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Functional traits as indicators of ecological strategies of savanna woody species under contrasting substrate conditions

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ABSTRACT

Environmental filters and functional adjustments of species to local conditions are major determinants of plant communities in stressing habitats. We set out to understand the role of different substrates in functional trait variation in wood plants by investigating key functional traits at the community and intraspecific levels in different types of Brazilian savanna: two sites of alluvial savannas (lowland savannas that occur in old alluvial deposits in riverbeds with sandy soils and low water-holding capacity), and two sites of typical savannas (upland savannas that occur in interfluvial zones, far from the influence of rivers, in which clay soils with higher fertility and water-holding capacity predominate). We conducted this study in four sites with savanna vegetation in the northeast region of the Cerrado Biome, nearby the transition with the Amazon. In each site we sampled six functional traits for each tree species: leaf area, leaf thickness, specific leaf area (SLA), stem-specific density, relative bark thickness and maximum plant height. We sampled 101 wood species, ranging from 26 to 62 species within each site. In both community and intraspecific levels, alluvial savanna plants showed higher SLA and specific-stem density, and lower leaf area, leaf thickness, bark thickness, and plant height compared with the typical savanna. We also found that, at a given leaf thickness, species from typical savanna exhibited ~20% higher SLA. In addition, at a given plant height, typical species showed ~56% higher bark thickness and ~20% lower specific-stem density. Our findings suggest that savanna tree species growing on alluvial savannas tend to adopt strategies related to water acquisition while species growing on typical savannas invest in both water conservation strategies and protection against high-intensity fires. We conclude that water deficit and fire, both related to substrate properties, play a key role in determining the woody plant communities functioning in savannas.

1. Introduction

Variability in environmental conditions may act at distinct spatial scales, selecting the functional traits of plant communities (Cadotte and Tucker, 2017; Cavender-Bares et al., 2009), and resulting in differences in vegetation structure and species composition (Hoffmann et al., 2012; Maracahipes et al., 2018; Mews et al. 2014; Power et al., 2019). For example, on a large scale, the water deficit and nutrient limiting in soils can be key determinants of tree adaptations and of their distribution in tropical environments (Oliveira et al., 2019; Oliveras and Malhi, 2016; Souza et al., 2016). Thus, water and nutrient availability act as a filter that determine the functional characteristics of the set of plant species in a given community, modulating the patterns of richness and functioning (Cássia-Silva et al., 2017; Maracahipes et al., 2018). However, not all plant traits respond similarly to environmental factors and their interaction, and not all species in a community can adjust to different habitat

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conditions (Thuiller et al., 2009), implying that the most common functional adjustments of species in a community may indicate which are the most relevant environmental filters.

In general, on a large scale, plants occurring under different environmental conditions can adopt strategies for the use of available resources that range from the conservative to the-acquisitive spectrum (Reich et al. 1999; Wright et al., 2004). Habitats with low resource availability (i.e., stressing habitats) select for conservative strategy is favored, which is characterized by slow growth, tissue protection, reserve organs, long-lived leaves with low nutrient concentrations, a low photosynthetic rate, a low respiration rate, and high investment in dry mass per area (Díaz et al., 2016; Donovan et al., 2011; Wright et al., 2004). The recognition of these strategies adopted by plants is fundamental to the understanding of species composition and the functioning of savanna communities in different stress levels. For example, the limited and patchy availability of resources, especially water and nutrients, promotes the coexistence of different functional groups (Oliveras and Malhi, 2016). Therefore, the leaf economics spectrum framework is particularly useful to disentangle strategies in tropical savanna ecosystems.

Describing ecological strategies of plants, however, can be challenging. Multiple functional traits can have contrasting responses to a given environmental stressor at the local scale; therefore, ecological strategies of a given plant community may sets of functional traits. The six key functional plant traits that represent distinct ecological processes and are normally recommended to be measured are: 1. leaf area, a trait related to the capacity of absorption and use of light and water loss by the leaves (Wright et al., 2017); 2. leaf thickness, a trait related to resistance to physical damage, water deficit and efficiency in the acquisition and use of resources (McBurney, 1992), 3. specific leaf area (SLA), a trait related to the investment in the acquisition and conservation of resources by the plant, such as nitrogen content, photosynthetic rate, foliar longevity and carbon fixation capacity (Wright et al., 2004); 4. stem-specific density, a trait related to resistance to physical damage and structural vigor of the plant (Chave et al., 2009; Díaz et al., 2016); 5. bark thickness, a trait that acts as protection of living tissues against desiccation and damage caused by fire (Pausas, 2015); and 6. maximum plant height, a trait related to competitive ability, resistance to environmental disturbance, and seed dispersal (Westoby, 1998).

In the Neotropical savannas, which present wide variation in phytophysiognomies (i.e., vegetation types), the occurrence and establishment of plant species are determined by functional adjustment to a large number of environment characteristics. Among environmental filters acting on a local scale, we can list soil acidity (Furley and Ratter, 1988; Haridasan, 2008), texture, fertility (Furley and Ratter, 1988), water availability (Motta et al., 2002), and fire frequency and severity (Dantas et al., 2013; Gomes et al., 2018; Moreira, 2000). Also, the species pool of a specific phytophysiognomie may be adapted to different soil depths (Pinheiro and Monteiro, 2010; Oliveira et al., 2005), soil acidity levels (Furley and Ratter, 1988; Haridasan, 2008), and climate seasonality (Gottsberger and Silberbauer-Gottsberger, 2006). Normally, the seasonal climate imposes certain water restrictions on plants (Oliveira-Filho and Ratter, 2002), favoring accidental fires in the dry season (Schmidt et al., 2018). In the case for Cerrado, the largest Neotropical savanna, different physiognomies might occur due to substrates with different types of relief, depths, variability of soil physical and chemical properties, and water availability (Oliveira-Filho and Ratter, 2002; Silva et al., 2006; Mews et al. 2014). Together, those environmental drivers can determine the physiognomies, species composition, structure, and functioning of plant communities.

The distinction between the different physiognomies in the Cerrado, in some cases, is not limited to the structure of its vegetation and species composition. For example, *typical cerrado*, the most representative physiognomy of the Cerrado, occurs predominantly in interfluves, is characterized by trees with twisted trunks and irregular branches, where shrubs and subshrubs are scattered, and a roughly continuous grass stratum, which grows fast in the rainy season and becomes fuel for fire in the dry period (Ribeiro and Walter, 2008). However, there is a distinct and much more uncommon type of *typical cerrado* phytophysiognomy, the alluvial savanna, in which the community composition and/or dynamic are still poorly known, such as the vegetation that occurs in patches on sandy hilltops along the margins of the Araguaia River (Eiten, 1985 – see Fig. 1). This formation is established on quartz sands derived from sediments forming sand mounds, where the water retention and clay content are low (Eiten, 1985; Valente and Latrubesse, 2012), and the water table shallow (RADAMBRASIL, 1999). Unique systematic and comparative studies of the flora of alluvial and typical savannas highlighted the floristic particularity of the alluvial savanna, where plant species generally occur in more xeric environments (e.g., *Commiphora leptophloeos* (Mart.) J.B.Gillett and *Cereus bicolor* Rizzini & A.Mattos) (Veríssimo et al., in review). This suggests that the floristic and structural distinction between these two savannas may be determined by species adaptations to local water deficit, mainly in dry season. Therefore, it is expected that savanna species that are able to establish themselves in contrasting substrates, as observed in alluvial and typical savannas, would show different adaptations to adjustment to the local environmental stressors.

One of the most suitable approaches to identify these different functional adjustments of plant species to different environmental filters is assessing the intra- and interspecific variation of functional traits (Cianciaruso et al., 2009; Siefert et al., 2015). Variability of functional traits of a same species in habitats with different environments condition help to understand species acclimation responses, while interspecific differences across habitats highlight species' adaptations to contrasting environmental conditions (e.g., water deficit and nutrient limiting) (Dantas et al., 2013; Cássia-Silva et al., 2017; Maracahipes et al., 2018). On the other hand, general trade-offs between traits depend on how plants respond to local environmental conditions, shaping different ecological strategies related to the use and allocation of resources in different habitats (Lavorel and Garnier 2002).

Here we studied different sites of alluvial and typical savannas, by analyzing the interspecific variation between communities and the intraspecific variation within species common to both environments. As water availability and soil fertility are lower in alluvial savanna environments (Veríssimo et al., in review; Valente and Latrubesse, 2012), we expected that: 1) plants in the alluvial savanna have more conservative resource use strategy (i.e., thicker leaves, thicker bark, shorter, and have denser wood), which provides greater tolerance to environmental stress, whereas plants in the typical savanna will display a more acquisitive resource use strategy (i.e., produce leaves with a larger area and a higher specific area); 2) species co-occurring in the two environments (intraspecific level) will present functional traits related to dominant strategy of each habitat (the conservative strategy in alluvial savanna and the acquisitive strategy in typical savanna); 3) although similar coordination between traits are expected for both sites, such as scaling relationships between leaf area, leaf thickness and SLA, the expected distinct resource use strategies between the two distinct cerrado communities will reflect in slope and/or elevation differences between traits bivariate relationships (Reich et al., 1999; Wright et al., 2001). By comparing analysis between the community level and the intraspecific level, we could investigate if the predominance of distinct ecological strategies within the different habitats are related to differences in species composition (i.e., environmental filters driving community assembly processes) or to species individual adaptation to local conditions (i.e., plant species are able to adjust physiological responses to survive in each environment).

2. Materials and methods

2.1. Study sites

We conducted this study in four sites with savanna vegetation

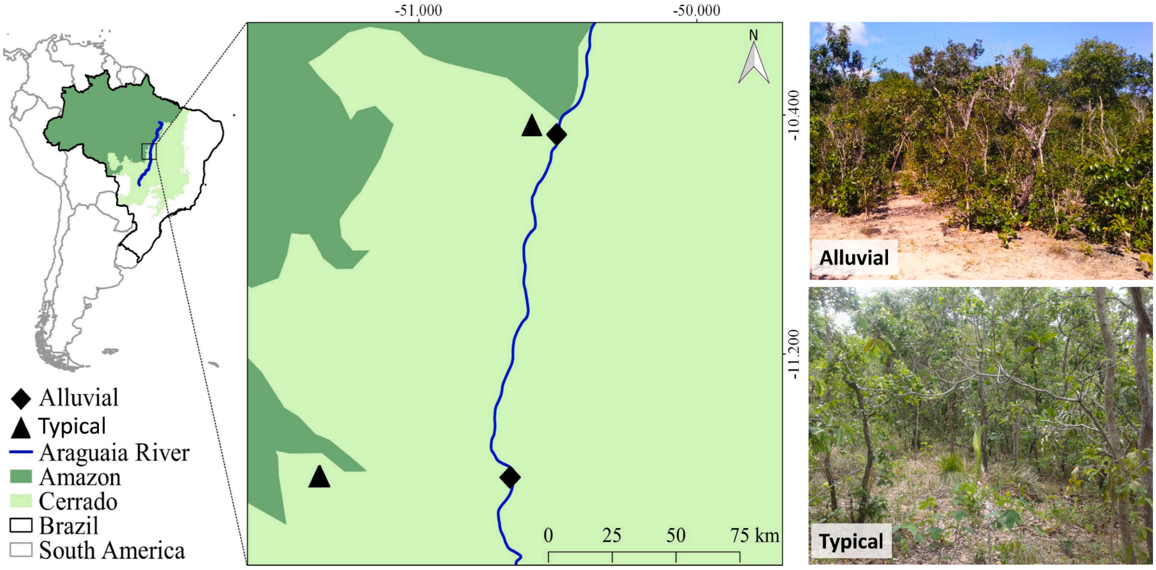

Fig. 1. Map of South America, with emphasis on the Araguaia River Basin (blue line) and the location of the sampling sites of alluvial (diamond symbols and picture on the top) and typical (triangle symbols and picture on the bottom) savanna, in the transition region between the Cerrado (light green area) and Amazon (dark green area) biomes according to IBGE (2018) classification. The pictures highlight contrasting substrate differences of the species living in these habitats, e.g., microsites of exposed soils only in the Alluvial Savanna. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(locally called Typical Cerrado), located in the Araguaia River basin, in the northeast region of the Cerrado Biome, nearby the transition with the Amazon (Fig. 1), in three municipalities (Alto Boa Vista, São Félix do Araguaia and Santa Terezinha), Mato Grosso State. Two sites are established on substrates formed by sandy alluvial deposits, located on the banks of the Araguaia River; for this reason, here we call it, "alluvial savanna". Two sites occur in the interfluvium, on flat relief, deep and well drained soils and were classified as "typical savanna", according to the requirements proposed by Ribeiro and Walter (2008). For study sites, the alluvial savanna and typical savanna has a mean (±SD) for calcium of 0.36 (±0.23) and 0.34 (±0.29) cmolc/dm^{-3}, for potassium of 0.09 (±0.07) and 0.11 (±0.07) mg/dm^{-3}, for phosphorous of 4.28 (±2.87) and 15.67 (±21.42) mg/dm^{-3}, and for sand of 85.9 (±3.9) and 77.7 (±10.9) g/kg, respectively (Veríssimo et al., in review). The vegetation of the alluvial savanna was briefly described by Eiten (1985), while the nature and the formation process of alluvial deposits on the banks of the Araguaia River were described by Valente and Latrubesse (2012). Although the vegetation of the alluvial savanna and the typical savanna are classified as typical savanna, we distinguished the two environments based on the different sedimentary processes and times of formation. While we find recent substrates in strongly weathered alluvial savanna and old substrates in typical savanna, there are also edaphic, floristic, and structural differences between the vegetation (Veríssimo et al., in review).

2.2. Data collection on vegetation and functional traits

At each site, we delimited 10 permanent plots with 20 × 50 m (total of one hectare) and with a minimum distance of 100 m from each other. We sampled and identified all woody plants, including lianas and monocotyledons (diameter at the trunk base ≥5 cm at 30 cm from the ground), from which we measured the total height and diameter of the main stem and the other stems when the plants had two or more stems. The methodology described above follows the protocol of the Biogeography Project of the Cerrado Biome (Felfili et al., 2004). Detailed flora information, including the list of abundances of all species sampled at each site are presented in Veríssimo et al. (in review). This list was used as a reference for sampling species in our study (see Table S1). We divided each plot into 10 subplots of 10 × 10 m, with a total of 100 subplots in each studied site. Next, we randomly selected 10 subplots at each site, and sampled 10 individuals of each species whenever possible. For those species with low abundance ($n < 10$), i.e., locally rare, we sampled nearby individuals outside the plots.

We collected the following functional traits, following the protocol proposed by Pérez-Harguindeguy et al. (2013): leaf area, leaf thickness, specific leaf area, stem-specific density, bark thickness and maximum plant height. The detailed functional and ecological significance of each trait, as well as the predictions about these traits in both environments studied, are presented in Table S2.

For leaf traits, we collected between three and five fully expanded sun leaves. These collections were carried out during the peak of the rainy season (January to February). We measured the thickness of fresh leaves in the field (specifically in the mid-leaf and avoiding leaf ribbing), using a micrometer with a resolution of 0.001 mm (Digital Electronic Micrometer Digimess). To calculate the leaf area, we scanned fresh leaves using a digital scanner (CanoScan LiDE 120). Then, to calculate total leaf area, we manipulated the scanned images to remove any possible dirt and completed the leaf area lost due to physical damage or herbivory, using GIMP software version 2.10.6. We quantified the actual leaf area (without filling) and total (with filling) using the "EBImage" package in the R environment (Team R Development Core, 2020). Subsequently, leaves were dried for 48 h at 60 °C, until a constant weight was reached. We weighed the dry leaves individually using a digital scale with a precision of 0.0001 g (Mars AD500) and calculated the SLA, by dividing the actual leaf area by the dry leaf weight.

To calculate the specific-stem density, we collected a sample from a terminal branch with evident secondary growth and regular diameter and removed all outer bark with the assistance of a stylet or a knife. Then, we measured the length and diameter (in cm) of each branch using a digital caliper (150 mm MTX). For the diameter, we took measurements in three positions on the branch (one in the center and two close to the branch edges) and in two directions, with an angle of 90° to each other, to obtain the height (H) and the width (W). We calculated the volume of the branches (V in cm^3) using the formula: $V = C * W * H$). Then, we kept the branches in a drying greenhouse with air circulation, for 72 h at a temperature of 60 °C (MARCONI 480 liters), until the material reached a constant weight. We measured the dry weight (P in grams) of the branches on a digital scale with a precision of 0.0001 g (Mars AD500). Finally, we calculated the specific-stem density (g.cm^{-3}) of each branch using the formula: $D = P / V$.

In the field, we took the measured thickness of the outer bark or rhytidome at three random points of the main stem, always at a height of 30 cm. We removed only the suber from a 3 cm x 3 cm area with a chisel and measured bark thickness using an analog caliper (Digimess 1000.003). We then calculated the bark thickness average of each plant at the three collection points. Relative bark thickness was calculated in relation to the trunk diameter at 30 cm from the ground (Cássia-Silva et al., 2017).

For the maximum plant height, we measured the longest plant length from ground level to the tallest living branch with leaves, using a laser measuring tape (GLM 40, Bosch 06010729000-000). Specifically, for this trait, all plants in the 10 plots of 20 × 50 m in each site were measured.

2.3. Data analysis

We performed the analyses at two levels: (1) at the community level, in which we compared traits of the entire set of species sampled between the two environments (alluvial versus typical), and (2) at the intraspecific level, in which we compared the traits only between individuals of the species common to both environments.

At the community level analysis, as at the intraspecific level, we used a MANOVA considering all six functional traits as response variables and the habitat type as predictor variables, followed by individual ANOVAs to compare each trait separately. All measured individuals were used. For the community level, species identity was considered a covariate in the model (all species were used), while for the intraspecific level, only the 28 species common to the two habitats were used, as species identity was considered a model error.

We used MANOVA because it is adequate when sets of dependent variables are correlated (Scheiner, 1993). In the analysis at the community and intraspecific levels, we considered the species as an error to avoid possible effects of pseudo-replicates. For MANOVA we used the “stats” package and for ANOVA, the “aov” function of the R base.

To understand bi-variate relationship shifts between communities, we performed correlations between log-transformed traits and compared the slopes using the SMATR package (Warton et al., 2012). To examine the amount of trait variation explained by differences across sites and cerrado types, we partitioned traits variance within and among species, sites and cerrado types. The decomposition of variance was applied according to Messier et al. (2010), using the package ‘cati’ (Taudiere and Violle 2015).

All response variables were examined and normalized when necessary prior to the analyses. All analyses were performed in an R environment (Team R Development Core, 2020), and we adopted a 5% significance level.

3. Results

We sampled 1,310 individuals from 101 species (26–31 species from the two alluvial savanna sites and 60–62 species in the typical savanna sites), representing 81 genera from 37 families. Among all sampled species, 10 occurred exclusively in the alluvial savanna, while 63 species only occurred in the typical savanna, and 28 species were found in both habitats (Table S1).

All six plant traits studied differed between alluvial and typical savannas. Species from the typical sites showed thicker leaves and lower SLA compared with alluvial species when considering all species (community level analysis) (Fig. 2; Table S3 and S2.1) or only the 28 species shared between both habitats (intraspecific level analysis)

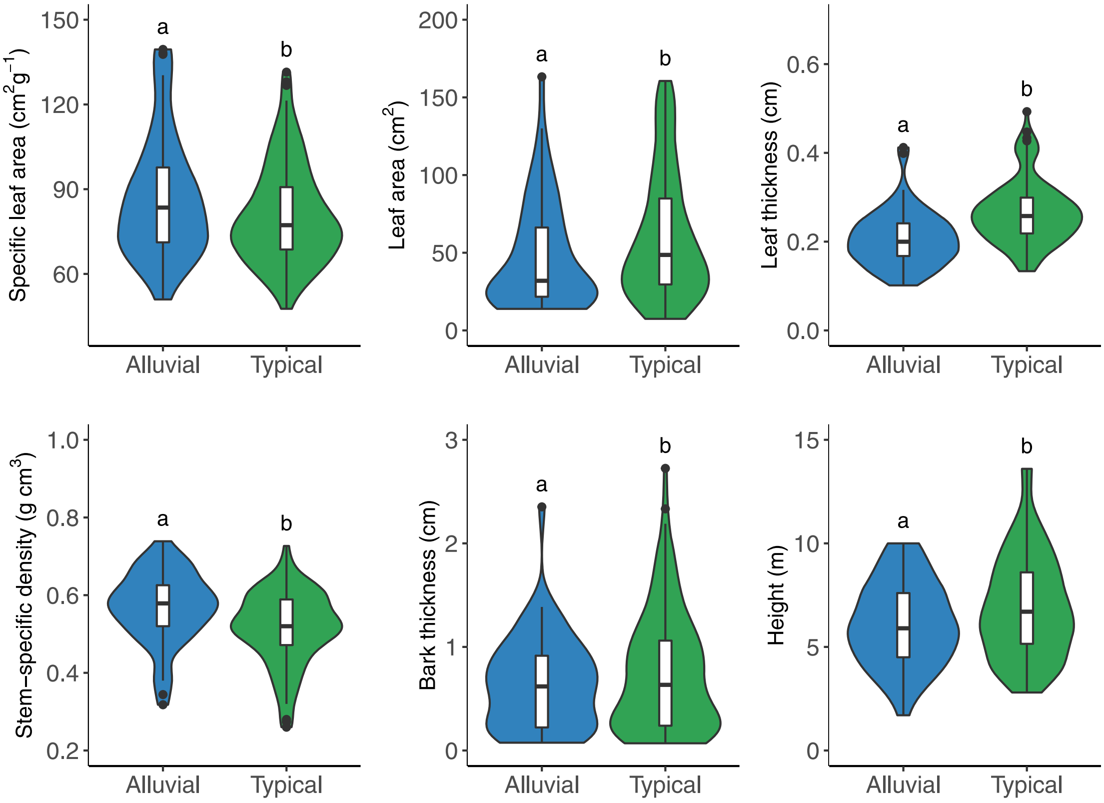

Fig. 2. Violin plot (boxplots combined with kernel density plots) comparing functional traits between woody plant communities from alluvial (blue) and typical (green) savanna located in the eastern region of the Cerrado Biome, Brazil. Boxplots showing median and 25° and 75° percentiles. Vertical curves represent kernel density estimates as a function of the probability density for each parameter. Distinct letters show significant differences between areas (ANOVA, $P < 0.05$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

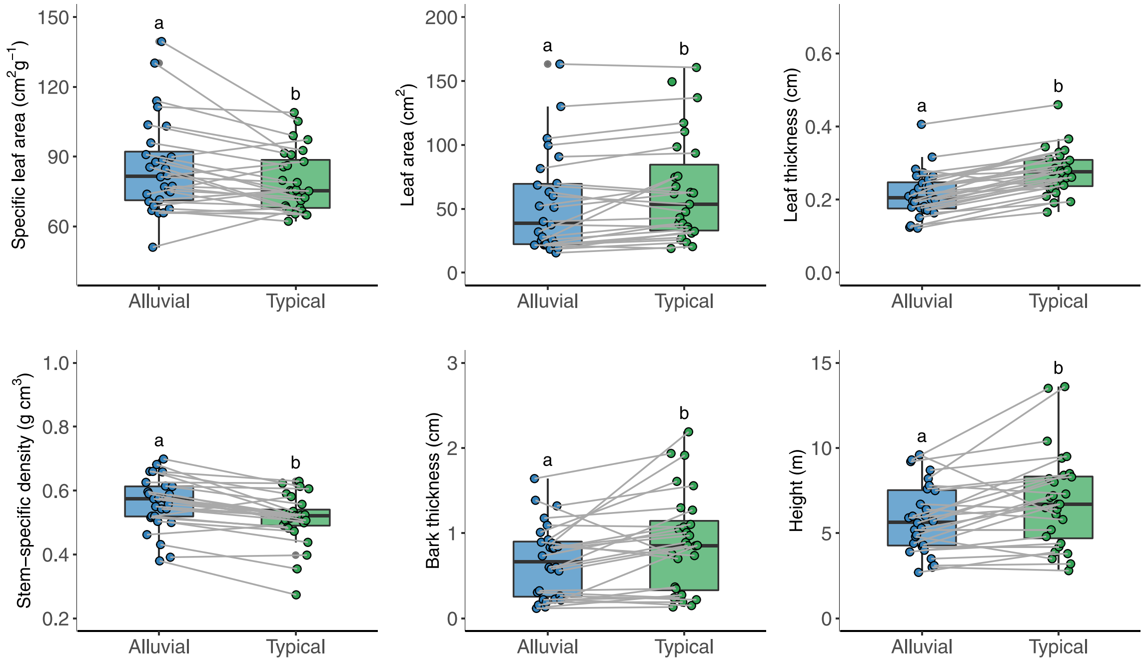

Fig. 3. Boxplots comparing functional traits between shared woody plant species (intraspecific level) between the alluvial (blue) and typical (green) savanna located in the eastern region of the Cerrado Biome, Brazil. Boxplots showing median and 25° and 75° percentiles. Distinct letters show significant differences between areas (ANOVA, $P < 0.05$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Fig. 3; Table S4 and S3.1). Similarly, plants occurring in the alluvial savanna produced generally shorter leaves, thinner bark, and denser wood compared with plants in the typical savanna, at both the community and intraspecific levels (Figs. 2 and 3, respectively). These results indicate a clear effect of the environment on the six key traits regardless of the level of analysis (Table S5). In general, differences among species and cerrado type explained trait variability (Fig. S1), while the variability among sites was relatively lower for all traits.

There was a negative relationship between SLA and leaf area for alluvial (r = -0.21, p=<0.001); and between SLA and leaf thickness also for both alluvial (r = -0.57, p<0.001) and typical savanna (r = -0.48, p<0.001; Table 1). While at a given leaf thickness value species from typical savanna exhibited a 20% higher SLA (similar slopes with difference in intercepts: Wald test = 14.72; $P < 0.001$, Fig. 4a), the slope for the leaf area and SLA relationship was steeper for the alluvial savanna (differences in slopes: Wald test: 4.07, $P = 0.030$, Fig. 4b).

There was a negative relationship between bark thickness and plant height for Alluvial (r = -0.37, p<0.001) and Typical savanna (r = -0.20, p<0.001). Also, there were a positive relationship between plant height and wood density (r = 0.23, p<0.001 for Alluvial and r = 0.22, p<0.001 for the Typical savanna; Table 1), meaning that small plants tend to have relatively thicker bark and softer wood. Between the two plant communities, at a given plant height, typical savanna species showed ~56% thicker bark (similar slopes with difference in intercepts: Wald test = 19.40; p< 0.001, Fig. 4c) and ~20% softer wood (similar slopes with a difference in intercepts: Wald test = 5.11; p = 0.024, Fig. 4d).

Interestingly, we found a positive relationship between leaf thickness and bark thickness for the two plant communities (Table 1), a negative relationship between specific-stem density and leaf area and leaf thickness for the typical savanna (Table 1), and between bark thickness and SLA for the alluvial and typical savanna species (Table 1), which suggests coordination between leaf traits and other organ-level functions.

4. Discussion

4.1. General patterns

Many morphological plant traits are highly plastic, allowing the same species to establish in habitats with different environmental conditions (Cássia-Silva et al., 2017; Maracahipes et al., 2018) and influencing the functioning of the community as a whole (Via, 1993; Via and Russel, 1985). Indeed, we have shown here, at both the community and intraspecific levels, that plants of the alluvial savanna produce smaller

Table 1
Pearson's correlation (r and P-values) between plant traits for alluvial and typical savanna plant communities. Significant correlations (P-values lower than 0.05) shown in bold. Specific leaf area (SLA), leaf area (LA), leaf thickness (LT), relative bark thickness (BT), maximum plant height (HTOT) and stem-specific density (SSD) .

Functional trait	Savanna type	LA	LT	BT	HTOT	SSD
SLA	Alluvial	-0.21 (<0.001)	-0.57 (<0.001)	-0.24 (<0.001)	0.07 (0.180)	-0.13 (0.016)
	Typical	-0.07 (<0.075)	-0.48 (<0.001)	-0.08 (0.033)	-0.18 (<0.001)	-0.04 (0.238)
LA	Alluvial	–	-0.03 (0.586)	0.14 (0.007)	-0.07 (0.185)	-0.16 (0.002)
	Typical	–	-0.01 (0.791)	-0.11 (0.004)	0.01 (0.805)	-0.30 (<0.001)
LT	Alluvial	–	–	0.19 (<0.001)	-0.22 (<0.001)	-0.06 (0.223)
	Typical	–	–	0.14 (<0.001)	-0.04 (0.200)	-0.25 (<0.001)
BT	Alluvial	–	–	–	-0.37 (<0.001)	-0.02 (0.722)
	Typical	–	–	–	-0.20 (<0.001)	-0.04 (0.220)
HTOT	Alluvial	–	–	–	–	0.23 (<0.001)
	Typical	-	-	–	–	0.22 (<0.001)

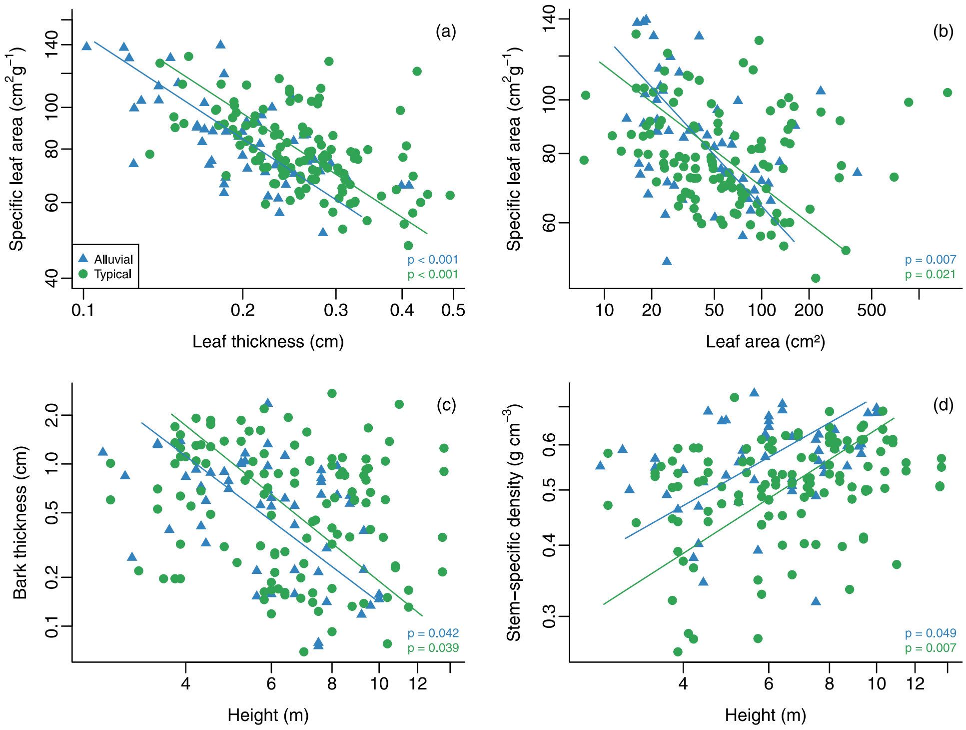

Fig. 4. Bi-variate relationships between (a) specific leaf area and leaf thickness; (b) specific leaf area and leaf area; (c) plant height and bark thickness; (d) plant height and wood density for alluvial (blue) and typical (green) savanna located at the east region of Cerrado Biome, Brazil. Each datapoint represents different species. Significant regression slopes ($P < 0.05$) shown as solid lines. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and thinner leaves, with higher SLA compared with plants in the typical savanna. Moreover, plants in the alluvial savanna are small and have denser wood and thinner bark. These differences between the two environments studied here, evidence the adaptive adjustment of the species to habitat-specific environmental stress (e.g., the stronger water and nutritional limitation of the soils in the alluvial savanna) and disturbance (higher fire severity in the typical savanna). We also demonstrated functional trade-offs between leaf traits (SLA, leaf thickness and leaf area), as well as between structural traits of individuals (plant height, specific-stem density and bark thickness).

4.2. *Leaf traits*

Our findings partially contradict our expectations. Contrary to what we hypothesized, at the community and intraspecific levels, alluvial savanna species showed smaller, thinner leaves and higher SLA than plants in the typical savanna. Smaller leaves favor a decrease in water loss through transpiration. This pattern seems to be well established among the different vegetation types of the Cerrado, where plants from more humid vegetation showed larger and thinner leaves than the more xeric savanna plants (Cássia-Silva et al., 2017; Hoffmann et al., 2005; Maracahipes et al., 2018).

Nonetheless, alluvial savanna plants presented thinner leaves with higher SLA than those in the typical savanna, which are related to higher water loss through transpiration (Westoby et al., 2002), lower leaf production costs (Villar and Merino, 2001), and greater efficiency in the synthesis of organic compounds, via photosynthesis (Lambers et al., 2008; Westoby et al., 2002). These strategies are usually described as an adaptation to more dystrophic environments (Pérez-Harguindeguy et al., 2013; Rossatto and Kolb, 2013; Rossatto et al., 2015) to be contradictory. However, as demonstrated by the bi-variate relationships (Fig. 4), at a given leaf thickness, species from the typical savanna showed higher SLA, suggesting that the driver of leaf traits in the alluvial savanna (high SLA, thin and small leaves) may be a shortage of resources, most likely nutrient limitations (Niinemets, 1999; Niinemets and Kull, 2003). Indeed, thinner leaves are more efficient at capturing light and consequently maximizing photosynthesis in environments poor in nutrients for plants (Cássia-Silva et al., 2017; Hoffmann et al., 2005; Meziane and Shipley, 2001, Wright et al., 2001).

Additionally, even though thinner leaves with higher SLA are more related to greater water loss, we noticed that the deciduousness of the plants is more evident in the alluvial savanna and the water economy could be guaranteed by the earlier loss of leaves and later regrowth in that environment (Souza et al., 2020; Veríssimo et al., in review). During the dry season, alluvial savanna plants lose their leaves earlier and produce new leaves later than the typical savanna plants (personal observation). This implies that leaves in the alluvial savanna have a short time during the year to photosynthesize, which seems to be compensated by the greater photosynthetic efficiency, inferred from the higher SLA. Thus, suggest that woody plants that establish in the typical alluvial savanna invest in leaves with lower production costs, adjusting to both water deficit and nutrient shortcut.

Considering the aspects discussed above, we suggest that the three leaf traits analyzed here are very labile, as also noted in other studies (Cássia-Silva et al., 2017; Maracahipes et al., 2018; Valladares et al., 2014) and therefore allow the establishment of woody plants of savanna formations in environments with contrasting conditions in terms of water and nutrient availability in the soil. The plasticity of the leaf traits showed here can both minimize water loss (smaller leaf area in the alluvial savanna) – a conservative strategy – and maximize nutrient synthesis (smaller thickness and greater SLA in the alluvial savanna) – an acquisitive strategy. Together, our results suggest a conservative strategy for the use of water in the alluvial savanna, considered more xeric, than the typical savanna (Veríssimo et al., in review).

4.3. *Stem-specific density*

The higher woody density from alluvial savanna plants also suggests greater water and nutritional restrictions for plants in this environment compared with the typical savanna. The investment in higher wood density is associated with resistance to cavitation, making the plant more resistant to water deficit, which can cause embolism and lead to plant death (Haccke et al., 2001; Pooter et al., 2009). Contradicting our results, some studies in the Cerrado have found that environments with lower water availability could favor species with soft wood, which could be important for storing water (Dantas et al., 2013; Maracahipes et al., 2018). However, this trend seems to be restricted to xeric but eutrophic environments, such as dry Cerrado forests (Apgaua et al., 2014). Thus, we suggest, based on our findings that the higher wood density in the alluvial savanna is a consequence of the limitation of both water and nutrients (Bucci et al., 2006; Pellegrini, 2016). In addition, the positive relationship between plant height and specific-stem density we found for both sites indicates that growing taller requires mechanical support and possibly more fibers and a lower vessel diameter to prevent embolism, implying a higher wood density (Hacke et al., 2001; Chave et al., 2009). Surprisingly, there are mixed results of positive and negative relationships between height and wood density worldwide (Chave et al., 2006; Falster and Westoby, 2005; Van Gelder et al., 2006), and species-specific life habit stress tolerance adaptations and ecological strategies (successional stage, light requirement, etc.) are suggested to explain these contrasting patterns, especially considering biomass allocation (Puglielli et al., 2021). We show here, for the first time, that in an open environment, with no light availability limitation, this relationship is weak, but consistently positive.

4.4. *Bark thickness*

The lower bark thickness of alluvial savanna plants can make them more sensitive to fire compared with typical savanna plants, since thicker bark would provide greater fire protection by thermal insulation of living tissues (Lawes et al., 2011; Pausas, 2015; Pausas et al., 2017). We note that in the alluvial savanna, the grassy layer is discontinuous, incipient, and less dense compared with that of the typical savanna (see also Fig. 1). Considering that this layer is the main fuel source for fire in the Cerrado (Gomes et al., 2018; Hoffmann et al., 2012), we believe that a greater severity of the fire in the typical savanna (inferred from the greater biomass of fuel material) is selecting individuals or species that produce thicker bark. In the Cerrado and other tropical savannas, the species selection process is well documented in studies comparing forest formations, where plants have thinner bark and are more sensitive to fire than savanna formations, where plants have thicker bark and are therefore more tolerant to fire (Pérez-Harguindeguy et al., 2013). Thus, we believe that there is a causal association between grass biomass and the bark thickness of woody plants between the alluvial and typical savanna.

4.5. *Maximum plant height*

The lower height of plants in the alluvial savanna also seems to result from the lower availability of water and nutrients in the soils to sustain their growth, as discussed previously for wood density. One of the consequences of small plants in the alluvial savanna is that they may be more exposed to flames during occasional fires (Gomes et al., 2014; Hoffmann et al., 2009). In fire-prone environments, a trade-off is observed between investing in bark thickness or tree height, as two possible strategies to survive after fire (Dantas and Pausas, 2013; Moreira et al., 2003; Pausas et al., 2017; Scalon et al., 2019). Indeed, the allometric negative relationship between plant height and bark density we found for both sites corroborate this trade-off, even for plants occurring in the alluvial savanna, which may not be highly prone to fire, due to the discontinuous grass layer, as discussed above. With increasing fire frequency and shifts in natural fire regimes due to land-use changes (Pivello, 2011), plants in the alluvial savanna, which are small and have thinner outer bark, may be less resistant to fires that could lead to local extinctions in the short term, an aspect worthy of investigation in future studies.

5. Conclusion

All six functional traits evaluated here suggest that plants species adopted distinct resource-use strategies to the different abiotic conditions of the two environments studied. This adaptive response of plant traits occurs due to the greater water deficit and limitation of nutrients in the soils of the alluvial savanna and the possible greater severity of the fires in the typical savanna, showing that factors such as water, nutrients, and fire act on multiple adaptive properties of the species. We conclude that:

1. Smaller leaves in the alluvial savanna represent a conservative resource strategy, minimizing water loss;
2. The smaller leaf thickness and the larger SLA area of the alluvial savanna plants represent a resource acquisition strategy, as they allow species to maximize the photosynthetic rate;
3. The lower heights of the plants and the higher density of the wood in the alluvial savanna are functional adjustments in response to the lower availability of water and nutrients for the plants;
4. The thicker bark makes the shrub species of the typical savanna more resistant to burning, and this seems to be a consequence of the greater biomass of combustible material (grasses) (personal observation) in this environment, since in the alluvial savanna the herbaceous-grassy stratum is discontinuous and incipient.

Data accessibility statement

The plant functional traits and community data used in this work are the primary data obtained by authors. The species abundances per site are available in electronic Supplementary Information (Appendices S1). The statistical analysis scripts, values of functional traits per individuals as well as the abundance of individuals per plots are available upon request from the corresponding author.

Authors' contributions

A.C.A., L.M., D.V.S., J.M., M.V.F. and E.L. conceived of the research idea; A.C.A., A.A.V., L.A.G., D.C., J.M. and E.L. collected data; J.N.C., L. M., M.C.S., D.V.S., M.V.F. and E.L. performed statistical analyses; J.N.C., L.M., M.C.S., D.V.S. and E.L. wrote the paper; all authors discussed the results and commented on the manuscript.

Declaration of Competing Interest

None.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.flora.2021.151925.

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