Santos Martins et al. *New Zealand Journal of Forestry Science* (2023) 53:8
https://doi.org/10.33494/nzjfs532023x232x
E-ISSN: 1179-5395
Published on-line: 20/08/2023

Research Article **Open Access**

New Zealand Journal of Forestry Science

Above-ground biomass accumulation in Cerradão managed by the mass ratio

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(Received for publication 2 April 2022; accepted in revised form 26 June 2023)

Abstract

Background: Forests have a huge potential to mitigate global warming through CO_2 accumulation in their living biomass. Thus, understanding the functioning of these ecosystems is crucial for revealing factors that drive biomass accumulation. Functional diversity helps us understand ecosystem services, including biomass accumulation. Within this context, this work aimed to investigate the role of functional diversity in biomass accumulation for woody vegetation of the Cerradão.

Methods: We estimated above-ground biomass (AGB) of 50 Cerradão stands in Brazil and measured five different functional traits associated with tree species' survival and growth. For each stand, we calculated five community-weighted means (CWMs), based on each functional trait, and three functional diversity metrics. We specifically explored the relationship between CWMs describing functional diversity metrics and AGB. After that, exponential regressions were adjusted, using the variables that presented significant correlation as independent variables and AGB as a dependent variable. Regressions with more than one independent variable were fitted in a way that avoided collinearity. Based on the strongest correlation coefficient (r) and the lowest Akaike value (AIC), we chose the best regression to explain the majority of the variance in AGB.

Results: Our results showed the role of function in determining AGB. In particular, bivariate correlations show that four CWM functional traits and two functional diversity metrics are significantly associated with AGB production, with CWM showing AGB estimation variables. However, multiple regression analyses show that maximum height is the only trait significantly associated with AGB and it alone provides the best model fit.

Conclusions: The accumulation of AGB in Cerradão is explained by the mass ratio theory, and this ecosystem services is directly related to the presence and abundance of species with greater potential tree height (Ht_{max}).

Keywords: niche complementarity; CWM (Community Weighted Mean); FRic (Functional Richness); maximum height; SLA

Introduction

Forests are dynamic ecosystems with a predominance of woody species that, through photosynthesis, accumulate carbon in the form of biomass, thereby providing an important ecosystem service in the face of climate change (Hubau et al. 2020; Souza et al. 2016; Terrer et al. 2019). Climate change, in particular global warming, has increased the intensity and frequency of extreme heat and severe drought conditions, as well as natural disasters such as storms, hurricanes, cyclones, and floods (Seneviratne et al. 2021), which directly affect the lives of human beings in terms of damage to houses and cities, health effects, and decreasing agricultural production. Therefore, understanding factors that drive biomass accumulation is crucial for mitigating these changes (Finegan et al. 2015).

Communities' functional diversity and traits have increased our understanding of ecosystem processes and services, particularly the relationship between different facets of biodiversity and biomass accumulation (Bruelheide et al. 2018; Díaz et al. 2007; Vargas-Larreta et al. 2021). Among different aspects of biodiversity, functional diversity has been shown to be associated with biomass. Functional diversity refers to species' functional traits and also to their variation and distribution among species within a community (Díaz et al. 2007, 2011; Tilman et al. 2001).

Functional traits are species' characteristics, generally associated with their morphology, ecophysiology, and phenology, which represent their competitive ability in an environment (Pérez-Harguindeguy et al. 2016; Violle et al. 2007). These characteristics may be related to the way in which ecosystem processes, such as biomass accumulation, occur (Díaz et al. 2004, 2007; Pérez-Harguindeguy et al. 2016). Using biomass accumulation as an example, depending on the environment, species in stands with higher specific leaf area may have a competitive advantage over species with lower specific leaf areas, promoting an increase in the total leaf area of these species assemblages, increasing their photosynthetic potential and consequently their total biomass. A conventional method for examining ecosystem processes using functional traits is by using trait mean, maximum, or variance values, weighted by the number of individuals within a community; a "community weighted mean" (CWM) (Ali et al. 2017; Finegan et al. 2015; Garnier et al. 2004; Lavorel et al. 2008; Terra et al. 2021).

When the CWM of traits is not, on its own, a good proxy to explain the variance of an ecological process, functional metrics can complementarily act as significant mechanisms (Díaz et al. 2007; Mason & De Bello 2013). Measuring the variation, distribution, and divergence of species within functional space is likely to improve the explained variance of an ecological process, because these aspects are directly related to functional traits (Mammola et al. 2021; Mason et al. 2005; Mouchet et al. 2010; Violle et al. 2007). Within a number of functional diversity metrics, the most widely used are functional richness (FRic), which reflects the number of functional characteristics within a community; equitability (FEve), which reflects how functional characteristics are distributed within species in a community; and divergence (FDiv) (Mammola et al. 2021; Mouchet et al. 2010).

Not only correlations and regressions between ecosystem processes, such as biomass accumulation, but also functional traits and metrics may help to identify the contribution(s) of the mediating agent(s) of ecosystem processes (Ali et al. 2017; Díaz et al. 2007; Vargas-Larreta et al. 2021). When the key driver is a functional trait, for example functional dominance, represented by CWM, the underlying process is probably associated with species mass ratio theory (Grime 1998). However, when key drivers are variance and functional trait distribution in space, the underlying process may occur through niche complementarity and the coexistence of divergent species (Begon et al. 2005; Mouchet et al. 2010). In mass ratio theory, patterns are determined by the presence or absence of dominant species with high productivity associated with a specific functional trait, such as maximum height (Grime 1998) or greater wood density, for example. For niche complementarity, there is optimization in the use or sharing of resources, such as light and nutrients, where coexisting species occupy distinct niches because they have divergent functional traits, thereby boosting an ecological process (Begon et al. 2005; Chesson 2000; Letten et al. 2017).

The use of CWM traits and functional metrics is becoming increasingly common worldwide (Ali et al. 2017; Finegan et al. 2015; Sonkoly et al. 2019; Vargas-Larreta et al. 2021). For the Brazilian savannah (Cerrado biome), studies have been conducted to verify strategic differences between species from contrasting environments (Freitas et al. 2012; Hoffmann et al. 2005, 2012; Maracahipes et al. 2018), to determine the relationships between ecosystem processes and functional diversity (Meira Junior et al. 2016; Terra et al. 2018, 2021) and to verify functional changes in veetation over time (Meira Junior et al. 2016). However, these studies have been primarily conducted only in cerrado sensu stricto and semi-deciduous forests.

Forested savannah (Cerradão) is a forest formation of the Cerrado biome, and it is associated with interfluves and well-drained soils of low and medium fertility, characterized by a continuous canopy with an average height of 8 to 15 m, tree cover between 50 and 90 %, and a sparse or non-existent herbaceous stratum (Eiten 1972; Oliveira-Filho & Ratter 2002; Ribeiro & Walter 2008). Although floristically similar to savannah formations, Cerradão also contains characteristic species of other forest formations, such as seasonal forests and gallery forests, and thus, structurally, Cerradão is more similar to forest than to savannah formations (Oliveira-Filho et al. 2002; Ribeiro & Walter 2008). Within Cerradão, floristic, structural, and edaphic studies have been extensively conducted and are well known (Miguel et al. 2017; Rodrigues & de Araújo 2013; Solórzano et al. 2012). In contrast, above-ground biomass (Marimon et al. 2014; Miguel et al. 2017; Morais et al. 2013) and functional diversity (Terra et al., 2018) within this physiognomy remain understudied. To tackle this issue and considering the potential of this physiognomy to mitigate climate change, we investigated the role of tree species' functional characteristics on biomass accumulation and total above-ground biomass for woody vegetation of the Cerradão.

Methods

Study site

The study area was near the Cerrado-Amazonia transition, within the boundaries of Lajeado State Park (LSP), located in the municipality of Palmas (Tocantins state - TO) with central coordinates 10°6'32" S and 48°13'26″ W (Figure 1). The LSP is a fully-protected state conservation unit, created by Law no. 1.224, on 11 May 2001 in Tocantins official journal no. 1039, and is located in the midwestern region of the state of Tocantins, near the city of Palmas, within the Environmental Protection Area (APA) of Serra do Lajeado, Brazil.

According to the Koppen and Geiger (1936) classification system, the climate of the region is the "Aw" type, characterised by a moderately dry season (winter) from May to September and a rainy season (summer) from October to April. The average rainfall is between 1300 and 1500 mm (Alvares et al. 2013). The relief of the region varies from flat to undulated, and the predominant soil is non-hydromorphic dark red latosol with a latosolic B horizon (Santos et al. 2013).

The site vegetation is Cerradão (as defined by Ratter 1971, Oliveira-Filho et al. 2002, Ribeiro & Walter 2008, phytophysiognomic characterisations). The canopy is closed, with 70–90% tree cover, sparse undercover that is open for most vegetation, and a sparse or non-existent herbaceous stratum. The study area is located between 10º10' 55" and 10º11'20″ S and 48º10'50" and 48º10'30″ W, presenting a continuous extension of 10.15 hectares (Figure 1).

Vegetation sampling

Sampling was conducted systematically with transects subdivided into plots (Kershaw et al. 2016; Péllico Netto & Brena 1997). Eight transects were sampled of 20 m in width and varying lengths (from 40 to 220 m), positioned 60 m apart. Each transect was subdivided into 400 m^2 plots (20 m × 20 m), totalling 50 plots and two hectares of sampling (Figure 1), according to the methodological suggestion for monitoring Cerradão vegetation (Felfili et al. 2005).

All living woody individuals, except for lianas, with diameters at 1.30 metres above-ground level (DBH) ≥ 5.0 cm were sampled and their DBH values, total height (Ht), and species were recorded. The height of each individual was measured with the aid of an 18 m telescopic height pole. Heights greater than 18 m were estimated visually using the pole as a reference. For individuals with multiple trunks above ground level, the quadratic mean diameter and Lorey's height were used as references, based on the basal area and height of each bifurcation (Kershaw et al. 2016).

The species were grouped into families based on the Angiosperm Phylogeny Group (APG IV 2016) classification system. The accepted species name and botanical synonym were verified using the Brazilian Flora List 2020 of the Botanical Garden of Rio de Janeiro (Forzza et al. 2021). Botanical vouchers of all species were collected, and the samples were deposited in the herbarium of the Federal University of Brasilia (UB-Herbarium).

The set of species that comprised each of the 50 plots was treated as an assemblage. Therefore, the total sampling included 50 species assemblages.

Above-ground biomass calculation

The above-ground biomass of each plot was calculated as the sum of the biomass of all living individuals, totalling 50 assemblages. The biomass per individual was obtained using Equation (1), which was developed

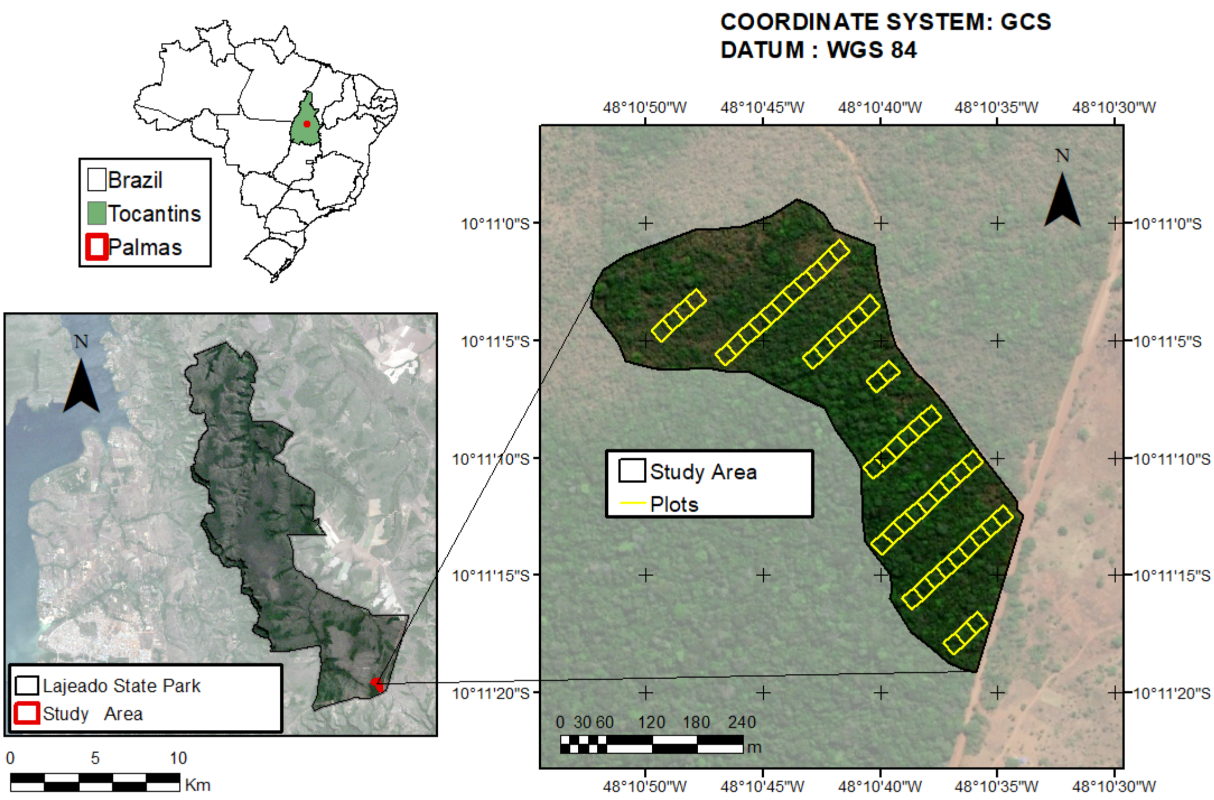

FIGURE 1: Location of the study area in Lajeado State Park, Tocantins State, Brazil. Sampling design, with the transects and their respective number of plots.

for woody vegetation of the Cerradão (Souza 2020).

$$AGB = (231\ 600 + 11\ 600 * (DBH * Ht * WD)\ 0.71) / (231\ 600 + ((DBH * Ht * WD) 0.71)) \quad (1)$$

where AGB= individual above-ground biomass, DBH= trunk diameter (cm) at 1.30 metres above-ground level, Ht= total height (m), and WD= woody density (g cm^{-3}).

Collecting and processing functional traits

The handbook for standardising the collection of functional traits establishes a minimum number of individuals for each trait, with at least ten individuals for maximum height and five individuals for leaf traits when possible (Pérez-Harguindeguy et al. 2016). In addition, for estimates relating functional diversity and ABG, either the number of species that together represent 80% of the total biomass, or of the total number of individuals of the community should be used (Pakeman & Quested 2007; Pérez-Harguindeguy et al. 2016). Increasing this percentage represents an increase in the accuracy of the desired estimate, which must be balanced with the human and financial effort required to collect the traits (Pakeman & Quested 2007).

To achieve 80% of the ABG in the study area, 14 species (20.28% of total richness) would be required; however, since a considerable number of the species and the possible variation in traits would not be measured or considered to predict ABG, we evaluated functional traits of all 69 species recorded in the study area. Considering the density of individuals of the species within the sample, it was not possible to collect the leaf traits of five individuals for 23 of the species (33% of the richness), or maximum heights of 10 individuals for 34 species (49% of the richness) (Table 1).

Five functional traits [Specific Leaf Area (SLA – mg mm^{-2}), Wood Density (WD - g cm^{-3}), Crown Area (CA – m^2), Diameter at maximum breast height (DBH_{max} - cm), and maximum height (Ht_{max} - m)], related to the growth and survival of woody species and, consequently, to AGB, were evaluated (Finegan et al. 2015; Pérez-Harguindeguy et al. 2016; Poorter & Rozendaal 2008; Wright et al. 2010). Whenever possible, a minimum of ten individuals was measured for Ht_{max} and DBH_{max} and five individuals for SLA and CA.

For SLA measurements, five mature, sun-exposed leaves, without evident symptoms of pathogens and herbivory, were collected from each individual of each species (Pérez-Harguindeguy et al. 2016). The collected leaves were digitised, considering the petiole and rachis, and overlaps between leaves or curled leaf blades were avoided. The leaf area was calculated using ImageJ software from the package LeafArea (Katabuchi 2015) of the R studio (R Core Team 2021). After digitisation, the leaves were stored in paper bags and placed in an oven at 70°C for 72 h (Pérez-Harguindeguy et al. 2016). The weight of dried SLA was then calculated by dividing the green leaf area by its dry weight (mm^2 mg^{-1}) (Pérez-Harguindeguy et al. 2016). The average of the traits was considered as a function of the number of individuals sampled for each species.

Wood density was obtained from secondary data available in the literature, some of which used samples of trees from the Cerrado biome, including plants within the study area (Vale et al. 2002; Silva, 2015; Souza, 2020), and others were obtained from a pantropical database, restricted to South American, using the "getWoodDensity" function of the BIOMASS package of the R software (Chaveet al. 2009; Réjou-Méchain et al. 2017). For seven species, it was not possible to determine the density at the species level; therefore, the average wood density at the genus level was used (Chave et al. 2009; Réjou-Méchain et al. 2017). Table 1 presents the wood density values for each species recorded in Cerradão vegetation.

Crown area (CA) was obtained by calculating the area of a circle ($\pi*[(R_1+R_2)/2]^2$). For this, the length of the crown projection was measured in the field in two directions: the direction of the greatest length of crown projection, and the transverse direction to the first measurement (Machado & Figueiredo Filho 2006). The crowns of 409 individuals distributed among 69 species were measured, to include as much of the variation in DBH as possible.

All trees sampled in the inventory were used to determine the maximum diameter value and total height. The maximum diameter value was calculated from the DBH measured in the field for each species. The same procedure was adopted for the maximum height, which was considered to be the height at 95% of the hypsometric distribution (Souza et al. 2016).

Community weighted mean and functional metrics

Based on the set of species that make up each plot, their respective five functional traits, and the number of individuals of each species, the community weighted mean (CWM) was calculated (Lavorel et al. 2008). The CWM represents the average of a functional trait weighted by the abundance of individuals of each species (Garnier et al. 2004; Lavorel et al. 2008). Therefore, a CWM index was calculated for each of the five traits: CWM_DBH_{max}, CWM_Ht_{max}, CWM_CA, CWM_WD, and CWM_SLA, in each plot, based on the species presence in each plot and their abundance.

Additionally, we calculated functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv), which are the three main facets of functional diversity (Mason et al. 2005; Mouchet et al. 2010; Villéger et al. 2008), and represent the types of measurements within a functional space. FRic represents the functional volume occupied by species; FEve is directly proportional to the regularity of the distribution of species abundances within a functional space; and FDiv measures the distance between species in a functional space, detecting variation of traits between species, with higher values representing assemblies where species with divergent functional traits coexist with abundant populations (Mason et al. 2005; Mouchet et al. 2010; Villéger et al. 2008). These metrics were obtained for each plot, using the same five functional traits used for the CWM index and the presence and abundance matrix of species in each plot.

TABLE 1: Woody species sampled in the Cerradão vegetation in Lajeado State Park, Tocantins State, Brazil, their respective number of individuals (Ni), frequency in the plot where they were sampled (AF), biomass, and significant functional traits to explain the biomass.

Species	Ni	AF (%)	AD (ind ha^{-1})	Biomass (Mg ha^{-1})	Ht_{max} (m)	CA (m^2)	DBH_{max} (cm)	SLA (mg mm^{-2})	WD (g cm^{-3})	% Biomass
Emmotum nitens (Benth.) Miers	221	90	110.5	14.29	16	52.42	53	164.34	0.93	**80**
Tapirira guianensis Aubl.	150	76	75	6.06	15	37.11	48.83	92.11	0.57	
Myrcia fenzliana O.Berg	307	80	153.5	5.86	9.95	10.03	28.27	66.47	0.73	
Parkia platycephala Benth.	46	52	23	4.99	14.75	63.99	51.94	103.79	0.69	
Ocotea canaliculata (Rich.) Mez	111	82	55.5	4.17	15.5	36.69	45.4	80.98	0.48	
Mezilaurus itauba (Meisn.) Taub. ex Mez	77	40	38.5	4.13	16.4	40.46	55.1	101.9	0.73	
Caryocar coriaceum Wittm.	47	50	23.5	3.82	15.4	32.99	51	88.1	0.69	
Tachigali vulgaris L.G.Silva & H.C.Lima	40	46	20	3.5	19.1	58.93	40.5	63.19	0.74	
Xylopia aromatica (Lam.) Mart.	175	88	87.5	3.35	14.65	18.75	22.01	78.5	0.59	
Qualea parviflora Mart.	92	66	46	2.45	11.45	15.43	40	67.4	0.73	
Pouteria ramiflora (Mart.) Radlk.	24	30	12	2.37	16.85	44.99	53	74.02	0.77	
Sacoglottis guianensis Benth.	103	62	51.5	2.35	14	32.77	37	73.81	0.67	
Miconia cuspidata Naudin	66	42	33	2.04	16	30.27	22.5	101.88	0.88	
Bowdichia virgilioides Kunth	11	20	5.5	1.78	21	46.29	47.8	80.77	0.86	
Byrsonima sericea DC.	70	66	35	1.75	14	41.28	28.07	78.91	0.72	**90**
Simarouba versicolor A.St.-Hil.	49	48	24.5	1.34	16.6	25.55	39.4	60.81	0.44	
Maprounea guianensis Aubl.	64	54	32	1.34	13.85	21.43	39	128.5	0.7	
Bocageopsis multiflora (Mart.) R.E.Fr.	73	54	36.5	1.26	16	10.74	26.8	107.71	0.61	
Miconia albicans (Sw.) Triana	187	70	93.5	0.89	7	6.83	12.3	100.78	0.69	
Diospyros sericea A.DC.	10	12	5	0.89	17.55	26.04	47	79.27	0.6	
Mouriri pusa Gardner	3	6	1.5	0.65	14.95	16.64	44	51.06	0.84	
Aniba heringeri Vattimo-Gil	15	20	7.5	0.65	15.49	15.9	35.73	98.87	0.59	**100**
Machaerium acutifolium Vogel	9	14	4.5	0.58	13	14.52	27.8	92.3	1.12	
Inga alba (Sw.) Willd.	24	22	12	0.53	16.93	21.98	21	115.02	0.61	
Physocalymma scaberrimum Pohl	5	6	2.5	0.45	14.6	18.04	31.49	122.82	0.85	

TABLE 1: *continued*

Species	Ni	AF (%)	AD (ind ha^{-1})	Biomass (Mg ha^{-1})	Ht_{max} (m)	CA (m^2)	DBH_{max} (cm)	SLA (mg mm^{-2})	WD (g cm^{-3})	% Biomass
Qualea grandiflora Mart.	21	36	10.5	0.41	10	12.33	24.5	88.33	0.61	
Vatairea macrocarpa (Benth.) Ducke	29	40	14.5	0.39	11	8.65	19.3	86.91	0.79	
Didymopanax morototoni (Aubl.) Decne. & Planch.	2	4	1	0.38	14.98	85.48	45.2	73.03	0.46	
Virola sebifera Aubl.	19	26	9.5	0.36	14.1	14.02	20.6	95.86	0.65	
Plathymenia reticulata Benth.	9	18	4.5	0.34	11	13.77	31	155.4	0.5	
Licania egleri Prance	9	12	4.5	0.3	17.2	16.66	29.3	74.16	0.64	
Licania octandra (Hoffmanns. ex Roem. & Schult.) Kuntze	19	20	9.5	0.29	11.75	11.27	20	92.04	0.76	
Himatanthus articulatus (Vahl) Woodson	7	12	3.5	0.25	15.7	10.37	24.5	90.85	0.49	
Erythroxylum squamatum Sw.	43	38	21.5	0.22	8	17.82	12.84	120.95	0.71	
Matayba guianensis Aubl.	17	18	8.5	0.19	11.7	16.64	19.7	137.1	0.81	
Kielmeyera lathrophyton Saddi	6	10	3	0.19	9.98	5.01	21.2	89.27	0.67	
Ouratea hexasperma (A.St.-Hil.) Baill.	23	30	11.5	0.16	6.45	6.07	19.33	81.73	0.63	
Byrsonima pachyphylla A.Juss.	12	16	6	0.13	9.5	9.69	14.5	53.62	0.68	
Vochysia gardneri Warm.	19	22	9.5	0.13	9.55	10.66	14.8	58.01	0.38	
Aspidosperma macrocarpon Mart. & Zucc.	10	20	5	0.12	11.28	7.51	14.6	75.65	0.71	
Dalbergia miscolobium Benth.	4	8	2	0.12	11.4	7.4	21.7	148.26	0.62	
Protium heptaphyllum (Aubl.) Marchand	10	10	5	0.1	10.55	13.14	14.6	107.08	0.63	
Hirtella glandulosa Spreng.	1	2	0.5	0.08	10.86	10.43	20.02	122.54	0.93	
Hancornia speciosa Gomes	11	14	5.5	0.06	7	7.04	14	116.35	0.68	
Mabea fistulifera Mart.	3	6	1.5	0.06	13.8	18.02	15	123.31	0.64	
Byrsonima crassifolia (L.) Kunth	5	10	2.5	0.05	8.2	10.64	11	85.36	0.58	
Myrcia splendens (Sw.) DC.	9	12	4.5	0.05	9.2	8.86	10.12	97.76	0.8	
Lafoensia pacari A.St.-Hil.	5	10	2.5	0.05	10.1	2.82	12.3	155.93	0.8	
Andira cordata Arroyo ex R.T.Penn. & H.C.Lima	4	6	2	0.04	8.43	3.43	12.3	71.88	0.77	

TABLE 1: *continued*

Species	Ni	AF (%)	AD (ind ha^{-1})	Biomass (Mg ha^{-1})	Ht_{max} (m)	CA (m²)	DBH_{max} (cm)	SLA (mg mm^{-2})	WD (g cm^{-3})	% Biomass
Dimorphandra gardneriana Tul.	5	10	2.5	0.04	7.5	8.69	10.8	115	0.79	
Cordiera sessilis (Vell.) Kuntze	10	14	5	0.04	7.05	10.68	8	106.37	0.68	
Roupala montana Aubl.	2	2	1	0.04	10.8	8.3	13.9	74.41	0.78	
Buchenavia tetraphylla (Aubl.) R.A.Howard	1	2	0.5	0.04	16.5	23.76	14.2	102.35	0.62	
Eriotheca gracilipes (K.Schum.) A.Robyns	7	12	3.5	0.03	8.49	4.15	10.3	65.32	0.47	
Handroanthus serratifolius (Vahl) S.Grose	1	2	0.5	0.02	12	2.69	11	59.48	0.92	
Hymenaea stigonocarpa Mart. ex Hayne	3	6	1.5	0.02	6.68	4.91	11.3	123.24	0.9	
Mouriri glazioviana Cogn.	1	2	0.5	0.01	10	11.34	9.4	66.29	0.84	
Heteropterys byrsonimifolia A.Juss.	3	4	1.5	0.01	7.7	1.01	7.5	103.19	0.61	
Agonandra brasiliensis Miers ex Benth. & Hook.f.	3	6	1.5	0.01	6.45	3.33	7.6	108.16	0.82	
Copaifera langsdorffii Desf.	1	2	0.5	0.01	8.5	9.62	10	130.76	0.65	
Thyrsodium spruceanum Benth.	2	4	1	0.01	8.9	3.56	8.4	88.75	0.64	
Davilla elliptica A.St.-Hil.	2	4	1	0.01	5	4.27	11.01	92.16	0.49	
Hymenolobium petraeum Ducke	1	2	0.5	0.01	7	7.55	8.1	76.6	0.71	
Casearia arborea (Rich.) Urb.	2	4	1	0.01	10.83	2.41	5.5	84.92	0.57	
Licania kunthiana Hook.f.	1	2	0.5	0	7	9.62	6	113.03	0.88	
Eriotheca pubescens (Mart. & Zucc.) Schott & Endl.	1	2	0.5	0	6	2.84	6.8	62.34	0.5	
Kielmeyera coriacea Mart. & Zucc.	1	2	0.5	0	5	1.77	5.2	53.01	0.56	
Rourea induta Planch.	1	2	0.5	0	4	3.14	5.8	83	0.47	
Inga cylindrica (Vell.) Mart.	1	2	0.5	0	5.5	18.86	5	135.67	0.48	
Total	**2325**	**-**	**1162.5**	**76.28**	-	-	-	-		

Ni: Number of individuals sampled in two hectares of survey; AF: Absolute frequency of plots in %; AD: Absolute Density (number of individuals/hectare); Ht_{max}: Maximum height in meters. DBH_{max}: Maximum diameter at 1.3 m height from the ground; SLA: Specific leaf area; WD: Wood density

Both CWM and functional metrics were calculated using the FD package (Laliberté et al. 2014) in R studio (R Core Team 2021).

Statistical analysis: Correlation and regressions

Spearman's correlation analysis was performed on AGB, functional trait CWMs, and functional metrics from each plot (Spearman 2010). These correlations were verified using the Rstudio platform (R Core Team 2021) using the function corr.test (method="spearman").

For functional traits and metrics that were significantly correlated with AGB, bivariate exponential model regressions (composed of one dependent and one independent variable) were fitted with each trait and metric separately, with biomass as the dependent variable. Exponential models were chosen because of the exponential behaviour of the CWM distribution of traits and functional metrics with respect to biomass (see Figures 2 & 3). The CWM of traits and metrics that showed significant p-values ($p < 0.05$) to explain the variance of AGB were associated with each other in multiple exponential regressions (one dependent variable and two independent variables) to verify collinearity between the independent variables (Table 3). Based on the strongest correlation value between actual AGB and estimated biomass and the lowest AIC (Akaike 1998), the regression that explained the majority of the variance in AGB was chosen (Díaz et al. 2007; Finegan et al. 2015). The fits of the nonlinear regressions were performed on the R platform (R Core Team 2021) using the minpack.lm package and the nlsLM function (Elzhov et al. 2016).

Results

We found 1163 living individuals per hectare, consisting of 69 species and an AGB of 76.82 Mg ha^{-1} (Table 2). The mean values of the functional traits for the total woody vegetation (69 species) were 11 m for Ht_{max}, 17.5 m^2 for CA, 23 cm for DBH_{max}, 94 mm^2 mg^{-1} for SLA, and 0.68 for WD.

The following were found for the group of species that together represented 90% of the biomass (21 species – 30% of richness; and 963 ind. ha^{-1} – 82% of the absolute density): Ht_{max} 7 –21 m (mean 15 m); CA 6.80 – 64 m^2 (mean 31 m^2); DBH_{max} 12 – 55 cm (mean 39 cm); SLA 51.06 –164.34 mm^{-2} mg^{-1} (mean 87.88 mm^{-2} mg^{-1}); and WD 0.44 – 0.93 g cm^{-3} (mean 0.70 g cm^{-3}). The results for the group that accounted for 80% of the ABG

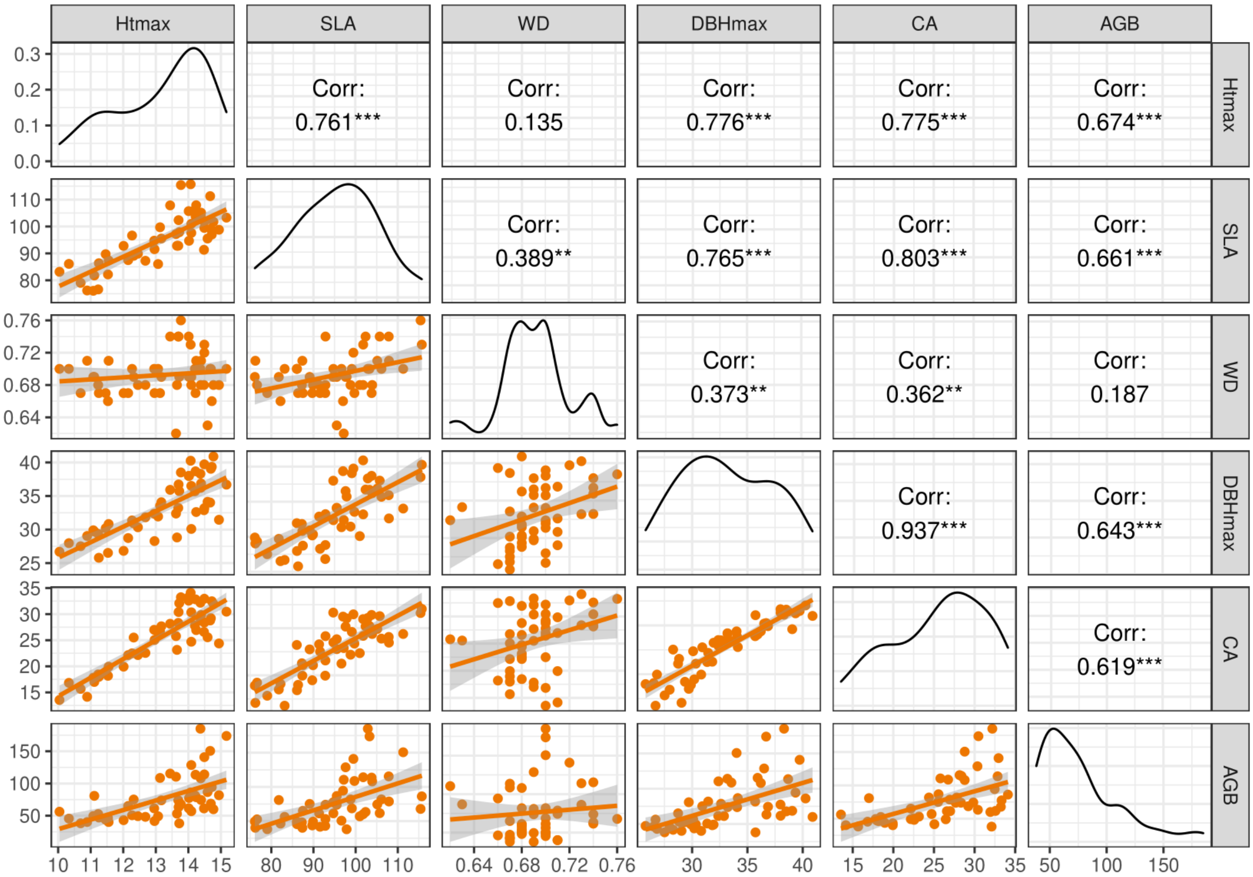

FIGURE 2: Spearman's correlation between functional traits and above-ground biomass for woody vegetation in an area of the Cerradão in Lajeado State Park, Tocantins State, Brazil. *: significant correlation at 95% probability; ** or ***: significant correlation at 99 % probability. Ht_{max}: maximum height (m); CA: canopy area (m^2); DBH_{max}: diameter at 1.3 meters from the ground (cm); SLA: specific leaf area (mm^2 mg^{-1}); WD: wood density (g cm^{-3}); *AGB:* above-ground biomass (Mg ha^{-1}).

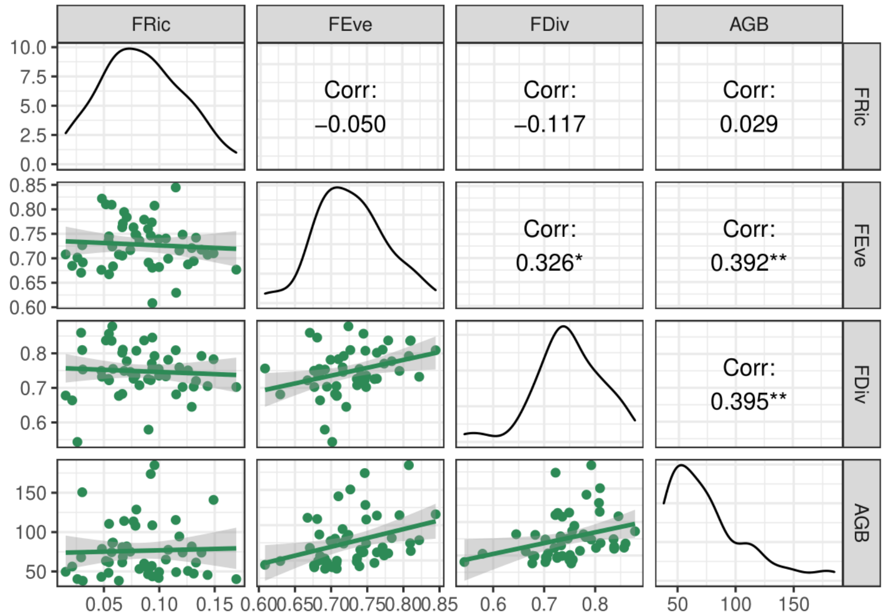

FIGURE 3: Spearman's correlation between functional metrics and above-ground biomass for woody vegetation of the Cerradão in Lajeado State Park, Tocantins State, Brazil. *: significant correlation at 95% probability; ** or ***: significant correlation at 99 % probability. Richness: species richness; FRic: Functional Richness; FEve: Functional Equitability; FDiv: Functional Divergence; AGB: above-ground biomass (Mg ha^{-1}).

14 species - 20.2% of richness; and 725 ind ha^{-1} – 62.33% of the absolute density) were: Ht_{max} 10–21 m (average 15 m); CA 10–64 m^2 (mean 37 m^2); DBH_{max} 22 – 55 cm (mean 42 cm); SLA 63.20–164.34 mm^{-2} mg^{-1} (mean 88 mm^{-2} mg^{-1}); and WD 0.48 – 0.90 g cm^{-3} (mean 0.72 g cm^{-3}). The values of functional traits of each species, as well as their respective absolute densities (number of individuals per hectare), frequencies (percentage of plots where the species was recorded), and biomasses (Mg ha^{-1}) are presented in Table 1, in which species are arranged in descending order of AGB and separated into three groups: 80, 90, and 100% of total ABG.

The group of species that represented up to 90% of the biomass included species such as *Emmotum nitens, Tapirira guianensis, Parkia platycephala, Mezilaurus itauba,* and *Bowdichia virgilioides*, which presented high values of potential growth traits (Ht_{max}, CA, and DBH_{max}) and SLA, and *Myrcia fenzliana, Xylopia aromatica*, and *Qualea parviflora*, were also present, which revealed lower values for the same traits (Table 1). These species were sampled simultaneously in more than one vegetation assembly.

The average CWM of the 50 assemblages for Ht_{max} was 13.18 m, CA was 25.63 m^2, DBH_{max} was 33.15 cm, SLA was 95.31 $mm^2.mg^{-1}$, and WD was 0.69 g cm^{-3}. For the functional metrics, the mean values of the 50 assemblages were 0.08 for FRic, 0.73 for FEve, and 0.75 for FDiv (Table 2).

Positive and significant correlations ranging from 62% to 67% were found between the Ht_{max}, CA, SLA,

TABLE 2: Minimum, maximum, mean, and standard deviation values of CWM parameters of each trait and functional metrics and biomass for woody vegetation of the Cerradão in Lajeado State Park, Tocantins State, Brazil.

Measure	Minimum	Maximum	Mean	Standard deviation
CWM Ht_{max} (m)	10.04	15.17	13.18	1.40
CWM CA (m^2)	13.55	34.1	25.63	5.69
CWM DBH_{max} (cm)	25.79	40.89	33.15	4.15
CWM SLA (mg mm^{-2})	76.09	115.7	95.31	9.76
CWM WD (g cm^{-3})	0.62	0.76	0.69	0.03
FRic	0.02	0.17	0.08	0.04
FEve	0.61	0.84	0.73	0.05
FDiv	0.54	0.88	0.75	0.07
Biomass (Mg ha^{-1})	38.12	185.01	76.28	35.10

Ht_{max}: Maximum; DBH_{max}: Maximum diameter at 1.3 m height from the ground; SLA: Specific leaf area; WD: Wood density, FRic: Functional richness; FEve: Functional equitability; FDiv: Functional divergence

DBH_{max}, and the AGB (Figure 2), whereas no significant correlation was observed with WD. Functional diversity metrics showed significant and positive correlations with AGB, FEve, and FDiv (Figure 3), while there was no significant correlation with FRic. The traits Ht_{max}, CA, SLA, and DBH_{max} showed significant and positive correlations among them, ranging from 76% to 94%, and the metrics FEve and FDiv showed a significant and positive correlation of 33%. Figures 2 and 3 represent two correlation matrices which verify the significance of the correlation (*), as well as the correlation value among the traits or metrics and between them and the AGB (right diagonal of the figures). The left diagonal of the figures represents the dispersion of the data among the functional traits and functional metrics and between the traits and functional metrics and AGB.

CWM of functional traits

CWM values of the traits significantly correlated with AGB showed significant coefficients when used as predictor variables in bivariate exponential regressions. The highest correlation coefficient (0.6170) and lowest AIC value (478.79) were observed for Ht_{max}. This was followed by CA (r = 0.5476 and AIC = 484.89), DBH_{max} (r = 0.5302 and AIC = 481.96), and SLA (r = 0.5288 and AIC = 486.34) (Figure 4). Furthermore, Figure 4 indicates that the fitted regression (red line) with the CWM of Ht_{max} was the closest to the local regression (blue line) among the CWMs of the significant functional traits.

Functional diversity metrics

Two functional diversity metrics significantly correlated to AGB also showed significant coefficients when used as predictor variables in bivariate exponential regressions. The highest correlation coefficient (r = 0.3460) and lowest AIC value (AIC = 496.33) were observed for FEve. This was followed by FDiv (r = 0.2989 and AIC = 498.03) (Figure 5). Figure 5 shows that the fitted regression (red line) with FEve was the closest to the local regression (blue line) between the two functional metrics. However, despite the exponential trend, the scatter of the points for the two metrics reveals that there was no directly proportional distribution pattern between the metric values and the AGB results. Furthermore, the estimation parameters of the models with the metrics were inferior to those of the functional CWMs.

Multiple regressions

The combinations of two independent variables in the multiple models showed little improvement in the

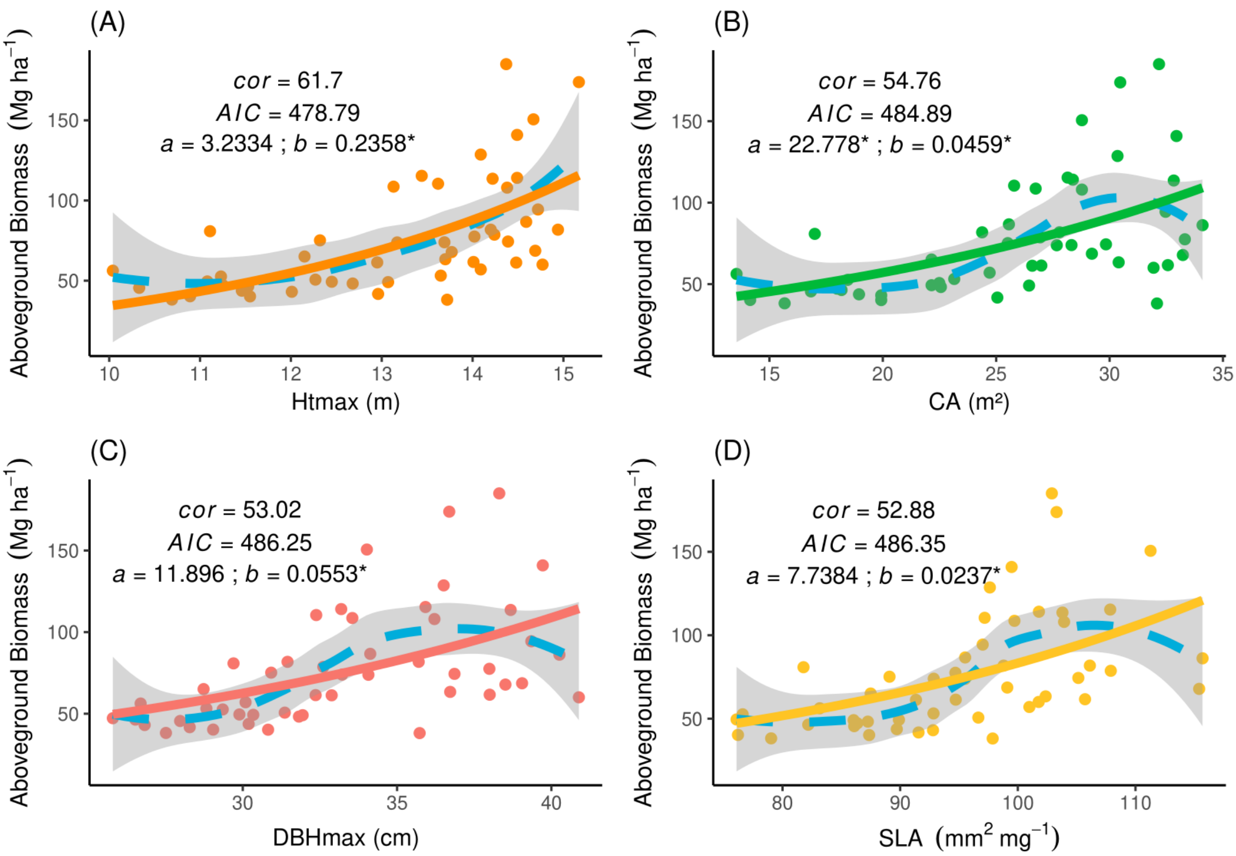

FIGURE 4: Distribution of significant functional traits in relation to above-ground biomass, their respective correlation coefficients (cor), Akaike's information criteria (AIC), and the coefficients of the regression fit for woody vegetation of the Cerradão in Lajeado State Park, Tocantins State, Brazil. *: significant coefficient at 95% probability; red line: values estimated by fitted exponential model; blue line: local non-linear regression; grey spot: confidence interval of local non-linear regression.

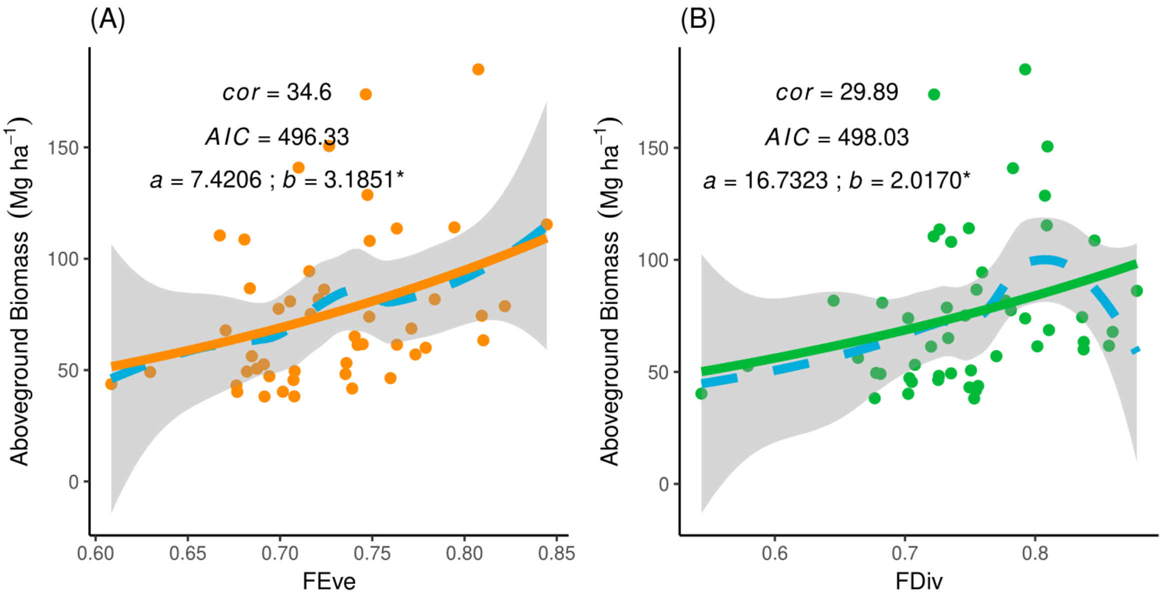

FIGURE 5: Distribution of significant functional metrics in relation to above-ground biomass, their respective correlation coefficients, Akaike's information criteria, and the coefficients of the regression fit for woody vegetation of the Cerradão in Lajeado State Park, Tocantins State, Brazil. *: significant coefficient at 95 % probability; red line: values estimated by fitted exponential model; blue line: local non-linear regression; grey spot: confidence interval of local non-linear regression.

parameter estimates over the bivariate models, with correlation coefficients ranging from 0.5514 to 0.6267 and AICs ranging from 479.85 to 486.58, respectively, which are values similar to those found in the bivariate models (Table 3).

Furthermore, when different traits and functional metrics were combined in the models, none of the multiple regression models showed significant coefficients, indicating collinearity between traits and functional metrics, and only Ht_{max} had a significant coefficient. Thus, the multiple models with the best estimates were those that used CWM Ht_{max} among the predictor variables; therefore, this variable was the superior predictor of AGB (Table 3).

Discussion

There were significant positive relationships between accumulation biomass and functional diversity for woody vegetation in Cerradão. The community-weighted means of functional traits, especially maximum height, were better predictors of above-ground biomass than functional metrics, as they showed higher correlation values and lower AIC values. Furthermore, in the association of functional traits and metrics in multiple regression models, both functional evenness and functional divergence were no longer significant variables. Despite the lower potential to explain biomass variation, functional evenness and functional divergence showed significant relationships with above-ground biomass in bivariate regressions.

The significant positive relationship between above-ground biomass and functional evenness reflects assemblages with optimised resource use and, consequently, more likelihood of presenting greater amounts of above-ground biomass. This is because functional evenness is directly proportional to the regularity of occupation of the functional space in relation to the abundance of species, and more equitably occupied spaces signify a better use of resources (Mason et al. 2005; Mouchet et al. 2010; Villéger et al. 2008).

The significant positive relationship with functional divergence revealed that some of the Cerradão assemblages with higher biomass values comprised abundant species with divergent functional traits, such as those with the presence of *Emmotum nitens* and *Myrcia fenzliana*, which are species with contrasting functional trait values. The coexistence of species with distinct, complementary functional traits, increases the above-ground biomass by more effective use or sharing of resources (Begon et al. 2005; Bernhardt-Romermann et al. 2011; Pérez-Ramos et al. 2019).

The fact that the community-weighted means of the potential growth traits and the specific leaf area were well correlated with above-ground biomass estimation indicates that these variables represent the competitive vigour, survival, and growth of the species (Finegan et al. 2015; Maracahipes et al. 2018; Pérez-Harguindeguy et al. 2016). Forests, such as the Cerradão vegetation, are closed canopy environments where light resources are limited; thus, higher growth potential and lower growth investment strategies determine species survival and growth (Finegan et al. 2015; Hoffmann et al. 2012; Poorter & Rozendaal 2008; Wright et al. 2010). In addition, positive relationships between potential growth traits, especially maximum height, and above-ground biomass corroborate studies that have evaluated the ability of community-weighted means to estimate

TABLE 3: Models fitted with CWM of functional traits and functional metrics, their respective relative error value (Syx%), correlation coefficient (r), Akaike value (AIC), and coefficients for woody vegetation of the Cerradão in Lajeado State Park, Tocantins State, Brazil. Arranged in ascending order of AIC value.

Model	Syx (%)	r	AIC	*a*	*b*	*c*	Regression
$AGB = a * exp^{(b*Ht_{max})}$	36.60	0.6170	478.79	3.2338	0.2359*	-	B
$AGB = a * Ht_{max}^{b} * SLA^{c}$	36.65	0.6267	479.85	0.0019	2.3590	0.9815	M
$AGB = a * DBH_{max}^{b} * Ht_{max}^{c}$	36.76	0.6232	480.15	0.0152	0.6689	2.3835	M
$AGB = a * Ht_{max}^{b} * CA^{c}$	37.03	0.6167	480.89	0.0405	2.4756	0.3458	M
$AGB = a * Ht_{max}^{b} * FE_{ve}^{c}$	37.12	0.6135	481.15	0.0537	2.8659	0.5255	M
$AGB = a * Ht_{max}^{b} * FD_{iv}^{c}$	37.27	0.6097	481.53	0.0303	3.0263	0.0315	M
$AGB = a * DBH_{max}^{b} * SLA^{c}$	38.33	0.5786	484.36	0.0032	1.1274	1.3441	M
$AGB = a * CA^{b} * FEve^{c}$	38.39	0.5766	484.50	3.3028	1.0775	1.1542	M
$AGB = a * CA^{b} * SLA^{c}$	38.43	0.5752	484.62	0.0302	0.7314	1.1956	M
$AGB = a * exp^{(b*CA)}$	38.90	0.5476	484.89	22.7776*	0.0459*	-	B
$AGB = a * CA^{b} * FDiv^{c}$	38.62	0.5695	485.10	0.4926	1.4640	-0.9932	M
$AGB = a * SLA^{b} * FDiv^{c}$	38.67	0.5682	485.22	$1.75 * 10^{-5}$	3.2664	-1.3298	M
$AGB = a * DBH_{max}^{b} * FEve^{c}$	38.68	0.5679	485.25	0.2718	1.7142	1.1905	M
$AGB = a * DBH_{max}^{b} * CA^{c}$	38.88	0.5615	485.77	0.4001	0.8471	0.7020	M
$AGB = a * exp^{(b*DBH_{max})}$	39.44	0.5302	486.25	11.8929*	0.0554*	-	B
$AGB = a * exp^{(b*SLA)}$	39.48	0.5288	486.35	7.7384	0.0238*	-	B
$AGB = a * SLA^{b} * FEve^{c}$	39.11	0.5544	486.35	0.0051	2.1653	0.8810	M
$AGB = a * DBH_{max}^{b} * FDiv^{c}$	39.20	0.5515	486.58	0.0208	2.2845	-0.6624	M
$AGB = a * exp^{(b*FEve)}$	43.62	0.3460	496.33	7.4206	3.1851*	-	B
$AGB = a * exp^{(b*FDiv)}$	44.37	0.2989	498.03	16.7325	2.0170*	-	B

Where: a, b and c: model coefficients, AGB: above-ground biomass (Mg ha^{-1}); Ht_{max}: CWM of maximum height (m), CA: CWM of crown area (m^2), DBH_{max}: CWM of maximum diameter at 1.30 m height from the ground; SLA: CWM of specific leaf area (mm^2 mg^{-1}); FEve: Functional evenness; FDiv: Functional divergence. B: bivariate regression and M: Multiple regression. Coefficient values with an asterisk represent significant coefficients; Syx (%): Residual standard error (%); r: correlation coefficient between estimated and observed values; AIC: Akaike's information criteria.

ecosystem properties and processes (Ali et al. 2017; Finegan et al. 2015; Terra et al. 2021; Vargas-Larreta et al. 2021).

Among the functional traits, community-weighted means of maximum height was the best predictor of above-ground biomass. Maximum height represents the potential growth that adult individuals can achieve at a site (Pérez-Harguindeguy et al. 2016; Poorter & Rozendaal 2008). Species with greater potential for vertical growth have a competitive advantage for light by reaching higher strata of the canopy (Finegan et al. 2015; Maracahipes et al. 2018; Pérez-Harguindeguy et al. 2016; Poorter & Rozendaal 2008). Thus, because of their competitive advantage for obtaining resources and their larger maximum size, species with greater maximum height are more likely to present higher biomass values.

The community-weighted means of diameter at maximum breast height reflects the successful establishment, survival, and secondary growth of species in the assemblages. Diameter at breast height is a key variable in woody community surveys, as it is readily measured in the field and highly correlated with other traits, such as height (Kershaw et al. 2016; Pretzsch 2009). The 0.77 significant correlation between the community-weighted means of maximum height and diameter at maximum breast height revealed that there was a predominance of situations in which the two variables were intrinsically related to all assemblages. In general, the assemblages in Cerradão that presented greater heights tended to present higher values of diameter at maximum breast height; therefore, the combination of the two variables explained the variation in above-ground biomass. It is worth noting that the residence time (survival) and biomass accumulation were directly related to the ecological group and wood density of the species (Chave et al. 2006; Hubau et al. 2020; Letcher & Chazdon 2009), which can modify the accumulated biomass in relation to diameter at maximum breast height.

Despite being a less commonly used trait in the literature, crown area showed potential as a community-weighted means to explain biomass accumulation in vegetation. Crown biomass represents, on average, 52% of the total biomass of trees and up to 58% for individuals larger than 35 cm diameter at breast height in Cerradão vegetation (Miguel et al. 2017).

Species with larger canopy areas tend to have a greater leaf area and improved light absorption, increasing their competitive dominance by using light more efficiently, and ensuring greater growth for the species (Kitajima et al. 2005). In addition, plasticity in the shape of the crown, which is related to the direction and extension of the growth of branches in relation to the main stem, promotes greater biomass production through the optimised occupation of canopy spaces (Souza et al. 2019; Jucker et al. 2015; Kitajima et al. 2005).

The positive relationship between specific leaf area and biomass found in our research points to the light optimisation and accelerated growth of some species, corroborating the findings of Finegan et al. (2015) and Ali et al. (2017). Higher specific leaf area values represent greater efficiency in light capture and use, as well as lower energy investment for leaf production, conferring a competitive advantage over species with lower specific leaf area in forest environments (Díaz et al. 2004; Maracahipes et al. 2018; Pérez-Harguindeguy et al. 2016). In addition, because of the characteristics of the environment, forest species tend to have higher specific leaf area (Díaz et al. 2004; Hoffmann et al. 2005; Maracahipes et al. 2018; Pérez-Harguindeguy et al. 2016).

Although wood density improves estimates of woody species biomass and represents a trade-off between growth and survival (Chave et al. 2006; Pérez-Harguindeguy et al. 2016; Souza, 2020), no significant relationships were found between community-weighted means of wood density and above-ground biomass in the assemblages, unlike the results of Ali et al. (2017), de Souza et al. (2019), and Vargas-Larreta et al. (2021), who found significant relationships between community-weighted means of wood density and biomass. The relationship between these variables may have been affected by the present scale of analysis, since the variance of wood density (mean values) occurred at larger spatial scales, following gradients of temperature and precipitation, and edaphic characteristics (Oliveira et al. 2022; Terra et al. 2018, 2021).

When the community-weighted means of functional traits and functional metrics with significant relationships with biomass were subjected to multiple regressions, they showed collinearity among themselves. Maximum height, maximum diameter, and crown area were all related to the potential growth and survival of the species, and they showed high correlation values.

Although the community-weighted means of specific leaf area is more related to the average leaf tissue investment strategy of the species, it showed a correlation between 76% and 80% with the community-weighted means of potential size traits, which may have led to collinearity with the community-weighted means of the other traits in the multiple regressions. However, the positive correlation between community-weighted means of specific leaf area and community-weighted means of potential growth traits indicates that assemblages with greater biomass predominantly and simultaneously have larger species with stronger light capture abilities.

Our results indicate that the above-ground biomass for woody vegetation in Cerradão assemblages was managed mainly by the mass ratio theory, in which a group of species with higher density and frequency and with traits of competitive advantage mediated the accumulation of biomass (Grime 1998). Among the functional traits with significant relationships, the most suitable for predicting biomass was the maximum height, although others presented good estimates.

Three final considerations are required. Soil is a determining variable in the processes and properties of an ecosystem (Oliveira et al. 2022; Quesada et al. 2012; Terra et al. 2018). Future investigations involving physical and chemical properties of soils may explain a larger percentage of the variance in biomass, although they are more expensive and more labour-intensive to obtain than dendrometric variables.

Although functional evenness was not significant in multiple regressions associated with functional traits, high functional evenness values may be an indication of environmental filtering (Mouchet et al. 2010; Villéger et al. 2008). Complementing the analyses with canopy opening and physical and chemical soil data may generate more conclusive results regarding the actual filtering effect on above-ground biomass accumulation.

Similarly, due to the correlation and significance of functional divergence with aerial biomass and the divergent characteristics of functional traits, especially among species that represent 80% of the biomass, part of the biomass accumulation is related to better utilisation or partitioning of resources. Therefore, it is not possible to completely exclude niche complementarity, but it is a weaker predictor of biomass than functional traits.

Conclusions

The community-weighted means of potential growth traits and specific leaf area are good predictors of above-ground biomass, and community-weighted means of maximum height were the most suitable. Furthermore, the process of biomass accumulation is managed more by the presence and abundance of species with functional traits of potential growth and foliar investment, than by the variance and distribution of the functional traits in a functional space.

Thus, we conclude that assemblages composed of species with higher potential height values were those with greater above-ground biomass. Considering the difficulty of measuring height in native forest environments, other potential growth traits, such as crown area and diameter at maximum breast height, are alternatives. Our results are in agreement with research on woody vegetation in savannah formations of the Brazilian savannah, in which the community-weighted means of diameter at maximum breast height, a variable of potential growth and survival, was directly proportional and explained the majority of the variance in above-ground biomass.

List of abbreviations

DBH; diameter at breast height;
CWM: Community Weighted Mean;
FRic: Functional Richness;
FEve: Functional Evenness;

FDiv: Functional Divergence;
SLA: Specific Leaf Area;
WD: Wood Density;
CA: Crown Area;
DBH_{max}: Diameter at maximum breast height;
HT_{max}: maximum height

Competing interests

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

Authors' contributions

Matheus Martins: Conceptualization, Methodology, Investigation, Software, Formal analysis, Writing–original draft, Visualization, Validation. **Eder Pereira Miguel**: Conceptualization, Methodology, Formal analysis, Writing – review & editing, Supervision and Validation. **José Roberto Rodrigues Pinto**: Formal analysis, Writing – review & editing, Validation. **Milton Serpa de Meira Junior**: Conceptualization, Software, Writing – review & editing, Formal analysis. **Fernanda Coelho de Souza**: Writing – review & editing, Formal analysis. **Hallefy Junio de Souza**: Software, Data curation, Writing – review & editing.

Acknowledgements

We would like to thank the Research and Innovation Support Foundation of the Federal District (FAP-DF, Brazil) and the Coordination for Higher Education Enhancement (CAPES, Brazil), both research funding institutions, and the Nature Institute of Tocantins (NATURATINS, Brazil), for managing Lajeado State Park. The authors are grateful to CNPq ("*Conselho Nacional de Desenvolvimento Científico e Tecnológico*", Brazilian government agency) for scholarship productivity of E.P. Miguel (process 309054/2021-4) and J.R.R. Pinto (process 312571/2021-6).

Funding

This work was supported by the Research and Innovation Support Foundation of the Federal District (FAP-DF, Brazil), which financed the field data collection.

The Coordination for Higher Education Enhancement (CAPES, Brazil) financed the master's scholarship of the first author.

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