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ANATOMICAL FUNCTIONAL TRAITS AND HYDRAULIC VULNERABILITY OF TREES IN DIFFERENT WATER CONDITIONS IN SOUTHERN AMAZONIA

[1, 2]Norberto G. Ribeiro-Júnior, [1]Ben Hur Marimon Junior*, [1]Beatriz S. Marimon, [1]Wesley J. A. Cruz, [3]Ivone V. Silva, [4]David R. Galbraith, [4]Emanuel Gloor & [4]Oliver L. Phillips

[1] **Programa de Pós-graduação em Ecologia e Conservação, Universidade do Estado de Mato Grosso**, Rua Prof. Dr. Renato Figueiro Varella, 78690-000 Nova Xavantina-MT, Brasil.

[2] **Diretoria Regional de Educação de Sinop, Secretaria de Estado de Educação de Mato Grosso**, Rua dos Lírios, 78500-007 Sinop-MT, Brasil.

[3] **Programa de Pós-graduação em Biodiversidade e Agroecossistemas, Universidade do Estado de Mato Grosso**, Avenida Perimetral Rogério Silva, 4930, 78580-000 Alta Floresta-MT, Brasil.

[4] **School of Geography, University of Leeds**, Leeds, LS2 9JT, UK.

* Author for correspondence:

Tel: +55 66 99919-4105 Email: bhmarimon@unemat.br

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ANATOMY AND HYDRAULIC VULNERABILITY OF AMAZON TREES

Abstract

Premise: Understanding tree species' responses to drought is critical for predicting the future of tropical forests, especially in regions where the climate is changing rapidly.

Methods: We compared the anatomical and functional traits of the dominant tree species of two tropical forests in Southern Amazonia, one on deep, well-drained soils (cerradão-CD) and one in a riparian environment (gallery forest-GF), to examine potential anatomical indicators of resistance or vulnerability to drought.

Results: CD species generally had thicker leaf cuticle, upper epidermis and mesophyll than GF, traits that are indicative of adaptation to water deficit. In the GF, the theoretical hydraulic conductivity of the stems was significantly higher, indicating lower investment in drought resistance. The anatomical functional traits of CD species indicate a greater potential for surviving water restriction compared to the GF. Even so, it is possible that CD species may also be affected by extreme climate changes due to the more water-limited environment.

Conclusions: As well as the marked anatomical and functional differences between these phytophysiognomies, tree diversity within each is associated with a large range of hydraulic morphofunctional niches. Our results suggest the strong potential for floristic and functional compositional shifts under continued climate change, especially in the GF.

Keywords: Brazilian Cerrado; cavitation; functional traits; leaf blade; Tropical Rainforest; water deficit.

INTRODUCTION

Climate change is affecting the structure and functioning of tropical forests worldwide, especially due to increases in drought and heat events (Flato et al., 2013; Hubau et al., 2020), which are also key factors driving the increasing risk of ecosystem tipping points in Amazonia (Brando et al., 2014; Lovejoy and Nobre, 2019). While models have related morphological and physiological characteristics to the resilience of plants to some of these variations (Fortunel et al., 2019), more information is required on anatomy of plant tissue and related anatomic functional traits (e.g., stomatal properties) to determine how these characteristics interact to influence hydraulic performance of plants during drought (Bartlett et al., 2016). Few studies have assessed how anatomy of wood and leaf tissues of tropical tree species respond to climate change, especially under high temperature and low water availability (Bonan, 2008; Binks et al., 2016). Anatomical and functional differences within and between tropical forests are associated with a wide variety of hydraulic morphofunctional niches, with wetter soil species being hydraulically more homogeneous. This condition may be a 'risk factor' for such communities (Sperry and Love, 2015), suggesting a strong potential for large changes in floristic and functional composition if and when droughts and climate change dries these soils.

In recent decades, there has been widespread increases in tree mortality in Amazonia in response to severe drought (Phillips et al., 2009; Rowland et al., 2015; Jiménez-Muñoz et al., 2016, Hubau et al., 2020) and temperature increase, especially in Southern Amazonia (e.g., Esquivel-Muelbert et al., 2019, Nogueira et al., 2019, Meira Junior et al., 2020). These climate-induced changes are concerning, given the major roles that tropical forests play in the regulation of the global climate system (Pan et al., 2011, Spracklen et al., 2012), which are critical for global water and carbon cycles due to the large geographic extent and high productivity of tropical forests (Giardina et al., 2018). In order to better infer the vulnerability of tropical vegetation to climate change, and particularly to repeated droughts, it is necessary to understand better the anatomy of the wood and leaf tissues of the tree species that dominate in Amazonia, particularly for those growing close to the current climatic edge of the biome.

The Amazon is highly heterogeneous, with its forests varying in structure, floristic and functional composition, and dynamics (ter Steege et al., 2006; Quesada et al., 2012; Esquivel-Muelbert et al., 2020). This is especially so in the Southern and Southeastern border in contact with the Cerrado biome (savanna), a huge ~6000 km belt known as the Amazonia/Cerrado transition (ACT) (Marques et al., 2019). The climate in the ACT is strongly seasonal with the vegetation composed of a complex mix of different, hyperdynamic forests and savannas (*sensu* Marimon et al., 2014) existing in a mosaic of savanna-forest contacts (Marques et al., 2019). Among these phytophysiognomies, “cerradão” represents a unique, filtered mix of forest and savanna tree species (Marimon et al., 2014) growing in well-drained soils with species adapted to drier environments prevailing and together acting as a “border barrier” that protects the core forest against the impact of extreme climate and fire (Marimon-Junior et al. in revision). The absence of fire and higher soil clay content than the adjacent cerrado (savanna facies) facilitates the establishment of forest species such as the hyperdominant *Tachigali vulgaris* and *Emmotum nitens* (Marimon-Junior and Haridasan, 2005). Similarly, those soils with the greatest water availability in the ACT along streams also act as a different species filter, with niche selection favouring the establishment of those adapted to greater soil water availability (Elias et al., 2019). These particular conditions generate the riparian vegetation known as “gallery forests”, which play important roles not least because of their ecological function of protecting watercourses (Wantzen et al., 2012).

Several studies have attempted to understand how tree species respond to environmental stressors acting together at a local scale, especially under conditions of higher temperatures and decreased water availability (e.g., Tyree and Ewers, 1991; Cochard et al., 2008; Bieras and Sajo, 2009; Markesteijn et al., 2011; Binks et al., 2016; Blackman et al., 2018). Such local-scale information can contribute for regional-scale understanding of stress, tipping point vulnerability, growth and adaptability of tree species to future scenarios. However, there are insufficient studies and data on how the dominant plant species here differ in hydraulically important aspects of plant tissue anatomy, including density and diameter of stem xylem vessels, cuticle thickness, epidermis, leaf parenchyma and stomatal density (Cetin et al., 2018).

Indeed, the whole tropical forest-savanna contact zone between South America's two largest biomes remains chronically understudied. In the face of a rapidly changing climate impacting a region which is already naturally dynamic in its floristic composition, the southern Amazon forest-savanna transition represents a globally-critical natural laboratory to investigate impacts of climate and climate change. Already highly seasonal, warming and drying rates in this region are much greater than other regions of the Amazon (Tiwari et al., 2020). The high seasonality of the ACT (Marimon et al., 2014) may be expected to act as a strong filter to favor tree species with anatomical-functional adaptations of the leaf and wood tissue that prevent excessive water losses by transpiration. Such a niche-selection effect may reach its extreme in locally enhanced conditions of environmental stress, particularly where low soil water availability combines with high temperatures (Poorter et al., 2010), especially at mean maximum temperatures above 32°C, beyond which forest biomass declines rapidly (Sullivan et al., 2020). Since water deficit in leaf tissue affects many physiological key processes (e.g., photosynthesis and respiration) (El Aou-ouad et al., 2017), trees in the ACT must deal with strongly contrasting water availability between the dry and wet seasons, adjusting water losses by plasticity in cell-tissue characteristics (Bastias et al., 2018). Xylem cavitation resistance may also be an important factor for many tree species to prevent hydraulic failure in the cell-tissue system (Cochard et al., 2008; El Aou-ouad et al., 2017). Or even without investing in water use regulatory strategies, many species may have been selected over time due to leaf deciduousness to avoid desiccation (Kunert et al., 2021) and thus overcome the period of greatest water stress of the ACT. This study aimed to evaluate the hydraulic anatomical properties of ACT-dominant tree species in two forests environments. We compared the anatomical functional traits of ten dominant tree species in a seasonally dry (cerradão forest) with ten dominant tree species in an environment with less water deficit during the year (gallery forest), and used these to address the following questions: (i) Which morpho-anatomical characters differ among dominant tree species in these communities? (ii) Does the lower level of water deficit in the gallery forest favor species with more efficient resource acquisition and utilization strategies, selecting non-xeric anatomical characteristics? To answer these questions, we tested the following hypotheses: (i) tree species of seasonally water-limited forests in ACT exhibit leaf and woody anatomical adaptations to water restrictions similar to those of tree species from seasonally water restricted savannas; (ii) trees from forests in ACT with more abundant water, such as gallery forests, possess an anatomical pattern of mesophytes, without desiccation-tolerant tissues of leaves and stems, such as large proportion of palisade parenchyma and fibers.

MATERIAL AND METHODS

Study sites

The gallery forest is located on the banks of the Bacaba Stream, in the Bacaba Municipal Park (BMP) (14°43'06.5“S, 52°21'43.1“W), municipality of Nova Xavantina, State of Mato Grosso, Brazil, Central South America (Fig. 1). The annual temperature and rainfall in the BMP vary between 26ºC (± 5.1) and 1500 mm (± 220) (Alvares et al., 2013). The Bacaba Stream has perennial flow, providing vegetation with more regular water availability throughout the year. The site has a litholic neosol, with rocks exposed at various points and is well-preserved from human activity. The stream arises out within the limits of the BMP, crossing throughout the 492 ha conservation unit (Elias et al., 2019).

[FIGURE 1]

The cerradão (augmentative of cerrado in Portuguese) is located in the municipality of Ribeirão Cascalheira, State of Mato Grosso (12°49'22.1“S, 51°46'13.5“W), with almost identical climate, with a mean annual temperature of 26ºC (±4.5) and rainfall of 1600 mm (±200) (Alvares et al., 2013). It has a continuous canopy, understory vegetation and no grasses (Marimon et al., 2014). Unlike the gallery forest, it occurs on interfluvial land, characterized by severe water shortage in the dry months, which we will denote here as having a seasonal water deficit (SWD). The cerradão site predominantly consists of primary forest, with no obvious signs of human activity and is within a private area. The tree species and forest structural characteristics can be found in Marimon et al. (2006) and Passos et al. (2018). The climate in both areas is continental Köppen Aw, with two well-defined seasons, a rainy season from October to March and a dry season from April to September, with significant inter-seasonal variability in temperature and water availability.

Sample Collection and Processing

Fieldwork was conducted from March to October 2017, the dry season in the region, by sampling the ten most representative tree species from each area according to the Importance Value Index (IVI) which takes into account the relative frequency, abundance and dominance of each species in the community (Mueller-Dombois and Ellenberg, 1974) (Table 1). We randomly selected five adult individuals of each species (> 10 cm diameter at breast height - DBH) between 12- and 15-meters height in a permanent well-preserved 1-ha plot of each community, Cerradão and Gallery Forest. The two permanent plots belongs to CNPq/PELD- Amazon Forest Transition Project and the RAINFOR Network (www.rainfor.org) and were both re-measured three times between 2008 and 2018 at three- to five-year intervals for vegetation dynamics studies.

[TABLE 1]

We collected at least three leaves and one stem sample (branch) from the canopy base of each individual, totaling 15 leaves/species/site and five stems/species/site. Leaves with the least amount of damage caused by herbivores or pathogens and fully expanded were used, thus minimizing effects of leaf development stage on its size. The leaves were pressed and dried in the field and young stem samples about 5 cm long and 1.5 cm in diameter were taken from the same leaf collection branch and stored in 70% ethanol bottles for transport.

In the laboratory, leaf area of samples was measured with a Licor 3100 leaf area meter, and leaf dry mass content was measured on a precision balance. All leaves were thereafter rehydrated following Smith and Smith (1942), where we immersed the samples in water at 90ºC and glycerin (3:1) in a beaker, allowing it to cool naturally and rest for 12 hours. For leaf tissue analysis, cross sections were made in the center region of five individuals per species (three leaves/individual/species/site) by random sampling.

Sections were stained with astra blue and basic fuchsin (Kraus et al., 1998). From the centers of the same leaves, samples of the leaf blade with approximately 2 cm^2 were taken and the epidermal adaxial and abaxial surfaces were distinguished through the modified Jeffrey dissociation method (Johansen, 1940), in which we stained with basic fuchsin (Kraus and Arduin, 1997), and mounted on histological slides with glycerinated gelatin for photographic recording and Entellan® for storage.

The stem samples were split in half and one part was boiled (water + glycerin, 3: 1) for 2 days on average for softening and microtome sectioning (Kraus and Arduin, 1997) with 12 to 20 µm sections. The sections were subjected to alcohol dehydration and basic fuchsin staining (Kraus et al., 1998). The processed stem samples were then cooked in a solution of hydrogen peroxide glacial and acetic acid (1:1, 75 ºC) for complete softening and subsequent maceration (Kraus and Arduin, 1997). The fragmented material was washed in running water and stained with 1% aqueous safranin. All histological slides of stems were mounted on glycerin (Purvis et al., 1964) for photographic recording and permanent slides with Entellan® for storing.

From the histological slides, photomicrographs with magnification of 100, 200 and 400 times were taken by means of the Leica® Digital Image capture (LAS E.Z. 1.7.0), coupled to a Leica® ICC50 microscope. In the photos, we measured the tissues with the aid of Anati Quant 2® UFV (Aguiar et al., 2007) and Image J software. The evaluated functional traits are listed in Table 2.

[TABLE 2]

From the initial measurements we calculated SIND (Stomatal index) with the equation SIND = NS/(EC + NS), where NS is the number of stomata and EC the number of epidermal cells per mm^2 (Cutter, 1986). SLA (specific leaf area) was calculated as $SLA = \frac{LA}{LDM}$, where LA is leaf area and LDM is leaf dry mass. PP-SP (Leaf blade parenchyma ratio) was calculated as $PP \cdot SP = \left(\frac{PALI}{PALI+SPON}\right) * 100$, where PALI corresponds to the thickness of the palisade parenchyma and SPON to the thickness of the spongy parenchyma. K$_h$, the theoretical hydraulic conductivity (in kg m MPa^{-1s-1}) was calculated according to Hagen-Poiseuille law, following Tyree and Ewers (1991) and Poorter et al. (2010) as $K_h = (\pi \ * \ p_W \ / \ 128^{\eta}) * XDEN * \ D_h^4$, where ρ_w is the density of water at 20 ºC (998.2 kg m^{-3}), η is the viscosity of water at 20 ºC ($1.002 \cdot 10^{-3}$ Pa s), XDEN is the vessel density (vessels mm^{-2}) and Dh is the hydraulically weighted vessel diameter (mm). Dh was determined by the average diameter in mm of 30 xylem vessels with the equation $D_h = (\Sigma d^4 \,/\, N)^{1/4}$, where “d” is the diameter of each vessel and “N” the number of vessels measured per sample. We determined the diameter of each vessel in photomicrographs of 100x and 200x magnification. For the cases of elliptical vessels, we estimated the diameter by the average of the lengths of the smaller and larger axes.

Data analysis

We rescaled the data and centered them around the zero mean before analysis. We calculated the correlation between anatomical-functional attributes with the function *correlation()* from the R *correlation* package (Makowski et al., 2020) in each forest independently to check for differences in configuration and tissue organization between the communities. In addition, we generated three other correlation matrices. One matrix included with the total quantitative data of the species of both sampled forests. The other two matrices contained data from either evergreen or deciduous species. This classification of evergreen or deciduous was based on data from herbaria accessed via Flora e Funga do Brasil (2022) and served to investigate possible patterns for the entire data set or for each phenological group. We determined the statistical significance of strong correlations (greater than 0.7) using adjust the p-value for multiple comparisons with false discovery rate correction (fdr) and we highlight strong correlations with p-value < 0.001.

To better understand how plant functional attributes varied across species and communities, we ran a PCA (Principal Component Analysis, on the dataset where Species were in rows and Traits in columns) using the function *PCAmix()* in the *PCAmixdata* package (Chavent et al., 2017), then extracted the PCA axis scores. We tested whether the PCA axes were composed of statistically different samples between the two forests by applying a Student's t-test on the PCA axis scores. As the distribution of residuals did not meet normality assumptions, we applied the Mann-Whitney test using the function *wilcox.test ()* with Bonferroni correction of the same R package. Finally, we calculated the effect size with the *kruskal_effsize ()* function of the rstatix package (Kassambara, 2020). We also constructed four other PCAs with subsets of our filtered data: (1) Cerradão, (2) Gallery, (3) Evergreen species, and (4) Deciduous species. We then applied the same score extraction procedure and Mann-Whitney test. We also used the Mann-Whitney test with Bonferroni correction by quantitative functional trait comparing the samples from the two forests.

To understand the variable distribution for the key traits, we fitted linear mixed models for each response variable using the *lme()* function of the nlme package (Pinheiro et al., 2021). In each model we included forest, phenology (evergreen versus deciduous), species and individual as nested random factors, to assess how the variability of characteristics was distributed among these different levels of organization (Rosas et al., 2019).

RESULTS

In the cerradão, which experiences a seasonal water deficit (SWD) due to rainfall seasonality interacting with deep, freely draining soils, we detected few strong correlations between the functional traits. The only association that occurred exclusively in the cerradão was a positive correlation between thickness of the upper leaf epidermis and fiber thickness of the midrib (ADEP x MIDF). In the gallery forest (non-SWD), more traits were more clearly associated with one another. This includes positive correlations between the thickness of the leaf abaxial epidermis (ABEP) and palisade parenchyma (PALI), ABEP and the contribution of the palisade layer to total parenchyma thickness (PP-SP), PALI and the thickness of the mesophyll (MESO), PALI and PP-SP, in addition to a negative correlation between PALI and the thickness of the spongy parenchyma (SPON). All of these relationships are exclusive to the gallery forest. These correlations between the functional anatomic traits measured in each forest were thus very distinct, revealing important differences in the structure of plant tissues in the two communities (Table 3, Appendix S1; see the Supplementary Data with this article). The forests also showed some similar patterns of correlation that are noteworthy, such as the positive correlations between density (SDEN) and stomatal index (SIND), SPON and MESO, leaf dry mass (LDM) and leaf area (LA), theoretical hydraulic conductivity (K_h) and mean area of the vessel lumen (XARE). In the principal component analysis (PCA) combining leaf and stem functional traits, the first five axes explained a cumulative 56.67% of the variation. SLA, PALI, ADEP and MESO contributed most to axis 1, being the most relevant for the graphical separation of the samples (Fig. 2, Appendix S2); the central fibers midrib (MIDF), trichome density (TRIC), ABAC and mean lumen area of xylem vessels (XARE) were the most relevant to axis 2.

[FIGURE 2]

[TABLE 3]

We detected a significant difference between the cerradão and gallery forest communities by statistically comparing the PCA axes scores (Fig. 2). In PCA, scores of functional traits of the cerradão tended to be higher than the gallery forest (axes 1 and 3), however traits such as SLA, LDM and SDEN, which are greater in the gallery forest, mitigate the differences (Fig. 3). The differences are not only quantitative but visually clear too (Fig. 4), with distinct patterns for epidermis and mesophyll of the leaf blade observed for both forest types. Many functional traits differed strongly between sites, indicating adaptive differences of the tree species. Notably, cerradão species are endowed with thicker leaves, reflecting greater thickness of the adaxial epidermis for some species, and photosynthetic parenchyma. Meanwhile, in two species of the gallery forest (*Apuleia leiocarpa* and *Hymenaea courbaril* – deciduous and semi-deciduous, respectively) there is greater investment in palisade parenchyma (Figs. 3 and 4). The differences among stem functional traits are less evident, with the species of cerradão having longer fibers (FIBL) and species of gallery forest having higher values of theoretical hydraulic conductivity (K_h). Although four species have K_h higher than 100 kg m $MPa^{-1}s^{-1}$, the main species responsible for the greater mean K_h was *Mabea pohliana* (Fig. 4), which had much wider vessels than other species. Other gallery forest species such as *A. leiocarpa, H. courbaril* and *P. gardneri* also had xylem ducts diameters that contribute to high mean values of the vessel lumen area (XARE) of the gallery forest community (Fig. 5J-K).

Considering species leaf deciduousness and analyses by subgroup, both evergreen and deciduous species differed significantly in investment in morphoanatomical structures between forests. The traits with greater contribution to separating the groups in the PCA of the evergreen species are MESO, PALI, and SLA. For deciduous species, the traits SLA, PALI, MESO, ABEP, and XARE contributed most (see Appendix S3).

The partition of variance by models revealed a high environmental influence of environment on the traits that most contribute to the PCA axes (SLA 46.4%, PALI 52.1%, MESO 52.1%, and ADEP 24.5%). At the same time, the phenology (evergreen versus deciduous) was associated with investment in photosynthetic tissues (MESO, SPON, and PALI) and stomatal density (SDEN). The influence of species on variation in each trait evaluated is relevant and predominant in most functional traits and PCA axes (except axis 1, which accounted for 65% of the variation explained by the environment. We highlight here the low intraspecific variance identified in most of the characters and in the variance of the PCA axes (Fig. 6).

[FIGURE 3]

[FIGURE 4]

[FIGURE 5]

[FIGURE 6]

DISCUSSION

The low number of significant correlations among functional traits of the cerradão community related to seasonal water deficit indicates a diversified pattern of investment in the stem and leaf tissues of the dominant species of this community. This is consistent with a decoupling of the leaf economy and stem hydraulic safety functional spectra (Baraloto et al., 2010; Braga et al., 2016) (Table 3 and Fig. 2A). The hypothesis that the leaves of the cerradão community would exhibit xeromorphic characteristics was clearly supported, indicating selection of species based on soil water availability. However, contrary to our expectations, such selection or niche variety also allowed the establishment of species with more conservative strategies in the gallery forest community, where xeromorphic traits were also present in several species. This is evident when analyzing the stomatal index (SIND) and the fiber distribution in the leaf blade (MIDF and SSE) (Fig. 3).

An explanation for the surprising occurrence of xeromorphism recorded in the gallery forest may be that the site itself is heterogeneous, including an upper, well-drained slope with outcrop of sandstone rocks dominated by large tree species such as *Apuleia leiocarpa* and *Hymenaea courbaril*, which have more xeric characteristics. In the other gallery forest species, anatomical-functional traits are less related to drought tolerance, responding positively to the water availability of the ecosystem that guarantee regular water supply with low need to investment in hydraulic safety. Larger vessels and smaller proportions of adaxial epidermis and palisade parenchyma, are characteristics of plants with some degree of leaf deciduousness, where the senescence of leaves in the dry period of the year is a strategy to prevent water loss by the plant (Ribeiro et al., 2022). We emphasize that seven of the ten species from the gallery forest exhibit some degree of deciduousness (deciduous or semi-deciduous).

Even so, the dominance of the relatively xeric *A. leiocarpa* and *H. courbaril* in the upper slope of the gallery forest is an indication that dry conditions can promote the replacement of dominant species of the gallery forest with others originally from drier forests. We note that tropical dry forests are characterized by an abundance of species with more plastic hydraulic functional traits, especially deciduous species, than those of more humid forests (Aguirre-Gutierres et al., 2019). The species *A. leiocarpa* and *H. courbaril* have deciduous behavior (Appendix S4), although during our sampling we observed these plants to retain abundant leaves in their canopy in the dry season. Considering the 20 tree species that we used as representatives of gallery forests and cerradão, we have a similar ratio of evergreen:deciduous species. Although leaf deciduousness can strongly explain seedling death in tropical forests (Poorter and Markesteijn, 2008), for adult trees the explanation tends to be much more complex (Kunert et al., 2021). Microstructural information such as that presented in this study can help understand how deciduous trees are distributed and affected by increased water stress resulting from climate change.

Such variation of flora related to the variation of relief in the landscape of the study area is consistent with floristic sensitivities recently described by Elias et al. (2019), where tree species micro-distributions correspond with edaphic and topographic variation. The consistency between floristic, functional, and plant tissue variation shows that the key factor organizing communities on a landscape scale here is the hydrological niche. More widely, the diversity of functional characteristics of tree species in a community is related to the ability of each species to deal with environmental stressors (da Costa et al., 2010; Bartlett et al., 2012; Binks et al., 2016), including for congeneric species that coexist in similar environments (Markesteijn et al., 2011; Castagneri et al., 2017). It is also relevant that individuals of the same species growing on environments with higher water seasonality in the Cerrado may present functional traits with less efficient strategies for water transport and safer against embolism when compared to individuals with continuous water abundance (Sonsin et al., 2012). This can be attributed to the phenotypic plasticity that several Cerrado species exhibit (Ariano et al., 2022).

Turning now to the individual anatomical and hydraulic traits, the higher specific leaf area (SLA) that characterizes our gallery forest species (Fig. 3) can be attributed to satisfactory water availability throughout the year, and may explain the higher water use efficiency for savanna (Hoffmann et al., 2005) and cerradão species. Lower SLA is common in nutrient-poor environments, probably because it allows for longer leaf longevity and higher nutrient-use efficiency, improving carbon balance under warmer and drier conditions and thus increasing the tree survival rates (Sakschewski et al., 2016). High SLA combined with high water availability, high solar irradiation and high surface temperature are further associated with shorter leaf pay-back time (Niinemets, 2001), potentially allowing for faster carbon capture in the gallery forest. Environmental factors combine with the high occurrence of deciduous species in the gallery forest and the potential phylogenetic conservatism of the SLA trait (see Appendix S5), contributing to the competitive ability of these species.

Stomatal density (SDEN) is an important ecophysiological parameter in plant response to various environmental factors. These include drought tolerance (Larcher, 2004) and it is commonly related to water stress by several authors (Cutler et al., 1977; Fahn and Cutler, 1992; Cetin et al., 2018), although others instead relate SDEN to the light intensity that penetrates the canopy (Binks et al., 2016; Simioni et al., 2017). Here, given that the canopy structure is continuous and similar in both cerradão and gallery forests, and that the cerradão has reasonable water retention capacity in soils (Marimon-Junior and Haridasan, 2005), the predominance of higher SDEN in the gallery forest, , despite the large variation for this community suggests that species that are excellent competitors under high supply of resources (water) predominate there. Despite similar SDEN values for the tree species of *Pouteria*, the trait does not show a tendency for phylogenetic conservatism (see Appendix S5). Thus, we assume that, despite the evolutionary history and phylogenetic relationships having an influence on the formation of these communities (see Appendix S5), the pattern of the anatomical-functional characters can be decisive for the maintenance or replacement of these species in the places where they occur, considering that variation in phylogenetic divergence and ecological differentiation are not necessarily correlated (Rios et al., 2014).

While there is no direct evidence that the two communities studied are severely affected by water deficit, the soils of the cerradão ecosystem are clearly drier than the gallery forest (Elias et al., 2019). The predominance of larger, supra-epidermal structures, such as thick cuticle and dense presence of tector trichomes in the cerradão, may be among the main morphological functional traits responsible for the water conservation of this vegetation. Tector trichomes are associated with possible reduction of water loss by evapotranspiration and leaf blade heating (Larcher, 2004), and may inhibit phytophagous animals (Theobald et al., 1979). These structures and their diversity are widely recorded in anatomical descriptions of Cerrado (Brazilian savanna) trees (Beiguelman, 1962; Bieras and Sajo, 2009; Ariano and Silva, 2016; Simioni et al., 2017, Ariano et al., 2022) and are described among the physiological mechanisms that limit water loss, even when not subjected to severe water stress. The presence of high xeromorphism in the Cerradão is further evidence of the successional process that can occur in cerrado *strictu sensu* under soils that can provide some nutritional support to larger plants, such as trees (Marimon-Junior and Haridasan, 2005), and are not exposed to fire.

The greater thickness of leaf lining tissues and potential water storage tissues (hypodermis or thick epidermis) in the cerradão community here are known to be relevant for maintaining leaf physiological stability (Larcher, 2004) and are proportionally larger in forests with lower water availability (Sugden, 1985) when comparing groups along rainfall gradients or at very different water availability sites (Bieras and Sajo, 2009; Ariano and Silva, 2016; Binks et al., 2016; Simioni et al., 2017; Cetin et al., 2018). These epidermises tend to be composed of thicker-walled cells, and cases of epidermal sclerification are reported (Fahn and Cutler, 1992; Bieras and Sajo, 2009), found here in *Roupala montana* of the cerradão community. Possession of a hypodermis layer, as we found for *Brosimum virgilioides* (Morretes and Ferri, 1959;

Ferreira et al., 2015), has been reported in some Cerrado tree species (Metcalfe and Chalk, 1950; Bieras and Sajo, 2009) to be important for leaf water storage.

The PP-SP (leaf blade parenchyma) ratio of each habitat reveals a higher occurrence of spongy parenchyma in the gallery forest species and, moreover, the leaf blade mesophyll is composed of conspicuous intercellular spaces (Fig. 5 D, F). In this case, the larger amount of spongy parenchyma in the leaf blade is associated with the lower investment in hydraulic safety and drought resistance (Binks et al., 2016) and a more efficient resource acquisition strategy for deciduous plants (Ribeiro et al., 2022). Palisade parenchyma (PALI) values ≥ 50% are commonly recorded in neotropical savanna trees (Bieras and Sajo, 2009; Ferreira et al., 2015; Ariano and Silva, 2016; Simioni et al., 2017) and this functional trait is associated with direct sun exposure, being able to distribute light more evenly across leaf layers (Vogelmann, 1993) and facilitate CO_2 uptake while maintaining photosynthesis under dry conditions (Oliveira et al., 2019). The presence of greater proportions of palisade parenchyma in the cerradão may be associated with greater light penetration through the canopy or even more efficient control of water transport in leaf tissues in plants under water stress (Scoffoni et al., 2017), therefore decreasing the risks of embolism in the stem. The leaf blade mesophyll is also thick for most cerradão leaves (Fig. 5 A-C), and as there is less space among cells, it is reflected in the larger dry mass of leaves of this community. There are other factors that contribute most strongly to the leaf dry matter (DM) composition, but as there is no large difference in the amount of fiber (MIDF) between the habitats, PALI seems to be decisive in contributing to DM.

Leaf succulence is strongly correlated with leaf mesophyll thickness (Niinemets, 2001) and can be calculated from the amount of leaf blade parenchyma. Ecophysiologists attribute leaf succulence to the organ's water storage capacity (Schwinning and Ehleringer, 2001; De La Riva et al., 2016), with high values usually associated with xerophytes. Consequently, we infer that cerradão plants tend to accumulate more water in their leaves. As well as properties that confer moisture retention in leaves, we need to evaluate the mechanisms for water transport to the canopy. Conductive ducts, vessels and tracheids are the connecting routes and must promote such transportation in a safe manner capable of keeping an intact column of water under negative pressure (Rowland et al., 2015; El Aou-ouad et al., 2017).

A key issue to be addressed in relation to plant tissue and environmental stressors is the relationship between a plant's hydraulic architecture, its ecological niche and cavitation vulnerability (Tyree and Ewers, 1991). Gleason et al. (2016) compiled data from dozens of studies and identified a weak correlation between safety and hydraulic efficiency in vessels. More curious is the fact that the authors identify several species that have low efficiency and low hydraulic safety. In our analysis, we discovered that many gallery forest species invest little in drought resistance, considering the K_h (theoretical hydraulic conductivity) which depends directly on vessel diameter. There are relevant differences between the xylem vessel diameter of the species, where narrow conducting vessels tend to provide greater hydraulic safety for dry forest trees (Markesteijn et al., 2011), therefore greater drought resistance. This is clearest for the cerradão species, which have a smaller average vessel lumen area (XARE) than the gallery forest species, except for *Aspidosperma subincanum*. This exception compensates partially for low XARE values with a vessel density of three to four times higher than other species of the same phytophysiognomy, which confers decreased potential conductivity and greater safety against vessel embolism (Gleason et al., 2016). Species in which xylem ducts diameters contribute to high mean values of the vessel lumen area (XARE) (e.g., *A. leiocarpa*, *H. courbaril* and *P. gardneri* of the gallery forest) demonstrates the importance of evolutionary factors and which individual characteristics of species are determinant in the formation of plant communities. While we detected consistent variation in theoretical hydraulic conductivity (K_h) in each habitat, the highest values were found in gallery forest species and the lowest in cerradão species (Fig. 5 G-L). High conductivity is a sign that the species of the gallery forest species are not consistently adapted for greater hydraulic safety, especially if we consider that the thickness and density of xylem vessels exhibit a high phylogenetic signal (see Appendix S5), indicating potential vulnerability to an increase in the frequency and intensity of drought and heat events in the region. Given that drought intensity and frequency is already increasing in southern Amazonia (Sullivan et al., 2020), and that deforestation and other destructive land use in the interfluves can also affect gallery forests, including by reducing the water table (Bruijnzeel, 2004), there is a risk that the current combination of land misuse with climate change may prove fatal for many tree species in the remaining gallery forests.

As for xylem fibers, the species with predominance of longer fiber length (FIBL) and thickness (FIBT) are common in the cerradão, and many of them occur in Cerrado savanna (*Myrcia splendens*, *Emmotum nitens*, *Roupala montana*, *Qualea grandiflora, Pouteria ramiflora* and *Xylopia sericea*). The long fibers in hydraulic architecture of trees are commonly related to less resistance for support of xylem conduits, but with no direct relationship with cavitation resistance (Lens et al., 2011). It is possible that the mechanical properties of xylem fibers as well as other vessel-associated cell types interfere with the chances of vessel embolism (Jacobsen et al., 2005), but these interactions are not yet fully understood. Overall, the hydraulic architecture of the wood indicates a lesser vulnerability of the cerradão community in the likely event of an increase in the already naturally high climatic seasonality of the region, via increased frequency and intensity of drought and heat waves. However, this does not guarantee the survival of cerradão species, which may not withstand more severe drought periods, and there may be a strong change in the floristic composition of these communities due to species selection pressure in case of climate change. This is already possible when we analyze the population dynamics of these communities in the last decade (Table 4 – Prestes et al. in preparation). We note that Sullivan et al. (2020), analyzing how forest biomass varies spatially as a function of long-term climate, projected significant reductions in the forest carbon stocks in South America by reduced tree growth and by high temperatures and drought, which enhance mortality. Given that the most important tree species in gallery forest have anatomical characteristics clearly indicating higher daily water demand (e.g., non-xerophyte tissue), an increase in the frequency and intensity of dry events could also be fatal to these forests.

[TABLE 4]

The different hydraulic characteristics of gallery forest and cerradão that we find reflect how different functional traits contribute to both the diversification and the coexistence of species within tropical forests (Oliveira et al., 2019), corroborating the premise that different degrees and forms of adaptation and resistance to low water availability occur in the tropics (Bartlett et al., 2012). Here, our key discovery is the fact that interspecific variation in anatomical structures of the leaves and young stems of the gallery forest tree species is more uniform than in the Cerradão (Figs. 3-4), probably due to the resource acquisition capacity that allows greater productivity without the need to invest in hydraulic safety structures, mostly of high energetic cost. We thus demonstrate, as proposed by Sperry and Love (2015), 'risk factors' for the community. This makes the gallery forest, and perhaps all riparian communities, especially sensitive to the intensification of drought events. Even if species with deciduous strategies to avoid water loss occur in them.

CONCLUSIONS

Our analysis reveals that tree species from cerradão communities are endowed with greater anatomical-functional xerophytic adaptations than the dominant species of gallery forests. However, despite the structural and functional differences between the two groups, both may be vulnerable to more extreme climatic conditions, as the soils in the cerradão have limited water storage capacity. While the main anatomical properties of the dominant gallery forest species are not consistent with the likely level of hydraulic safety needed as climates warm and dry, the ability of leaf deciduousness to prevent excessive water loss and the phenotypic plasticity that these species may present still need to be investigated in detail.

Despite the predominance of xerophyte characteristics in the cerradão community and lower investment in hydraulic safety in the dominant gallery forest species, many anatomical and functional traits of these communities are similar and appear in species which are phylogenetically distant. Thus, the closeness of many values for the functional traits of the two communities reveals the strong environmental pressure exerted on the tree species composition on the wood and leaf tissue anatomy of both.

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AUTHOR CONTRIBUTIONS

N.G.R.J and B.H.M.J designed the study, B.H.M.J managed the field sample collections, N.G.R.J., J.A.C and I.V.S processed, analyzed and measured the plant samples. N.G.R.J. performed the statistical analyses and wrote the first version of the manuscript, which was intensively discussed and revised by B.S.M, E.U.G., D.R.G. and O.L.P.

DATA AVAILABILITY

Data are available from the Figshare Digital Repository: https://doi.org/10.6084/m9.figshare.20063096 and https://doi.org/10.6084/m9.figshare.20063264 (Ribeiro-Júnior et al., 2022).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information section at the end of the article.

Appendix S1. Pearson's correlation matrix for quantitative functional traits with the entire Cerradão and Galeria Forests dataset (a). Pearson's correlation matrix by subgroups of species considering deciduousness: Evergreen Species (b) and Deciduous Species (c).

Appendix S2. Output of the analysis of main components of mixed data accompanied by the percentage contribution of the traits anatomical-functional attribute for the axes.

Appendix S3. Figure and tables with PCA of the forests considering species deciduousness as a factor and statistical differences by species subgroups considering deciduousness.

Appendix S4. Qualitative characterization of six anatomical functional traits of tree species with the highest importance value index in two forest formations in southern Amazonia.

Appendix S5. Tables with phylogenetic signals (Pagel's Lambda, Blomberg's K and K star) of functional traits measured in the two forests and phylogenetic hypothesis for the species list based on backbone phylogeny.

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TABLE 1. The most frequent tree species in the permanent plots monitored by the CNPq/PELD Cerrado-Amazon Forest Transition Project (UNEMAT-NX) and the Amazon Forest Inventory Network (RAINFOR), showing number of individuals (N) with diameter ≥ 10 cm, total basal area in m² (BA) and relative dominance (D%) of the species in the community.

Cerradão					**Gallery forest**				
Species	**Family**	**N**	**BA**	**D(%)**	**Species**	**Family**	**N**	**BA**	**D(%)**
Xylopia sericea A.St.-Hil.	Annonaceae Juss.	73	0.30	13.54	*Aspidosperma subincanum* Mart.	Apocynaceae Juss.	17	0.09	3.35
Pterodon pubescens (Benth.) Benth.	Fabaceae Lindl.	50	0.24	10.91	*Protium heptaphyllum* (Aubl.) Marchand	Burseraceae Kunth	12	0.02	0.77
Mezilaurus crassiramea (Meisn.) Taub. ex Mez	Lauraceae Juss.	37	0.85	37.43	*Ephedranthus parviflorus* S.Moore	Annonaceae Juss.	11	0.01	0.60
Myrcia splendens (Sw.) DC.	Myrtaceae Juss.	33	0.01	0.59	*Tetragastris altissima* (Aubl.) Swart	Burseraceae Kunth	10	0.20	7.30
Emmotum nitens (Benth.) Miers	Metteniusaceae Schnilz.	29	0.07	3.35	*Apuleia leiocarpa* (Vogel) J.F. Macbr.	Fabaceae Lindl.	9	0.46	16.36
Pouteria ramiflora (Mart.) Radlk.	Sapotaceae Juss.	29	0.09	4.35	*Hymenaea courbaril* L.	Fabaceae Lindl.	8	0.65	22.99
Qualea grandiflora Mart.	Vochisiaceae A.St.-Hil.	19	0.04	2.07	*Unonopsis guatterioides* (A.DC.) R.E.Fr.	Annonaceae Juss.	7	0.30	10.80
Roupala montana Aubl.	Proteaceae Juss.	16	0.02	1.08	*Mabea pohliana* (Benth.) Müll. Arg.	Euphorbiaceae Juss.	7	0.01	0.39
Bowdichia virgilioides Kunth.	Fabaceae Lindl.	15	0.19	8.74	*Pouteria gardneri* (Mart. & Miq.) Baehni	Sapotaceae Juss.	7	0.09	3.17
Tachigali vulgaris L.G.Silva & H.C.Lima	Fabaceae Lindl.	12	0.05	2.49	*Pouteria torta* (Mart.) Radlk.	Sapotaceae Juss.	7	0.69	24.65

TABLE 2. Functional traits measured in order to compare the two tree communities.

Functional Trait	Symbol	Unit of measurement	Function *
Adaxial cuticle	ADAC	min / slim /mild / thick	Transpiration reduction and UV- B protection [1 2]
Abaxial cuticle	ABAC		
Presence of trichomes	TRIC	A /B / C / D	
Adaxial epidermis thickness	ADEP	μm	Conservation of water in the organ [1 3]
Abaxial epidermis thickness	ABEP	μm	
Stomatal index	SIND	%	Regulation of water loss and leaf respiration [1 4 5]
Stomatal density	SDEN	Stomata mm^{-2}	
Hypodermis	HYPO	yes / no	Conservation of water in the organ [1 3]
Substomatic chamber	SUBC	yes / no	Control of pressure on the leaf conducting vessels [6]
Spongy parenchyma thickness	SPON	μm	
Palisade parenchyma thickness	PALI	μm	Limit water loss, increase mesophyll capacitance and light diffusion under excess light [7 5]
Leaf blade parenchyma ratio	PP-SP	%	
Leaf blade mesophyll thickness	MESO	μm	
Sclerenchymatic sheath extension	SSE	out / being	Mechanical support for leaves exposed to wind [2]
Central midrib fiber thickness	MIDF	μm	
Specific leaf area	SLA	g cm^{-2}	Carbon assimilation and biomass investment in light capture [8 5]
Leaf dry mass	LDM	g	
Leaf area	LA	cm^{2}	
Xylem vessel density	XDEN	vessels mm^{-2}	Regulate the "down up" transport of water, hydraulic safety and resistance to cavitation [9 10 11 12]
Average lumen area of xylem vessels	XARE	μm^{2}	
Theoretical hydraulic conductivity	K_h	Kg m MPa^{-1s-1}	
Average fiber length	FIBL	μm	Assist in supporting xylem ducts and wood density [13 14]
Average fiber thickness	FIBT	μm	
Leaf Cycle	CYCLE	Evergreen / deciduous / semideciduous	Strategy to avoid or not to lose water in the dry season.

* Cited authors: [1] Cutter (1986), [2] Bieras e Sajo (2006) [3] Larcher (2004), [4] Binks et al. (2016), [5] Oliveira et al. (2019), [6] Scoffoni et al. (2017), [7] Vogelmann (1993), [8] Westoby et al. (2000), [9] Poorter et al. (2010), [10] Markesteijn et al. (2011), [11] Rowland et al. (2015), [12] El Aou-ouad et al. (2017), [13] Jacobsen et al. (2005) and [14] Lens et al., 2011).

TABLE 3. Pearson correlation matrix for quantitative functional traits of tree communities of cerradão and gallery forest formations. Bottom left diagonal – cerradão (seasonal water restrictions); Top right diagonal - gallery forest. See Table 2 for legends of functional traits. The Pearson correlation matrices with total data and by deciduousness subgroups are available in Appendix S1.

	Correlation cerradão								***Correlation gallery***								
	ADEP	**ABEP**	**SIND**	**SDEN**	**MIDF**	**PALI**	**SPON**	**MESO**	**PP/SP**	**SLA**	**LDM**	**LA**	**XDEN**	**XARE**	**K_h**	**FIBL**	**FIBT**
ADEP	-	0.60	0.15	0.34	0.10	0.43	-0.31	0.44	0.39	-0.32	-0.05	-0.24	-0.21	0.18	0.10	0.08	0.25
ABEP	0.24	-	0.15	0.27	-0.30	**0.70**	-0.65	0.62	**0.70**	-0.56	-0.09	-0.45	-0.28	0.33	0.12	0.03	-0.04
SIND	0.45	-0.08	-	**0.85**	-0.06	-0.06	-0.01	-0.11	0.06	-0.25	-0.22	-0.32	0.12	0.12	0.12	-0.32	-0.03
SDEN	0.09	-0.34	**0.78**	-	0.14	0.13	-0.20	0.05	0.24	-0.37	-0.11	-0.31	-0.03	-0.02	-0.05	-0.38	-0.03
MIDF	**0.74**	0.11	0.49	0.04	-	-0.36	0.42	-0.25	-0.35	0.03	0.23	0.28	0.18	-0.40	-0.24	-0.14	0.33
PALI	0.17	0.42	-0.13	-0.29	0.06	-	**-0.88**	**0.92**	**0.93**	-0.59	0.22	-0.21	-0.28	0.20	0.01	0.25	-0.19
SPON	-0.15	0.20	-0.23	-0.11	-0.12	-0.04	-	-0.62	**-0.96**	0.57	-0.05	0.33	0.41	-0.21	0.03	-0.12	0.24
M	-	0.3	-	-	-	0.4	**0.8**	-	**0.7**	-	0.3	-	-	0.1	0.	0.3	-

ESO	0.05	8	0.27	0.24	0.08	4	**8**		**5**	0.50	1	0.08	0.13	7	04	1	0.11
PP/SP	0.24	0.03	0.21	0.07	0.09	0.40	**-0.90**	-0.61	-	-0.69	0.12	-0.33	-0.35	0.21	-0.02	0.15	-0.19
SLA	-0.24	-0.24	-0.15	0.09	-0.27	-0.14	-0.51	-0.53	0.40	-	-0.19	0.42	0.20	-0.20	-0.10	0.03	0.14
LDM	0.33	0.24	-0.11	-0.24	0.29	0.12	0.25	0.28	-0.21	-0.24	-	**0.78**	0.26	-0.23	-0.09	0.07	-0.09
LA	0.26	0.13	-0.15	-0.21	0.20	0.03	0.04	0.05	-0.07	0.15	**0.90**	-	0.38	-0.35	-0.15	0.06	0.04
XDEN	0.26	-0.30	0.66	0.52	0.41	-0.35	-0.17	-0.33	0.01	-0.09	-0.08	-0.09	-	-0.56	-0.32	-0.32	0.13
XARE	-0.29	0.09	-0.43	-0.28	-0.35	-0.10	0.43	0.34	-0.42	-0.03	-0.13	-0.15	-0.39	-	**0.87**	0.34	-0.15
K_h	-0.29	-0.06	-0.19	-0.05	-0.27	-0.24	0.34	0.19	-0.41	0.00	-0.24	-0.24	-0.01	**0.90**	-	0.20	-0.21
FIBL	0.24	0.03	0.17	0.15	0.14	0.20	0.35	0.41	-0.21	-0.34	0.00	-0.13	0.12	0.16	0.18	-	0.16
FIBT	0.65	0.04	0.44	0.18	0.59	-0.04	-0.17	-0.17	0.20	-0.14	0.00	-0.04	0.29	-0.18	-0.15	0.35	-

Strong correlation (≥ |0.7) is highlighted in bold. Pairwise correlation analysis significance = $p < 0.001$).

TABLE 4. Number of individuals per species sampled in three consecutive censuses between 2008 and 2018. Only trees with DBH ≥ 10 cm were remeasured. Percentage variation from the first census (*Δ %*). Evergreen species are marked with 🍃 .

Forest	**Species**	*Census 1*	*Census 2*		*Census 3*		
			Death	*Recruit*	*Death*	*Recruit*	*Δ %*
Cerradão	*Bowdichia virgilioides*	15	0	0	1	0	-6.6%
	Emmotum nitens 🍃	16	1	7	0	11	106%
	Mezilaurus crassiramea	40	2	0	3	0	12.5%
	Myrcia splendens 🍃	18	0	11	9	7	50%
	Pouteria ramiflora	29	2	2	0	0	0%
	Pterodon pubescens	30	0	17	0	5	73.3%
	Qualea grandiflora	16	0	3	1	0	12.5%
	Roupala montana	13	2	5	1	0	15.3%
	Tachigali vulgaris 🍃	0	0	9	3	7	--
	Xylopia sericea 🍃	68	8	6	7	13	5.8%
	Average variation of species in the plot →						**29.8%**
Gallery	*Apuleia leiocarpa*	10	1	0	0	0	-10%
	Aspidosperma subincanum	33	2	2	1	1	0%
	Ephedranthus parviflorus	26	3	3	0	0	0%
	Hymenaea courbaril	8	0	0	0	0	0%
	Mabea pohliana 🍃	11	0	2	1	1	18.2%
	Pouteria gardneri	14	1	0	0	0	7.1%
	Pouteria torta	7	1	1	0	0	0%
	Protium heptaphyllum	21	1	4	0	0	14.3%
	Tetragastris altissima 🍃	18	1	3	2	0	0%
	Unonopsis guatterioides 🍃	16	2	0	2	2	12.5%
	Average variation of species in the plot →						**4%**

FIGURE 1. Study area in the Cerrado/Amazon transition, Brazil. Different shades of green represent the vegetations based on the original biomes mapping from RADAMBRASIL-IBGE project (IBGE 1982). Boundaries of Amazonia and Cerrado biomes are broken by bands of transitional vegetation. The map was generated in QGIS v.3.14 using background maps from the Brazilian Ministry of Environment's database (https://www.mma.gov.br/)

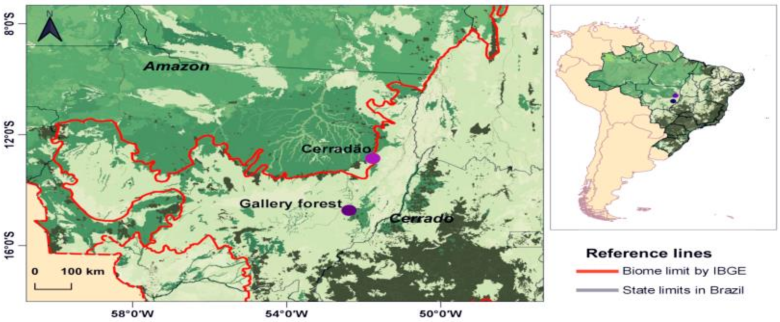

FIGURE 2. Principal component analysis (PCA) showing the distribution of functional traits vectors of cerradão and gallery forest (a). Axes with statistical differences by Mann-Whitney test (b). PCA by species subgroups considering leaf deciduousness (c) and (d). More details on the factorial load of the traits per axis – Appendix S2 (see the Supplementary Data with this article). PCAs by Forest and statistical difference by subgroups considering deciduousness – Appendix S3.

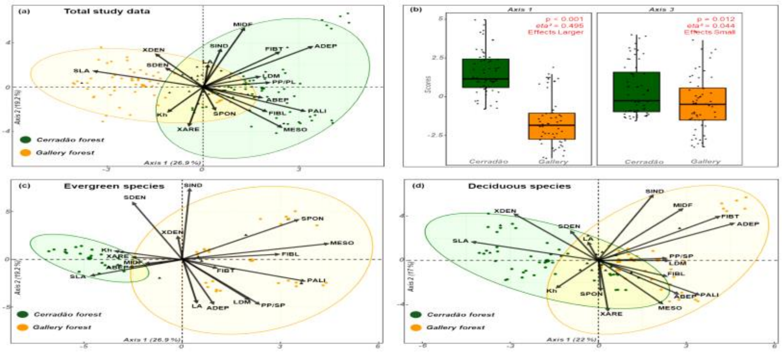

FIGURE 3. Main leaf traits measured in species from two forest of the Amazon-Cerrado Transition. ABEP = Abaxial epidermis thickness; ADEP = Adaxial epidermis

thickness; PALI = Palisade parenchyma thickness; SPON = Spongy parenchyma thickness. The traits highlighted with an asterisk (*) differed significantly in the Mann-Whitney hypothesis test when comparing the two forests. * = 0.05, ** = 0.001, *** = 0.0001 and ^{ns} = not significant. Evergreen species are marked with 🍃. See Supplementary Material for more details on the evaluated qualitative traits – Appendix S4.

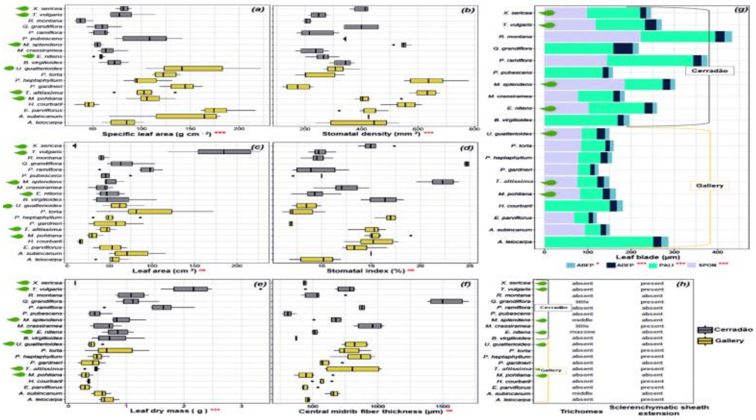

FIGURE 4. Xylem traits of the stem measured in the species from two forest of the Amazon-Cerrado Transition. The traits highlighted with an asterisk (*) differed significantly in the Mann-Whitney hypothesis test when comparing the two forests. * = 0.05, ** = 0.001 and *** = 0.0001. Evergreen species are marked with 🍃.

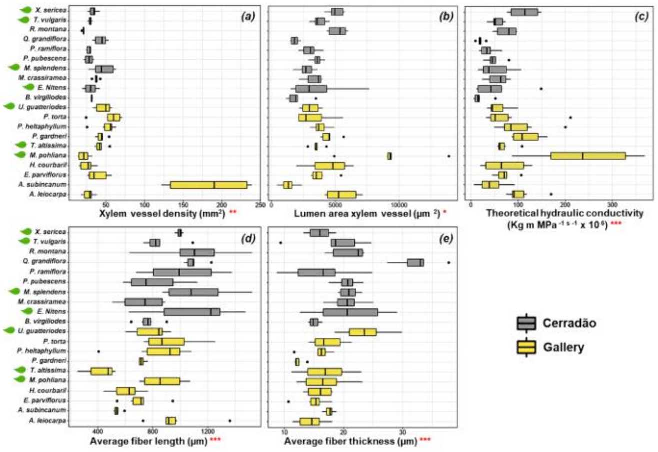

FIGURE 5. Cross sections of leaves (A-F) and young branches (G-L) of dominant species from tree communities of two Cerrado forest formations. Cerradão dominants' leaves: trichomes in *Emmotum nitens* (A), thick epidermis in *Pterodon pubescens* (B), thick cuticle in *Pouteria ramiflora* (C); Gallery forest leaves, with dorsiventral mesophyll and showing much greater spacing in the spongy parenchyma: *Aspidosperma subincanum* (D), *Ephedranthus parviflorus* (E) and *Unonopsis guatterioides* (F). Cerradão plants with higher vessel density and smaller vessel diameter (G - *Myrcia splendens*, H - *Tachigali vulgaris* and I - *Mezilaurus crassiramea*); Gallery forest plants with lower vessel density and larger vessel diameter (J - *Pouteria gardneri*, K - *Apuleia leiocarpa* and L - *Mabea pohliana*). Bars: 150 µm (A-F), 200 µm (G-L).

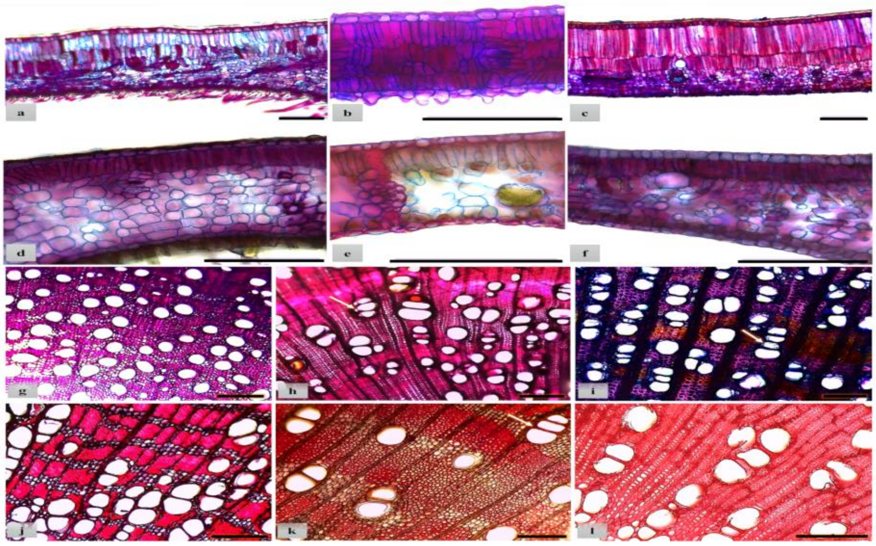

FIGURE 6. Partitioning the variance of nested linear mixed models of the functional traits of two tree communities in the Amazon-Cerrado transition. Specific leaf area (SLA), palisade parenchyma thickness (PALI), leaf blade mesophyll thickness (MESO), adaxial epidermis thickness (ADEP), palisade parenchyma thickness (PP-SP), spongy parenchyma thickness (SPON), average lumen area of xylem vessels (XARE) and axes of the PCA. Within means the residual error, all data were transformed (log-10) before analysis.