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Ecological adaptation of five woody species of forested savanna of Cerrado (Cerradão)

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ABSTRACT

The forested savanna (cerradão) is an important vegetation type of Cerrado in terms of carbon stock and biodiversity. Describing the morphological and anatomical characteristics of plants allows for a better understanding of the processes that sustain species co-occurrence in these forests. This study evaluated the ecological adaptations of five woody species from the cerradão that are important in terms of aboveground biomass, through the analysis of their functional traits. Leaf and stem traits of plants occurring in a remnant of cerradão were measured. Two main strategies related to resource use were observed: acquisitive and conservative. However, cerradão species can also combine elements of both strategies and be described as generalist species. This description shows how Cerrado forest formations are composed of species with high variability in their traits and ecological strategies.

Keywords: Cerrado vegetation, leaf anatomy, plant morphology, plant traits, generalist species.

Adaptações ecológicas de cinco espécies lenhosas que ocorrem no Cerrado

RESUMO

O cerradão é um tipo de formação florestal do Cerrado importante em termos de estoque de carbono e biodiversidade. A descrição das características morfológicas e anatômicas das plantas permite a compreensão dos processos que sustentam a co-ocorrência das espécies nessas florestas. Este estudo avaliou as adaptações ecológicas de cinco espécies lenhosas de cerradão importantes em termos de biomassa aérea por meio da análise de suas características funcionais. Foram mensuradas características das folhas e do caule das plantas que ocorrem em um remanescente de cerradão. Observamos duas estratégias principais relacionadas ao uso de recursos: aquisitiva e conservadora. Entretanto, as espécies de cerradão também podem combinar elementos de ambas as estratégias e serem descritas como espécies generalistas. Essa descrição mostra como as formações florestais do Cerrado são compostas por espécies com alta variabilidade em suas características e estratégias ecológicas.

Palavras-chave: Vegetação do Cerrado, anatomia foliar, morfologia vegetal, atributos funcionais, espécies generalistas.

Introduction

The Cerrado (Brazilian savanna) is a phytogeographic domain with high heterogeneity of vegetation types in the landscape (Ratter et al., 2003; Ribeiro & Walter, 2008). This biome encompasses a variety of ecosystems, including grasslands, savannas and forests, each distinguished by structural vegetation, predominant plant life forms and seasonality (Oliveira Filho & Ratter, 2002; Ribeiro & Walter, 2008). Each of these vegetation types are shaped by factors such as soil fertility, climate, and the frequency and intensity of fires (Costa et al., 2023; Lira-Martins et al., 2022; Ribeiro & Walter, 2008).

Although certain Cerrado species can thrive in a range of environmental conditions, others exhibit more specific habitat requirements (Maracahipes et al., 2018). Solar irradiation availability is one of the resources with the highest variability among the vegetation types (Ronquim, 2004). Within forests, light availability constrains species lacking ecological adaptations for light absorption, such as those with large leaves and a significant investment in aerial biomass (Franco, 2002). Unlike savanna species, forest species are vulnerable to fire, high light intensity, and water deficit (Hoffmann & Franco, 2003).

Cerrado forests can occur along watercourses (riparian and gallery forests) or in interfluvial areas (dry seasonal forests or forested savannas) (Ribeiro & Walter, 2008). The forested savanna, called cerradão, is characterized by a canopy cover ranging from 50 to 90%, with woody plants reaching heights of eight to 15 meters, forming a continuous canopy (Ribeiro & Walter, 2008). Cerradão can be diverse in terms of structure and species composition. These forests can vary in woody plant density and share species of other vegetation types as savannas or dry seasonal forests (Solórzano et al., 2012).

Understanding how woody species adapt to the unique environmental conditions of the cerradão, a rare and ecologically important forest type within the Brazilian Cerrado, is a significant challenge. The cerradão occupies just 1% of the Cerrado's territory (Marimon Junior & Haridasan, 2005), yet it plays a crucial role in carbon storage and biodiversity due to its dense woody vegetation (Miranda et al., 2014; Reis et al., 2023). The functional traits and adaptations that allow species to thrive in this environment remain poorly understood, especially in light of the increasing threats posed by climate change and habitat loss.

The description of functional traits plays a crucial role in comprehending plant communities. Functional traits are morphological, anatomical, and physiological features of the species that affect the growth, reproduction, and survival (Violle et al., 2007). The responses of the plants to the environmental conditions and resource availability can be driven by their traits and can be related to the plant ecological strategies (Cornelissen et al., 2003; De Bello et al., 2010; Pérez-Harguindeguy et al., 2016). The composition of Cerrado plant traits results from adapting plants to biotic and abiotic conditions and rather than phylogeny (Silva & Batalha, 2011). Thus, the use of resources and the intra- and interspecific variability of plants provide information about the capacity of plants to respond to the local environment but also aid in understanding the ecosystem processes of forest communities (Maracahipes et al., 2018), as well as responses to climate change.

Anatomical traits of plants can vary between species (Zhou et al., 2021) or within species as responses to climatic conditions (Soheili et al., 2023) and to interactions with other species (Hanley et al., 2007). Incorporating intraspecific variation in anatomical traits allows for the prediction of plant responses to environmental changes (e.g., deficiency in hydraulic capacity due to the addition of nutrients, Costa et al., 2021), or to environmental gradients (e.g., increase in altitude is associated to thinner leaf mesophyll and epidermis (Yang et al., 2023). Consequently, the utilization of comparative anatomy remains a relevant tool for taxonomic classification and evaluating plants' ecological strategies in acquiring resources.

This study characterizes the potential ecological adaptations of five woody species from cerradão by analyzing their morphological, anatomical, and physiological functional traits. Two hypotheses were tested: (1) Cerradão species are expected to exhibit resource acquisition strategies aimed at optimizing light capture and structural resistance, with traits such as high plant height, large leaf area, high specific leaf area, high wood and bark density, as well as lower values for bark thickness, thin and smooth leaf cuticle, unistratified palisade parenchyma and extensive lacunose parenchyma of the leaf. (2) Generalist species, which occur in both forest and savanna environments, are hypothesized to display traits aligned with resource conservation and protection against fire, herbivory, and high light intensity. These traits include lower plant height, lower specific leaf area, lower wood density and bark density, larger bark thickness, thick leaf cuticle, high density of leaf tectorial trichomes, high stomata density, and extensive leaf palisade parenchyma.

Materials and methods

Study area

A cerradão patch was sampled within a private farm (Fazenda Buriti, 16°51'23.89''S, 49°59'29.95''W) located in the municipality of Palmeiras de Goiás, Goiás state, Brazil. The patch of cerradão has approximately 52 ha. It is the "Legal reserve" of the farm, i.e., a mandatory proportion of the private land covered with native vegetation that follows Brazilian environmental laws. The region's climate is Aw by Köppen-Geiger classification (wet summer and dry winter). The soil is predominately dystrophic, with dark red and red yellow latosoil (dos Santos, 2018). Random permanent plots were installed in this patch in 2017/2018 to study the woody cover (Reis et al., 2023; Vasconcelos et al., 2020), and details of the forest inventory can be accessed in Vasconcelos (2019).

Species selection and field sampling

Five species in the *cerradão* patch, based on their phytosociological relevance and contribution to aerial carbon stock, were selected following the criteria established by Vasconcelos (2019). The species were: *Emmotum nitens* (Benth.) Miers (Metteniusaceae), *Annona crassiflora* Mart. (Annonaceae), *Curatella americana* L. (Dilleniaceae), *Qualea grandiflora* Mart. (Vochysiacee) and *Roupala montana* Aubl. (Proteaceae). *Emmotum nitens* is a unique species classified as a forest specialist (Felifili & Silva Júnior, 1992). The other four species are classified as habitat generalists because they occur in forests and savannas. All but *A. crassiflora* are part of the 38 woody plants widely distributed in Cerrado savanna woodlands (Ratter et al., 2003).

The aboveground biomass (AGB) was estimated using the following equation: Ln (DM) = - 11,3710317049 + 2,433521972 * Ln (DBH) + 0,8433902218 * Ln (H), where DM = dry mass (Mg), DBH = diameter at breast height (cm) and H = plant height (m) (Scolforo et al., 2008).

Nine to ten individuals per species with a diameter of 30 cm from the soil surface $\geq$ 5 cm were randomly sampled. Plant traits were measured and collected following Cornelissen et al. (2003). From each individual, 20 leaves fully expanded, mature, exposed to the sun, and without herbivory, when possible, were collected. A terminal branch with regular secondary growth and a perimeter exceeding three centimeters was collected from each individual. Bark was removed and measured in 4 x 4 cm segments from approximately one-third of the stem's length, avoiding protuberances.

Leaf anatomical traits

Two leaf anatomical traits were measured: leaf mesophyll and stomatal density. To analyze the leaf mesophyll, samples from the middle region of the leaf were fixed in FAA 70, stored in 70% alcohol after 48 hours (Johansen, 1940), and leaf cross-sections were extracted. These leaf sections were clarified using a 15% sodium hypochlorite solution, stained with 1% alcian blue and 1% basic fuchsin (3:1 v/v) (adapted from Luque et al., 1996), and dehydrated in an ethyl alcohol series to mount permanent samples using colorless varnish (Paiva et al., 2006). Three samples were prepared for each species and digitized using a Leica DM500 optical microscope.

To analyse the leaf epidermis, the abaxial surface of fresh leaves was stamped onto microscope slides (Segatto et al., 2004). This trait was measured for nine to ten leaves per species, one per individual. The slides were observed under an optical microscope (40x), digitized (Leica DM500), and measured in four sections. Stomatal frequency was determined using the ImageJ program (Gavilanes et al., 2020; Santos et al., 2022). Stomatal density was calculated using the formula: total stomata/section area (mm²) (Gavilanes et al., 2020; Santos et al., 2022).

Leaf morphological traits

Five leaf traits were measured: leaf thickness (LT), leaf area (LA), specific leaf area (SLA), relative leaf water content (RLWC), and leaf density (LD). These traits were measured in ten leaves per individual per species, after removing the petiole. Leaf thickness was measured on fresh leaves using a digital micrometer (0 to 25 mm resolution), and leaf fresh mass (LFM) was weighed. The leaves were digitized and then dried at 60°C for 48 hours to determine leaf dry mass (LDM). Leaf area was measured using ImageJ (Schneider et al., 2012), and specific leaf area was calculated by SLA (mm²/mg) = LA (mm²) / LDM (mg). Relative leaf water content was calculated using the formula: RLWC (%) = (LFM - LDM) / LDM * 100. Leaf volume (LV) was calculated by multiplying leaf area by leaf thickness, and leaf density was calculated using the formula: LD (mg/mm^3) = LDM (mg) / LV (mm^3).

Wood traits

Five wood traits were measured: relative wood water content (RWWC), wood density (WD), bark thickness (BT), relative bark water content (RBWC), and bark density (BD). The bark was removed from terminal branches and rehydrated for 48 hours, followed by measuring the saturated wood and bark weight (SWW and SBW) and determining the wood and bark dry mass (WDM and BDM) after drying at 60°C for 72 hours. Relative wood and bark water content were calculated using the formula: RWWC or RBWC (%) = (WDM or BDM – SWW or SBW) / WDM or BDM * 100. Wood and bark density were determined using the formula: WD or BD (mg/mm^3) = WDM or BDM / Volume. Branch length and diameter were measured to calculate wood volume using the formula: $\pi * (\text{diameter} / 2)^2 * \text{length}$. Bark volume was calculated by multiplying bark thickness, length, and height.

Statistical analysis

Plant traits were compared both between and within species. The coefficient of variability (CV) was calculated to assess intraspecific trait variability. For interspecific variability, traits were compared using one-way analysis of variance (ANOVA). Traits with normal distributions (LT, SLA, LD, stomatal density, WD, BT, and BD) were analyzed using ANOVA and post hoc Tukey analysis. For traits without normal distributions (LA, RLWC, RWWC, and RBWC), the Kruskal-Wallis test and post hoc Dunn analysis were performed. All statistical analyses were conducted using the R program (ver. 4.2.1, R Core Team 2022) with the "rstatix" (Kassambara, 2021) and "multcompView" (Graves et al., 2019) packages.

Results

Aboveground biomass and community description

Within the *cerradão* patch, *Anonna crassiflora*, *Curatella americana*, and *Qualea grandiflora* occurred in all plots, while *Roupala montana* was present in 90% of the plots and *Emmotum nitens* in 40%. Among these, *E. nitens* had the lowest density (19 individuals per hectare), followed by *Q. grandiflora* (27 $ind.ha^{-1}$), *A. crassiflora* (36 $ind.ha^{-1}$), *C. americana* (79 $ind.ha^{-1}$), and *R. montana* (70 $ind.ha^{-1}$).

No large individuals (DBH ≥ 25 cm) were found for *A. crassiflora*, *C. americana*, and *R. montana* (Figure S1). Furthermore, 80% of individuals with diameters less than 15 cm belonged to *C. americana* and *R. montana* (Figure S1). The largest diameters were recorded for *Q. grandiflora* (28.9 cm) and *E. nitens* (51.4cm). In terms of height, 69% of *R. montana* individuals were less than 6 m tall, while 100% of *E. nitens* exceeded this height (Figure S2). The tallest individuals were *A. crassiflora* (12 m) and *E. nitens* (12.5 m), whereas the remaining species did not exceed 11 m in height (Figure S2).

In terms of aboveground biomass (AGB), *A. crassiflora* contributed 1.63 $Mg.ha^{-1}$, with most individuals (83.3%) having stem diameters between 10 and 19.9 cm, representing 79.5% of the AGB (Figure S1). Additionally, 63.9% of these individuals were between 6 and 7.9 m tall, accounting for 65.1% of the AGB (Figure S2). *C. americana* had an estimated AGB of 1.90 $Mg.ha^{-1}$, with 83.5% of individuals having stem diameters between 5 and 14.9 cm, corresponding to 52.7% of the AGB (Figure S1). Moreover, 73.4% of the individuals had heights less than 6.9 m, accounting for 46.9% of the AGB (Figure S2). *Q. grandiflora* contributed 1.53 $Mg.ha^{-1}$ of AGB. While 40.7% of the individuals had diameters under 10 cm, these accounted for only 5.7% of the total AGB (Figure S1). Larger diameter classes (15–29.9 cm) represented 48.1% of the individuals and 89.8% of the AGB (Figure S1).

Regarding height, 66.7% of *Q. grandiflora* individuals were between 5 and 7.9 m tall, contributing 64.4% of the AGB (Figure S2). *R. montana* provided 1.42 $Mg.ha^{-1}$ of AGB, with the first two DBH classes accounting for 55.6% of the total (Figure S1). Individuals below 6 m tall (68.6%) contributed 27.7% of the AGB, while the tallest individuals (7.0–10.9 m) accounted for 60.5% of the total AGB (Figure S2). Finally, *E. nitens* accounted for 1.99 $Mg.ha^{-1}$ of AGB. Although most individuals (89.5%) had DBH values below 20 cm, this class only represented 27.2% of the woody AGB (Figure S1). Conversely, the tallest individuals (10.0–12.9 m) contributed 85.4% of the estimated AGB, despite representing only 26.3% of the individuals (Figure S2).

Leaf anatomical traits

The leaf of *Anonna crassiflora* is hypostomatic with a uniseriate epidermis covered by a thick cuticle on the adaxial surface (Figure 1). The mesophyll is heterogeneous, featuring palisade parenchyma on both sides (1-2 layers) and lacunose parenchyma in the center (3-4 layers). Additionally, the leaf has a layer of hypodermis on the adaxial surface. The central vein (midrib) is structured in an open arch surrounded by fibers and secretory cavities (Figure 1). Trichomes are present on the adaxial surface, but only in the central vein region (Figure 1).

The leaf of *Curatella americana* was hypostomatic with a uniseriate epidermis and a thin cuticle on both surfaces (Figure 2). The stomata presented cells with straight anticlinal walls on both surfaces and within stomata crypts (Figure 2).

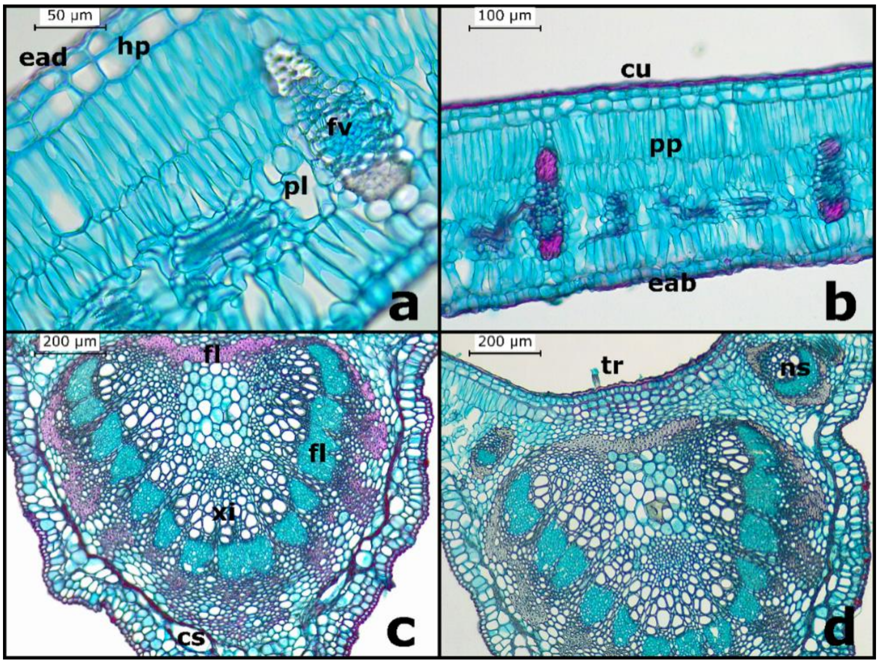

Figure 1. Leaf sections of *Annona crassiflora*. a - b: epidermis and mesophyll. c - d: Leaf central vein (midrib). Cs: secretory cavity; cu: cuticle; eab: abaxial epidermis; ead: adaxial epidermis; fi: fiber; fl: phloem; fv: vascular bundles; hp: hypodermis; ns: secondary veins; pp: palisade parenchyma; pl: lacunose parenchyma; tr: trichome.

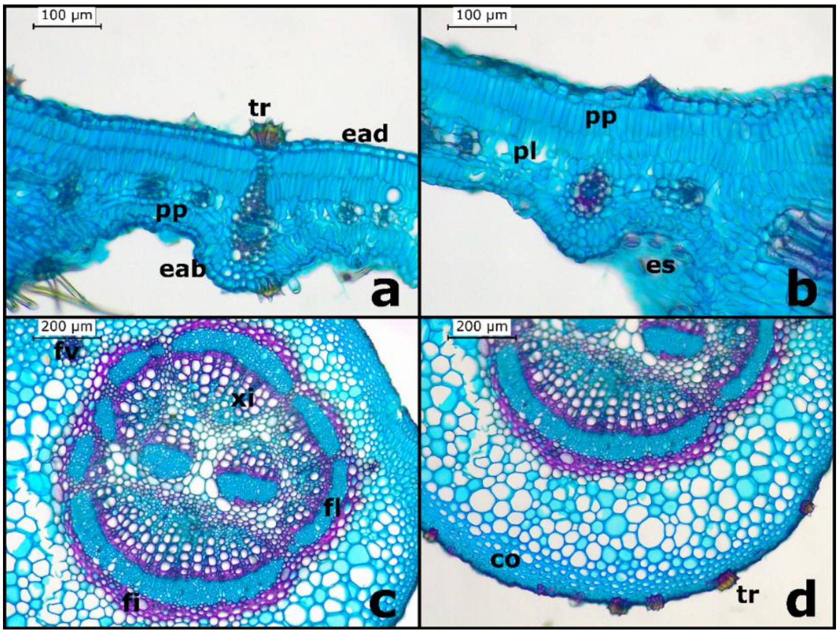

Figure 2. Leaf sections of *Curatella americana*. a - b: epidermis and mesophyll. c - d: Leaf central vein (midrib). Co: collenchyma; eab abaxial epidermis; ead: adaxial epidermis; es: trichomes; fi: fibers; fl: phloem; fv: vascular bundles; pl: lacunose parenchyma; pp: palisade parenchyma; tr: short trichomes.

The mesophyll was isobilateral, composed of two layers of palisade parenchyma on the adaxial surface and one on the abaxial surface (Figure 2).

The lacunose parenchyma consisted of a single layer in the center (Figure 2). The central vein has a closed-arched vascular system. Isolated vascular bundles were observed in the medullary region (Figure 2). Fibers surrounded the vascular system, extending into sheath-like structures in the lateral veins. Collenchyma was present, and both short and long tectorial trichomes were observed in the central vein region and between veins (Figure 2).

The leaf of *Qualea grandiflora* exhibited a uniseriate epidermis with large cells on the adaxial surface and unicellular tectorial trichomes on the abaxial surface (Figure 3). The abaxial surface also had stomatal crypts, stomatal ridges, and a heterogeneous mesophyll, tending towards homogeneity. The mesophyll consisted of one layer of palisade parenchyma and three layers of chlorophyllous parenchyma, with intercellular spaces typical of lacunose parenchyma. The central vein was organized in an open arch, and calcium oxalate crystals were present in the mesophyll and central vein (Figure 3).

The leaf of *Roupala montana* was hypostomatic with a uniseriate epidermis and a thin cuticle (Figure 4). Its mesophyll contained a single layer of palisade parenchyma and seven to eight layers of lacunose parenchyma. Fibers and sclereids were observed on both sides of the mesophyll, while the central vein had vascular bundles surrounded by fibers (Figure 4).

The single forest species, *Emmotum nitens*, had a hypostomatic leaf with a uniseriate epidermis, a thin cuticle, and short, irregular-shaped cells covered by tectorial trichomes on the abaxial surface (Figure 5). The stomata were elevated above the epidermis, and the mesophyll was heterogeneous, containing two layers of palisade parenchyma and three to four layers of lacunose parenchyma. Sclereids, collenchyma, and calcium oxalate crystals were also present, with an open-arched vascular system in the central vein surrounded by fewer fibers than the other species (Figure 5).

When comparing stomatal density, *A. crassiflora* had the lowest mean value, which was significantly different from *R. montana*, *C. americana*, and *Q. grandiflora*, all of which had higher stomatal densities (> 334 stomata/mm²; Table 1).

Leaf morphological traits

All the differences in the plant traits between the five species are in Table 2. Considerable intraspecific variation of the leaf morphological traits were observed, except for *Anonna crassiflora*, which had slight variation (CV < 30%).

The most significant variations occurred in the leaf area (LA) and specific leaf area (SLA) of the *Curatella. americana*, *Qualea grandiflora* and *Roupala montana*. Also, high variation in leaf density of *R. montana* (CV=50%) were observed. Regarding leaf thickness, *C. americana* had the highest mean value and differed statistically only from *Emmotus nitens*, which had the lowest mean value. *C. americana* had the largest SLA and differed from *R. montana*, which had the lowest value. The CV of SLA in *C. americana*, *E. nitens*, and *R. montana* was high (over 40%) but without statistical differences between all the species.

The leaf density (LD) of *C. americana* had the lowest average value, which was different from *E. nitens* and *R. montana*, which had the highest average values (Table 2). The relative leaf water content (RLWC) of *C. americana* had the highest mean value, differing statistically from *E. nitens* and *R. montana*, which had the lowest values. For this trait, the species studied showed low coefficients of variation, between 9.74 and 20.45% (Table 2).

Bark traits

Intraspecific variability in bark traits was observed across all species, with *R. montana* exhibiting the least variation (CV < 30%) (Table 2). *C. americana* and *E. nitens* showed high variability in wood density (WD; CV > 40%). Additionally, high variation in bark density (BD; CV > 50%) was observed in *E. nitens*, *Q. grandiflora*, and *A. crassiflora*. The most substantial variation in bark thickness (BT) was found in *E. nitens* (CV > 80%), although *Q. grandiflora* had the largest mean BT, significantly differing from *E. nitens*, which had the smallest value. The bark thickness (BT) of *A. crassiflora*, *C. americana*, and *R. montana* was statistically similar. For bark density, *A. crassiflora* and *C. americana* had the lowest mean values, while *E. nitens* and *R. montana* had the highest mean values.

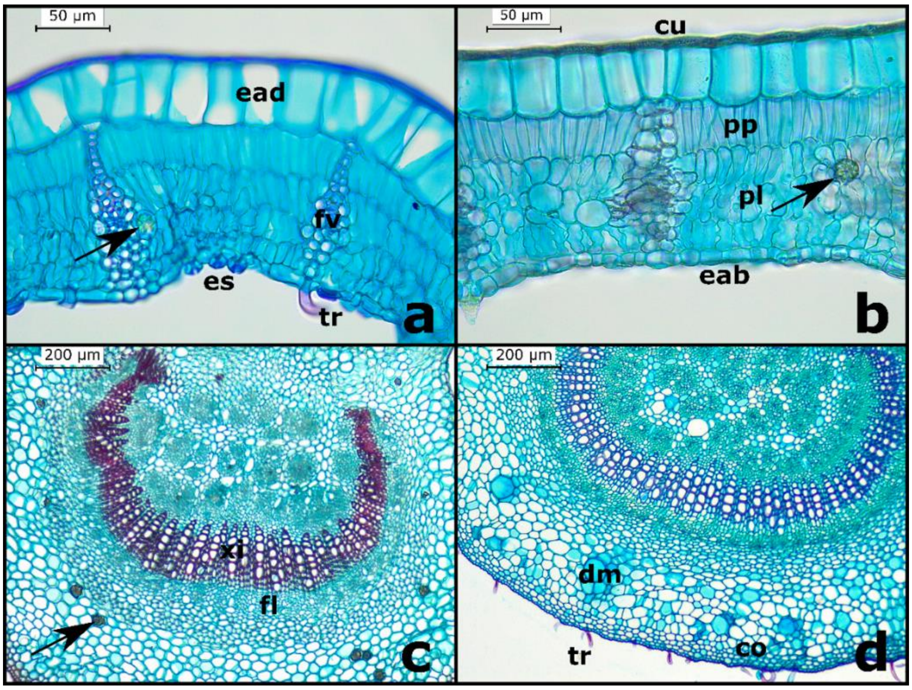

Figure 3. Leaf sections of *Qualea grandiflora*. A - B: epidermis and mesophyll. C - D: Leaf central vein (midrib). Co: collenchyma; cu: cuticle; eab abaxial epidermis; ead: adaxial epidermis; es: stomata; fi: fibre; fl: phloem; fv: vascular bundles; pl: lacunose parenchyma; pp: palisade parenchyma; tr: trichomes. Arrows indicate calcium oxalate crystals.

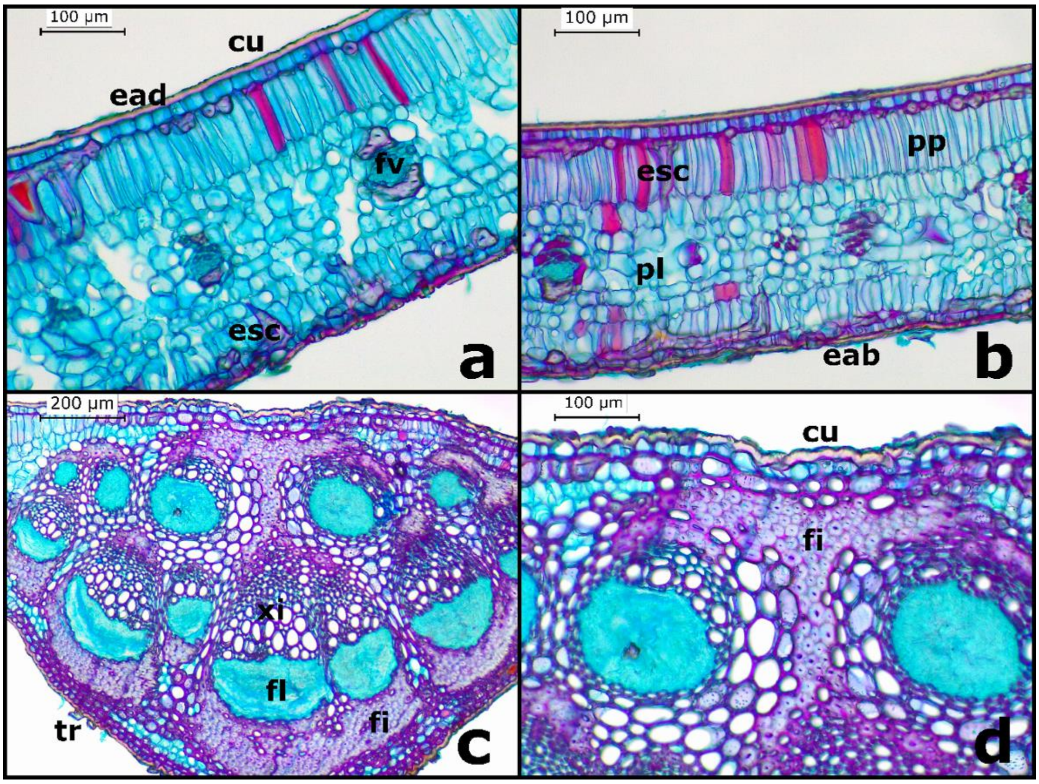

Figure 4. Leaf sections of *Roupala montana*. a - b: epidermis and mesophyll. c - d: Leaf central vein (midrib). Cu: cuticle; eab abaxial epidermis; ead: adaxial epidermis; es: stomata; esc: sclereids; fi: fibres; fl: phloem; pl: lacunose parenchyma; pp: palisade parenchyma tr: trichome.

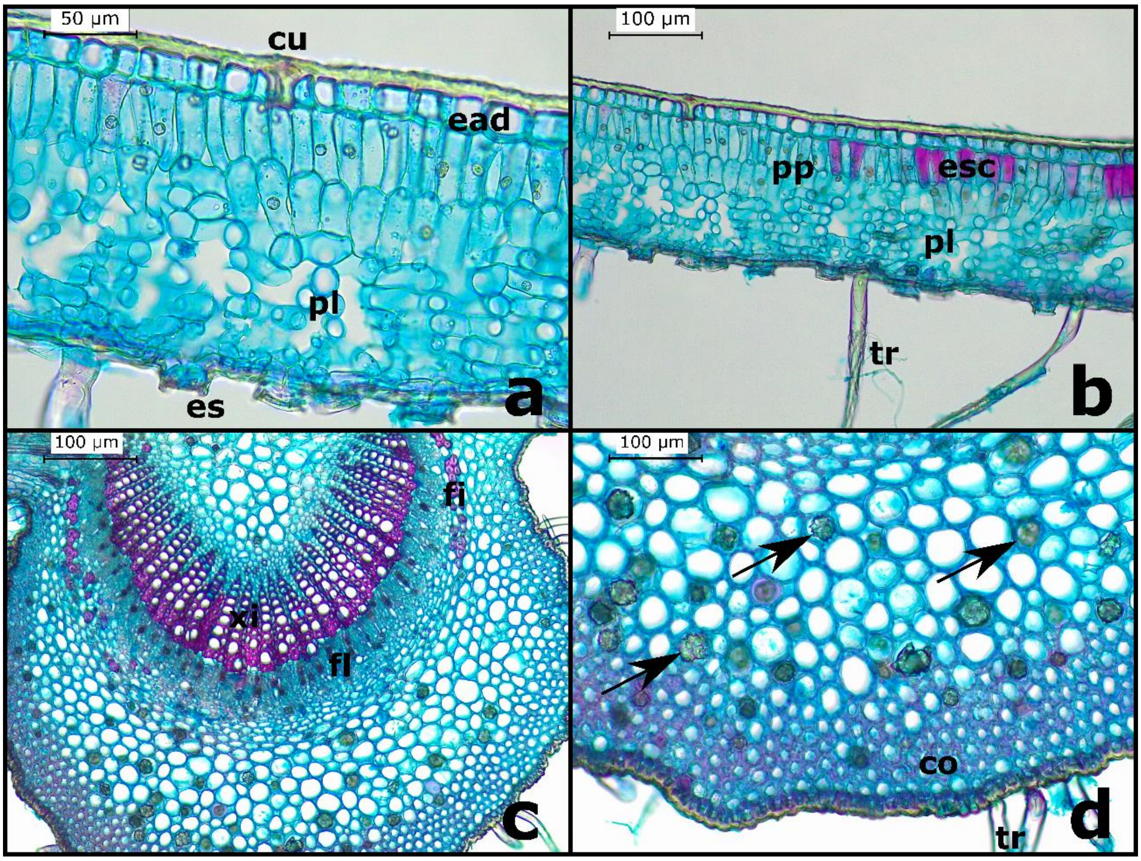

Figure 5. Leaf sections of *Emmotum nitens* a - b: epidermis and mesophyll. c - d: Leaf central vein (midrib). co: collenchyma; cu: cuticle; eab: abaxial epidermis; esc: sclereids; es: stomata; fi: fibres; fl: phloem; pl: lacunose parenchyma; pp: palisade parenchyma tr: trichome. Setas indicam drusas de cristais de oxalato de cálcio. Arrows indicate calcium oxalate crystals.

Table 1. Stomata density (stomata/ mm^2) of the five woody species of cerradão at Palmeiras de Goiás. Min.: minimum stomata density, Max.: maximum stomata density, CV: coefficient of variation (%). Compact letters indicate differences between the species (Tukey test, where p > 0.05).

	Annona crassiflora		*Curatella americana*		*Emmotum nitens*		*Qualea grandiflora*		*Roupala montana*	
Stomata density	Min. Max.	Mean (CV%)	Min. Max.	Mean (CV%)	Min. Max.	Mean (CV%)	Min. Max.	Mean (CV%)	Min. Max.	Mean (CV%)
	176,00 285,21	229,26**a** (13,68)	243,46 425,15	338,30**b** (14,39)	249,0 411,91	327,57**ab** (18,07)	320,5 848,09	506,00**b** (35,19)	278,9 425,61	334,76**b** (15,81)

Table 2. Functional traits of the five woody species of cerradão at Palmeiras de Goiás. Min = minimum, Max = maximum, CV = coefficient of variance (CV%), LT = leaf thickness (mm); LA = leaf area (mm^2); SLA = specific leaf area (mm²/mg); LD = leaf density (mg/mm³); RLWC = relative leaf water content (%); RWWC = relative wood water content (%); WD = wood density (mg/mm³); BT = bark thickness (mm); RBWC = relative bark water content (%); BD = bark density (mg/mm³). * Different letters on the same line indicate statistically significant differences.

	Annona crassiflora		***Curatella americana***		***Emmotum nitens***		***Qualea grandiflora***		***Roupala montana***	
	Min. - Max.	Mean (CV%)	Min. - Max.	Mean (CV%)	Min. - Max.	Mean (CV%)	Min. - Max.	Mean (CV%)	Min. - Max.	Mean (CV%)
LT	0,23 - 0,45	0,31**ab** (13,68)	0,28 - 0,54	0,38**a** (10,84)	0,21 - 0,51	0,28**b** (19,61)	0,20 - 0,72	0,36**ab** (32,84)	0,13 - 0,49	0,32**ab** (27,72)
LA	2.224,60 - 8.808,60	4.997,50**ab** (29,31)	2.024 - 20.460,80	7.241,07**c** (42,46)	2.252,40 - 15.269,70	6.836,96**ac** (33,70)	1.020,30 - 15.606,40	5.365,20**abc** (61,20)	1.684,30 - 11.194,60	4.771,68**b** (40,18)
SLA	5,42 - 17,03	10,43**a** (23,06)	2,67 - 43,72	11,53**a** (45,03)	5,27 - 15,73	8,94**a** (23,47)	3,78 - 26,61	10,51**a** (49,74)	3,98 - 22,58	8,54**a** (47,99)
LD	0,19 - 0,51	0,32**ab** (18,21)	0,05 - 0,89	0,25**a** (34,71)	0,25 - 0,61	0,41**b** (19,79)	0,14 - 0,48	0,31**ab** (24,33)	0,19 - 1,13	0,46**b** (50,35)
RLWC	33,33 - 82,89	63,12**ab** (9,74)	29,79 - 89,89	67,66**a** (12,97)	41,18 - 78,80	57,77**b** (11,01)	23,55 - 84,02	63,77 **ab** (15,71)	39,71 - 82,74	58,81**b** (20,45)
RWWC	51,61 - 78,21	65,69**a** (13,23)	24,93 - 74,27	60,80**ab** (24,21)	47,59 - 76,89	54,44 **ab** (14,95)	38,59 - 59,82	51,09**b** (14,11)	48,09 - 58,35	53,23**b** (6,04)
WD	0,13 - 0,42	0,30**a** (31,91)	0,41 - 1,78	0,67**b** (58,36)	0,50 - 3,20	0,90**b** (90,25)	0,51 - 0,82	0,61**b** (16,66)	0,51 - 1,06	0,83**b** (22,32)
BT	2,00 - 11,08	8,60**ab** (32,01)	4,37 - 12,97	7,50**ac** (38,21)	0,17 - 0,87	0,81**c** (89,05)	8,14 - 26,24	15,59**b** (36,39)	3,75 - 13,41	8,75**ab** (28,32)
RBWC	56,60 - 74,58	62,41**a** (10,76)	40,76 - 76,23	53,58**ab** (22,94)	38,89 - 71,83	52,32 **ab** (17,17)	25,60 - 55,96	42,96**b** (24,36)	39,17 - 75,58	53,91 **ab** (19,89)
BD	0,06 - 0,56	0,17**a** (86,58)	0,16 - 0,28	0,21**a** (15,39)	0,23 - 0,92	0,46**b** (43,03)	0,16 - 0,80	0,38**ab** (57,28)	0,32 - 0,52	0,43**b** (15,90)

Discussion

Leaf anatomical traits

The leaves of the five cerradão woody plants exhibit different degrees of scleromorphisms, characterized by distinct features such as a thin cuticle (except *Curatella americana*), extensive epidermal cells (*Qualea grandiflora*), hypodermis (*Anonna crassiflora*), large palisade parenchyma (*C. americana*), high density of tectonic trichomes (*Emmotum nitens*, *C. americana* e *Q. grandiflora*), stomata crypts (*C. americana* and *Q. grandiflora*), sclereids in the mesophyll (*E. nitens* e *Roupala montana*), abundant calcium oxalate crystals (*E. nitens* e *Q. grandiflora*) and substantial amounts of fibers in the main vascular bundles (except *Q. grandiflora* and *E. nitens*). These traits can affect species survival, establishment, and growth in seasonal environments with different light availability caused by the heterogeneous canopy, as observed in cerradão (Reis et al., 2023).

The outermost leaf surfaces provide insights into the resource storage strategies employed by these plants. The thick cuticle observed in *A. classifora*, *E. nitens*, *Q. grandiflora*, and *R. montana* is an important trait that avoids leaf water loss and protects the leaf from excessive solar radiation (Bi et al., 2017; Yavas et al., 2024). In contrast, *C. americana* exhibits a thin cuticle on both sides of its leaves (Araújo & Haridasan, 2007; Bieras, 2006). This trait differs from other savanna species, which have thick cuticle.

The high density of tectonic trichomes in *C. americana*, *E. nitens*, and *Q. grandiflora* also indicates the adaptation of Cerrado species to water deficit conditions. Trichomes can prevent water loss by avoiding excessive leaf transpiration and protecting from high solar radiation levels and herbivores (Liesenfeld et al., 2019). Under high solar radiation, leaves can also have extensive palisade parenchyma with large or highly stratified cells (Yavas et al., 2024), as observed in *C. americana* leaves.

Some important strategies of water retention related to the leaf stomata were observed. The presence of stomata crypts in the abaxial surface of the leaves of *C. americana* and *Q. grandiflora* suggests a characteristic strategy of scleromorphic species, i.e., decrease the exposure of the stomata to direct sunlight to reduce the respiration rate and protects the plant from excessive water loss in dry and hot conditions (Esposito-Polesi et al., 2011). The stomatal crypts create a humid microclimate in the leaf surface that avoids excessive transpiration during the opening of stomata (Alquini et al., 2006; Šantrůček, 2022).

High stomata density, as observed in *Q. grandiflora*, leads to an increase in photosynthetic efficiency (Wang et al., 2022) and a decrease in transpiration since plants can capture a greater amount of CO_2 by reducing the time of stomata opening (Franks & Farquhar, 2007).

The large concentration of calcium oxalate crystals in the leaf tissue is expected in savanna species (Konno et al., 2014). *E. nitens* and *Q. grandiflora* had central vein and mesophyll crystals, respectively. Calcium oxalate crystals are possibly related to protection against herbivores, ionic balance, tissue support, and rigidity (Franceschi & Nakata, 2005; Khan et al., 2023). In *R. montana*, the presence of fibers and sclereids in the mesophyll can indicate high tissue resistance to mechanical stress and prevent leaf collapse after dehydration (Dickison, 2000).

The leaves of *Q. grandiflora* had some peculiarities. Large epidermis cells of the adaxial surface of *Q. grandiflora* leaf lack chloroplasts and the vacuole storage water (Alquini et al., 2006). Another characteristic observed only in *Q. grandiflora* was a substance resembling mucilage, but no histochemical test was carried out to confirm this. Mucilage is a substance produced by the plant's metabolism for water retention and may contribute to dehydration resistance by binding water near the cell surface (Vieira et al., 2022).

Leaf morphological traits

The woody plants in this study share some leaf traits related to resource acquisition and protection against natural enemies. In shaded environments, increasing leaf area is an ecological strategy to maximize light uptake (Cornelissen et al., 2003; Maracahipes et al., 2018). Leaves with significant areas lose more water through transpiration, but within the forest, that is compensated by higher water availability in the soil (Rossatto et al., 2010). A dense leaf with low SLA provides higher resistance to physical damage and prevents damage from generalist herbivores, increasing leaf lifespan (Cornelissen et al., 2003; Poorter, 2009; Poorter & Bongers, 2006).

More rigid leaves are also more effective at withstanding dehydration in the dry season (Barros & Soares, 2013). Although there were no differences in SLA between *Curatella americana*, *Qualea grandiflora*, and *Anonna crassiflora,* those species had large SLA. This trait is directly related to the plant's photosynthetic efficiency and biomass allocation (Cornelissen et al., 2003; Vale et al., 2021). In closed canopy environments, where light availability is a strong environmental filter, high SLA is an acquisitive trait that can result in higher plant productivity (Prado Júnior et al., 2015).

The SLA is a relevant trait in physiological terms, as it is directly related to investment in leaf structures and represents the plant's biomass allocation (Cornelissen et al., 2003; Umaña et al., 2021). This allows us to understand the plant community's water use mechanisms and carbon cycles (Araújo & Haridasan, 2007). The SLA is correlated to the maximum photosynthetic capacity of the plant (Cornelissen et al., 2003) and to the carbon sequestration capacity of Cerrado species (Franco et al., 2005). Larger values of SLA are usually observed in shadow species as the investment is less in leaf tissue thickness and lignification (Dahlgren et al., 2006, Reis et al., 2023). In contrast, high SLA values represent high competition ability for light, but it reduces the resistance to stress caused by excessive irradiation (Rossatto et al., 2010).

In our study, *C. americana* showed the highest mean value of leaf thickness. This trait can represent the morphological response of the species to reduce water loss and the direct incidence of light through reflectance, avoiding overheating of the mesophyll (Costa et al., 2021). The occurrence of thick leaves in Cerrado woody species can be related to high leaf venation that indicates copious water transport (Souza & Vale, 2019). Those traits can favor the abundance of *C. americana*, a widely distributed species in cerrado *lato sensu* that occurs in more than 50% of the areas studied by Ratter et al. (2003). This species has high scleromorphism because of its thick leaves with a coriaceous texture, a high density of leaf trichomes, tortuous trunks, and thick bark (Amaral et al., 2016).

The thick bark is another relevant adaptative trait that protects the plant meristems and shoots. Thick bark prevents the plant from fire and avoids top kill (Chiminazzo et al., 2023; Scalon et al., 2021). Among the species only *Q. grandiflora* could have the chance to avoid top kill in 50% under high-intensity fire because the bark thickness was greater than 9.1 mm (Hoffmann et al., 2012; Scalon et al., 2021). Forest plants are more vulnerable to fires (even low-intensity ones) than savanna plants because forest plants have thinner bark (Hoffmann et al., 2009), as observed for *E. nitens* (0.81 mm). This supports the idea that *E. nitens* is a forest species since its set of traits potentially limits the species' occurrence in other vegetation types at high density.

In terms of relative wood and bark water content, *A. crassiflora* had the higher mean value (Table 2). One role of the stem bark is the water storage reservoir of plants (Scalon et al., 2021). This water can be used as a complementary mechanism to improve the water supply for the leaves. It is also an intermediate water source for leaf transpiration and is important in regulating diurnal water deficits in Cerrado woody species (Epron et al., 2021; Scholz et al., 2007).

E. nitens and *R. montana* had mean wood density larger than 0.80 mg/mm3 (Table 2). According to Coradin et al. (2010) and Silveira et al. (2013), species with WD higher than 0.73 mg/mm3 are dense wood species (heavy wood). Dense wood is related to unsuitable environmental conditions that constrain plant growth and generally indicate water deficit and low soil fertility since the plant's cambial and physiological activity is reduced (Roque & Tomazello Filho, 2009). In our study, *A. crassiflora* had the lowest wood density (0.30 mg/mm3) compared to the other woody species and can be classified as a low-density wood (Coradin et al., 2010; Silveira et al., 2013).

Wood density is a trait that correlates with different ecological, morphological, and physiological properties of the species and is an important parameter for estimating carbon stock in terrestrial biomes (Baker et al., 2004; Chave et al., 2006). Wood density is related to plant performance, such as survival and growth (Chave et al., 2009), and is related to structural strength, wood durability, and above-ground carbon storage (Batalha et al., 2011; Cornelissen et al., 2003).

Bark density is related to the structure of the tissue, which produces small cells with thick cell walls to provide mechanical resistance and protection against pathogens (Scalon et al., 2020). In our study, *E. nitens* also stood out as the species with the highest average bark density.

Morphological and functional relationships between species

In general, plants have two main strategies for acquiring and using resources available in the environment, which are called acquisitive and conservative strategies (Becklin et al., 2021; Donovan et al., 2011). However, based on the characteristics presented here, this distinction was unclear for the species studied.

Our first hypothesis was that species of cerradão would show a predominance of strategies for acquiring resources related to light capture and structural resistance, i.e., higher values for total height, leaf area, SLA, wood density, and bark density, as well as lower values for bark thickness, thin and smooth cuticle, unistratified palisade parenchyma and extensive lacunose parenchyma. Among the species analyzed, *E. nitens* is classified as a forest species (Felfili & Silva Júnior, 1992). This species had high plant height, high wood density and bark density, and low bark thickness. Extensive lacunose parenchyma was corroborated regarding anatomical traits, although it is loose with three to four layers. However, the palisade parenchyma had two layers, and the cuticle was thick.

For the generalist species, our hypothesis identifies characteristics related to resource conservation and protection against fire, herbivory, and high light intensity that affect the establishment and survival of the plant in different environments (e.g., savanna and forest). Thus, were expected that "generalist" species have lower height, SLA, wood density, bark density, and large bark thickness, presence of thick cuticles, high density of tectorial trichomes, high stomata density, and developed palisade parenchyma. However, our results differed among the generalist species (*A. crassiflora*, *C. americana*, *Q. grandiflora*, and *R. montana*). There was a high variation in plant height. *R. montana* was the species with higher wood density and bark density. In terms of leaf anatomy, *C. americana* did not have a thick cuticle. Tectorial trichomes were found in high density on *C. americana* and *Q.*

grandiflora. The presence of extensive palisade parenchyma was observed in *C. americana.* The lowest stomata density was found in *A. crassiflora*.

Conclusion

The traits of the five species analyzed suggest that plants are adapted to the physical and biotic conditions of the studied cerradão patch, as indicated by the interspecific analysis. The functional traits measured express two resource acquisition and use strategies: acquisitive and conservative. Species exhibiting both strategies, such as *A. crassiflora*, *C. americana*, *Q. grandiflora*, and *R. montana*, can be found in cerradão patches, demonstrating generalist behavior. *E. nitens* showed some consistency with traits expected for forest specialists, though variation was present even within this species. Consequently, species' strategies can be classified based on their traits, although this generalization is limited by the wide variability within each species, resulting in a gradient of traits that allow survival in heterogeneous environments.

The high variability of anatomical, morphological, ecological, and functional traits among species is notable. Over millions of years, these traits, spanning both morphological/anatomical and physiological aspects, have been shaped by gradual selection to enhance survival, adaptation, and reproduction. Understanding this complexity is crucial, especially in the context of the climate impacts caused and intensified by human activity. The latest Intergovernmental Panel on Climate Change-IPCC report (Sixth Assessment Report) warns that such rapid changes could threaten the ability of many native species to adapt and survive in the short term, potentially leading to biodiversity loss in natural ecosystems. Recognizing the complexity of plant traits and their evolutionary history is essential for developing strategies to mitigate climate change's impact on ecosystems and preserving biodiversity in the face of these unprecedented challenges.

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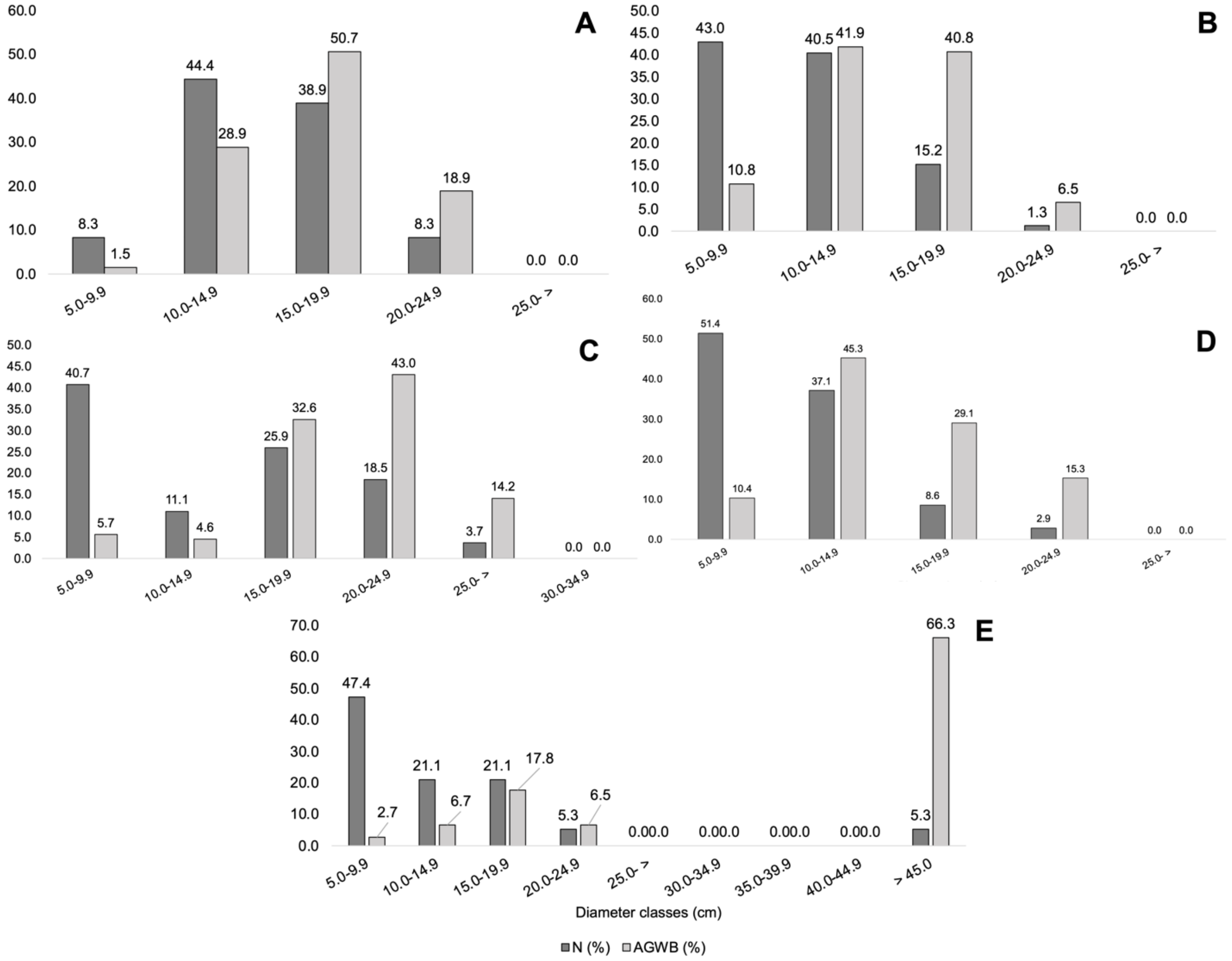

Figure S1: Distribution of the number of individuals (N %) and above-ground woody biomass (AGWB %) in different diameter classes at breast height (DBH) (cm) for the five woody species of the cerradão. A= *Annona crassiflora*; B= *Curatella americana*; C= *Qualea grandiflora*; D= *Roupala montana*; E= *Emmotum nitens*.

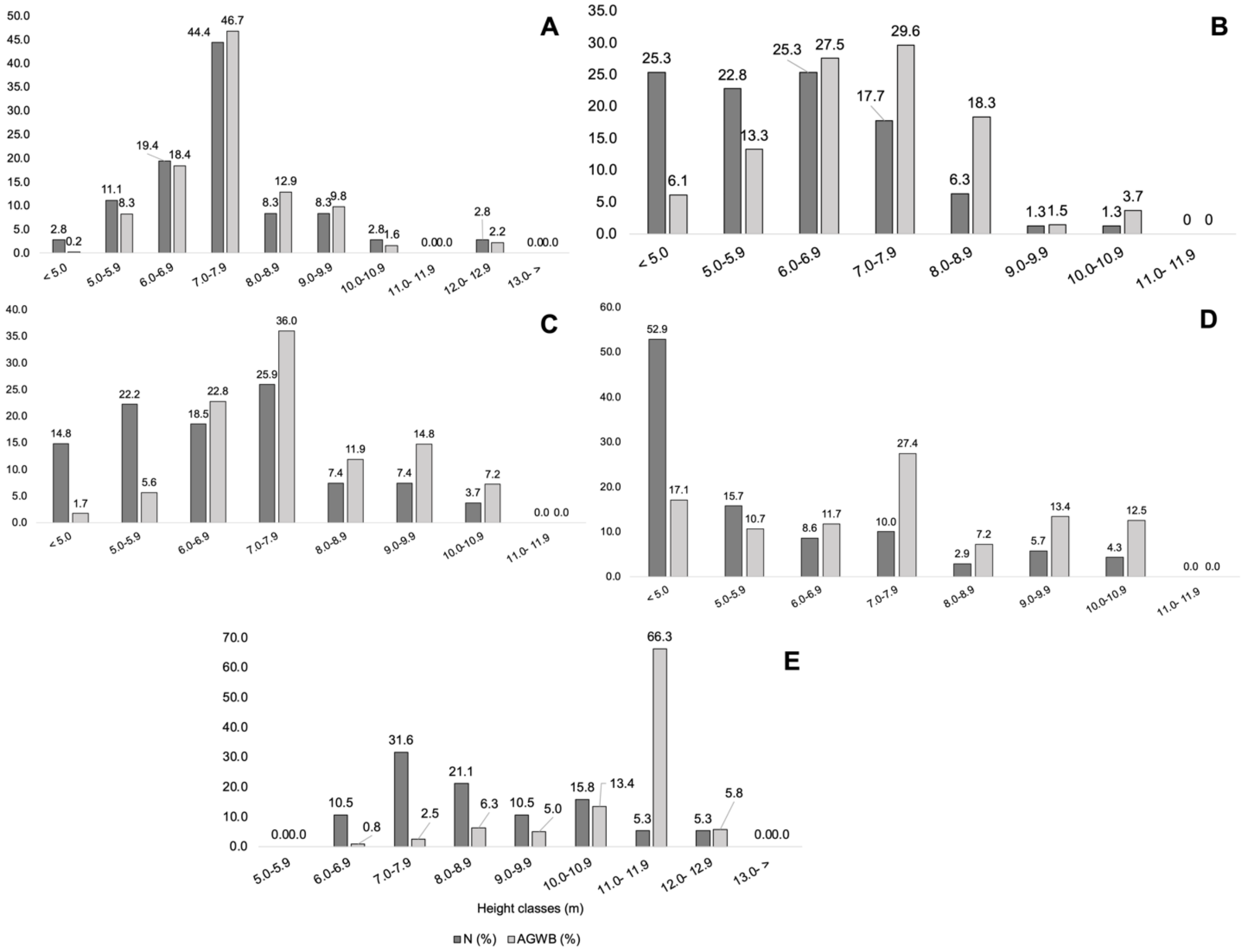

Figure S2: Distribution of the number of individuals (N %) and above-ground woody biomass (AGWB %) in different height classes (m) for the five woody species of the cerradão. A= *Annona crassiflora*; B= *Curatella americana*; C= *Qualea grandiflora*; D= *Roupala montana;* E= *Emmotum nitens*.