466–472, 1986.

Cunha, H. F. V., Andersen, K. M., Lugli, L. F., Santana, F. D., Aleixo, I. F., Moraes, A. M., Garcia, S., Di Ponzio, R., Mendoza, E. O., and Brum, B.: Direct evidence for phosphorus limitation on Amazon forest productivity, Nature, 608, 558–562, 2022.

Davies, S. J., Tan, S., LaFrankie, J. V, and Potts, M. D.: Soil-related floristic variation in a hyperdiverse dipterocarp forest, in: Pollination ecology and the rain forest: Sarawak studies, Springer, 22–34, 2005.

Demarchi, L. O., Scudeller, V. V., Moura, L. C., Dias-Terceiro, R. G., Lopes, A., Wittmann, F. K., and Piedade, M. T. F.: Floristic composition, structure and soil-vegetation relations in three white-sand soil patches in central Amazonia, Acta Amaz., 48, 46–56, 2018.

Demarchi, L. O., Klein, V. P., Aguiar, D. P. P., Marinho, L. C., Ferreira, M. J., Lopes, A., da Cruz, J., Quaresma, A. C., 600 Schöngart, J., and Wittmann, F.: The specialized white-sand flora of the Uatumã Sustainable Development Reserve, central Amazon, Brazil, Check List, 18, 187–217, 2022.

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., and Colin Prentice, I.: The global spectrum of plant form and function, Nature, 529, 167–171, 2016.

Esquivel-Muelbert, A., Phillips, O. L., Brienen, R. J. W., Fauset, S., Sullivan, M. J. P., Baker, T. R., Chao, K.-J., Feldpausch, 605 T. R., Gloor, E., and Higuchi, N.: Tree mode of death and mortality risk factors across Amazon forests, Nat. Commun., 11, 5515, 2020.

Esteban, E. J. L., Castilho, C. V, Melgaço, K. L., and Costa, F. R. C.: The other side of droughts: wet extremes and topography as buffers of negative drought effects in an Amazonian forest, New Phytol., 229, 1995–2006, 2021.

Ferraz, J. B. S., Higuchi, N., Santos, J. dos, Biot, Y., Marques, F., Baker, K., Hunter, I., Baker, R., and Proctor, J.: Distribuição 610 de nutrientes nas árvores e exportação de nutrientes pela exploração seletiva de madeira, BIONTE-Biomassa e Nutr. Florestais, Vol. 1, pg. 134-149, 1997.

Flores, B. M., Montoya, E., Sakschewski, B., Nascimento, N., Staal, A., Betts, R. A., Levis, C., Lapola, D. M., Esquível-Muelbert, A., and Jakovac, C.: Critical transitions in the Amazon forest system, Nature, 626, 555–564, 2024.

Gimenez, B., Bomfim, B., Camelo, S., Oliveira, R., Chambers, J., Higuchi, N., Lima, A. Comparative analysis of nutrient
615 concentrations in generalist and specialist tree species and soils, Manaus, Brazil. 1.0. NGEE Tropics Data Collection. (dataset),
2024. https://doi.org/10.15486/ngt/2377278

Gonçalves, N. B., Rosa, D. M., do Valle, D. F., Smith, M. N., Dalagnol, R., de Almeida, D. R. A., Nelson, B. W., and Stark,
S. C.: Revealing forest structural" fingerprints": An integration of LiDAR and deep learning uncovers topographical influences
on Central Amazon forests, Ecol. Inform., 81, 102628, 2024.

620 Gorgens, E. B., Nunes, M. H., Jackson, T., Coomes, D., Keller, M., Reis, C. R., Valbuena, R., Rosette, J., de Almeida, D. R.
A., and Gimenez, B.: Resource availability and disturbance shape maximum tree height across the Amazon, Glob. Chang.
Biol., 27, 177–189, 2021.

Gray, E. F., Wright, I. J., Falster, D. S., Eller, A. S. D., Lehmann, C. E. R., Bradford, M. G., and Cernusak, L. A.: Leaf: wood
allometry and functional traits together explain substantial growth rate variation in rainforest trees, AoB Plants, 11, plz024,
625 2019.

Guilbeault-Mayers, X., Lambers, H., and Laliberté, E.: Coordination among leaf and fine-root traits along a strong natural soil
fertility gradient, Plant Soil, 1–17, 2024.

Guilbeault-Mayers, X. and Laliberté, E.: Root phosphatase activity is coordinated with the root conservation gradient across a
phosphorus gradient in a lowland tropical forest, New Phytol., 2024.

630 Heineman, K. D., Turner, B. L., and Dalling, J. W.: Variation in wood nutrients along a tropical soil fertility gradient, New
Phytol., 211, 440–454, 2016.

Holm, J. A., Medvigy, D. M., Smith, B., Dukes, J. S., Beier, C., Mishurov, M., Xu, X., Lichstein, J. W., Allen, C. D., and
Larsen, K. S.: Exploring the impacts of unprecedented climate extremes on forest ecosystems: hypotheses to guide modeling
and experimental studies, Biogeosciences, 20, 2117–2142, 2023.

635 Jiménez, E. M., Moreno, F. H., Peñuela, M. C., Patino, S., and Lloyd, J.: Fine root dynamics for forests on contrasting soils in
the Colombian Amazon, Biogeosciences, 6, 2809–2827, 2009.

John, R., Dalling, J. W., Harms, K. E., Yavitt, J. B., Stallard, R. F., Mirabello, M., Hubbell, S. P., Valencia, R., Navarrete, H.,
Vallejo, M., and Foster, R. B.: Soil nutrients influence spatial distributions of tropical tree species, Proc. Natl. Acad. Sci., 104,
864–869, https://doi.org/10.1073/pnas.0604666104, 2007.

640 Knox, R. G., Koven, C. D., Riley, W. J., Walker, A. P., Wright, S. J., Holm, J. A., Wei, X., Fisher, R. A., Zhu, Q., and Tang,

J.: Nutrient dynamics in a coupled terrestrial biosphere and land model (ELM-FATES-CNP), J. Adv. Model. Earth Syst., 16, e2023MS003689, 2024.

Koven, C. D., Knox, R. G., Fisher, R. A., Chambers, J. Q., Christoffersen, B. O., Davies, S. J., Detto, M., Dietze, M. C., Faybishenko, B., and Holm, J.: Benchmarking and parameter sensitivity of physiological and vegetation dynamics using the

645 Functionally Assembled Terrestrial Ecosystem Simulator (FATES) at Barro Colorado Island, Panama, Biogeosciences, 17, 3017–3044, 2020.

Larjavaara, M. and Muller-Landau, H. C.: Rethinking the value of high wood density, Funct. Ecol., 701–705, 2010.

Leff, J. W., Wieder, W. R., Taylor, P. G., Townsend, A. R., Nemergut, D. R., Grandy, A. S., and Cleveland, C. C.: Experimental litterfall manipulation drives large and rapid changes in soil carbon cycling in a wet tropical forest, Glob. Chang. Biol., 18,

650 2969–2979, 2012.

Lira-Martins, D., Quesada, C. A., Strekopytov, S., Humphreys-Williams, E., Herault, B., and Lloyd, J.: Wood nutrient-water-density linkages are influenced by both species and environment, Front. Plant Sci., 13, 778403, 2022.

Liu, S. T., Gille, C. E., Bird, T., Ranathunge, K., Finnegan, P. M., and Lambers, H.: Leaf phosphorus allocation to chemical fractions and its seasonal variation in south-western Australia is a species-dependent trait, Sci. Total Environ., 901, 166395,

655 2023.

Lopes, A. P., Nelson, B. W., Wu, J., de Alencastro Graça, P. M. L., Tavares, J. V., Prohaska, N., Martins, G. A., and Saleska, S. R.: Leaf flush drives dry season green-up of the Central Amazon, Remote Sens. Environ., 182, 90–98, 2016.

Lugli, L. F., Andersen, K. M., Aragão, L. E. O. C., Cordeiro, A. L., Cunha, H. F. V., Fuchslueger, L., Meir, P., Mercado, L. M., Oblitas, E., Quesada, C. A., Rosa, J. S., Schaap, K. J., Valverde-Barrantes, O., and Hartley, I. P.: Multiple phosphorus

60 acquisition strategies adopted by fine roots in low-fertility soils in Central Amazonia, Plant Soil, 450, 49–63, https://doi.org/10.1007/s11104-019-03963-9, 2020.

Luizão, R. C. C., Luizão, F. J., Paiva, R. Q., Monteiro, T. F., Sousa, L. S., and Kruijt, B.: Variation of carbon and nitrogen cycling processes along a topographic gradient in a central Amazonian forest, Glob. Chang. Biol., 10, 592–600, 2004.

Machado, M. R., Sampaio, P. de T. B., Ferraz, J., Camara, R., and Pereira, M. G.: Nutrient retranslocation in forest species in

665 the Brazilian Amazon, Acta Sci. Agron., 38, 93–101, 2016.

Martin, A. R., Erickson, D. L., Kress, W. J., and Thomas, S. C.: Wood nitrogen concentrations in tropical trees: phylogenetic patterns and ecological correlates, New Phytol., 204, 484–495, 2014.

Martin, A. R., Doraisami, M., and Thomas, S. C.: Global patterns in wood carbon concentration across the world's trees and forests, Nat. Geosci., 11, 915–920, 2018.

670 Martins, N. P., Fuchslueger, L., Fleischer, K., Andersen, K. M., Assis, R. L., Baccaro, F. B., Camargo, P. B., Cordeiro, A. L., Grandis, A., and Hartley, I. P.: Fine roots stimulate nutrient release during early stages of leaf litter decomposition in a Central Amazon rainforest, Plant Soil, 469, 287–303, 2021.

Martins, N. P., Valverde-Barrantes, O., Fuchslueger, L., Lugli, L. F., Grandis, A., Hofhansl, F., Takeshi, B., Ushida, G., and Quesada, C. A.: Fine root presence and increased phosphorus availability stimulate wood decay in a central Amazonian 675 rainforest, Oikos, e09996, 2023.

Medina-Vega, J. A., Zuleta, D., Aguilar, S., Alonso, A., Bissiengou, P., Brockelman, W. Y., Bunyavejchewin, S., Burslem, D. F. R. P., Castaño, N., and Chave, J.: Tropical tree ectomycorrhiza are distributed independently of soil nutrients, Nat. Ecol. Evol., 8, 400–410, 2024.

Meerts, P.: Mineral nutrient concentrations in sapwood and heartwood: a literature review, Ann. For. Sci., 59, 713–722, 2002.

680 Meng, L., Chambers, J., Koven, C. D., Pastorello, G., Gimenez, B., Jardine, K., Tang, Y., McDowell, N., Negron-Juarez, R., Longo, M., Araujo, A., Tomasella, J., Fontes, C., Mohan, M., and Higuchi, N.: Soil moisture thresholds explain a shift from light-limited to water-limited sap velocity in the Central Amazon during the 2015-16 El Niño drought, Environ. Res. Lett., 2022.

Monteiro, M.T.F.: Interações na dinâmica do carbono e nutrientes da liteira entre a floresta de terra firme e o igarapé de 685 drenagem na Amazônia Central (master's thesis). Programa em Biologia Tropical e Recursos Naturais do Convênio INPA, Manaus - AM. p. 112, 2005.

Nardoto, G. B., Ometto, J. P. H. B., Ehleringer, J. R., Higuchi, N., Bustamante, M. M. da C., and Martinelli, L. A.: Understanding the influences of spatial patterns on N availability within the Brazilian Amazon forest, Ecosystems, 11, 1234–1246, 2008.

690 Noguchi, H., Suwa, R., de SOUZA, C. A. S., da SILVA, R. P., Dos Santos, J., Higuchi, N., Kajimoto, T., and Ishizuka, M.: Examination of vertical distribution of fine root biomass in a tropical moist forest of the Central Amazon, Brazil, Japan Agric. Res. Q. JARQ, 48, 231–235, 2014.

Nogueira, E. M., Fearnside, P. M., Nelson, B. W., Barbosa, R. I., and Keizer, E. W. H.: Estimates of forest biomass in the Brazilian Amazon: New allometric equations and adjustments to biomass from wood-volume inventories, For. Ecol. Manage.,

695   256, 1853–1867, https://doi.org/http://dx.doi.org/10.1016/j.foreco.2008.07.022, 2008.

Norby, R. J., Gu, L., Haworth, I. C., Jensen, A. M., Turner, B. L., Walker, A. P., Warren, J. M., Weston, D. J., Xu, C., and Winter, K.: Informing models through empirical relationships between foliar phosphorus, nitrogen and photosynthesis across diverse woody species in tropical forests of Panama, New Phytol., 215, 1425–1437, 2017.

Nottingham, A. T., Gloor, E., Bååth, E., and Meir, P.: Soil carbon and microbes in the warming tropics, Funct. Ecol., 36, 1338–
700   1354, 2022.

Oliveira, R. S., Costa, F. R. C., van Baalen, E., de Jonge, A., Bittencourt, P. R., Almanza, Y., Barros, F. de V, Cordoba, E. C., Fagundes, M. V, and Garcia, S.: Embolism resistance drives the distribution of Amazonian rainforest tree species along hydro-topographic gradients, New Phytol., 221, 1457–1465, 2019.

Piva, L. R. de O., Jardine, K. J., Gimenez, B. O., de Oliveira Perdiz, R., Menezes, V. S., Durgante, F. M., Cobello, L. O.,
705   Higuchi, N., and Chambers, J. Q.: Volatile monoterpene 'fingerprints' of resinous Protium tree species in the Amazon rainforest, Phytochemistry, 160, 61–70, 2019.

Poorter, L., McDonald, I., Alarcón, A., Fichtler, E., Licona, J., Peña-Claros, M., Sterck, F., Villegas, Z., and Sass-Klaassen, U.: The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species, New Phytol., 185, 481–492, 2010.

710   Powers, J. S., Montgomery, R. A., Adair, E. C., Brearley, F. Q., DeWalt, S. J., Castanho, C. T., Chave, J., Deinert, E., Ganzhorn, J. U., Gilbert, M. E., González-Iturbe, J. A., Bunyavejchewin, S., Grau, H. R., Harms, K. E., Hiremath, A., Iriarte-Vivar, S., Manzane, E., De Oliveira, A. A., Poorter, L., Ramanamanjato, J.-B., Salk, C., Varela, A., Weiblen, G. D., and Lerdau, M. T.: Decomposition in tropical forests: a pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient, J. Ecol., 97, 801–811, https://doi.org/https://doi.org/10.1111/j.1365-
715   2745.2009.01515.x, 2009.

Quesada, C. A., Phillips, O. L., Schwarz, M., Czimczik, C. I., Baker, T. R., Patiño, S., Fyllas, N. M., Hodnett, M. G., Herrera, R., and Almeida, S.: Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate, Biogeosciences, 9, 2203–2246, 2012.

Reed, S. C., Townsend, A. R., Davidson, E. A., and Cleveland, C. C.: Stoichiometric patterns in foliar nutrient resorption
720   across multiple scales, New Phytol., 196, 173–180, 2012.

Reichert, T., Rammig, A., Fuchslueger, L., Lugli, L. F., Quesada, C. A., and Fleischer, K.: Plant phosphorus-use and-

acquisition strategies in Amazonia, New Phytol., 234, 1126–1143, 2022.

Ribeiro, G. H. P. de M., Chambers, J. Q., Peterson, C. J., Trumbore, S. E., Marra, D. M., Wirth, C., Cannon, J. B., Negrón-Juárez, R. I., Lima, A. J. N., and De Paula, E.: Mechanical vulnerability and resistance to snapping and uprooting for Central Amazon tree species, For. Ecol. Manage., 380, 1–10, 2016.

Rodrigues, J. R., Solander, K. C., Cropper, S., Newman, B. D., Collins, A. D., Warren, J. M., Negron-Juarez, R., Gimenez, B. O., Spanner, G. C., and Menezes, V. da S.: Soil water percolation and nutrient fluxes as a function of topographical, seasonal and soil texture variation in Central Amazonia, Brazil, Hydrol. Process., 38, e15148, 2024.

Sampaio de Souza, C. A. Turnover e biomassa de raízes finas e suas relações com o padrão de crescimento de árvores em uma floresta de terra firme na Amazônia central (Doctoral dissertation). Programa em Ciências de Florestas Tropicais. INPA, Manaus, Brazil. 153p, 2016.

Schreeg, L. A., Mack, M. C., and Turner, B. L.: Nutrient-specific solubility patterns of leaf litter across 41 lowland tropical woody species, Ecology, 94, 94–105, 2013.

Shen, J., Yuan, L., Zhang, J., Li, H., Bai, Z., Chen, X., Zhang, W., and Zhang, F.: Phosphorus dynamics: from soil to plant, Plant Physiol., 156, 997–1005, 2011.

Silva, R. P. da: Alometria, estoque e dinâmica da biomassa de florestas primárias e secundárias na região de Manaus (AM), 2007.

Da Silva, R. P., Dos Santos, J., Tribuzy, E. S., Chambers, J. Q., Nakamura, S., and Higuchi, N.: Diameter increment and growth patterns for individual tree growing in Central Amazon, Brazil, For. Ecol. Manage., 166, 295–301, 2002.

Silver, W. L., Neff, J., McGroddy, M., Veldkamp, E., Keller, M., and Cosme, R.: Effects of soil texture on belowground carbon and nutrient storage in a lowland Amazonian forest ecosystem, Ecosystems, 3, 193–209, 2000.

Soong, J. L., Janssens, I. A., Grau, O., Margalef, O., Stahl, C., Van Langenhove, L., Urbina, I., Chave, J., Dourdain, A., and Ferry, B.: Soil properties explain tree growth and mortality, but not biomass, across phosphorus-depleted tropical forests, Sci. Rep., 10, 2302, 2020.

Sousa, T. R., Schietti, J., Ribeiro, I. O., Emílio, T., Fernández, R. H., Ter Steege, H., Castilho, C. V, Esquivel-Muelbert, A., Baker, T., and Pontes-Lopes, A.: Water table depth modulates productivity and biomass across Amazonian forests, Glob. Ecol. Biogeogr., 31, 1571–1588, 2022.

Souza, F.C.: Dinâmica de uma floresta de terra firme na estação experimental de silvicultura tropical, Manaus - Amazonas (master's thesis). Programa em Ciências de Florestas Tropicais . INPA-UFAM. Manaus - AM. p. 110, 2011.

750   Spanner, G. C., Gimenez, B. O., Wright, C. L., Menezes, V. S., Newman, B. D., Collins, A. D., Jardine, K. J., Negrón-Juárez, R. I., Lima, A. J. N., Rodrigues, J. R., Chambers, J. Q., Higuchi, N., and Warren, J. M.: Dry Season Transpiration and Soil Water Dynamics in the Central Amazon, https://www.frontiersin.org/articles/10.3389/fpls.2022.825097, 2022.

Summers, P. M.: Estoque, decomposicao, e nutrientes da liteira grossa em floresta de terra-firme, na Amazonia Central, Ciencias Florestas Trop. Inst. Nac. Pesqui. da Amaz. Manaus, Brazil, 1998.

Trumbore, S., Brando, P., and Hartmann, H.: Forest health and global change, Science (80-.)., 349, 814–818, 2015.

Urbina, I., Grau, O., Sardans, J., Margalef, O., Peguero, G., Asensio, D., LLusià, J., Ogaya, R., Gargallo-Garriga, A., and Van Langenhove, L.: High foliar K and P resorption efficiencies in old-growth tropical forests growing on nutrient-poor soils, Ecol. Evol., 11, 8969–8982, 2021.

Vengavasi, K., Pandey, R., Soumya, P. R., Hawkesford, M. J., and Siddique, K. H. M.: Below-ground physiological processes
760   enhancing phosphorus acquisition in plants, Plant Physiol. Reports, 26, 600–613, 2021.

Venturas, M. D., Sperry, J. S., and Hacke, U. G.: Plant xylem hydraulics: what we understand, current research, and future challenges, J. Integr. Plant Biol., 59, 356–389, 2017.

Vitousek, P. M. and Matson, P. A.: Nitrogen transformations in a range of tropical forest soils, Soil Biol. Biochem., 20, 361–367, 1988.

765   Vitousek, P. M. and Sanford, R. L.: Nutrient cycling in moist tropical forest, Annu. Rev. Ecol. Syst., 137–167, 1986.

Ye, X., Luan, J., Wang, H., Zhang, Y., Wang, Y., Ma, J., and Liu, S.: Tree species richness and N-fixing tree species enhance the chemical stability of soil organic carbon in subtropical plantations, Soil Biol. Biochem., 174, 108828, 2022.

Ziemińska, K., Butler, D. W., Gleason, S. M., Wright, I. J., and Westoby, M.: Fibre wall and lumen fractions drive wood density variation across 24 Australian angiosperms, AoB Plants, 5, plt046, 2013.

770   Zuleta, D., Duque, A., Cardenas, D., Muller-Landau, H. C., and Davies, S. J.: Drought-induced mortality patterns and rapid biomass recovery in a terra firme forest in the Colombian Amazon, Ecology, 98, 2538–2546, https://doi.org/https://doi.org/10.1002/ecy.1950, 2017.

Zuleta, D., Russo, S. E., Barona, A., Barreto-Silva, J. S., Cardenas, D., Castaño, N., Davies, S. J., Detto, M., Sua, S., Turner,

B. L., and Duque, A.: Importance of topography for tree species habitat distributions in a terra firme forest in the Colombian
775   Amazon, Plant Soil, 450, 133–149, https://doi.org/10.1007/s11104-018-3878-0, 2020.

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

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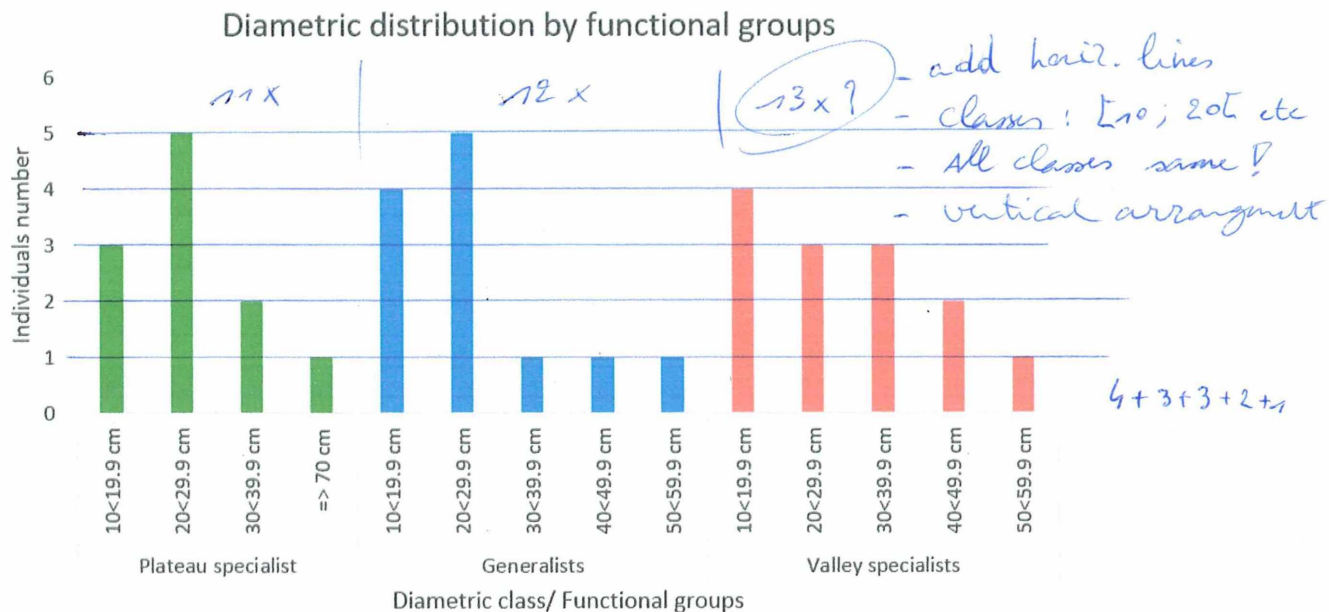
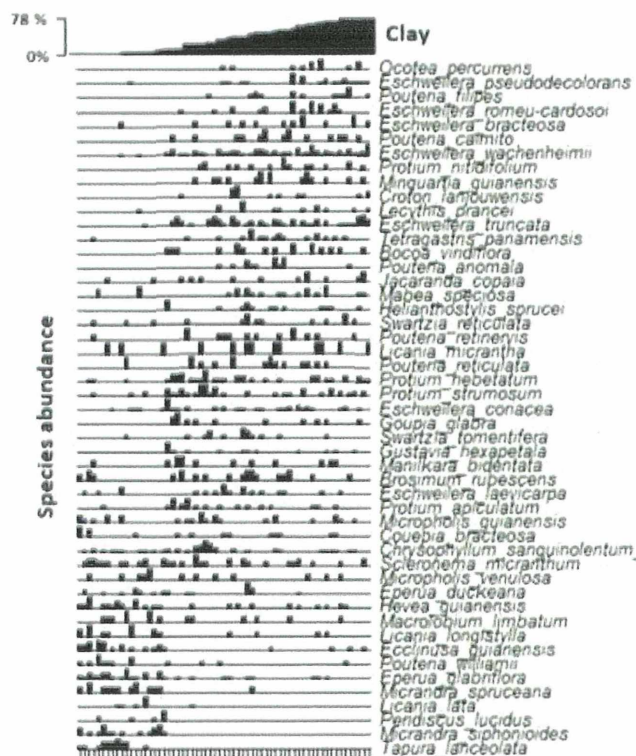
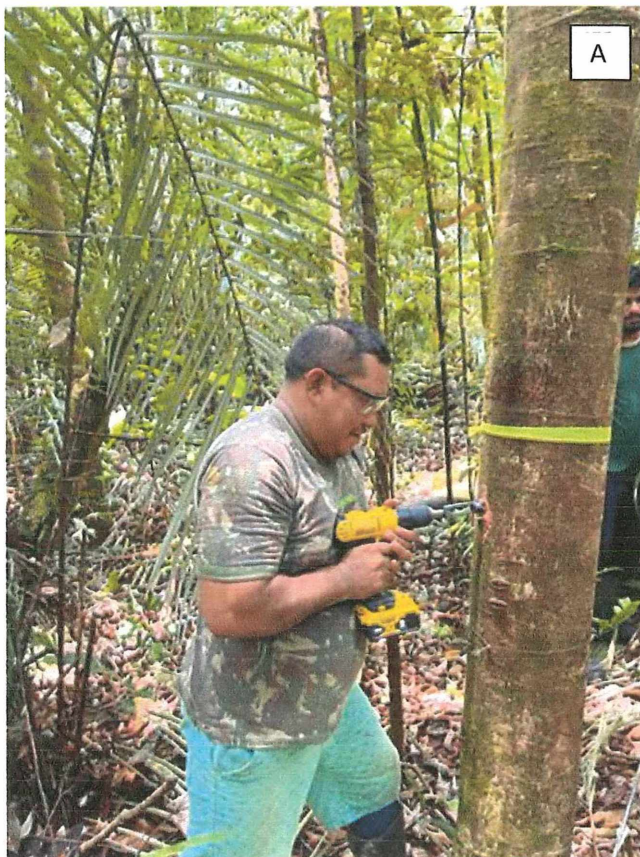
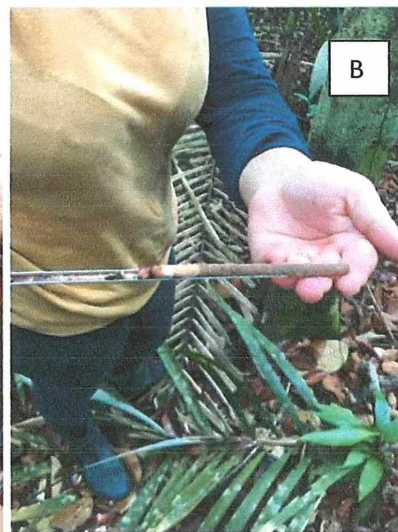
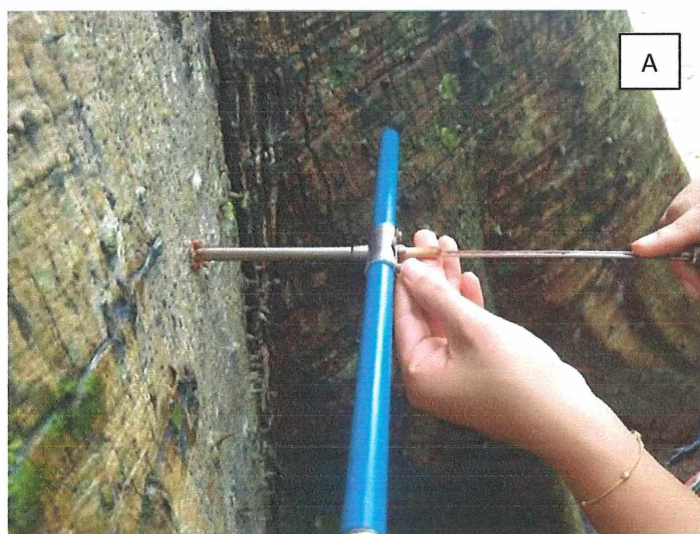
SUPPLEMENTARY MATERIAL

relative to ?

Supplementary Figure 1: Image of the topographic profile of the North - South Transect, where the green dots represent the trees where plant tissues (leaf and wood) were collected for nutrient analysis. ~~In this graph, we can see the variation in the topography of the area.~~ Image adapted from Higuchi et al. (1998)

- use ≠ colors for ≠ Categories (~ how separated are the classes ?)
- add classification where valley, where plateau,
e.g. what is this ?

Supplementary Figure 2: Diametric distribution (cm) of the individuals selected according to each functional group

Supplementary Figure 3: Distribution of the 50 most common tree species with DBH ≥ 10 cm inventoried in the transect along the soil texture gradient, represented by clay content (in %). This image is adapted from Souza (2011), which studied the dynamics of a terra firme forest in Central Amazonia

→ Give figure only for relevant species

Supplementary Figure 4: ~~The first image is a~~ photo of the collection of woody material in the field with a 25 mm diameter drill attached to a drill press (A), ~~in the second image~~ we have a photo of the drill used (B) *just use (A) & (B)!*

Supplementary Figure 5 Illustrative image of the Pressler drill embedded in a tree (A); sample obtained with the Pressler drill (B) to determine wood density

Supplementary Table 1: Table results of the analysis of variance for the nutritional concentration and carbon in the leaves between the different functional groups.

Variables	Source of variation	G.L	SQ	QM	F	P
C	Group	2	3004	1505	2.562	0.092
	Error	32	18760	586.3		
N	Group	2	219.1	109.53	15.93	1.6e-05
	Error	32	220	6.88		
P	Group	2	0.48	0.245	8.824	0.00089
	Error	32	0.89	0.028		
K	Group	2	241.1	120.54	15.58	1.9e-05
	Error	32	247.6	7.74		

G.L = Degrees of freedom; SQ = Sum of squares; QM = Mean square; F = F-statistic; P = P-value

Supplementary Table 2: Summary of the analysis of variance for nutritional variables that did not follow a normal distribution (Kruskal-Wallis test) in the leaves between the groups.

Variables	p-value
Ca	0.00092
Mg	0.031

Supplementary Table 3: Mean concentration and confidence interval (CI = 95%) in g.kg^{-1} of carbon and nutrients in the leaf.

	Functional Group		
Chemical elements in leaves	*Generalists*	*Plateau specialists*	*Valley specialists*
C	601.81 ± 13.86	613.09 ± 10.99*	590.23 ± 15.61
N	14.47 ± 1.02	19.63 ± 1.80···	14.05 ± 1.55
P	0.62 ± 0.05	0.65 ± 0.08	0.88 ± 0.12··
K	5.57 ± 0.99	3.40 ± 0.92··	9.56 ± 2.08··
Ca	2.75 ± 0.92	0.89 ± 0.33··	4.09 ± 1.99
Mg	1.09 ± 0.36	0.70 ± 0.11·	1.28 ± 0.34

***p <0,001; **p <0,01; *p <0,05

Supplementary table 4: Table of results of the analysis of variance for the nutritional concentration and carbon in the trunk between the different functional groups.

Nutrients	Source of variation	G.L	SQ	QM	F	P
N	Group	2	4.65	2.33	3.485	0.043
	Error	32	21.36	0.67		

G.L = Degrees of freedom; SQ = Sum of squares; QM = Mean square; F = F-statistic; P = P-value.

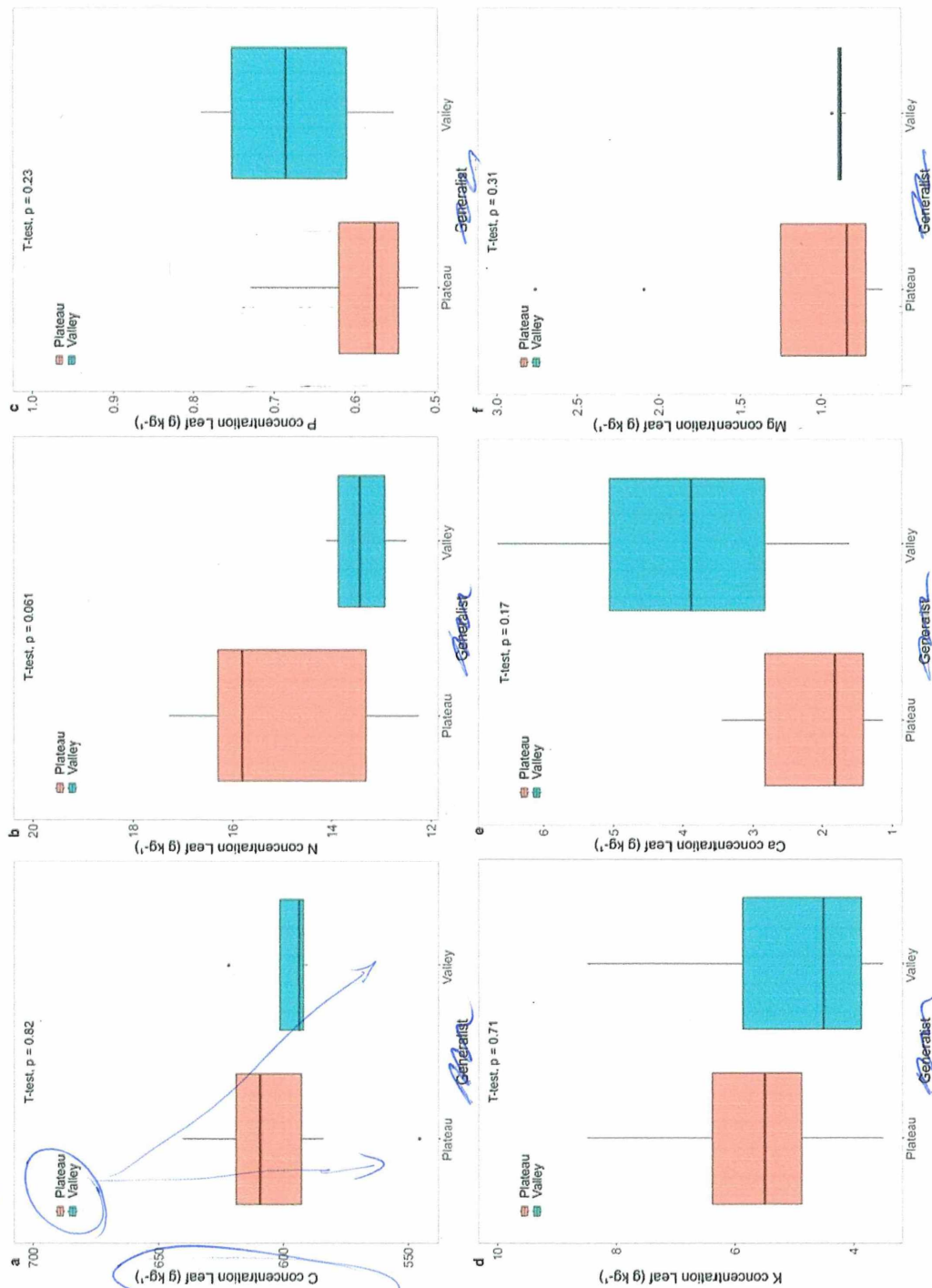
Supplementary Table 5: Summary of the analysis of variance for nutritional variables that did not follow a normal distribution (Kruskal-Wallis test) in the trunk between the groups

Variables	p-value
C	0.23
P	0.0013
K	0.0007
Ca	0.000064
Mg	0.003

Supplementary Table 6: Mean concentration and confidence interval (CI = 95%) in g kg⁻¹ of carbon and nutrients in wood.

same as for Table S3

Chemical elements in wood	Functional Group		
	Generalists	*Plateau specialists*	*Valley specialists*
C	560.4 ± 34.6	585.81 ± 33.95	597.27 ± 26.96
N	2.42 ± 0.35*	3.17 ± 0.38	3.2 ± 0.59
P	0.076 ± 0.021	0.066 ± 0.007	0.11 ± 0.01*
K	0.81 ± 0.27*	0.44 ± 0.04***	1.40 ± 0.30
Ca	2.21 ± 1.05	0.81 ± 0.16***	3.26 ± 0.95
Mg	0.82 ± 0.59	0.22 ± 0.08**	0.59 ± 0.15

***p <0,001; **p <0,01; *p <0,05

Supplementary Figure 7: Boxplots illustrating the concentrations of leaf C and nutrients in generalist species across different topographic positions (plateaus and valleys)

(handwritten annotations)

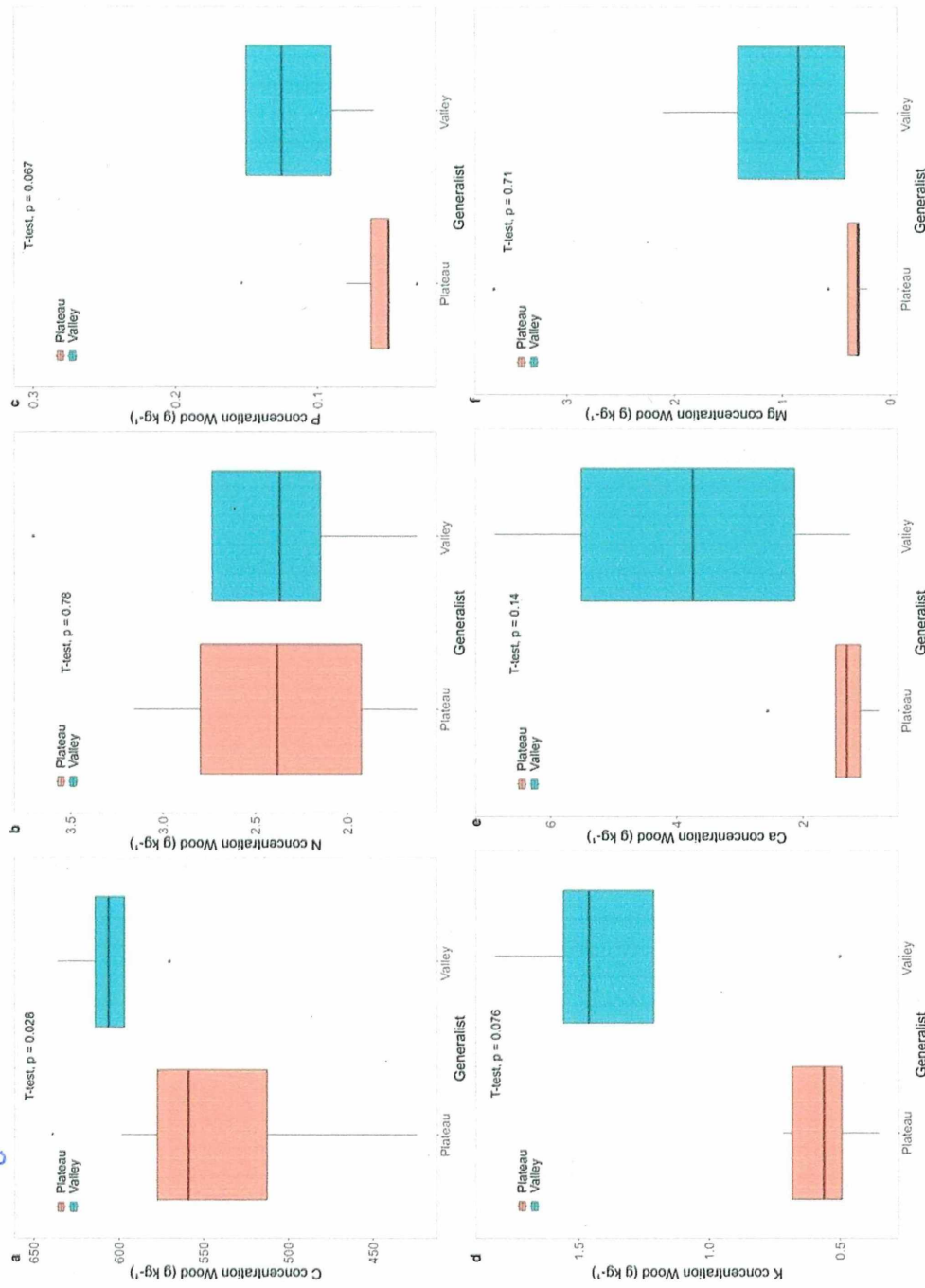
+ add data points

+ indication sign. diff.

" Fabian C (g c kg⁻¹) "

not informative

same comments as for S7.

+ add data
+ indication zijn diff. ?

Supplementary Figure 8: Boxplots illustrating the concentrations of trunk C and nutrients in generalist species across different topographic positions (plateaus and valleys)