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Functional Biogeography and Ecological Strategies of Trees Across the Amazon–Cerrado Transition

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ABSTRACT

Question: We asked how community functional traits differ among vegetation types at the transition zone between the Amazon forest and Cerrado savanna biogeographic domains, and which environmental variables best predict these changes in functional structure.

Location: The large transition zone between the Amazon and Cerrado biogeographic domains.

Methods: We field-collected and analyzed an extensive new database of 182 tree species from six vegetation types, resulting in 55,895 records of functional traits. We selected 15 traits that affect different aspects of ecosystem processes and ecological strategies of trees. Then we compared the distribution of functional traits among vegetation types and assessed their association with edaphic and macroclimatic variables.

Results: We recorded a functional continuum between the extremes of Cerrado (Typical Cerrado) and the Amazon (Open Ombrophilous Forest), with most traits forming a gradient along the vegetation types. Our data also indicate that tree-dominated Cerrado formations (Cerradão) are functionally intermediate between savannas and forests, reinforcing the importance of accounting for the full floristic and structural variation of neighboring biogeographic domains. Our work revealed that CEC, soil pH, mean temperature, maximum temperature, total precipitation, and climatic water deficit are consistently related to key functional traits across the Amazon–Cerrado transition.

Conclusions: Functional traits can be used to efficiently characterize and distinguish multiple communities where South America's two largest biogeographic domains meet. We were able to delimit morpho-physiological requirements that ensure tree species' maintenance in different vegetation types and to characterize the transition zone in terms of ecosystem functioning.

Woody vegetation can vary greatly in terms of ecological strategies. Hence, to understand the rules of assembly, boundaries, and full complexity of transitions, it is essential to account for functional differences.

1 | Introduction

Understanding the relationships of plant characteristics with abiotic and biotic factors has been a central goal of community ecology for decades (e.g., Lavorel and Garnier 2002; Grime 2006). Its importance is now all the greater because of the potential to use these relationships to better predict vegetation responses to disturbance and changes in ecosystem processes driven by anthropogenic changes. Critical to such understanding is the large-scale quantification of functional traits (Souza et al. 2016), as these represent the morphological, physiological, or phenological characteristics measurable in plants and which affect their growth, reproduction, and survival (Violle et al. 2007). The functional approach is based on ecological niche theory (Hutchinson 1957), according to which species are heterogeneous entities that respond to environmental conditions, with functional traits, rather than species, being selected over time through environmental filters (Violle et al. 2007).

Variation in plant functional traits is associated with important ecological processes such as climate change, land use, and biotic interactions (Kattge et al. 2011; Funk et al. 2017). Ecosystems respond to change by altering in both structure and function, caused mainly by environmental factors (Díaz and Cabido 2001). Thus, the association between functional traits and environmental conditions allows us to detect the assembly rules and coexistence patterns of organisms concerning selective forces (Díaz et al. 1999). Consistent patterns of association between functional traits of plants and the environment have been recorded (Grime 1998), with different functional groups performing the essential functions for each community (Díaz et al. 2004). The analysis of trait distribution across different ecosystems can be broadly defined as functional biogeography (Violle et al. 2014), which, in contrast to classical biogeography, offers a powerful lens for understanding how the ecological functions performed by species influence ecosystem structure and services.

The importance of the environment for the functional structure of vegetation types is highlighted by the transition zone between the two largest biogeographic domains in South America, the Amazon and the Cerrado. The vegetation of this transition zone is extensive, highly variable, and dynamic in space and time ("hyperdynamic"), due to strong environmental filters, and it has sharply declined due to anthropogenic pressures (Marimon et al. 2014; Marques et al. 2020). These conditions make this ecological stress zone an especially important natural laboratory and lend urgency to research to characterize, quantify, and understand the functional structure of contrasting vegetation types that span a large ecotone between these key tropical biogeographic domains (Neyret et al. 2016; Araújo, Marimon, Scalon, Fauset, et al. 2021; Jancoski et al. 2022).

Indeed, rather than there being simply an abrupt and obvious transition between the Cerrado and the Amazon, the transition is complex and extensive. It includes a range of distinct vegetation types with a variable mix of Amazonian and Cerrado species, within a zone up to 250 km wide and extending over 6000 km through central South America (Ratter et al. 1973; Marimon et al. 2006; Morandi et al. 2016; Marques et al. 2020). While the large-scale functional biogeography of this region has been largely neglected, it is to be expected that vegetation types here are predictably composed of different functional groups (e.g., fire-tolerant species, fast-growing species, species with high water use efficiency), due to the existence of distinct selective pressures at each site, and that ecological strategies of species will be reflected in their functional traits (Díaz et al. 1999; Zilli et al. 2014). In all, the vast scale and ecological diversity of the Amazon–Cerrado transition zone, together with the relative neglect by researchers, reinforces the need to investigate the assembly rules that govern the coexistence of its communities. Here, we aim to characterize the arboreal functional biogeography across the complex transition between South America's two largest biogeographic domains. To address this, we use the trait-based approach supported by the theoretical framework of Niche Theory, which suggests that different species can develop functional traits as a result of evolutionary pressures, to exploit specific niches depending on the abiotic conditions of the environment (Hutchinson 1957), and Environmental Filtering Theory, which suggests that environmental factors act as filters selecting species with specific functional traits (Weiher and Keddy 1995). Taken together, this theoretical basis helps to understand how tree species manage to coexist while exploiting different aspects of the Amazon–Cerrado transition.

To make our goal possible, we first made extensive, original field and laboratory measurements across 30 permanent plots that include almost 200 tree species and over 50,000 records of functional traits, all collected applying the same protocol standards. We analyzed these to investigate the distribution of traits across different vegetation types and evaluate how multivariate tree strategies change across the vegetation gradient in the biogeographic domains transition. Our questions and their respective hypotheses were as follows:

1. How does functional structure change between different vegetation types in the Amazon–Cerrado transition? We expected that functional traits would be distributed to form a coherent functional gradient from savanna to forest, following patterns of species composition (Morandi et al. 2016) and the regenerative functional traits of fruits and seeds (Cruz et al. 2021). We also expected that this vegetation mosaic would be composed of different sets of functional strategies. In communities established in more seasonally dry conditions (closer to the Cerrado), we expected to find species with more conservative functional strategies (Araújo, Marimon, Scalon, Cruz, et al. 2021).
2. How do environmental predictors relate to variation in functional structure along the Amazon–Cerrado transition? We expected that edaphic parameters and the precipitation regime are the key environmental factors for controlling variation in functional structure. This is due to evidence that some communities are located in regions with distinct soil types (Nardoto et al. 2014;

Lloyd et al. 2015) and due to the marked climatic seasonality onto which more frequent heat waves and extreme drought events have been superimposed recently (Marimon et al. 2020; Tiwari et al. 2021).

2 | Methods

2.1 | Study Area

We conducted the study in the Amazon–Cerrado transition region using a large network of 30 permanent plots, which in turn contributes to wider networks with more than 8000 plots in 70 countries tropics-wide where forests are monitored (ForestPlots.net et al. 2021). Each plot is 1 ha (100 × 100 m), established in Typical Cerrado (typical savanna), Cerradão (woodland savanna), Gallery Forest, Semi-deciduous Seasonal Forest, Evergreen Seasonal Forest, and Open Ombrophilous Forest. These vegetation types have been extensively documented elsewhere (Ratter et al. 1973; Marimon et al. 2002, 2006; Marimon-Junior and Haridasan 2005; Ivanauskas et al. 2008; Solórzano et al. 2012; Mews et al. 2012; Morandi et al. 2016; Cruz et al. 2021). Plot locations ranged from the southern portion of Pará state, skirting the southern edge of the Xingu Indigenous Park, to the north-central portion of Mato Grosso state (Figure 1; Appendix S1: Table S1). The regional climate is type Aw (tropical with dry winters) and Am (tropical monsoon), according to the Köppen classification (Alvares et al. 2013), and mean annual precipitation and temperature values range from 1511 to 2353 mm and 24.1°C to 27.3°C, respectively (Hijmans et al. 2005; Appendix S1: Table S1).

2.2 | Functional Traits

Our species database was based on the species lists generated by recent plot inventories (2014–2016) conducted by the research team of the Plant Ecology Laboratory of the Universidade do Estado de Mato Grosso (UNEMAT), Nova Xavantina, Mato Grosso, Brazil. The level of inclusion of stem diameters within these inventories was ≥ 10 cm at 1.3 m height (from the ground) for forest formations and 0.3 m height for savanna formations. The final list was composed of 182 tree species from 45 families, with all data deposited in the ForestPlots.net database (Lopez-Gonzalez et al. 2011). We classified the families according to APG IV (Chase et al. 2016) and revised the species names following the Flora do Brazil 2020 species list (http://floradobrasil.jbrj.gov.br/). The botanic material used to identify each species in our domain is deposited in the herbaria NX (UNEMAT, Nova Xavantina, MT), UB (University of Brasilia, Brasilia, DF), IBGE (Brazilian Institute of Geography and Statistics, Brasilia, DF), and CEN (Embrapa Genetic Resources and Biotechnology, Brasilia, DF).

For each 1-ha plot, we selected the most abundant species, which together contribute up to 80% of the basal area of the community. Thus, we ranked the species in each plot in order of abundance, then summed the accumulated basal area contribution until reaching 80%, thereby obtaining our sample target species for each plot. Faced with the challenge of accessing the functional traits of all the species in this biodiverse region (between 30 and 150 species per plot), this selection methodology enabled us to distribute the field data collection effort optimally among multiple locations in the Amazon–Cerrado transition.

For each species and plot, we then randomly selected five individuals, on which we measured and collected field samples to determine the functional traits: leaf area (LA, mm^2), leaf dry matter content (LDMC, mg/g), leaf mass per area (LMA, g/cm), leaf thickness (LT, mm), leaf nitrogen (N, mg/g) and phosphorus (P, mg/g) concentration, outer (OBT, mm) and inner (IBT, mm) bark thickness, bark density (D, mg/mm^3), maximum xylem length (MXL, mm), xylem lumen diameter (XLD, μm), xylem vessel density (XVD, mm^2), mean fiber length (FL, μm), mean fiber thickness (FT, μm), and fiber wall thickness (FWT, μm). The xylem vessel anatomy data (XLD, XVD, FL, FT, and FWT) were obtained only for: Cerradão, Semi-deciduous Seasonal Forest, Evergreen Seasonal Forest, and Open Ombrophilous Forest. We separated the bark into inner and outer because bark consists of a living inner portion, including the innermost periderm, and a nonliving outer portion made of dead cells. Inner bark is mainly involved in water storage and photosynthesis, while outer bark plays a protective role against fire and physical damage. The proportion of these layers varies among species, reflecting functional trade-offs (Rosell et al. 2014). We selected these 15 functional traits because they affect different ecosystem processes and respond to macroclimatic drivers (Bruelheide et al. 2018) and are anatomical indicators of resistance or vulnerability to drought (Ribeiro-Júnior et al. 2023; Appendix S1: Table S2). Field campaigns for the collection of functional traits were conducted between June 2016 and October 2018, always in the dry period.

We measured and calculated: LA using scanned leaves and ImageJ software (Rasband 1997); LMA as the ratio of fresh leaf area to dry leaf mass after 60 h drying in an oven at 65°C; LDMC as the ratio of saturated mass to dry leaf mass; LT, OBT, and IBT with a digital caliper (precision 0.001 mm); bark density (D) by the ratio of fresh bark volume to dry weight (Rosell et al. 2014); MXL using the air injection method (Skene and Balodis 1968); and determined N and P by Kjeldahl digestion and UV spectroscopy, respectively. To obtain XLD, XVD, FL, FT, and FWT measurements, we divided stem samples in half and boiled one part (water + glycerin 3:1) for 2 days for softening, then sectioned on microtome with sections of 12–20 μm. Photomicrographs were taken from the histological slides at 100, 200, and 400 × magnification using a Leica Digital Image capture camera (LAS E.Z. 1.7.0) coupled to a Leica ICC50 microscope. Using the photos, we measured the tissues with the aid of Anati Quant 2 UFV (Aguiar et al. 2007) and ImageJ software.

2.3 | Environmental Data

We extracted the macroclimatic variables (maximum temperature, average temperature, and total precipitation) from the WorldClim database (www.worldclim.org) with a resolution of 2.5 arc-minutes for the period from 2010 to 2018. We added the CWD (climatic water deficit), which characterizes the loss of

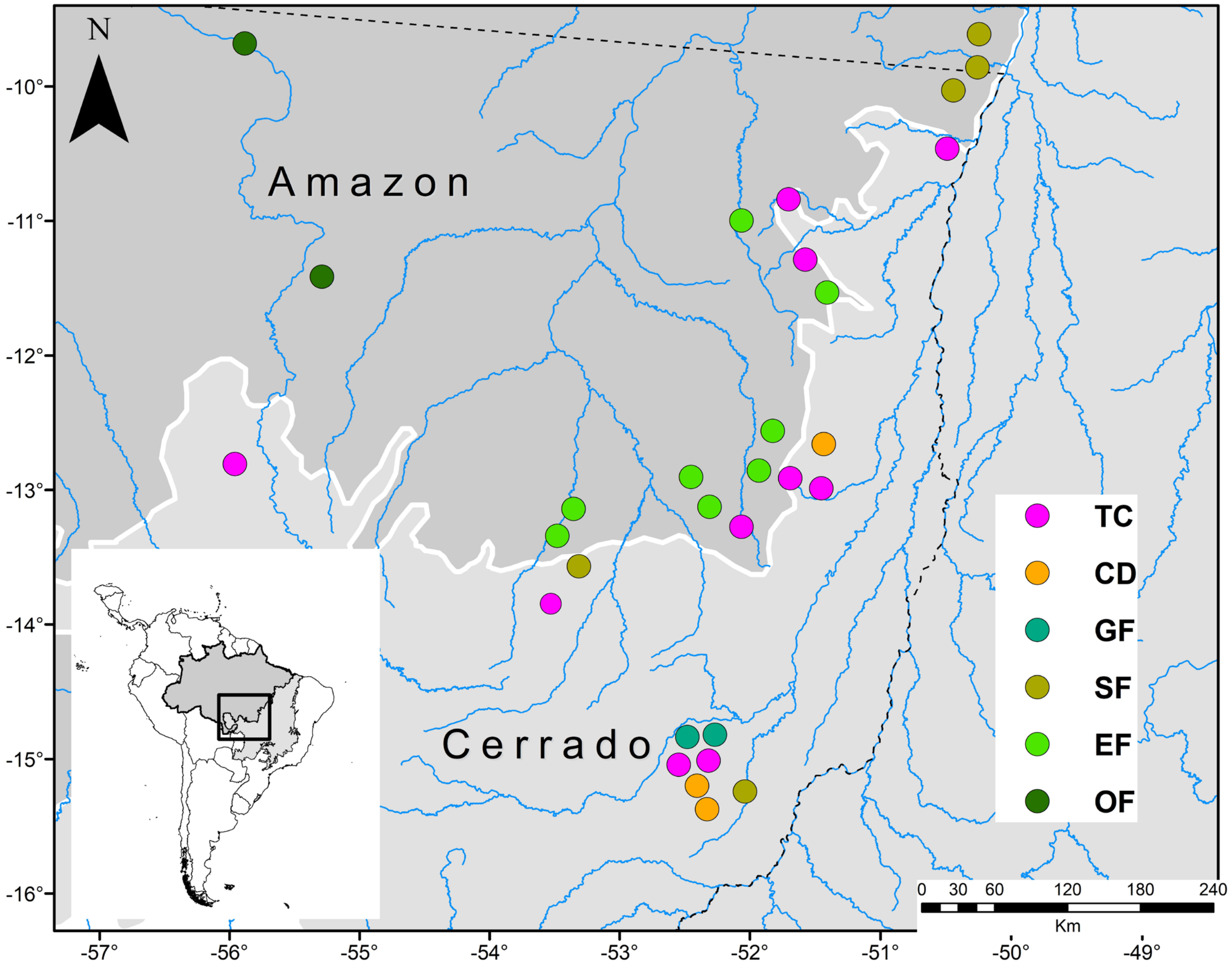

FIGURE 1 | Distribution of the thirty 1-ha plots assessed in the Amazon–Cerrado transition, each denoted by colors representing the vegetation types. The blue lines represent the main rivers and the dotted black line the boundaries of Mato Grosso state. The white line represents the official boundary (IBGE 2012) between the Amazon and Cerrado. CD = Cerradão, EF = Evergreen Seasonal Forest, GF = Gallery Forest, OF = Open Ombrophilous Forest, SF = Semi-deciduous Seasonal Forest, TC = Typical Cerrado.

water to the atmosphere during the driest months (the months when evapotranspiration is greater than precipitation). The CWD values were extracted from a layer with long-term averages of CWD and 2.5 arc-minutes resolution based on the projection of Chave et al. (2014). We also used edaphic variables (cation exchange capacity, pH in water, nitrogen, and carbon concentration in the soil) extracted from the SOILGRIDS Project (https://soilgrids.org/, licensed by ISRIC-World Soil Information), with a resolution of 250 m.

2.4 | Data Analysis

To compare the distribution of functional traits and their variation among vegetation types we fitted generalized linear mixed-effects models (GLMM) using the package `lme4` (Bates et al. 2015). We built alternative models using individual trait values as the response variable, vegetation type as a fixed effect predictor, species, and plot as a random effect factor, and the *Gaussian* error distribution. We fitted the alternative and a null model for each trait and tested the statistical similarity by a one-way ANOVA. To assess the differences in functional traits between vegetation types, we carried out the Tukey HSD pairwise test with the package `emmeans` (Lenth 2021). We chose GLMM because of its ability to model the grouping of traits considering species and plot as a random factor, and because the distribution of the full set of traits was not normally distributed. For each trait, we calculated the community-weighted mean (CWM) according to Garnier et al. (2004).

$$\mathrm{CWM}_{j.k} = \sum_{i}^{n.k} P_{i,k} t_{i,j}$$

where n is the number of species sampled in plot k, $P_{i,k}$ is the relative abundance of species i in plot k, referring to the sum of the abundances for all species with traits in the plot, and $t_{i,j}$ is the mean value of species i for trait j. We calculated this metric for all traits using the `FD` package (Laliberté and Legendre 2010).

To explore covariance in trait space, reveal gradients and identify underlying ecological strategies, we performed a principal component analysis (PCA) between the CWM values of the functional traits and the sampled plots. We rescaled the CWM values to mean = 0 and standard deviation = 1 and used them in a PCA by the `FactoMineR` (Lê et al. 2008) and `factoextra` (Kassambara and Mundt 2020) packages.

To assess the relationship between functional traits and the environment considering species turnover across the environmental gradient (Appendix S3: Figure S1), we used a model based on the "fourth corner problem" and RQL approach (Legendre et al. 1997; Brown et al. 2014). We used environmental variables (matrix R), with species functional traits (matrix Q), species abundance (matrix L), and their interactions to fit generalized linear models (GLMs) using the `mvabund` package (Wang et al. 2012). The models were implemented with a negative binomial distribution and selected using the LASSO (Least Absolute Shrinkage and Selection Operator) optimization algorithm to regularize and select variables. The negative binomial distribution is often preferred in RQL analyses and ecological models that deal with count data such as species abundance (matrix L). Statistical significance was assessed using a variance analysis with 1000 resamples. We divided this set of analyses into three datasets due to the difference in the number of species in each one: leaf, bark, and branch morphological traits (165 species), xylem vessel anatomy traits (96 species), and leaf nutrient traits (60 species). We performed all analyses in the R program (R Core Team 2023) and considered the significance level at 5% for all analyses.

3 | Results

Community values of LDMC (leaf dry matter content) were greatest in the Cerradão and lowest in the Open Ombrophilous Forest (Figure 2; Appendix S2: Tables S3 and S4). In the Typical Cerrado, we also observed thicker leaves (LT) than in forest formations, with the Cerradão having the highest values. Leaf N and P concentrations were lowest in the Typical Cerrado and greatest in the Open Ombrophilous and Gallery Forest. Both outer and inner bark thickness (OBT, IBT) were highest in the Typical Cerrado and Cerradão. Among the forest formations, the Gallery Forest showed the highest OBT value but did not differ from the Semi-deciduous Seasonal Forests. Bark density (D) was lowest in the Typical Cerrado and Cerradão but did not differ statistically among the other formations. MXL (maximum xylem length) was low for Evergreen Forest but similar to Open Ombrophilous Forest (Figure 2; Appendix S2: Tables S3 and S4). In terms of xylem vessel anatomy, Cerradão showed marked differences from the other forests, with lower XLD (mean xylem vessel lumen diameter) and higher FL (mean fiber length), FT (mean fiber thickness), and FWT (mean fiber wall thickness).

For N (leaf nitrogen concentration), P (leaf phosphorus concentration), and D (bark density), the distribution of means at the community level (CWM) increased significantly from Typical Cerrado toward Open Ombrophilous Forest, while LMA (leaf mass per area), LT, OBT, and IBT showed the inverse pattern (Figure 2). The CWM of traits LA (leaf area) and LDMC did not show a distribution pattern along the Amazon–Cerrado gradient, although they showed a statistical difference between the Open Ombrophilous Forest and the other forest formations (Figure 2). For xylem anatomy traits, we observed gradual changes between vegetation types for FT and FWT, with CWM decreasing toward the Open Ombrophilous Forest (Figure 2).

The relationship between functional traits at the community level was well captured by the first two axes of PCA, with a total of 71.8% of the variance explained (PC1 = 55.7% and PC2 = 16.1%), where axes 1 and 2 were determined by LMA and LDMC, respectively (Figure 3A,B; Appendix S2: Tables S5 and S6). By visual inspection, axis 1 clearly describes the functional distinction between savanna, forest, and transitional areas, while axis 2 separates the different forest types. We verified a gradient formed by two main continua, the first with communities characterized by high foliar N and P concentration and bark density, characterizing plants with traits linked to productivity (Figure 3A,B). The second was formed by thicker leaves and bark, high LMA, and longer xylem vessel lengths (Figure 3A,B). We also observed strong similarities between Semi-deciduous Seasonal Forest and Evergreen Forest plots, as well as the position of Cerradão as a functionally transitional vegetation type between forest and savanna formations.

The first two axes for the PCA performed with the xylem functional traits captured a total of 69.7% of the variation in functional space (PC1 = 45.4% and PC2 = 24.3%), with axes 1 and 2 determined by FWT and FL, respectively (Figure 3C,D; Appendix S2: Tables S5 and S6). The first axis of the PCA indicated a spectrum of variation between safety and hydraulic efficiency, where we found higher values of FWT and FT for the Cerradão plots, and higher XVD (xylem vessel density) for the Open Ombrophilous forests (Figure 3C,D).

The overall interaction between environmental variables and leaf, bark, and branch morphological functional traits was supported by the "fourth corner" modeling ($p = 0.02$; Figure 4). The LMA trait was positively correlated with TempMax (0.62) and Prec (0.87), while negatively correlated with Temp (−0.73; Figure 4). For LT we obtained positive correlations with CEC (1.26) and TempMax (1.20), and negative correlations with Temp (−0.94) and Prec (−0.82). Similarly, LDMC was negatively correlated with Prec (−0.67; Figure 4). The bark traits (IBT, OBT, and D) showed a strong correlation with soil pH, positive for OBT and IBT (0.84 and 0.82) and negative for D (−0.62; Figure 4). Regarding leaf nutrients, we also obtained strong and significant correlations ($p = 0.02$; Figure 4). Leaf phosphorous was positively correlated with pH (2.80) and Prec (2.90), while for leaf nitrogen there were positive correlations with SNC (−3.00) but negative correlations with CEC (−2.80) and pH (−3.03).

For the xylem anatomy, we found strong and significant associations with climate and soil ($p = 0.01$; Figure 4). Among the trait set, FWT and XLD had the highest number of strong correlations with environmental predictors (Figure 4). Both FWT and XLD were positively correlated with CEC (2.98) and pH (2.52 and 2.45), with only XLD being negatively correlated with Prec (−2.12; Figure 4). Meanwhile, XLD was negatively correlated with CWD (−1.72), and FWT was positively correlated with CWD (1.98) (Figure 4). The variation in ecological strategies along the longitudinal gradient was not supported (Appendix S3: Figure S2).

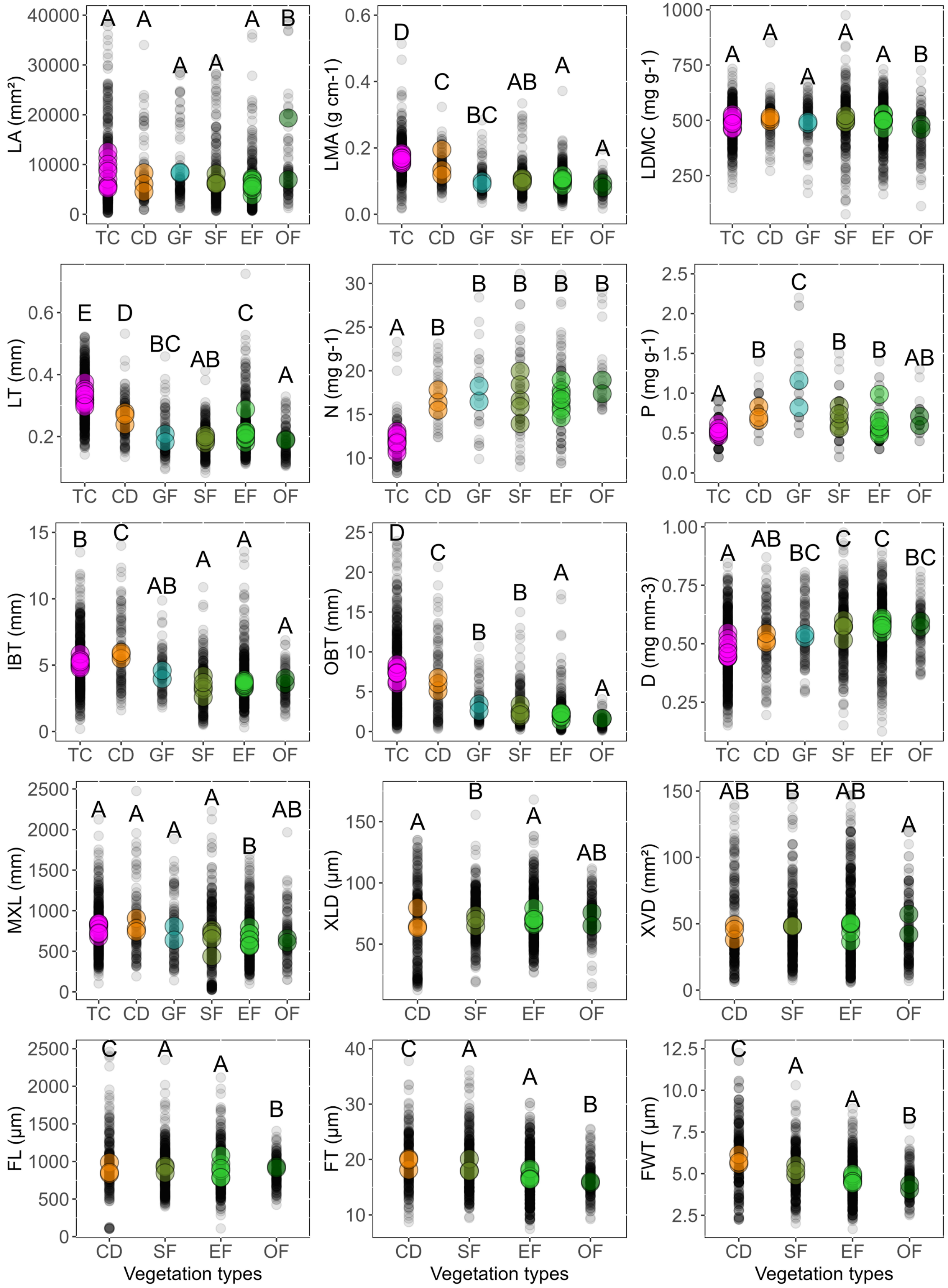

FIGURE 2 | Legend on next page.

FIGURE 2 | Variation of functional traits among vegetation types in the Amazon–Cerrado transition. The colored circles represent the trait community-weighted mean (CWM) for each sampled plot, and the black circles represent the trait values for each individual. *X*-axis (vegetation types): CD = Cerradão, EF = Evergreen Seasonal Forest, GF = Gallery Forest, OF = Open Ombrophilous Forest, SF = Semi-deciduous Seasonal Forest, TC = Typical Cerrado. *Y*-axis (functional traits): D = bark density, FL = mean fiber length, FT = mean fiber thickness, FWT = mean fiber wall thickness, IBT = inner bark thickness, LA = leaf area, LDMC = leaf dry matter content, LMA = leaf mass per area, LT = leaf thickness, MXL = maximum xylem length, N = nitrogen concentration, OBT = outer bark thickness, P = phosphorus concentration, XLD = mean xylem lumen diameter, XVD = xylem vessel density. Letters represent differences in means according to Tukey HSD pairwise post hoc comparisons.

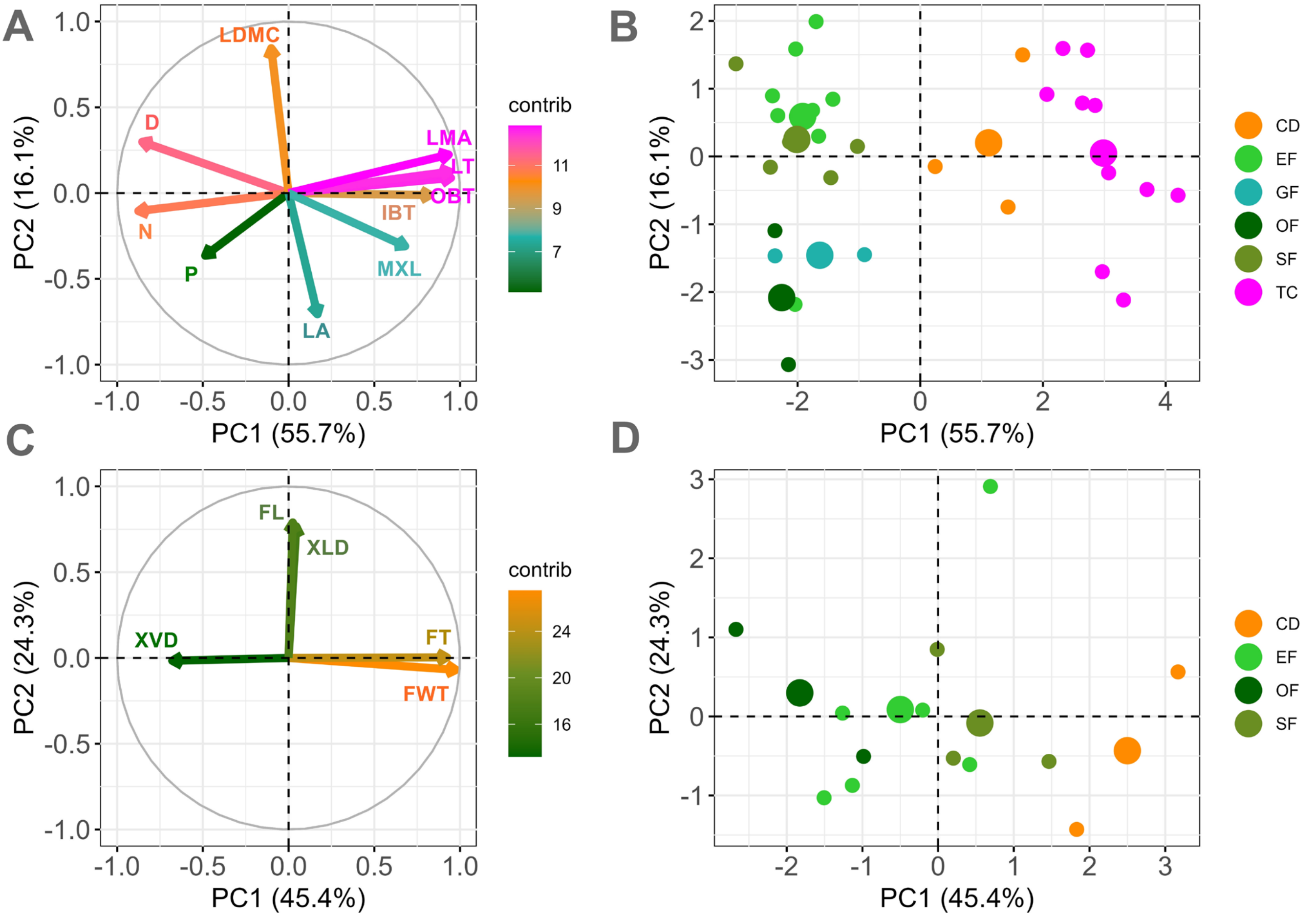

FIGURE 3 | Principal component analysis (PCA) based on 10 functional leaf, bark, and branch traits in 30 woody vegetation plots (A, B); and on 5 xylem functional traits in 15 woody vegetation plots from forest formations of the Amazon–Cerrado transition (C, D). CD = Cerradão, D = bark density, EF = Evergreen Seasonal Forest, FL = mean fiber length, FT = mean fiber thickness, FWT = mean fiber wall thickness, GF = Gallery Forest, IBT = inner bark thickness, LA = leaf area, LDMC = leaf dry matter content, LMA = leaf mass per area, LT = leaf thickness, MXL = maximum xylem length, N = nitrogen concentration, OBT = outer bark thickness, OF = Open Ombrophilous Forest, P = phosphorus concentration, SF = Semi-deciduous Seasonal Forest, TC = Typical Cerrado, XLD = mean xylem vessel lumen diameter, XVD = xylem vessel density. The larger dots in B and D represent the centroid of each vegetation type. Details of the loadings from PCA are available in Appendix S2: Table S6.

4 | Discussion

Answering the first question, our community-level analysis revealed a functional continuum among the vegetation types. They range functionally from Typical Cerrado at one extreme to Open Ombrophilous Forest at the other. Thus, most arboreal traits are distributed in a coordinated way along a gradient from savanna—with smaller trees and a more open canopy—to forest formations—with taller trees and a larger basal area—in line with the floristic composition. Based on the functional traits, we also found that Cerradão is functionally intermediate between savannas and forests, which is consistent with earlier findings addressing floristic and structural variation in the Amazon–Cerrado transition (Marimon et al. 2006; Torello-Raventos et al. 2013). We also found that Gallery Forests are functionally similar to Open Ombrophilous and Semi-deciduous Forests—even though Gallery Forest is by definition embedded in a savanna matrix and is thus a characteristic formation of the Cerrado biogeographic domain. This demonstrates the wide physiognomic variation contained within the Cerrado domain. Thus, from the functional traits evaluated here, it has been possible to assess and evaluate the diverse niches and strategies

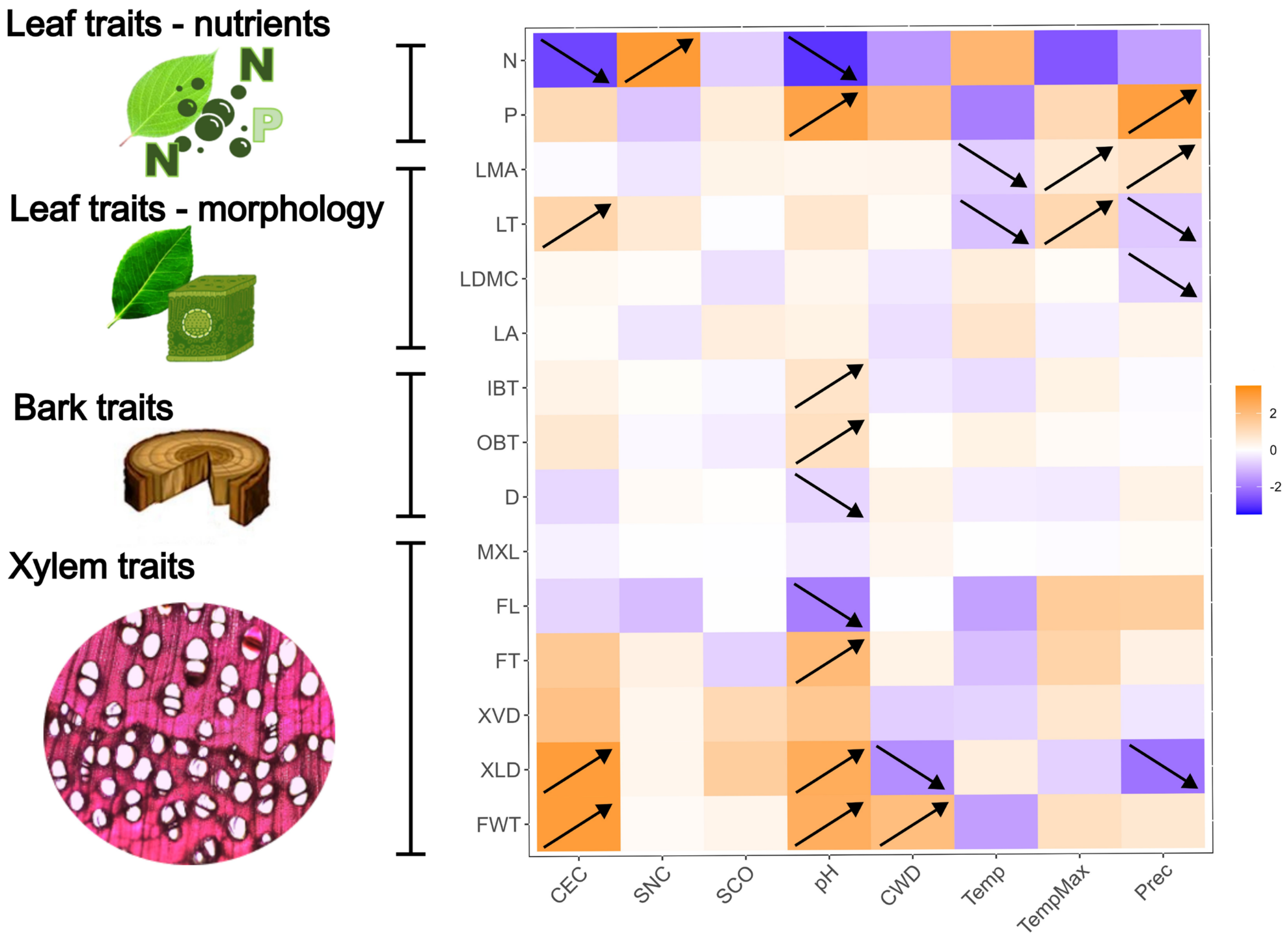

FIGURE 4 | Results of the fourth corner analysis. The significant correlations between functional traits and environmental variables are represented by the colored squares. Dark colors indicate stronger correlations within each set of traits. CEC = cation exchange capacity, D = bark density, FL = mean fiber length, FT = mean fiber thickness, FWT = mean fiber wall thickness, IBT = inner bark thickness, LA = leaf area, LDMC = leaf dry matter content, LMA = leaf mass per area, LT = leaf thickness, MXL = maximum xylem length, N = nitrogen concentration, OBT = outer bark thickness, P = phosphorus concentration, pH = soil pH, Prec = total annual precipitation, SCO = soil carbon, SNC = soil nitrogen concentration, Temp = average temperature, TempMax = maximum temperature, XLD = mean xylem lumen diameter, XVD = xylem vessel density.

of trees selected along the Amazon–Cerrado transition and to detect functionally "Amazonian" communities existing well within the savanna. In addition, our results help to position the different vegetation types on the leaf economic spectrum (Wright et al. 2004). Our study reveals contrasting investment in traits conferring hydraulic efficiency and hydraulic safety, showing notably that the Cerradão functional composition is characterized by hydraulic safety, a strategy adopted to avoid damage and collapse caused by the mechanical stress of water transport in the xylem (Bittencourt et al. 2016).

Regarding the second question, some functional traits of the leaf and xylem were related to the climate parameters evaluated, but the spatial climatic variation here was not always strong enough to drive large changes in functional structure (and were so mostly for bark traits) between the different vegetation types. This is reminiscent of the pattern found by Bruelheide et al. (2018), in which global scale plot variation in functional structure showed a remarkably weak association with climate and soil. However, our work did reveal that soil CEC and pH, as well as mean temperature, maximum temperature, total precipitation, and CWD, are consistently related to key functional traits across the Amazon–Cerrado transition. These traits are important for defense, resource acquisition/conservation, tree hydraulic safety, and fire resistance (Wright et al. 2004; Rosell et al. 2014; Bittencourt et al. 2016).

4.1 | Functional Biogeography in the Amazon–Cerrado Transition

The communities studied here are organized along a gradient in which functional structure changes progressively. This variation appears largely consistent with the "leaf economy" hypothesis (Wright et al. 2004), by which traits are directly related to the trade-off between plant growth and survival, whereby acquisitive species have high mortality while species with conservative strategies have high survival (Sterck et al. 2006). This trade-off contributes to explaining the hyperdynamic characteristic of the Amazon–Cerrado transition vegetation, and especially the fact that savanna formations have relatively low mortality rates and high recruitment, with forest formations having the opposite pattern, including some of the highest tree mortality rates in the world (Marimon et al. 2014). Similarly conservative characteristics have been observed for leaf traits in savannas elsewhere in Brazil and Peru (Hoffmann et al. 2005; Neyret et al. 2016) and for bark and wood traits in savannas of Tropical America, Africa, and Australia (Rosell et al. 2014; Pellegrini et al. 2017), in which functional traits also differed, comparing savanna and forest. While these earlier functional ecology studies have detected such patterns with savanna or forest, or in combination, ours is the first in which different vegetation formations have been evaluated in a standardized way at a large spatial scale, allowing us to reveal both the key trait combinations characterizing each environment and how functional structure changes along a trans-biogeographic domain vegetation gradient.

We recorded large differences in functional traits between Typical Cerrado and forest communities, which were expected based on other studies (Hoffmann et al. 2005, 2012; Araújo, Marimon, Scalon, Cruz, et al. 2021; Scalon et al. 2022). If Typical Cerrado and Open Ombrophilous Forests are functionally opposite extremes, the vegetation types between these can be considered "intermediate functional types" between a savanna and a typical Amazonian forest, as suggested in earlier smaller studies (Neyret et al. 2016; Araújo, Marimon, Scalon, Cruz, et al. 2021; Araújo et al. 2023). This was confirmed by our results that pointed to a gradual change between some functional traits in the community means (CWM). More surprising, perhaps, is the remarkable similarity we found in terms of functional traits among the various forest types (Gallery Forest, Semi-deciduous Forest, Evergreen Forest, and Open Ombrophilous Forest) analyzed here. This is despite these forests being structurally and floristically distinct (Ratter et al. 1973; Ivanauskas et al. 2008; Marimon et al. 2014; Morandi et al. 2016; Nogueira et al. 2019) and being established under very different conditions.

We recorded patterns defined by biochemical (N and P) and leaf structural traits, building on previous work (Viani et al. 2011; Nardoto et al. 2014; Singh et al. 2015; Dionizio et al. 2018; Scalon et al. 2022) that are determined mainly by nitrogen concentrations, with low values representing greater structural investment and leaf lifespan (Wright and Westoby 2003) and higher values indicating species that maximize carbon fixation (Shipley 2006), represented here by Seasonal, Evergreen and Open Ombrophilous Forests. The LMA (leaf mass per area) represents the ratio of investment between leaf mass and leaf area, where higher values represent species with slow return on investment in nutrients and leaf dry mass (Pérez-Harguindeguy et al. 2013). In this case, fast-return species (low LMA), such as those of the Open Ombrophilous Forest (a typical Amazonian forest type), will also show high leaf nutrient concentration, high rates of photosynthesis, respiration, and leaves with a short lifespan (Wright et al. 2004). On the other hand, slower return (high LMA) species, such as those in the Typical Cerrado, have longer lived leaves, more investment in building leaf biomass, and lower rates of photosynthesis and respiration (Wright et al. 2004; Gvozdevaite et al. 2018).

The Ombrophilous Forests are located in the far north of the Amazon–Cerrado transition belt and have functional traits linked to competition for light, resource acquisition, and hydraulic efficiency. An example is their low LDMC values, normally associated with high productivity and high relative growth rates (Smart et al. 2017). This implies that their leaves are less resistant to physical damage (herbivory and wind) and subject to rapid decomposition (Poorter et al. 2009). Taken together, their trait combinations indicate that these forests have high primary productivity, trophic transfer, litter decomposition, and nutrient and carbon cycling (Garnier et al. 2001; Díaz et al. 2004). Furthermore, the combination of low LMA and low LDMC recorded in our Open Ombrophilous Forests characterizes trees with a capacity for rapid production of aboveground biomass (Poorter and Garnier 2007). However, species with rapid growth bear the potential costs of having smaller hydraulic safety margins (Oliveira et al. 2021), and also characterize communities that are more vulnerable to drought and tree mortality by embolism in the event of pronounced seasonal drought. As observed in our study, such species allocate more resources to building other xylem tissues (Bittencourt et al. 2016) unrelated to maintaining hydraulic safety, with less investment in fiber thickness and fiber wall thickness.

The Gallery Forests, although located in the Cerrado biogeographic domain (Felfili 1995) and usually in direct contact with savanna areas or Seasonal Forests (Ratter et al. 1973), were characterized in our study as being functionally similar to Open Ombrophilous Forests, Semi-deciduous Seasonal Forests, and Evergreen Forests. The similarities found in leaf N and P concentrations between Gallery Forests and these reflect the fact that forests associated with streams are usually in more nutrient-rich environments (Asner et al. 2015). Gallery Forests, although somewhat floristically distinct, are classically thought of as potential long-term refugia of forest species (Ratter et al. 1973; Silva 1996; Morandi et al. 2016; Cabanne et al. 2019). Oliveira-Filho and Ratter (1995) observed that forests associated with rivers and streams in the Central region of Brazil form a connected, dendritic network that acts as a potential migration route for species and provides a long-term bridge between the floras of the Amazon, Cerrado, and Atlantic Forest. Our analysis thus provides contemporary functional evidence basis to support these key ideas about large-scale historical movements of species and vegetation with climatic fluctuations in South America.

The lower leaf concentrations of N and P that we recorded for the Typical Cerrado may not necessarily be related to the low availability of these nutrients in the soil (see Gvozdevaite et al. 2018), but could be explained by the low availability of water present in the soil, which prevents the uptake of these nutrients by the plant (Hu and Schmidhalter 2005). The low concentration of leaf N and P in Typical Cerrado species can also be explained by the ecological strategy adopted by these trees, where the allocation of these nutrients is concentrated in other plant organs such as the stem and roots (Scalon et al. 2022).

Cerradão is a forest formation of the Cerrado whose species have adaptations to withstand a strongly seasonal climate and avoid water loss when compared to other forests (Ratter and Dargie 1992; Jancoski et al. 2022). Our work confirms it as a transitional, intermediate type between the typical savanna formation (Typical Cerrado) and other forests, which, despite having xeromorphic characteristics (Bieras and Sajo 2009), have some of the functional structure of a forest. For example, and contrary to Haridasan (1992), we found clear differences in leaf N and P concentrations between Cerradão (higher) and typical Cerrado (lower). The only similarities between functional traits verified in our study between Cerradão and Typical Cerrado were for LDMC, inner bark thickness, and maximum xylem length. The shared high values of leaf thickness, outer bark thickness, and inner bark thickness, common in savanna species (Franco et al. 2005; Scalon et al. 2020), reflect the influence of fire on both typical Cerrado and Cerradão (Ratter et al. 1973; Reis et al. 2015). Thick bark and leaves are characteristics that allow tree species to resist fire (Rosell et al. 2014; Scalon et al. 2020) and prevent biomass and carbon loss (Pellegrini et al. 2017). Among the forest types evaluated here, Cerradão is also the one that includes species with a combination of xylem traits that indicate a wood architecture that confers greater hydraulic safety, such as smaller vessel lumen diameters and greater fiber and wall thicknesses. Its species survive under more negative water potential compared to species from Semi-deciduous Seasonal Forests in the same climatic region (Jancoski et al. 2022), and this structural reinforcement in the vessels allows trees to avoid implosive forces in the xylem (Jacobsen et al. 2005; Bittencourt et al. 2016).

4.2 | Relationship Between Functional Traits and the Environment

We found clear evidence that climatic and soil variables affect the distribution of functional traits of tree species in the transition zone between the Amazon and the Cerrado, and that different sets of traits are associated with different environmental drivers. All our communities are established at the southern limit of Amazonia, in a region where species are experiencing, in recent years at least, temperatures close to their limits of photosynthetic thermotolerance (Tiwari et al. 2021). Thus, the fact that some climatic variables did not show greater influence on functional traits may be explained by a widespread adaptation of species to the climatic characteristics of the region, since trees from a drier environment and exposed to consecutive heat waves have shown high functional and ecophysiological adaptability (Araújo, Marimon, Scalon, Cruz, et al. 2021; Araújo, Marimon, Scalon, Fauset, et al. 2021).

Our study includes many savanna and forest areas with trees that need to be able to survive environmental stress due to high temperatures and relatively low precipitation (Marimon et al. 2020; Morandi et al. 2020; Tiwari et al. 2021; Araújo, Marimon, Scalon, Cruz, et al. 2021; Araújo, Marimon, Scalon, Fauset, et al. 2021), so they may be expected to favor conservative ecological strategies in general (Westoby et al. 2002; Araújo, Marimon, Scalon, Cruz, et al. 2021). Indeed, we found strong relationships between functional traits linked to the leaf economic spectrum (e.g., LMA, LT, and LDMC) and all thermal and moisture climatic variables except for CWD. The strong relationship between LT and LMA with maximum temperature reflects ecological strategies adopted by the species throughout the transition, with species investing more in leaf thickness and mass in areas with the highest maximum temperatures, also expected to be environments where leaves must be able to regulate leaf water potential in the face of large vapor pressure deficits. Thicker leaf blades with more structural investment (based on mass) are widely considered adaptive to allow leaves to function under very dry conditions (Wright et al. 2005).

Soil pH is related to important functional traits that define the main ecological strategies of hydraulic safety and defense against fire of trees along the Amazon–Cerrado transition. We expected to find species with more conservative strategies in communities on more acidic soils, such as Typical Cerrado and Cerradão, and species with more acquisitive strategies in communities on less acidic soils, such as Evergreen and Open Ombrophilous Forests (Hoffmann et al. 2005). Instead, contrary to our expectation, Typical Cerrado communities are established in less acidic soils than Open Ombrophilous Forests, reflecting the presence of species with more conservative traits (e.g., high OBT, IBT, LT). We believe that this pattern was revealed due to the proximity and contact between forest and savanna areas, in which some forests showed pH values a few times higher than savannas. This does not demonstrate the expected difference in acidity between forest and savanna, although previous studies have shown that forest soils in the Amazon can be as acidic as savanna soils in the Cerrado, with differences in nutrient availability, organic matter deposition, and water retention (Haridasan 1992; Laurance et al. 2010; Quesada et al. 2011). Soil pH affects not only the availability of other soil nutrients and water but also the floristic differentiation of vegetation, shaping functional structure by filtering the pool of species tolerant to more acidic soils (Viani et al. 2014). Soil pH levels can also be indicative of water stress and drought, where woody vegetation, when established on acidic soils, can suffer from physiological stress, influenced by the soil's low water retention capacity due to its pH-influenced structure (Russell et al. 2018).

We found that communities that experience the most water stress and drought (high CWD), such as Semi-deciduous Seasonal Forests and Savannas, are characterized by species with functional traits and strategies adaptive for greater hydraulic safety. They invest more in fiber construction and vessels with a smaller lumen diameter, providing a more efficient hydraulic system against embolism and cavitation (Oliveira et al. 2021). High water deficit also tends to select for other adaptations to drought, including morphological and physiological traits (e.g., deep roots and leaves with high water use efficiency; O'Brien et al. 2017). On the other hand, in Open Ombrophilous Forests, plants have the highest vulnerability to hydraulic failure, with their hydraulic risk indicated by the configuration of xylem vessels with low investment in fibers (Bittencourt et al. 2016). All communities in the Amazon–Cerrado transition are expected to face more severe droughts and water deficits (Phillips et al. 2009; Feldpausch et al. 2016), and even those best adapted to drought conditions may become even drier, potentially pushing woody vegetation across the Amazon and neighboring biogeographic domains beyond its climatic and physiological limits (Tavares et al. 2023).

A limitation of this study was the unbalanced sampling, with an unequal number of plots, as well as the small number of sampling points for some vegetation types (Cerradão, Gallery Forest, and Open Ombrophilous Forest), and the spatial clustering of some. Future efforts should focus on increasing the spatial scale, sampling, and monitoring periods, especially for poorly inventoried vegetation types, which will support a more robust assessment of ecological patterns and more ability to compare and discern among vegetation types in this vast Amazon–Cerrado transition zone.

5 | Conclusions

This is the first study to address the distribution of functional traits and ecological strategies of trees in the transition zone between the two largest biogeographic domains in South America. In spite of these limitations, we showed that functional traits efficiently reflect functional differences among forest communities, savannas, and transitional formations, with multiple functional traits aligned along an environmental and vegetation cover gradient ranging from more open savanna formations to closed-canopy forests typical of the Amazon. Our results show that functional traits play a key role in adapting to environmental gradients, helping to explain the performance of tree species in this important transition zone. The Amazon–Cerrado transition has experienced strong drought events in recent years, coupled with extreme heat waves and anthropogenic fires, and these stressors are increasing. Our results have implications for understanding the functional responses and survival strategies of trees in the face of climate change and/or anthropogenic disturbances, helping us to identify the most potentially sensitive communities and vegetation types. In all, the woody vegetation in the transition between the Amazon and the Cerrado varies greatly in terms of ecological strategies. Examining the functional basis of these differences helps us to better understand the composition, limits, past, and future of these great South American biogeographic domains.

Author Contributions

W.J.A.C., B.S.M., and O.L.P. conceived the idea, questions, hypotheses, and led the writing of the manuscript; B.S.M., B.H.M.J., and O.L.P. secured the funding and supervised different stages of the study; W.J.A.C., B.S.M., and M.C.S. developed the study design and methodology; W.J.A.C., P.S.M., S.G.L., N.C.C.S.P., N.G.R.J., and E.A.O. performed the field measurements and data curation; W.J.A.C. and A.L. organized the database; W.J.A.C. performed the analyses and prepared the figures; P.S.M., S.M.R., N.C.C.S.P., M.C.S., and O.L.P. contributed to the revision of the manuscript. All authors critically contributed to the production of the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The CWM and environmental data are available as a data package on ForestPlots.net: https://doi.org/10.5521/forestplots.net/2025_3. The tree-level data used for all analyses were extracted on 21/03/2019 and are available on request from ForestPlot.net: https://www.forestplots.net/en/join-forestplots/working-with-data.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Supplementary plot and traits specification. **Table S1:** Characteristics of plots sampled in different vegetation types in the Amazon–Cerrado transition. Prec = total annual precipitation, Temp = mean annual temperature. The abbreviations of each area (plot code) are the same adopted in the ForestPlots.net platform (Lopez-Gonzalez et al. 2011). Temperature and precipitation data were extracted from the WorldClim database (Hijmans et al. 2005). **Table S2:** Functional traits established to characterize the functional structure of communities in the Amazon–Cerrado transition. **Appendix S2:** Supplementary statistical details. **Table S3:** Mean and standard deviation (in parentheses) of functional traits in vegetation types in the Amazon–Cerrado transition. CD = Cerradão, D = bark density, EF = Evergreen Seasonal Forest, FL = mean fiber length, FT = mean fiber thickness, FWT = mean fiber wall thickness, GF = Gallery Forest, IBT = inner bark thickness, LA = leaf area, LDMC = leaf dry matter content, LMA = leaf mass per area, LT = leaf thickness, MXL = maximum xylem length, N = nitrogen concentration, OBT = outer bark thickness, OF = Open Ombrophilous Forest, P = phosphorus concentration, SF = Semi-deciduous Seasonal Forest, TC = Typical Cerrado, XLD = mean xylem lumen diameter, XVD = mean vessel density. Averages followed by the same letters do not present significant difference in pairwise comparison by Tukey. **Table S4:** Statistics of comparisons between the alternative mixed models and null model by ANOVA. AIC = Akaike information criteria, D = bark density, DF = degrees of freedom, FL = mean fiber length, FT = mean fiber thickness, FWT = mean fiber wall thickness, IBT = inner bark thickness, LA = leaf area, LDMC = leaf dry matter content, LMA = leaf mass per area, LT = leaf thickness, MXL = maximum xylem length, N = nitrogen concentration, OBT = outer bark thickness, $p = p$ values, P = phosphorus concentration, XLD = mean xylem lumen diameter, XVD = mean vessel density, χ^2 = chi-squared. **Table S5:** PCA data output accompanied by the percentage contribution of morphoanatomical traits to the axes. The retention of PC axes follows the proposed Kaiser rule. **Table S6:** Loadings from principal component analysis (PCA) of morphoanatomical traits. D = bark density, FL = mean fiber length, FT = mean fiber thickness, FWT = mean fiber wall thickness, IBT = inner bark thickness, LA = leaf area, LDMC = leaf dry matter content, LMA = leaf mass per area, LT = leaf thickness, MXL = maximum xylem length, N = nitrogen concentration, OBT = outer bark thickness, P = phosphorus concentration, XLD = mean xylem lumen diameter, XVD = mean vessel density. **Appendix S3:** Supplementary analysis. **Figure S1:** Overlap in tree species composition across vegetation types in the Amazonia–Cerrado transition. Chord width is proportional to the number of shared species. **Figure S2:** Variation of the main axes (PC1 and PC2) of functional traits in relation to the latitudinal gradient, based on 10 functional leaf, bark, and branch traits in 30 woody vegetation plots (A, B); and on 5 xylem functional traits in 15 woody vegetation plots from forest formations of the Amazon–Cerrado transition (C, D). CD = Cerradão, EF = Evergreen Seasonal Forest, GF = Gallery Forest, OF = Open Ombrophilous Forest, SF = Semi-deciduous Seasonal Forest, TC = Typical Cerrado.