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Morpho-anatomical traits and leaf nutrient concentrations vary between plant communities in the Cerrado–Amazonia transition?

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ABSTRACT

Leaves are the most variable plant organ, responding and adapting to the environment in the long and short term. However, the link between leaf functional traits and environmental gradients is challenging, especially in systems of high diversity, such as transitional regions between savannas and tropical forests that are considered unstable. Here we evaluate anatomical and morphological traits and nutrient concentrations for the most representative woody species of four vegetation types (i.e., semideciduous forest, *cerradão*, typical *cerrado*, and *cerrado rupestre*) in the Amazonia–Cerrado transition to explore how vegetation will respond to changes in the environment. We found that closed-canopy species invested in traits related to rapid resource acquisition (e.g., higher leaf water content, larger stomata size, and higher maximum opening of the stomatal pore), while open-canopy species optimized traits related to resource conservation and protection from physical damage (e.g., higher leaf thickness, smallest maximum stomatal pore opening and smaller size of stomata). Our study shows that functional traits play an important role in adapting to environmental gradients and help explain the performance of trees in the Amazonia–Cerrado transition, opening the door to a more accurate prediction of plant community responses over time.

1. Introduction

Savannas and rainforests are important in terms of area occupied on the planet, biodiversity, and carbon stock (Torello-Raventos et al., 2013). Between the two largest South American biomes, the Brazilian Savanna, known as Cerrado, and Amazonia, there is an extensive transitional area, the Cerrado–Amazonia transition, with unique characteristics, such as a shared floristic composition and climatic parameters, and occurrence of fires, mainly in savanna formations (Furley and Ratter, 1988; Ratter, 1993; Marimon et al., 2006; 2014). The vegetation of this complex and inter-digitaded transition, which is more than 6000 km long (Marques et al., 2020), has higher baseline mortality and recruitment rates when compared to core areas of Amazonia and Cerrado (Marimon et al., 2014).

The Cerrado–Amazonia transition is an open-air laboratory to study the relationships between abiotic filters and functional traits of trees, due to the highly contrasting environments that occur next to each other, such as savanna formations (typical *cerrado* and *cerrado rupestre*; characterized by high water deficit and low soil fertility) and forest formations (*cerradão* and semideciduous forest; soils with high water availability) (Ratter, 1993; Marimon et al., 2006; 2014). The study of plant species adaptation in these distinct vegetation types can help improving our understanding on how different environmental drivers shape the functional traits of plant communities.

These transitional regions are relatively unstable and may be highly susceptible to global climate change (Marimon et al., 2014; Morandi et al., 2018; Tiwari et al., 2020; Araújo et al., 2021a). Climate predictions indicate that there will be a gradual increase in temperature

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over the coming decades (Gatti et al., 2014), leading to increasingly severe drought conditions (Coe et al., 2016), which will limit the ability of trees to recover and resist recurring droughts (McDowell, 2011). Therefore, understanding ecological strategies at the community level is fundamental to clarify how selective processes impact different species and to describe functional patterns (Pearson and Dawson, 2003). Environmental constraints drive acquisitive–conservative strategies of trees (Wright et al., 2006; Araújo et al., 2022). Functional traits are morpho-physiological-phenological characteristics that directly or indirectly affect plant performance through their effects on growth, survival, and reproduction (Violle et al., 2007) and are essential for the adaptation of the species along environmental gradients (Ghalambor et al., 2007). Modifications in functional traits enable species to overcome different environmental filters (Borges et al., 2019), particularly associated with availability of resources, such as water, nutrients, and light (Wellstein et al., 2017; Araújo et al., 2022).

In savannas, water deficit and low soil fertility (Ribeiro and Walter, 2008; Mews et al., 2011; Gomes et al., 2016) are considered the most relevant environmental filters that determine functional traits of the plant community (Cássia-Silva et al., 2017; Maracahipes et al., 2018; Carrijo et al., 2021). On the other hand, forests are environments where soils show higher percentages of clay, resulting in higher water availability throughout the year. Even though soil fertility is similar to savanna environments, water availability regulates the dynamics of soil nutrients and plants' absorption, which may lead to higher nutrient availability in forest environement (Marimon and Haridasan, 2005; Marimon et al., 2014). Generally, in trees growing under different environmental conditions, functional traits tend to vary over a gradient of strategies that ranges from fast acquisition to efficient resource conservation (Wright et al., 2004; Reich, 2014), reflecting the extremes of an ecological continuum (Grime, 1983; Craine, 2009).

In environments with water and nutritional deficit, species are selected to display more resource conservative strategies (Prado-Junior et al., 2016; Araújo et al., 2021b); these strategies reflect structural adjustments of the plants in the face of conditions of high irradiance and low water availability, for example, thicker and more succulent leaves that favor water storage (Rabelo et al., 2013), and homogenous distribution of light throughout the leaf mesophyll (Cornelissen and Fernandes, 2003; Rozendaal et al., 2006). In addition, thicker leaves may have a greater amount of usable water stored for long periods, allowing the maintenance of water status during periods of greater restriction of this resource (Niinemets, 2001). Plants with smaller specific leaf areas are common in low-nutrient environments because it relates to a greater leaf longevity, improving carbon balance in hotter and drier conditions and increasing tree survival rates (Sakschewski et al., 2016). Another structural strategy observed in species from limiting environments is the high density of trichomes on leaf surfaces, which acts in temperature regulation, as barrier to insects, and reduction of transpiration due to the increase in water vapor concentration around the leaf boundary layer (Fahn and Cutler, 1992; Larcher, 2000; Wagner et al., 2004). Species tend to have distinct anatomical characteristics, e. g. with respect to size and maximum opening of smaller stomatal pores to reduce atmospheric water loss (Franks et al., 2009, 2012). Furthermore, the concentration of nutrients in the leaves is related to the tree's response to the availability of nutrients in the soil (Rossatto et al., 2013; Dantas et al., 2013). In this context, trees growing in nutrient-limited soils or under disturbances like fire tend to have lower leaf nutrient concentrations (Cornelissen et al., 2003).

On the other hand, in environments with greater availability of water, species are selected with an acquisitive strategy; species usually invest in higher specific leaf areas to maximize light interception and with larger stomata to increase CO_2 assimilation (Casas et al., 2011), which enhances photosynthetic efficiency (Cornelissen et al., 2003) and enables higher tree growth rates (Ogburn and Edwards, 2010). In addition, leaf nutrient concentration reflects soil fertility. It is an important determinant of the species' performance in their habitats (Aerts and Chapin, 1999), reflecting physiological needs and potential growth (Field and Mooney, 1986).

In this study, we evaluated the variability of functional traits and the relationship between leaf nutrients and important morpho-anatomical characteristics related to efficiency in resource acquisition (e.g., specific leaf area) and regulation of water loss (e.g., stomata size) in four vegetation types located in the transition between the Amazon and Cerrado biomes. By combining morpho-anatomical traits and leaf nutrient concentration, we can examine in an integrated way the drivers of functional patterns, including convergence or divergence of traits linked to the foliar economic spectrum. This framework is crucial for understanding how plants adapt to the distinct environmental conditions in this critically endangered region. We hypothesize that community-level traits will display a gradient response going from acquisitive functional traits in species of cerradão and semideciduous forest (e.g., higher specific leaf area, higher leaf water mass content, higher leaf nutrient concentration, and larger stomata) to conservative functional traits in species of typical cerrado and cerrado rupestre (e.g., higher trichome density, higher leaf thickness, lower specific leaf area, and lower leaf nutrient concentrations and smaller stomata) (Wright et al., 2004; Rossatto et al., 2009; Reich, 2014; Monteiro et al., 2016).

2. Materials and methods

2.1. Study area

The four study areas are in Nova Xavantina, eastern Mato Grosso state, Central Brazil, in the Amazonia–Cerrado transition zone (Fig. 1). The climate is higly seasonal with two well-distinct periods, the rainy (October to March) and the dry (April to September), being Aw type, according to Köppen's classification (Alvares et al., 2013), with annual rainfall of 1.600 mm and mean monthly temperature of 25 °C, ranging from 21.5 to 28 °C (Marimon et al., 2010). For detailed climatic conditions throughout the year and fire frequencies in the area, please see Scalon et al. (2021). Three areas are located in the Municipal Park of Bacaba (14° 41′ 09" S, 52° 20′ 09" W; elevation 325 m). Our vegetation gradient includes the *cerrado rupestre* (open-canopy) which is a savanna phytophysiognomy with a tree cover of 10 to 37%, consists of an upper canopy 3 to 5 m tall, and occurs on shallow soils with rocky outcrops of the Neosol type; the flora in this phytophysiognomy is similar to the species of the typical *cerrado* (Gomes et al., 2016). The trees settle in the cracks between the rocks, where there is accumulation and decomposition of organic matter and sand deposition resulting from the weathering of the rocks (Maracahipes et al., 2011). Typical *cerrado*, an open savanna with a tree cover of 20 to 50%, consists of an upper canopy 3 to 7 m tall, with deciduous and evergreen trees (Ribeiro and Walter, 2008; Mews et al., 2011; Gomes et al., 2016). It occurs on deep, well-drained, dystrophic, acidic Latosols (Ferralsols) with high exchangeable aluminium contents (Marimon-Junior and Haridasan, 2005). *Cerradão* is a forest-type vegetation, with a tree cover of 20 to 60%, and consists of an upper canopy 5 to 17 m tall (Marimon-Junior and Haridasan, 2005; Reis et al., 2015) occurring on dystrophic soils, with higher percentages of clay that result in higher availability of water throughout the year for the trees. It features a mixture of forest and *cerrado* species (Marimon-Junior and Haridasan, 2005; Marimon et al., 2014). The other study area is a semideciduous forest (closed-canopy) at Vera Cruz farm (14° 49′ 32" S, 52° 06′ 20" W; elevation 39 m). The vegetation is characterized by typical Amazonia tall trees with a tree cover of 37 to 82%, and consists of an upper canopy 14 to 28 m tall; soils are characterized by low acid plinthosols with plinthics elements concretions and medium-textured soil demonstrating greater availability of water (Marimon et al., 2014; Marimon-Junior et al., 2020). For more information on soil physical and chemical property differences between vegetation types, see Marimon-Junior et al. (2020), Marimon-Junior and Haridasan (2005) and Marimon et al. (2014), and for microclimatic differences, see Araújo et al. (2021b).

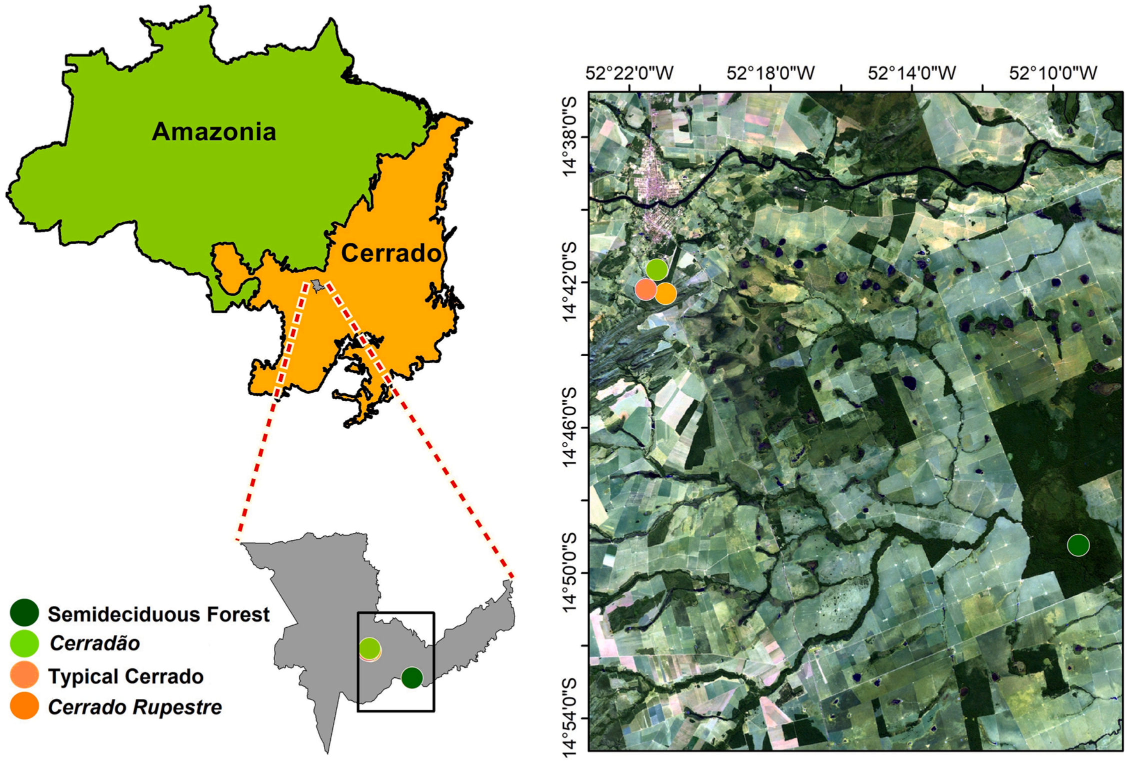

Fig. 1. Distinct vegetation types in the Amazonia–Cerrado transition. Open-canopy vegetation (typical *cerrado* and *cerrado rupestre*) and closed-canopy vegetation (semideciduous forest and *cerradão*).

2.2. Data collection

We selected seven species that represented >80% IVI in the plant communities in each vegetation type, according to the importance value index (IVI, Table 1), which considers species' relative density, frequency, and dominance (Reis et al., 2015; Gomes et al., 2016). We sampled the five largest trees and a trained climber harvested 1–2 canopy branches per individual fully exposed to the sun to avoid light variations throughout the day for each species. Thereafter, we placed the branches inside plastic bags and sealed the end so there was no contact with the external environment. We kept the plastic bags with the samples inside coolers during transport to the laboratory, which is very close to the studied areas, and on the same day, we digitized them. In the laboratory, for each tree, we randomly selected eight fully expanded and pathogen-free leaves (i.e., five leaves were used for morphological and nutrient analysis and additional three leaves for measurements of anatomical traits) in the rainy season peak (February).

2.3. Leaf morphological traits and nutrient analysis

Functional traits assessed in this study are listed in Table 2. We measured leaf thickness (mm) using an electronic digital micrometer (± 0.001 mm). Fresh leaves were scanned, and the leaf area was determined with ImageJ software (Abràmoff et al., 2004). We estimated the fresh mass of the leaves with a precision balance (± 0.001 g), then placed them in paper bags in an oven at 60 °C and, after 72 h, determined the dry mass. The leaf water content (mg g^{-1}) was calculated as the fresh and dry mass ratio. The specific leaf area (cm^2 g^{-1}) was calculated as the ratio between leaf area and leaf dry mass (Pérez-Harguindeguy et al., 2013). Dried samples were sent to the laboratory of the Soil Department of the Federal University of Viçosa (UFV, MG, Brazil) for nutrient concentration analyses. N was determined by Kjeldahl digestion and distillation procedure. P (g kg^{-1}) was determined by UV-Vis spectroscopy and the other nutrients (Ca, Mg, and K, g kg^{-1}) were determined by atomic absorption spectrometry after wet digestion with a tri-acid mixture (nitric acid 65%, sulfuric acid 99.99% and perchloric acid 70% – 10:1:2).

2.4. Leaf anatomical traits

We sampled three leaves of each tree and applied the foliar surface imprinting method on abaxial and adaxial leaf surfaces (Weyers and Johansen, 1985) using high molding technology silicone (Coltene). After drying, we obtained reverse imprints from the molds using colorless nail polish. We photographed the imprints on a light optical microscope (Zeiss Primo Star), with a coupled camera taken under microscopic magnification of 40 × . We randomly selected 10 fields from each leaf and processed the images with ImageJ software (Abràmoff et al., 2004). The measured parameters were: guard cell length ("L" in μm), guard cell pair width ("W" in μm), stomata size ("STS" estimated as $STS = L \times W$, according to Franks et al., 2009, 2012) and maximum area of the stomatal pore ("MOSP " in μm^2). The maximum area of the stomatal pore was calculated as ($MOSP = \alpha \times STS$, where $\alpha = 0.12$, according to Franks et al., 2009). Stomata density (mm^{-2}) was determined for each tree as the average number of stomata counted in a given area. The same area was used to determine trichome density (mm^{-2}) when present. A total of 25 stomata per tree were investigated, and stomata densities, lengths, and widths were averaged per species.

2.5. Statistical analysis

Before performing all analyses, we tested the normality and homoscedasticity of the data using the Shapiro-Wilk and Levene tests (Levene, 1961; Shapiro and Wilk, 1965). To test for differences in functional traits between vegetation types, we compared the functional traits using Generalized Linear Mixed Models (GLMM) in the lme4 package (Bates et al., 2014), with the vegetation type as predictors (fixed effect) and species as a random effect. We fitted a standardized central axis to

Table 1

Trees in distinct vegetation types in the Amazonia–Cerrado transition and their respective importance value index (IVI), calculated based on species' relative density, frequency, and dominance. We checked the species name, family, and authority according to Flora do Brasil 2020 (http://floradobrasil.jbrj.gov.br/). IVI values were extracted from Mews et al. (2011) for typical *cerrado*, Reis et al. (2015) for *cerradão*, Gomes et al. (2016) for *cerrado rupestre*, and Marimon et al. (2014) for the semideciduous forest.

Species	Family	IVI (%)
Cerrado Rupestre		
Qualea parviflora Mart.	Vochysiaceae	17.94
Vatairea macrocarpa (Benth.) Ducke	Fabaceae	13.66
Erythroxylum suberosum A.St.-Hil.	Erythroxylaceae	13.66
Anacardium occidentale L.	Anacardiaceae	10.60
Heteropterys byrsonimifolia A.Juss.	Malpighiaceae	10.14
Kielmeyera rubriflora Cambess.	Calophyllaceae	9.42
Eugenia aurata O.Berg	Myrtaceae	7.73
Typical *Cerrado*		
Qualea parviflora Mart.	Vochysiaceae	20.55
Davilla elliptica A.St.-Hil.	Dilleniaceae	15.07
Roupala montana Aubl.	Proteaceae	14.66
Guapira graciliflora (Mart. ex Schmidt) Lundell	Nyctaginaceae	10.50
Qualea grandiflora Mart.	Vochysiaceae	9.24
Eriotheca gracilipes (K.Schum.) A.Robyns	Malvaceae	7.29
Euplassa inaequalis (Pohl) Engl.	Proteaceae	6.27
Cerradão		
Hirtella glandulosa Spreng.	Chrysobalanaceae	44.28
Tachigali vulgaris L.G.Silva & H.C.Lima	Fabaceae	34.44
Tapirira guianensis Aubl.	Anacardiaceae	16.15
Myrcia splendens (Sw.) DC.	Myrtaceae	15.20
Xylopia aromatica (Lam.) Mart.	Annonaceae	14.91
Emmotum nitens (Benth.) Miers	Metteniusaceae	13.89
Eriotheca gracilipes (K.Schum.) A.Robyns	Malvaceae	7.97
Semideciduous Forest		
Ephedranthus parviflorus S.Moore	Annonaceae	33.18
Chaetocarpus echinocarpus (Baill.) Ducke	Peraceae	30.61
Mabea fistulifera Mart.	Euphorbiaceae	26.71
Amaioua guianensis Aubl.	Rubiaceae	26.69
Protium altissimum (Aubl.) Marchand	Burseraceae	24.51
Cheiloclinium cognatum (Miers) A.C.Sm.	Celastraceae	24.14
Brosimum rubescens Taub.	Moraceae	11.31

Table 2

Morpho-anatomical traits and their functional significance. [1] Schulten and Schnitzer, 1997; [2] Shen et al., 2011; [3] Leigh and Wyn Jones, 1984; [4] White and Broadley, 2003; [5] Maathuis, 2009; [6] Grime, 1983; [7] Rabelo et al., 2013; [8] Bündchen et al., 2015; [9] Wagner et al., 2004; [10] Pearce et al., 2006; [11] Abrams et al., 1994; [12] Rossatto et al., 2009.

Traits	Acronym	Unit	Functional significance
Leaf nitrogen	N	$g\ cm^{-2}$	Directly related to the maximum photosynthetic rate [1]
Leaf phosphorus	P	$g\ cm^{-2}$	Influences root development, plant growth, and productivity [2]
Leaf potassium	K	$g\ cm^{-2}$	Leaf osmoregulation, maintaining turgor and cell expansion in conditions of water deficit [3]
Leaf calcium	Ca	$g\ cm^{-2}$	Required for various structural roles in the cell wall and membranes [4]
Leaf magnesium	Mg	$g\ cm^{-2}$	Crucial for protein synthesis, chlorophyll pigments and cofactor in carbon fixation [5]
Specific leaf area	SLA	$cm^2\ g^{-1}$	Resource uptake, resource use efficiency, and growth strategies [6]
Leaf thickness	LET	mm	Resistance to physical damage [7]
Leaf water content	LWC	$mg\ g^{-1}$	Leaf temperature reduction and protection against desiccation [8]
Trichome density	TRD	mm^{-2}	Heat dissipation [9]
Stomata density	STD	mm^{-2}	Carbon assimilation [10]
Stomata size	STS	μm	Water use efficiency [11]
Maximum opening of the stomatal pore	MOSP	μm^2	Regulation of water loss [12]

understand how leaf morpho-anatomical traits are related to leaf nutrient concentrations; we estimated the allometric lines of best fit for the bivariate relationships. We tested for differences in inclination (slopes) and intercepts among the four vegetation types using the SMATR package (Warton et al., 2012). Variables were log10-transformed when necessary. All data analyses were performed using the R program, version 3.6.1 (R Core Team, 2019), with a 5% significance level.

3. Results

Species that grow in closed-canopy (*cerradão* and semideciduous forest) environments generally showed different values for leaf traits compared to species that grow in open-canopy (*cerrado rupestre* and typical *cerrado*) environments, except for leaf nutrient concentration at a mass basis and STD (Table 3; Table S1). Species in the semideciduous forest showed higher specific leaf area than species in other vegetation types (Table 3). Species in the semideciduous forest showed the maximum area of the stomatal pore and stomatal size similar to species that grow in *cerrado rupestre* (Table 3). On the other hand, species in open-canopy environments showed smaller SLA and thicker leaves, combined with higher trichome density than species in the semideciduous forest (Table 3). On a mass basis ($mg\ g^{-1}$), there was no difference between species from distinct vegetation types for leaf macronutrient concentrations (Table S1; Table S2). On an area basis ($g\ cm^{-2}$), however, species in the semideciduous forest showed lower leaf content of P than species in other vegetation types (Table 3). On the other hand, species in the *cerradão* showed higher leaf content of N than species in other vegetation types (Table 3). In contrast, the leaf content of Mg varied widely between vegetation types (Table 3). There were no differences in leaf K and Ca contents on an area basis between vegetation types (Table 3; Table S3).

Among individuals in all vegetation types, leaf N concentration was positively related to SLA (semideciduous forest: $R^2 = 0.37$, $P = 0.003$; *cerradão*: $R^2 = 0.43$, $P = 0.001$; typical *cerrado*: $R^2 = 0.22$, $P = 0.030$; *cerrado rupestre*: $R^2 = 0.27$, $P = 0.017$; Fig. 2a). Whereas semideciduous

Table 3

Morpho-anatomical traits and leaf nutrient contents on an area basis of trees in distinct vegetation types in the Amazonia–Cerrado transition. Leaf nitrogen (N, $g\ cm^{-2}$), leaf phosphorus (P, $g\ cm^{-2}$), leaf potassium (K, $g\ cm^{-2}$), leaf calcium (Ca, $g\ cm^{-2}$), leaf magnesium (Mg, $g\ cm^{-2}$), specific leaf area (SLA, $cm^2\ g^{-1}$), leaf thickness (LET, mm), leaf water content (LWC, $mg\ g^{-1}$), stomata density (STD, mm^{-2}), stomata size (STS, μm), trichome density (TRD, mm^{-2}) and maximum opening of the stomatal pore (MOSP, μm^2). SE = standard error, N = number of replicates and absent (0), different lowercase letters denote significant differences (Tukey, $P < 0.05$). Vegetation types: SF = semideciduous forest, CD = *cerradão*, TC = typical *cerrado*, CR = *cerrado rupestre*.

Traits	SF Mean ± SE (N = 35)	CD Mean ± SE (N = 35)	TC Mean ± SE (N = 35)	CR Mean ± SE (N = 35)
STD	246.95 ± 55.16a	181.40 ± 100.96a	153.31 ± 89.88a	240.86 ± 74.95a
STS	106.76 ± 66.34b	165.81 ± 70.86a	85.36 ± 54.06b	77.57 ± 69.01b
MOSP	12.81 ± 7.96b	19.89 ± 8.50a	10.24 ± 6.48b	9.30 ± 8.28b
SLA	97.10 ± 21.08a	67.50 ± 18.65b	72.51 ± 23.11b	75.42 ± 13.85b
LET	0.168 ± 0.02c	0.292 ± 0.06b	0.335 ± 0.06a	0.286 ± 0.05b
LWC	720.68 ± 91.44a	772.09 ± 154.76a	482.66 ± 81.47c	576.74 ± 135.17b
TRD	0.00 ± 0.00 c	75.27 ± 89.93ab	47.44 ± 26.03b	109.51 ± 71.87a
Leaf N	1.87 ± 0.36b	2.80 ± 0.60a	2.16 ± 0.81b	2.22 ± 0.53b
Leaf P	0.07 ± 0.01b	0.12 ± 0.03a	0.11 ± 0.05a	0.14 ± 0.05a
Leaf K	0.54 ± 0.18a	0.71 ± 0.23a	0.74 ± 0.31a	0.69 ± 0.23a
Leaf Ca	0.49 ± 0.30a	1.10 ± 1.04a	0.56 ± 0.33a	0.41 ± 0.13a
Leaf Mg	0.22 ± 0.07c	0.42 ± 0.22ab	0.56 ± 0.34a	0.33 ± 0.12bc

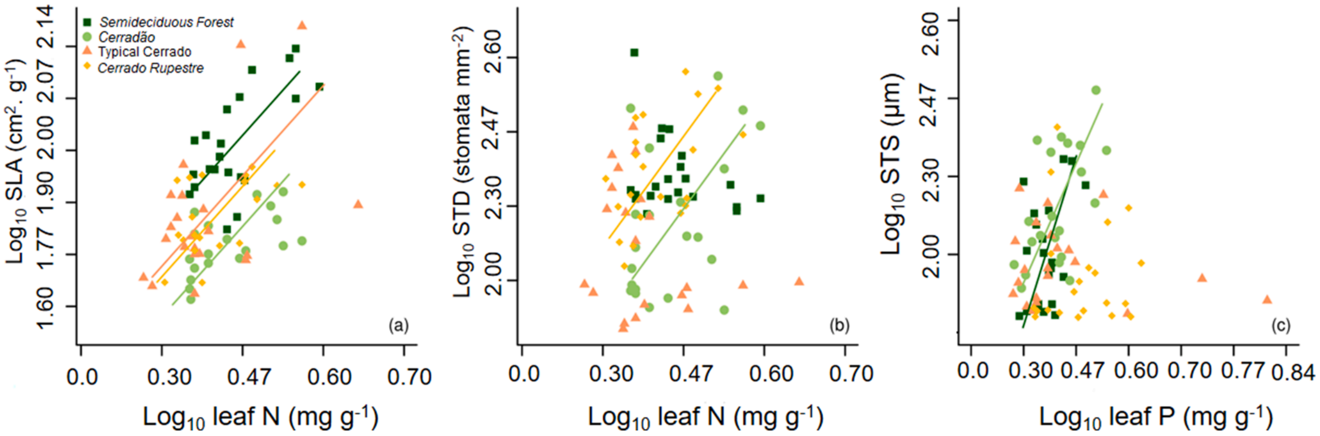

Fig. 2. Bi-variate relationships between leaf nutrient concentration and morpho-anatomical traits of trees in distinct vegetation types in the Amazonia–Cerrado transition. leaf nitrogen (N), leaf phosphorus (P), specific leaf area (SLA), stomata density (STD), and stomata size (STS). All data were log10 transformed.

forest exhibit higher SLA at a given N, cerradão showed the lowest SLA at a given N, and the open-canopy vegetation (typical cerrado and cerrado rupestre) were in between (Wald = 46.39, $P < 0.0001$; Fig. 2a). Furthermore, there are no differences in slope between the four vegetation types. Stomata density was also positively related to leaf N concentration, but only for *cerradão* and *cerrado rupestre* (*cerradão*: $R^2 = 0.19$, $P = 0.042$; *cerrado rupestre*: $R^2 = 0.24$, $P = 0.023$; Fig. 2b). There was also a positive relationship between leaf P concentration and stomata size for the two closed-canopy communities (semideciduous forest: $R^2 = 0.15$, $P = 0.048$; *cerradão*: $R^2 = 0.33$, $P = 0.006$; Fig. 2c).

4. Discussion

Our findings reveal different ecological strategies for resource use, including relevant traits of trees in contrasting habitats in the Amazonia–Cerrado transition (Table 3). Closed-canopy (cerradão and semideciduous forest) habitat species invest in trait values related to rapid resource acquisition (e.g., higher leaf water content, larger stomata size, and higher maximum opening of the stomatal pore), while open-canopy (typical cerrado and cerrado rupestre) habitat species optimize trait values related to resource conservation and protection from physical damage (e.g., higher leaf thickness, smallest maximum stomatal pore opening and smaller size of stomata) (Rozendaal et al., 2006; Maracahipes et al., 2018). Therefore, our results show that plant communities are under different environmental effects (Marimon-Junior and Haridasan, 2005; Marimon et al., 2014) and, to persist in their habitat, these species have developed different resource use strategies (Abrams et al., 1994), validating the leaf economic spectrum and reflecting the environmental differences between these vegetation types (Wright et al., 2004; Marimon-Junior and Haridasan, 2005; Araújo et al., 2021b). In the *cerrado rupestre*, where access to water and soil nutrients is more limited (Marimon-Junior and Haridasan, 2005), we observed that the maximum stomatal pore area and stomatal size were smaller than the values recorded in the semideciduous forest (Table 3), although the differences were not significant. In this case, there may be a synergy between the traits, reflecting on combinations of morpho-anatomical strategies, for example, the greater thickness of the leaves (Table 3) and the high occurrence of trichomes (≈110 mm^{-2}) in the *cerrado rupestre* and, the total absence of trichomes on the leaves of trees in the semideciduous forest. The low water availability and high irradiance in the *cerrado rupestre*, in addition to influencing the structural aspects of leaves, can also affect photosynthetic processes. Under these conditions, plants tend to decrease stomatal conductance to avoid water loss through evapotranspiration, thus increasing resistance to CO_2 entry into the leaves and compromising CO_2 assimilation (Flexas et al., 2012). On the other hand, the lower stomatal conductance favors greater efficiency in water use (Vitória et al., 2016, 2018); these mechanisms minimize the effects of the seasonal water deficit in these areas.

The similarities in stomatal density (Table 3) between leaves from closed-canopy and open-canopy trees can be explained by the strong effect of seasonal climate (Marimon et al., 2014). Indeed, Pearce et al. (2006) observed that stomatal density is strongly associated with seasonal environments and reflects climate adaptations. Larger stomata, which are commonly found in leaves of closed-canopy environments (e.g., *cerradão*, Table 3), help to increase CO_2 assimilation capacity and evapotranspiration rates, and consequently promote higher growth rates (Galmés et al., 2007; Ogburn and Edwards, 2010), as recorded for *cerradão* in previous studies (Marimon et al., 2014). On the contrary, high temperature and light incidence, and low air humidity influence open-canopy environment species (Franco, 2002; Araújo et al., 2021b). The relatively higher trichome densities observed in *cerrado rupestre* species may also reflect adaptation to control water loss due to increased water vapor concentration around the leaf boundary layer (Fahn and Cutler, 1992; Larcher, 2000).

Species in the semideciduous forest had thinner leaves and higher specific leaf area than those in open-canopy environments (Table 3), which is associated with low leaf production costs (Villar and Merino, 2001) and high efficiency in the production of organic compounds through photosynthesis (Westoby et al., 2002; Lambers et al., 2008). Generally, these strategies are more common in high-nutrient soils (Pérez-Harguindeguy et al., 2013; Rossatto and Kolb, 2013; Rossatto et al., 2015), indicating that the determinant factor that characterize leaf traits between the semideciduous forest (high specific leaf area and thinner leaves) and other vegetation types can be nutrient availability.

We also found that species in all vegetation types showed a positive relationship between leaf N concentration and SLA. We believe that closed-canopy species use this strategy to ensure greater resource acquisition, maximize photosynthesis and invest in rapid primary growth, revealing competitive (higher trees) and efficient resource capture strategies (higher SLA) (Grime, 1983; Cornelissen et al., 2003; Casas et al., 2011; Marimon et al., 2014). On the other hand, photosynthetic maximization for open-canopy species is less efficient due to their thicker leaves (Table 3). Therefore, species in habitats with low water availability and limited nutrients usually invest in maximizing the conservation of resources, investing in nutrient remobilization, allowing species to store nutrients to use early in the next growing season and begin rapid and sustained growth (Wilson et al., 1999; Weatherall et al., 2006; Netzer et al., 2017).

Furthermore, species from open-canopy environments invested in higher leaf thickness that helps reduce leaf damage caused by herbivores and increases leaf lifespan (Grime, 1983; Bündchen et al., 2015). Interestingly, species from the cerradão showed markedly similar traits compared to species from cerrado rupestre and typical cerrado, such as SLA, TRD, and P, K, Ca and Mg leaf contents on an area basis (Table 3), indicating a convergence of ecological strategies in response to different environmental drivers. These findings reinforce the idea that cerradão is typical to contact areas between savannas and forests (Ratter, 1993; Marimon-Junior and Haridasan, 2005), especially in the Amazonia–Cerrado transition (Marimon et al., 2014; Marques et al., 2020). These different combinations of ecological strategies in *cerradão* can be advantageous in dealing with different environmental pressures, an essential condition for species persistence over time.

The positive relationship between N leaf tissue concentrations and stomata density for cerrado rupestre and cerradão species may suggest a stronger pressure to optimize resources in these vegetations because it is a low-cost combination to acquire the resources, particularly water, and nitrogen, probably to maximize photosynthesis (Wright et al., 2003). Moreover, P and stomata size scaled positively, but only for forest formations, where plants should invest in primary growth to reach the canopy and compete for light. Whereas P limitation is associated with lower wood density and greater hydraulic conductivity (De Dios et al., 2013), the coordination between P availability and stomata size in low-P soil and light-limited vegetation might be a key adaptation for closed-canopy environments. Thus, the interaction between nutrients and water availability may have critical implications for the future distribution of plants and their responses to increasing drought severity and length (Cramer et al., 2009). Notably, the similar leaf nutrient concentration on a mass basis (Table S2) and similar stomata density (Table 3) between trees of all vegetation types suggest some common environmental drivers, such as likely nutrient limitation and climate seasonality, which may be expected in a transition zone characterized by ecological tensions (Furley and Ratter, 1988; Ratter, 1993; Marimon et al., 2006; 2014; Oliveras and Malhi, 2016).

Therefore, our results demonstrate that species adopt different functional strategies to maintain themselves in distinct and adjacent vegetation types in the Amazonia–Cerrado transition. Our results highlight the importance of the interaction between the environment and functional traits to understand how selective pressures act on the functional diversity of tree communities in the Amazonia–Cerrado transition. Our study shows that functional traits play an important role in adapting to environmental gradients and help explain the performance of trees in the Amazonia–Cerrado transition, opening the door to a more accurate prediction of plant community responses over time.

CRediT authorship contribution statement

Igor Araújo: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft. **Marina C. Scalon:** Conceptualization, Methodology, Writing – review & editing. **Izabel Amorim:** Investigation, Methodology. **Imma Oliveras Menor:** Formal analysis, Writing – review & editing. **Wesley J.A. Cruz:** Formal analysis. **Simone Matias Reis:** Writing – review & editing. **Priscila F. Simioni:** Writing – review & editing. **Beatriz S. Marimon:** Conceptualization, Methodology, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Supplementary materials

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