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Aboveground Similarity, Belowground Dominance: Biomass Allocation in Cerrado *sensu stricto* and Carrasco Vegetation in the Brazilian Semi-Arid

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Abstract

This study quantified total biomass stocks in Carrasco (CAR, n = 12), a dense tropical deciduous vegetation type from the Brazilian semi-arid region for which biomass information remains scarce. We also evaluated differences in floristic composition, diversity, structure, and biomass allocation patterns relative to Cerrado *sensu stricto* (CSS, n = 40). Forest inventories were conducted in southeastern Brazil. Woody biomass was estimated using a regional allometric equation. Roots were sampled in a position adjacent to the plots, and litter was collected at the center of each plot using a frame. Necromass was assessed along a linear transect corresponding to the length of each plot using the line-intersect method. Biomass differences between vegetation types were assessed using generalized linear and mixed-effects models (GLMs and GLMMs). Total biomass reached 45.24 Mg ha^{-1} in CSS and 59.01 Mg ha^{-1} in CAR. In CSS, woody biomass predominated (20.47 Mg ha^{-1}; 45%), followed by roots (18.47 Mg ha^{-1}; 41%), litter (5.49 Mg ha^{-1}; 12%), and necromass (0.81 Mg ha^{-1}; 2%). In CAR, roots were the dominant component (32.37 Mg ha^{-1}; 55%), followed by woody biomass (16.57 Mg ha^{-1}; 28%), litter (8.39 Mg ha^{-1}; 14%), and necromass (1.68 Mg ha^{-1}; 3%). CSS and CAR shared only 10% of their species and showed significant differences in total biomass (TB) and belowground biomass (BGB), while aboveground biomass (AGB), aboveground woody biomass (AGWB), litter, and necromass did not differ significantly ($\alpha = 0.05$). The BGB/AGWB ratio was <1 in CSS and >1 in CAR, resembling global patterns of savanna/shrubland and grassland formations, respectively. Considering the sampling design adopted, despite the higher stem density in CAR, larger individuals in CSS compensated for structural differences, resulting in similar aboveground biomass stocks. Our findings reinforce the floristic and structural distinctiveness of Carrasco and reveal contrasting biomass allocation strategies, with a strong dominance of belowground biomass in CAR. These results demonstrate that aboveground-based assessments can substantially underestimate total biomass in semi-arid transitional vegetation and highlight the need to incorporate non-forest ecosystems into biomass inventories, conservation planning, and climate change mitigation strategies.

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1. Introduction

Savannas represent an important component of global vegetation, covering approximately one-sixth of the Earth's terrestrial surface [1]. In Brazil, savannas occur predominantly in the Cerrado [2,3], the second largest biome in South America, characterized as a vegetation mosaic composed of savanna, forest, and grassland formations [2,4]. Despite its high biodiversity [5,6], relatively little attention has been given to its ecosystem services [1,7].

Land-use changes in the Cerrado have occurred at an accelerated pace [8–10], resulting in high greenhouse gas (GHG) emissions in Brazil [11]. Consequently, the biome ranks among the largest carbon dioxide emitters in the country, second only to the Amazon [11,12].

With the global climate crisis [13], the number of studies aimed at obtaining accurate estimates of carbon stocks in biomass has increased [14]. Given that biomass is a proxy for carbon [15,16], that climate change is actively altering plant communities in this important Neotropical savanna, where prolonged dry seasons tend to reduce biomass [17], and that most existing studies have evaluated only woody biomass [18], it is necessary to expand knowledge of biomass stocks across the different vegetation compartments.

In addition to the Cerrado, Carrasco [19] is another important vegetation type that occurs naturally in a fragmented pattern within the Brazilian savanna and forms transition zones with another Brazilian biome, the Caatinga [20], the predominant and exclusive biome of Brazil, characteristic of the semiarid region.

Although Carrasco is considered a vegetation type of the Caatinga, particularly due to its deciduousness, its structural characteristics, such as high stem density, an apparently single-layered structure, and the near absence of cacti and bromeliads, justify its recognition as a distinct transitional vegetation type [20,21].

Despite these distinct structural and floristic characteristics observed in transitional zones between the Cerrado and the Caatinga [19], it remains unclear how they influence biomass allocation patterns between aboveground and belowground compartments, especially in the absence of biomass stock estimates for this vegetation type.

This knowledge gap is relevant not only at the regional scale but also in the context of global patterns, where biomass allocation between roots and shoots represents a fundamental adaptive strategy that enables terrestrial ecosystems to enhance their carbon sequestration capacity [22]. In this context, global root-to-shoot allocation patterns in savannas, shrublands, and grasslands have been widely described [23] and used to predict biomass distribution across different vegetation types [24].

It is within this context that Carrasco is situated. In Central Brazil, this vegetation type is found near the boundaries with Northeastern Brazil and in the northern region of the state of Minas Gerais [25]. Studies on this vegetation are still developing, particularly regarding its proposed relationship with Cerrado vegetation [19,26–29].

The few existing studies on Carrasco vegetation are primarily related to floristics [27], as well as the phenology and dispersal of woody species [30] and the ethnopharmacology of medicinal plants [31]. Studies aimed at evaluating its relationships with Cerrado vegetation are scarce, and, to our knowledge, none have focused on biomass.

Therefore, considering that Carrasco (CAR) is a distinct transitional vegetation type and that no studies have focused on its biomass, we quantified its total biomass stocks for the first time and tested the hypothesis that its structural and floristic differences relative to Cerrado *sensu stricto* (CSS) in the semiarid region of Minas Gerais State, Brazil, are also reflected in its biomass allocation strategies.

2. Materials and Methods

2.1. Study Area

The study was carried out in areas of Cerrado *sensu stricto* (CSS) and Carrasco (CAR) [19,21,26], within the Rio Pardo and Urucuia basins, located in the northern and northwestern regions of the state of Minas Gerais (MG), Brazil (Figures 1 and 2).

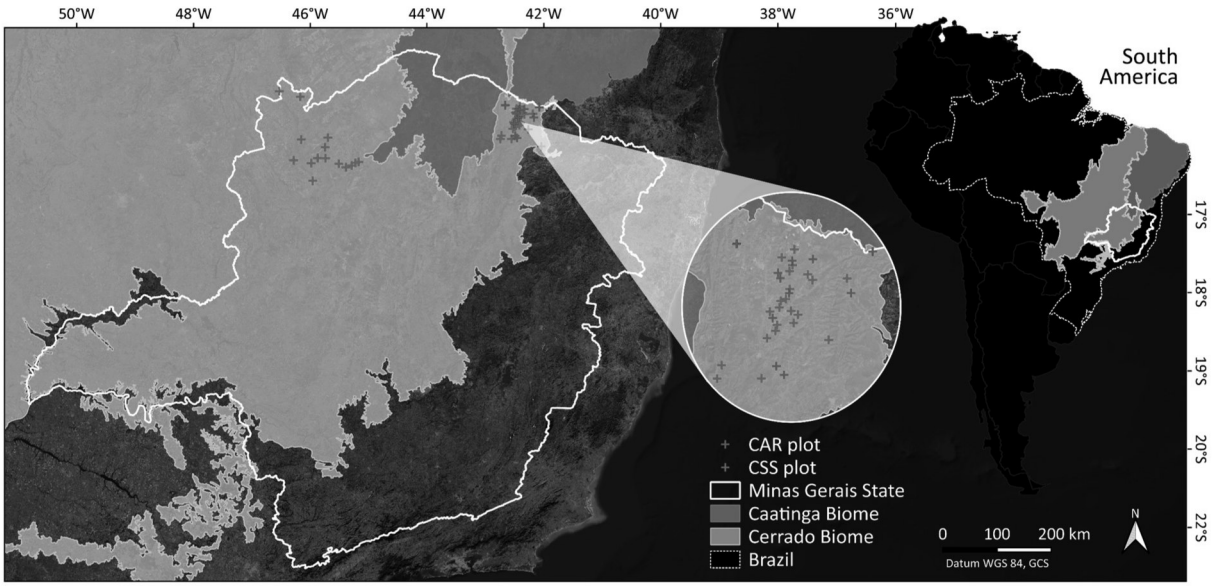

Figure 1. Distribution of sampling units from the forest inventory conducted in areas of Cerrado *sensu stricto* (CSS) and Carrasco (CAR), located in the Rio Pardo and Urucuia basins, in the northern and northwestern regions of the state of Minas Gerais, Brazil.

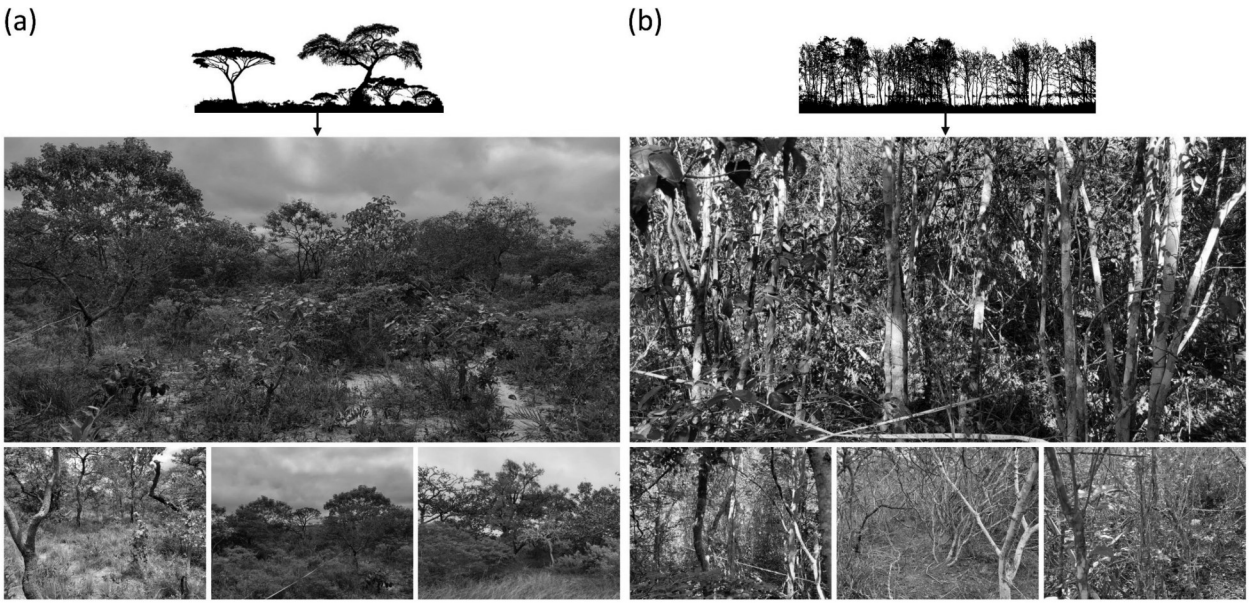

Figure 2. Landscape view of the sampling units of (**a**) Cerrado *sensu stricto* (CSS) and (**b**) Carrasco (CAR), located in the Rio Pardo and Urucuia basins, in the northern and northwestern regions of the state of Minas Gerais, Brazil.

The Brazilian Rural Environmental Registry System (SICAR) was used to identify the number and geographic location of rural properties within the two river basins. The properties are distributed across the municipalities of Vargem Grande, Montezuma, Indaiabira, Rio Pardo, São João do Paraíso, and Taiobeiras in northern Minas Gerais, and Pintópolis,

Urucuia, Riachinho, Bonfinópolis, Uruana de Minas, Arinos, and Formoso in northwestern Minas Gerais.

The CSS areas were sampled in all municipalities listed above, except Taiobeiras. In contrast, CAR areas were evaluated only in the municipalities of Taiobeiras, Rio Pardo, São João do Paraíso, Vargem Grande, and Montezuma, located in northern Minas Gerais.

The region is characterized by a tropical savanna climate (Aw, tropical (A) with a dry winter (w) and mean temperature of the coldest month $\geq$ 18 °C), according to the Köppen–Geiger classification [32,33].

Climate normals from the National Institute of Meteorology weather stations (1991–2020) indicated a mean annual precipitation of approximately 1100 mm and a mean annual temperature of 25 °C for the northwestern region (Arinos-MG station), and 820 mm and 24 °C for the northern region (Salinas-MG station) [34].

2.2. Data Collection

2.2.1. Forest Inventory

Temporary sampling units (Figure 1) were established within the study area, considering rural properties previously selected using SICAR. Socio-environmental studies and assessments of silvopastoral systems in the study area preceded the establishment of the temporary sampling units [35]. In each property, the native vegetation type was confirmed by specialists, and a random sampling point was subsequently defined using QGIS. Only one plot was installed per property within the same vegetation type to reduce autocorrelation among the collected data.

A total of 52 sampling plots were established, of which 40 were located in Cerrado *sensu stricto* (CSS) and 12 in Carrasco (CAR). In CSS, the plots measured 1000 m^2 (20 × 50 m), whereas in CAR they measured 100 m^2 (10 × 10 m). Plot sizes (Figure 3) were defined according to the Permanent Plot Manual for the Cerrado and Pantanal Biomes [25], which recommends smaller plots for Carrasco due to its naturally fragmented distribution and more homogeneous structure, whereas larger plots are recommended for CSS because of its greater spatial continuity and structural heterogeneity. Field inventories were conducted in March 2024 and 2025 in the northern and northwestern regions, respectively.

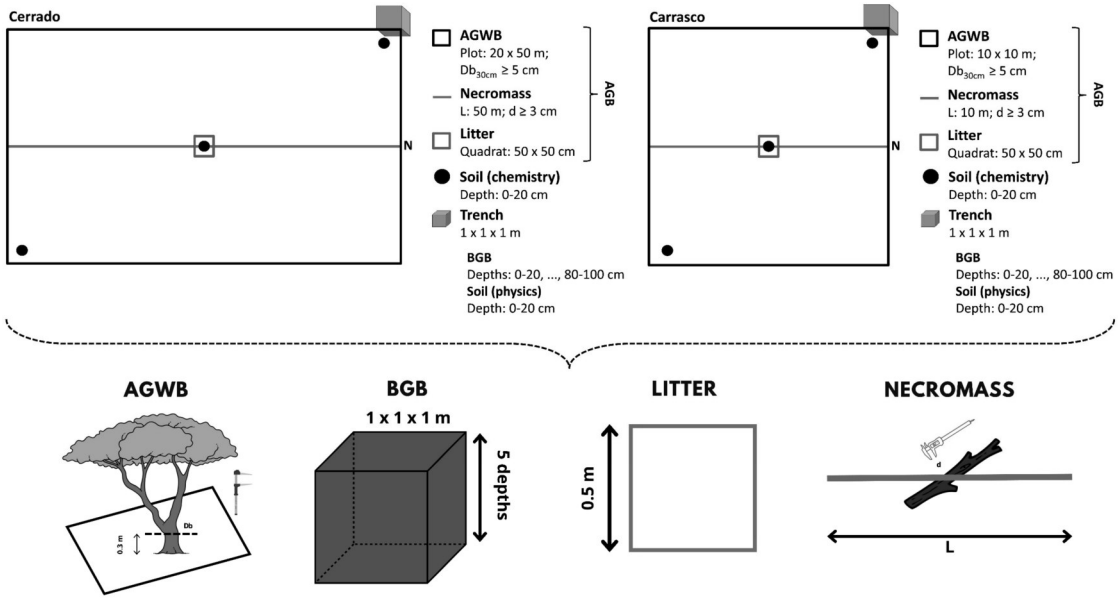

Figure 3. General schematic of the sampling design applied to Cerrado *sensu stricto* (CSS) and Carrasco (CAR) areas. AGB and BGB = aboveground and belowground biomass, respectively; AGWB = aboveground woody biomass; Db = basal diameter; d = diameter; L = line length.

All biomass estimates were standardized to Mg ha^{-1}, allowing direct comparisons between vegetation types and reducing, although not completely eliminating, potential scale effects associated with differences in plot area.

In both vegetation types (CSS and CAR), all woody individuals with a basal diameter (Db), measured at 30 cm above ground level, equal to or greater than 5 cm were recorded and botanically identified by a specialist according to APG IV [36] and the Brazilian Herbaria Reflora 2020 [37]. Basal diameter was measured using a diameter tape. For multi-stemmed individuals, all stems with Db $\geq$ 5 cm were included in the survey.

Although this inclusion criterion is widely used in forest and savanna inventories, it is acknowledged that it may partially underestimate the structural complexity of Carrasco, as this vegetation type is characterized by a high density of smaller individuals and multiple slender stems. Thus, woody stems below the adopted threshold were not included, which may lead to an underestimation of aboveground biomass and structural density in CAR compared with CSS. Therefore, a uniform inclusion threshold was applied across both vegetation types to minimize the introduction of additional methodological differences between them, thereby allowing the analysis of relative biomass allocation patterns.

Sampling sufficiency was evaluated based on species richness and rarefaction and extrapolation curves, as described in the Section 2.3. The stabilization of richness estimates within each vegetation type supported the adequacy of the sampling effort despite differences in the size and number of sampling plots.

2.2.2. Estimation of Total Biomass Stock (TB)

For the estimation of total biomass (TB) in CSS and CAR, both aboveground (woody biomass of trees and shrubs, necromass, and litter) and belowground (root biomass) compartments were considered.

Aboveground Woody Biomass (AGWB)

Using forest inventory data from the CSS and CAR areas, the AGWB of each sampled tree and shrub individual was estimated to obtain the woody biomass for each sampling unit.

The aboveground biomass of each woody individual in each vegetation type was estimated using Equation (1) [38], with an inverse transformation to the original scale using the Sprugel correction factor [39]. The equation accounts for the biomass of the commercial stem with bark (measured to a minimum top diameter of 3.0 cm), branches (due to their irregular shape, variable-length sections were adopted, and the circumference was measured at the midpoint of each section), and leaves (weighed separately), following the procedures of the Forest Inventory of Minas Gerais [40]. For multi-stemmed individuals, the equivalent diameter was used and calculated for each individual as the square root of the sum of the squared diameters of all stems (i.e., $Db_{eq} = \sqrt{\sum(Db_i)^2}$), thereby representing a single diameter value per individual.

$$AGWB = e^{-10.87846+2.84969 \cdot \ln(Db_i)} \cdot 1.0085 \quad (1)$$

where AGWB = woody biomass of individual i (Mg); Db_i = basal diameter of individual i, measured at 30 cm above the ground (cm); R^2adj (adjusted coefficient of determination) = 0.94; SEE (standard error of the estimate) = 0.1301 (Mg) and 61.74 (%).

The dataset used by Morais et al. [38] came from the Minas Gerais Forest Inventory for Cerrado *sensu stricto* [41]. A total of 868 trees belonging to 99 species, distributed in 70 genera and 37 families, were sampled across 20 forest fragments in different regions of the state. Individual tree volumes were obtained using Huber's method, and biomass was calculated as the product of volume and wood basic density, determined from discs collected at five positions along the commercial height.

Furthermore, the absence of allometric equations specifically developed for CAR, combined with the lack of destructive sampling data and legal restrictions on such sampling in native vegetation, limits model development. In this context, the use of an equation derived from CSS should be interpreted not only as a methodological limitation but also as evidence of the need for further studies focused on CAR, which remains poorly understood beyond its floristic characteristics.

Necromass

Necromass was estimated using the line-intersect method [42]. A sampling line was allocated at the center of each CSS and CAR sampling unit. In CSS, the line length (L) was 50 m, while in CAR it was 10 m. The line lengths were chosen to sample necromass across the entire extent of each plot without exceeding its boundaries.

Due to multiple terminologies associated with dead wood [43], necromass was defined as woody debris, including branches, stumps, and dead fallen trees or shrubs, i.e., non-living woody biomass not counted as litter [44]. All woody debris with a diameter ≥ 3 cm intersecting the line (L) or its vertical projection was included. Debris diameters were measured using a digital caliper. Debris was also classified by decomposition stage as: (1) fresh, (2) initial decomposition, and (3) advanced decomposition [45,46] (Table 1).

Table 1. Classification of necromass according to decomposition stages.

Decomposition Class	Characteristic
1—Fresh	Presence of branches and intact wood texture.
2—Initial decomposition	Remnants of bark, without branches and firm wood.
3—Advanced decomposition	Without bark or branches and wood in a moderate to advanced stage of decomposition, crumbling.

Brazilian Forest Service [45].

The necromass for each sampling unit was obtained using Equation (2) [42]. Necromass was calculated as the product of volume and the mean basic density (ρ) (Table 2) of the woody debris that intersected the line (L) in each sampling unit (Equation (2)).

$$\text{Necromass} = \pi \cdot \frac{\sum_{i=1}^{n} d_i^2}{8 \cdot L} \cdot \rho_i \quad (2)$$

where necromass = deadwood mass (Mg ha^{-1}); d_i = diameter (cm) of each piece that intercepted L; L = line length (m); ρ_i = mean basic density of debris per plot (g cm^{-3}), considering the diameter and its respective decomposition class.

Table 2. Basic density (ρ) (g cm^{-3}) according to the degree of decomposition and diameter of the woody debris.

Diameter Class (cm)	Decomposition Class		
	1	2	3
$2 < d < 4$	0.52	0.31	0.28
$4 \leq d < 6$	0.63	0.43	0.35
$6 \leq d < 8$	0.75	0.45	0.37
$8 \leq d < 10$	0.78	0.48	0.45
≥ 10	0.62	0.44	0.36

Luccas [47].

Litter

At the center of each sampling unit established for the CSS and CAR inventories, a 50 × 50 cm frame was installed to collect litter, i.e., fine, non-woody debris (diameter < 3 cm). The litter from each frame was collected and weighed to obtain the total fresh mass. A subsample from each frame was taken, weighed, and dried in a forced-air oven at 70 ± 2 °C until constant mass was reached (variation ≤ 1%) to determine the dry mass, thus allowing the calculation of the total dry litter biomass per unit area [48].

The dry mass of litter was obtained using the proportional method [49], according to Equation (3). After determining the dry mass, values were extrapolated to megagrams per hectare.

$$DM = WM \cdot \frac{Dm}{Wm} \quad (3)$$

where DM = dry mass of the field sample (g); WM = fresh mass of the field sample (g); Dm = dry mass of the subsample (g); Wm = fresh mass of the subsample (g).

Belowground Biomass (BGB)

For root sampling in CSS and CAR areas, a trench measuring 1 m × 1 m × 1 m (1 m^3) was excavated adjacent to the perimeter of each sampling unit established for the woody vegetation inventory. Only roots with a diameter greater than 2 mm were collected, as smaller roots cannot be reliably distinguished from soil organic matter [50]. It is important to note that trench-based methods tend not to include roots of larger diameters. Despite this limitation, this component is hereafter referred to as total belowground biomass (BGB) in this study. Roots were collected in 20 cm layers, corresponding to 0–20, 20–40, 40–60, 60–80, and 80–100 cm. Using sieves, roots were separated from the soil.

For each layer, the total fresh mass of roots from each sample was obtained. Subsequently, a subsample was taken from each depth sample and dried in a forced-air oven at 70 ± 2 °C until constant mass was reached (variation ≤ 1%) to determine the dry mass, thus allowing the calculation of the total dry root biomass per layer [48].

The determination of root dry mass followed the same procedure used for litter dry mass determination.

2.2.3. Soil Physical and Chemical Variables

For fertility and texture analyses, soil samples were collected within the forest inventory sample plots. For bulk density (BD), samples were collected from the trench. Disturbed samples used for fertility analysis were collected using a Dutch auger, forming a composite sample from the 0–20 cm layer. This composite sample was obtained from three subsamples collected along the diagonal of the plot, two near the ends and one at the center (Figure 3). Soil sample preparation used 10-mesh (2 mm) sieves in order to isolate the fine earth fraction, which is the fraction most accessible to plant roots, as described by the Soil Survey Staff [51].

Soil chemical and physical variables included pH, aluminum (Al), organic matter (OM), calcium (Ca), magnesium (Mg), phosphorus (P), potassium (K), sand, silt, and clay contents, as well as bulk density (BD). Chemical and textural analyses were performed in a commercial laboratory that reports using the Manual of Soil Analysis Methods [52]. A soil texture triangle was generated for each vegetation type using the TT.plot function from the soiltexture package [53].

To determine soil bulk density (BD), undisturbed samples were collected from the 0–20 cm layer directly from the trench profile using cylinders of known volume. Samples were oven-dried with air circulation and renewal at 103 ± 2 °C until constant mass was reached (variation ≤ 1%), in order to obtain soil dry mass [48]. After drying, the

material was sieved to separate the coarse fraction (>2 mm) from the active soil fraction (fine earth < 2 mm), which was used for bulk density determination. The volume of the coarse fraction was determined by water displacement according to Archimedes' principle. Bulk density was then calculated as the ratio between the dry mass of the fine earth fraction and the effective volume occupied by this fraction (Equation (4)), obtained as the difference between the ring volume and the gravel volume (Equation (5)):

$$BD = \frac{M_{FE}}{V_{FE}} \quad (4)$$

$$V_{FE} = V_{ring} - V_{gravel} \quad (5)$$

where BD = bulk density of the fine earth fraction (g cm^{-3}); M_{FE} = dry mass of the fine earth fraction (<2 mm) (g); V_{FE} = effective volume of the fine earth fraction (cm^3); V_{ring} = total volume of the sampling ring (cm^3); V_{gravel} = volume occupied by the gravel fraction (>2 mm) (cm^3).

2.3. Data Analysis

2.3.1. Vegetation Structure, Floristics and Diversity

Vegetation structure was assessed through phytosociological analysis of each vegetation type following the classical framework proposed by Mueller-Dombois and Ellenberg [54], based on species density, frequency, and dominance, from which the Importance Value (IV%) was calculated. The IV% expresses the ecological relevance of each species sampled within each vegetation type and is calculated as the sum of the relative values of the metrics mentioned above (Table 3). In addition, the horizontal structure of the vegetation was evaluated through the diameter class distribution of individuals using 5 cm class intervals.

Table 3. Formulas used in the phytosociological analysis of woody vegetation in Cerrado *sensu stricto* (CSS) and Carrasco (CAR).

Variable	Unit	Formula
Basal area of species i (G_i)	m^2	$G_i = \sum_{i=1}^{n} \frac{\pi \cdot Db_i^2}{40{,}000}$
Absolute density of species i (AD_i)	Individuals ha^{-1}	$AD_i = \frac{n_i}{A}$
Relative density of species i (RD_i)	%	$RD_i = \frac{AD_i}{\sum_{i=1}^{n} AD_i} \cdot 100$
Absolute dominance of species i (ADo_i)	m^2 ha^{-1}	$ADo_i = \frac{G_i}{A}$
Relative dominance of species i (RDo_i)	%	$RDo_i = \frac{ADo_i}{\sum_{i=1}^{n} ADo_i} \cdot 100$
Absolute frequency of species i (AF_i)	%	$AF_i = \frac{P_i}{\sum_{i=1}^{n} P_i} \cdot 100$
Relative frequency of species i (RF_i)	%	$RF_i = \frac{AF_i}{\sum_{i=1}^{n} AF_i} \cdot 100$
Importance value of species i (IV_i)	%	$IV_i = \frac{RD_i + RDo_i + RF_i}{3}$

Db_i = basal diameter, measured 30 cm above the ground of individual *i* (cm); P_i = number of plots where species *i* occurs; A = total sampled area; n_i = number of sampled individuals of species *i*.

Floristics in CSS and CAR were evaluated by species richness (S) and diversity. Richness considered the number of families, genera, and species recorded in each vegetation type.

Shannon-Wiener [55] and Pielou's evenness (J') indices [56,57] were used to assess floristic diversity (Table 4). In general, the Shannon-Wiener index (H') ranges from 1.5 to 3.5 and, exceptionally, exceeds 4.5. When using natural logarithms, the mathematical

properties of H′ provide greater consistency and coherence. Therefore, the use of nats per individual is strongly recommended [58], following the global trend toward natural-log bases [55,59]. The relative proportion of species (J′) is derived from H′ and reflects the degree of uniformity in the distribution of individuals among species present.

Table 4. Formulas used for floristic and diversity analysis of woody vegetation in Cerrado *sensu stricto* (CSS) and Carrasco (CAR).

Index	Formula
Shannon–Wiener diversity (H′)	$H' = -\sum_{i=1}^{S} p_i \cdot \ln(p_i)$
Pielou's evenness (J′)	$J' = \frac{H'}{\ln(S)}$
Jaccard similarity (J)	$J(A, B) = \frac{\lvert A \cap B \rvert}{\lvert A \cup B \rvert}$

S = species richness; p_i = proportion of the *i*th species in the population; A, B = CSS and CAR, respectively.

Floristic similarity between CSS and CAR was assessed using a Venn diagram and the Jaccard similarity index (J) [54], which considers the number of species shared between two areas and the number of species exclusive to each area (Table 4).

Sample sufficiency is a quantitative concept used to indicate whether the sample employed is representative of the plant community under study [54]. To assess this, sample sufficiency regarding species diversity was evaluated using rarefaction and extrapolation curves for q = 0 (species richness—S), where q is a numeric value specifying the order of diversity in Hill numbers [60].

Extrapolations were performed using species diversity data as a function of the number of sampling units, with 1000 bootstrap replications and 95% confidence intervals [61], using the iNEXT package [62] in R software (version 4.5.0) [63].

It is recommended that the minimum area not be defined solely as the point where the curve becomes horizontal, but more rigorously as the area in which a 10% increase in sampled area results in a maximum increase of 5% in total species number [64].

2.3.2. Biomass Analysis

Total biomass (TB) for Cerrado *sensu stricto* (CSS) and Carrasco (CAR) was calculated as the sum of aboveground biomass (AGB: AGWB, necromass, and litter) and belowground biomass (BGB: roots).

Differences between vegetation types for all biomass components were evaluated using Generalized Linear Models (GLMs). Total biomass, aboveground biomass, aboveground woody biomass, litter biomass, and total root biomass were analyzed using Gamma-distributed models with a log link function, fitted with the glm function in R. Necromass was modeled using a GLM implemented in the glmmTMB package, assuming a Tweedie distribution with a log link function, which is appropriate for data containing true zeros [65]. Models included vegetation type (CSS and CAR), spatial gradient (region: north and northwest), and soil textural gradient, represented by clay content (%) in the 0 to 20 cm soil layer as a proxy variable.

Root biomass by soil layer was analyzed using a Generalized Linear Mixed Model (GLMM) with a Gamma distribution and log link function, fitted with the glmmTMB package [65]. The model included vegetation type, soil layer, and their interaction as fixed effects, while plot was included as a random effect. The use of a mixed-effects model was justified by the hierarchical structure of the data, with root biomass measurements across soil layers nested within plots, resulting in non-independent observations.

When significant effects were detected, differences among groups were assessed using estimated marginal means (EMMs), obtained with the emmeans function from the emmeans package [66].

For all models, residual diagnostics were assessed using the simulateResiduals function from the DHARMa package [67].

The significance level adopted was $\alpha < 0.05$. All statistical and graphical analyses were performed using R software (version 4.5.0) [63].

3. Results

3.1. Vegetation Structure, Floristics and Diversity

Regarding the horizontal structure of each vegetation formation, the distribution of individuals across diameter classes followed a reverse-J or negative exponential model, with most individuals concentrated in the smaller classes. The first diameter class (5–10 cm) accounted for 69% and 82% of the total individuals per hectare in CSS and CAR, respectively. The next class (10–15 cm) represented 21% and 13% of the sampled individuals in CSS and CAR, respectively (Figure 4).

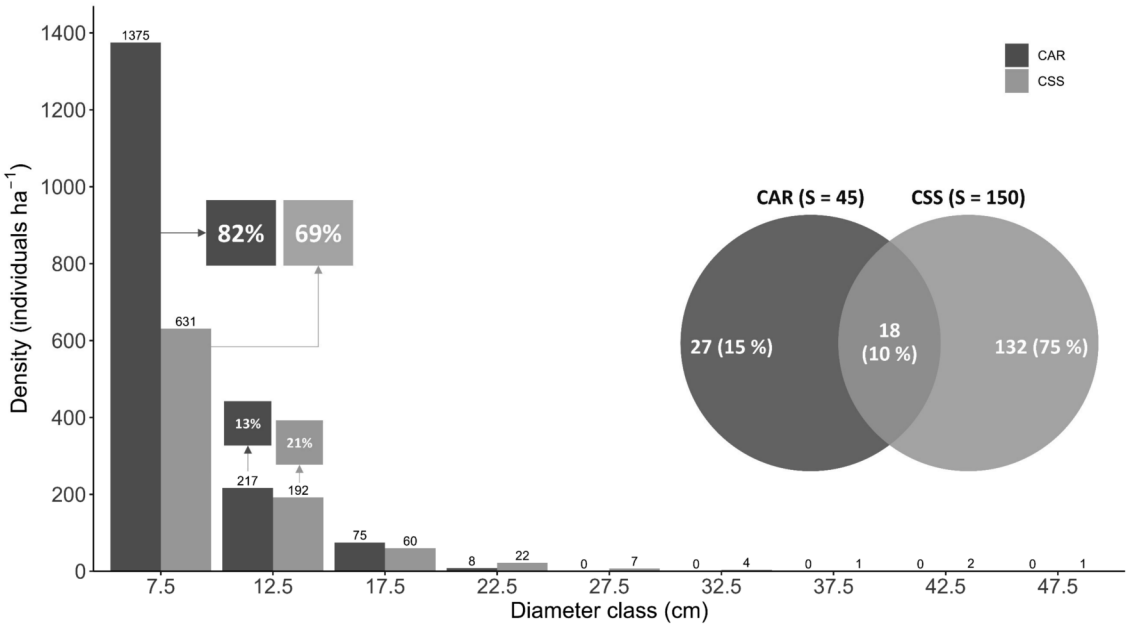

Figure 4. Horizontal structure and Venn diagram of species richness (S) in Cerrado *sensu stricto* (CSS) and Carrasco (CAR) vegetation in the North and Northwest regions of Minas Gerais, Brazil.

The Venn diagram shows species richness (S) of 150 and 45 for the CSS and CAR areas, respectively (Figure 4). The two formations share only 10% (18 species) of the total species, corresponding to a Jaccard similarity index (J) of 0.10 (Table 5).

Table 5. Estimated vegetation parameters in Cerrado *sensu stricto* (CSS) and Carrasco (CAR) areas, Minas Gerais, Brazil.

Vegetation Type	Mean Db	Max. Db	G	N	S	H′	J′	J
	(cm)		(m^2 ha^{-1})	(Individuals ha^{-1})	(No. Species)			
CSS	9.3	48.8	8.0744	920	150	3.80	0.80	0.10
CAR	7.1	21.0	9.3486	1675	45	3.13	0.82	

Db = mean and maximum basal diameter, measured at 0.3 m above the ground ≥ 5 cm; G = basal area; N = number of woody individuals; S = species richness; H′ = Shannon-Wiener diversity index; J′ = Pielou's evenness index; J = Jaccard similarity index.

For the CSS areas, 920 individuals ha^{-1} were recorded, distributed across 44 botanical families and 150 species. Taxonomic identification was performed by specialists following the APG IV classification system [36] and the Reflora 2020 [37]. Among the identified families, those richest in species number were Fabaceae with 32 species, Vochysiaceae with 11 species, Myrtaceae with 9 species, Rubiaceae with 7 species, Bignoniaceae with 6 species, and Malpighiaceae with 5 species. The most numerous families, with over 100 individuals ha^{-1}, were Vochysiaceae (201 ind. ha^{-1}), Fabaceae (182 ind. ha^{-1}), Myrtaceae (152 ind. ha^{-1}), and Combretaceae (53 ind. ha^{-1}). Families Boraginaceae, Celastraceae, Chrysobalanaceae, Lamiaceae, Rutaceae, and Solanaceae had only one individual per hectare and were therefore considered rare in the community.

The species with the highest number of individuals per hectare were *Eugenia dysenterica* (145 ind. ha^{-1}), *Qualea parviflora* (77 ind. ha^{-1}), and *Callisthene fasciculata* (52 ind. ha^{-1}). The three main species in terms of relative density, frequency, and dominance were *Eugenia dysenterica*, *Qualea parviflora*, and *Qualea grandiflora*, with Importance Values (IV%) of 11.2, 6.7, and 4.0%, respectively, summing to 22% of the total IV%. The Shannon-Wiener index (H′) was 3.80, and Pielou's evenness (J′) was 0.80 (Table 5).

For the CAR areas, 1675 individuals ha^{-1} were recorded, distributed across 18 botanical families and 45 species. Among the identified families, those richest in species number were Fabaceae with 17 species, Euphorbiaceae with 4 species, Erythroxylaceae and Myrtaceae with 3 species each, and Annonaceae, Rutaceae, Rubiaceae, and Combretaceae with 2 species each. Sapotaceae, Salicaceae, Apocynaceae, Polygonaceae, Sapindaceae, Vochysiaceae, Solanaceae, Lauraceae, Malvaceae, and Proteaceae each had only one species.

The most numerous families, with over 100 individuals ha^{-1}, were Fabaceae (800 ind. ha^{-1}), Vochysiaceae (275 ind. ha^{-1}), Rutaceae (150 ind. ha^{-1}), and Euphorbiaceae (92 ind. ha^{-1}).

The species with the highest number of individuals per hectare were *Pityrocarpa brenanii* (308 ind. ha^{-1}), *Callisthene major* (275 ind. ha^{-1}), and *Metrodorea mollis* (133 ind. ha^{-1}). These three species were also the main ones in terms of relative density, frequency, and dominance, with Importance Values (IV%) of 18.6, 11.4, and 6.8%, respectively, summing to 37% of the total IV%. The Shannon-Wiener index (H′) was 3.13, and Pielou's evenness (J′) was 0.82.

The CSS community showed a species richness (S) of 150, with the potential to reach just over 180 species based on extrapolation. The CAR community exhibited a species richness (S) of 45, with the potential to reach approximately 60 species through extrapolation. However, achieving this would require doubling the current sampling effort. If the number of sampled plots were increased by 10%, the gain in species number would be less than 5% (Figure 5).

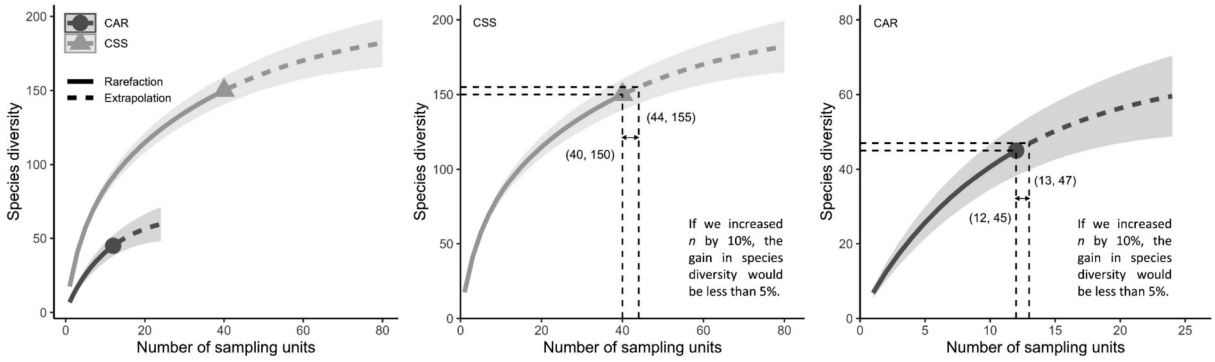

Figure 5. Species richness accumulation curve as a function of the number of sampled plots in Cerrado *sensu stricto* (CSS) and Carrasco (CAR), Minas Gerais, Brazil. q = 0, where q refers to the Hill number (0 = species richness). Rarefaction (solid line) and extrapolation (dashed lines) represent mean values and standard error intervals, with confidence intervals (α = 0.05).

3.2. Soil Physics and Chemistry

On average, soils under CAR exhibited higher clay (38.0 vs. 25.2%), silt (8.0 vs. 5.9%), and organic matter contents (2.0 vs. 1.3%), as well as lower pH (3.9 vs. 4.2) and bulk density (1.11 vs. 1.33 g cm^{-3}) compared with CSS. Both vegetation types occurred on soils with low availability of Ca, Mg, K, and P (Table 6).

Table 6. Physical and chemical characteristics of surface soils (0–20 cm) in Cerrado *sensu stricto* (CSS) and Carrasco (CAR) in northern and northwestern Minas Gerais, Brazil.

Variable	Unit	CSS	CAR
Sand	(%)	68.90 (±15.69)	54.00 (±12.43)
Clay	(%)	25.20 (±13.26)	38.00 (±10.63)
Silt	(%)	5.90 (±2.67)	8.00 (±1.86)
OM	(%)	1.28 (±0.56)	2.02 (±0.43)
pH	-	4.21 (±0.18)	3.89 (±0.15)
Al^{3+}	cmolc dm^{-3}	0.42 (±0.27)	1.47 (±0.32)
Ca	cmolc dm^{-3}	0.37 (±0.28)	0.26 (±0.05)
Mg	cmolc dm^{-3}	0.15 (±0.07)	0.14 (±0.05)
K	cmolc dm^{-3}	0.10 (±0.09)	0.10 (±0.04)
P	mg dm^{-3}	1.69 (±1.54)	1.80 (±2.02)
BD	g cm^{-3}	1.33 (±0.14)	1.11 (±0.06)

Values are presented as mean ± standard deviation. OM = soil organic matter; pH = pH in $CaCl_2$ solution; Al^{3+} = aluminum; Ca = calcium; Mg = magnesium; K = potassium; P = phosphorus extracted by the Mehlich I method; BD = bulk density.

Regarding soil texture classes, CAR areas occurred predominantly on sandy clay loam, sandy clay, and clay soils, whereas CSS was found not only on these textural classes but also on sandy loam, loamy sand, and sand soils (Figure 6).

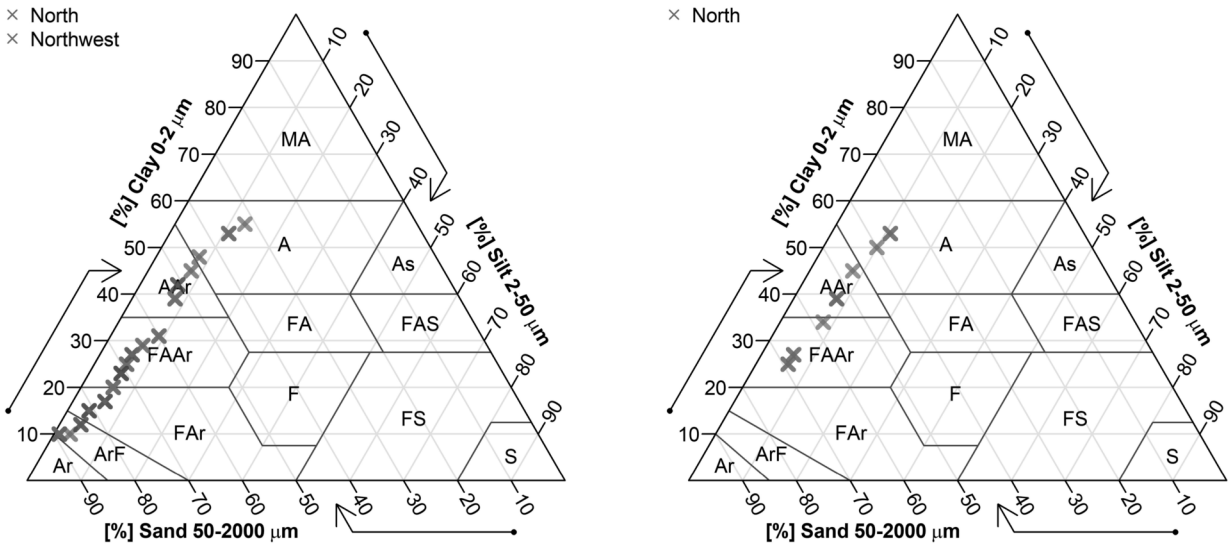

Figure 6. Soil texture triangle for plots located in (**a**) Cerrado *sensu stricto* (CSS) and (**b**) Carrasco (CAR) in Minas Gerais State, Brazil. MA = muito argilosa (heavy clay); A = argila (clay); AS = argilossiltosa (silty clay); AAr = argilarenosa (sandy clay); FA = francoargilosa (clay loam); FAS = franco-argilossiltosa (silty clay loam); FAAr = franco-argiloarenosa (sandy clay loam); F = franca (loam); FS = francossiltosa (silt loam); FAr = francoarenosa (sandy loam); S = silte (silt); ArF = areia franca (loamy sand); Ar = areia (sand). Textural classes follow the Brazilian Soil Classification System [68].

3.3. Biomass Stocks

The estimated total biomass stock for CSS was 45.24 Mg ha^{-1}, distributed in descending order among the analyzed compartments as follows: aboveground woody biomass (AGWB) (20.47 Mg ha^{-1}; 45%), belowground biomass (BGB) (18.47 Mg ha^{-1}; 41%), litter (5.49 Mg ha^{-1}; 12%), and necromass (0.81 Mg ha^{-1}; 2%). Total aboveground biomass (AGB) was 26.77 Mg ha^{-1}. The BGB:AGB ratio was 0.69, and the BGB:AGWB ratio was 0.90 (Table S1).

For CAR, the estimated total biomass stock was 59.01 Mg ha^{-1}. In descending order, the contribution of each biomass compartment was: BGB (32.37 Mg ha^{-1}; 55%), AGWB (16.57 Mg ha^{-1}; 28%), litter (8.39 Mg ha^{-1}; 14%), and necromass (1.68 Mg ha^{-1}; 3%). Total AGB was 26.50 Mg ha^{-1}. The BGB:AGB ratio was 1.22, and the BGB:AGWB ratio was 1.95 (Table S1).

For CSS, belowground biomass decreased with depth. Values were 8.49 Mg ha^{-1} in the 0–20 cm layer, 5.01 Mg ha^{-1} in 20–40 cm, 2.75 Mg ha^{-1} in 40–60 cm, 2.19 Mg ha^{-1} in 60–80 cm, and 1.37 Mg ha^{-1} in 80–100 cm (Table S1).

In CAR, root biomass also decreased with depth: 18.37 Mg ha^{-1} in 0–20 cm, 6.43 Mg ha^{-1} in 20–40 cm, 3.13 Mg ha^{-1} in 40–60 cm, 2.58 Mg ha^{-1} in 60–80 cm, and 1.86 Mg ha^{-1} in 80–100 cm (Table S1).

Only roots with diameters between 2 mm and 5 cm were found in the samples. Roots smaller than 2 mm cannot be reliably distinguished from soil organic matter [50]. Roots with d $\geq$ 5 cm were not recorded, as this size class is not adequately sampled by the trench method at a single point in the sampling unit. Roots of this size are usually included in destructive sampling of woody individuals, which allows excavation of the entire root system.

Vegetation type had a significant effect on TB (z = −2.39, p = 0.02) and BGB (z = −2.40, p = 0.02), both of which were higher in CAR than in CSS (Figure 7a,f). In contrast, AGB, AGWB, litter, and necromass were not significantly affected by vegetation type ($p > 0.05$) (Table S2; Figure 7b–e).

Region had a significant effect on AGWB (z = −2.58, p = 0.01) and BGB (z = 2.20, p = 0.03). AGWB was lower in the northern region than in the northwestern region, whereas BGB was higher in the northern region. TB, AGB, litter, and necromass were not significantly affected by region ($p > 0.05$) (Table S2).

BGB decreased progressively with soil depth ($p < 0.001$ for all comparisons), with the highest values observed in the 0–20 cm layer and the lowest in the 80–100 cm layer. The interaction between vegetation type and soil depth was not significant ($p \geq 0.08$), indicating that the vertical distribution pattern of BGB was similar between CAR and CSS (Table S3; Figure 7g). Nevertheless, CAR maintained higher BGB values throughout the entire soil profile.

Clay content did not have a significant effect on TB, AGB, AGWB, litter, or BGB ($p > 0.05$). The only exception was necromass, which showed a negative association with clay content (z = −2.03, p = 0.04) (Table S2).

For all models, residual diagnostics can be found in the Supplementary Material (Figures S1–S7).

For CSS, the three species contributing the most to aboveground woody biomass were *Caryocar brasiliense* (2.86 Mg ha^{-1}), *Eugenia dysenterica* (2.29 Mg ha^{-1}), and *Qualea parviflora* (1.74 Mg ha^{-1}), together representing 34% of total woody biomass (Table 7).

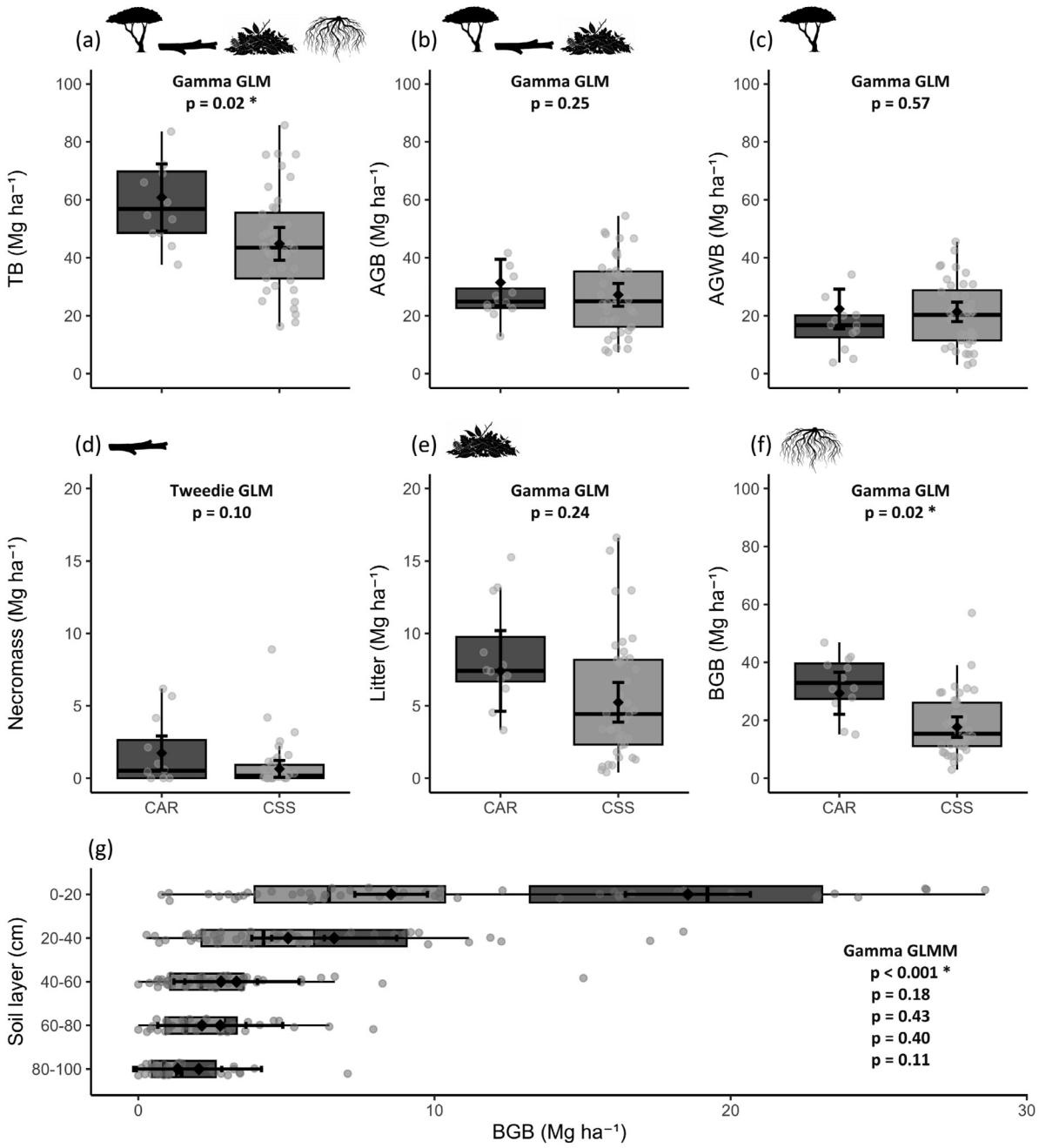

Figure 7. Stocks of total biomass (TB) (**a**), aboveground biomass (AGB) (**b**), aboveground woody biomass (AGWB) (**c**), necromass (**d**), litter (**e**), and belowground biomass (BGB) (**f**), as well as their vertical distribution across soil depth (**g**), in Cerrado *sensu stricto* (CSS) and Carrasco (CAR) areas in the North and Northwest regions of Minas Gerais, Brazil. Boxplots show the median, interquartile range, and data dispersion. Gray circles represent raw data points, black diamonds indicate predicted means from gamma and tweedie GLMs and gamma GLMM, and error bars represent 95% confidence intervals. * indicates a statistically significant difference among the physiognomies, whereas its absence indicates that no statistically significant difference was detected.

In CAR, the three most important species according to VI% were also those storing the most aboveground woody biomass: *Pityrocarpa brenanii* (5.19 Mg ha^{-1}), *Callisthene major* (1.86 Mg ha^{-1}), and *Metrodorea mollis* (1.84 Mg ha^{-1}). Together, they accounted for more than half (54%) of the total aboveground woody biomass in this vegetation type (Table 7).

Table 7. Phytosociology of the 10 species ranked by aboveground woody biomass stock in Cerrado *sensu stricto* (CSS) and Carrasco (CAR) areas, Minas Gerais, Brazil.

Species	Author	Family	AGWB	AF	RF	AD	RD	ADo	RDo	IV
Cerrado										
Caryocar brasiliense	Cambess.	Caryocaraceae	2.8627	37.5	2.1	15.3	1.7	0.6526	8.1	4.0
Eugenia dysenterica	(Mart.) DC.	Myrtaceae	2.2883	72.5	4.1	145.0	15.8	1.1070	13.7	11.2
Qualea parviflora	Mart.	Vochysiaceae	1.7397	65.0	3.7	77.3	8.4	0.6522	8.1	6.7
Terminalia fagifolia	Mart.	Combretaceae	1.5090	35.0	2.0	32.0	3.5	0.4339	5.4	3.6
Hymenaea stigonocarpa	Mart. ex Hayne	Fabaceae	0.8875	47.5	2.7	21.0	2.3	0.2953	3.7	2.9
Qualea grandiflora	Mart.	Vochysiaceae	0.8339	57.5	3.3	40.0	4.3	0.3580	4.4	4.0
Callisthene fasciculata	Mart.	Vochysiaceae	0.7877	12.5	0.7	52.3	5.7	0.3820	4.7	3.7
Vochysia thyrsoidea	Pohl	Vochysiaceae	0.7556	17.5	1.0	11.3	1.2	0.2211	2.7	1.7
Tachigali subvelutina	(Benth.) Oliveira-Filho	Fabaceae	0.6141	25.0	1.4	12.8	1.4	0.2108	2.6	1.8
Machaerium opacum	Vogel	Fabaceae	0.5942	47.5	2.7	18.0	2.0	0.2253	2.8	2.5
Total (Top 10 species ranked by biomass)			12.8728	417.5	23.8	425	46.2	4.5383	56.2	42.1
Total (All species)			20.4711	1752.5	100	920	100	8.0744	100	100
Carrasco										
Pityrocarpa brenanii	(G.P.Lewis & M.P.Lima) L.P.Queiroz & L.M.Borges	Fabaceae	5.1933	75.0	11.0	308.3	18.4	2.4728	26.5	18.6
Callisthene major	Mart.	Vochysiaceae	1.8625	33.3	4.9	275.0	16.4	1.2096	12.9	11.4
Metrodorea mollis	Taub.	Rutaceae	1.8263	16.7	2.4	133.3	8.0	0.9330	10.0	6.8
Copaifera langsdorffii	Desf.	Fabaceae	0.8752	41.7	6.1	66.7	4.0	0.4618	4.9	5.01
Dalbergia miscolobium	Benth.	Fabaceae	0.7753	16.7	2.4	33.3	2.0	0.3436	3.7	2.70
Aspidosperma oliganthum	Woodson	Apocynaceae	0.6306	25.0	3.7	33.3	2.0	0.3050	3.3	2.97
Calliandra macrocalyx	Harms	Fabaceae	0.5452	8.3	1.2	66.7	4.0	0.3374	3.6	2.94
Erythroxylum daphnites	Mart.	Erythroxylaceae	0.4788	8.3	1.2	50.0	3.0	0.2968	3.2	2.46
Machaerium acutifolium	Vogel	Fabaceae	0.4174	8.3	1.2	41.7	2.5	0.2223	2.4	2.03
Roupala montana	Aubl.	Proteaceae	0.2810	33.3	4.9	41.7	2.5	0.1980	2.1	3.16
Total (Top 10 species ranked by biomass)			12.8856	266.7	39.0	1050	62.7	6.7803	72.5	58.1
Total (All species)			16.5718	683.3	100	1675	100	9.3486	100	100

AGWB = aboveground woody biomass (Mg ha^{-1}); AF = absolute frequency (%); RF = relative frequency (%); AD = absolute density (individuals ha^{-1}); RD = relative density (%); ADo = absolute dominance (m^2 ha^{-1}); RDo = relative dominance (%); IV = importance value (%).

4. Discussion

4.1. Vegetation Structure, Floristics and Diversity

From a structural perspective, both vegetation types showed a concentration of individuals in the smallest diameter classes, a pattern commonly observed in tropical plant communities [69] and consistent with a negative exponential (reverse J-shaped) distribution [70]. However, in terms of number of individuals per unit area, CAR presented on average approximately 1.8 times more individuals than CSS, a pattern that would become even more pronounced if the minimum diameter inclusion criterion were set at 3 cm, as recommended by the Permanent Plot Manual for the Cerrado and Pantanal Biomes [25]. In addition, CSS showed a greater diameter range, with individuals reaching approximately 45–50 cm in diameter, whereas in CAR the largest diameters were concentrated around 20–25 cm. This contrast indicates that, despite the higher stem density in CAR, CSS is composed of fewer but larger individuals, a characteristic that directly influences its biomass accumulation potential.

The low floristic similarity observed between the areas, expressed by the low Jaccard index [71], confirms that CAR has a distinct floristic identity, as previously suggested by other studies [19]. In CSS, the dominance of families such as Vochysiaceae, Fabaceae, Malpighiaceae, and Myrtaceae is consistent with widely recognized patterns for the biome, in which these groups are considered hyperdominant [72]. At the species level, the genus *Qualea*, which includes *Q. parviflora* and *Q. grandiflora* and is abundant in the study areas, is among the most dominant in the Brazilian Cerrado [72,73]. Supporting these observations, *Q. parviflora* ranked second and third in both importance value (IV%) and aboveground woody biomass (AGWB) in CSS. Although the literature on Carrasco remains relatively limited, the results obtained are consistent with previous studies that also identified Fabaceae and Euphorbiaceae as the main families in terms of species richness [19,30].

The species that contributed most to AGWB belong to taxonomic groups with functional traits that favor biomass accumulation and maintenance in ecosystems within the Cerrado domain. Species from the Fabaceae family are frequently associated with biological nitrogen fixation, a strategy that increases nitrogen availability in nutrient-poor soils and promotes plant growth [74]. The Vochysiaceae family is widely recognized for its tolerance to acidic and aluminum-rich soils, a trait considered an important adaptation to the edaphic conditions of the Cerrado [75,76]. These functional characteristics enhance resource acquisition, increase tolerance to environmental stress, and promote species persistence over time, thereby contributing to the biomass stocks observed in the studied communities.

Regarding sampling sufficiency, and considering the methodological recommendations for vegetation sampling in each formation type [25], as well as criteria related to incremental sampling effort and expected gains in species richness [64], we conclude that, despite the limitations and differences in plot size and number of sampling units between CSS and CAR, the sampling effort was sufficient to characterize species richness.

Overall, these results highlight marked differences between CSS and CAR in both structure and floristic composition, reinforcing that these vegetation types represent ecologically distinct communities in these aspects.

4.2. Biomass Stocks and Allocation

The higher total biomass (TB) observed in CAR compared with CSS was primarily driven by differences in belowground biomass (BGB), as no significant differences were detected between vegetation types for aboveground biomass (AGB), aboveground woody biomass (AGWB), litter, or necromass. This result highlights that structural and floristic differences between vegetation formations do not always translate into contrasts in aboveground biomass compartments but may instead be expressed in belowground compartments. Therefore, the

inclusion of root biomass is essential for a more realistic assessment of biomass and carbon stocks in vegetation within the Neotropical savanna domain.

Although CSS showed a greater contribution of AGWB associated with larger individual size, while CAR was characterized by higher stem density, this structural contrast was not sufficient to generate statistically detectable differences in aboveground biomass. This pattern reinforces the idea that individual size, mainly represented by stem diameter and height, exerts a stronger influence on biomass accumulation than population density alone, with these variables being widely used and reported in biomass and carbon estimation models [77,78].

This result suggests that structurally distinct vegetation formations may converge in some biomass compartments, such as aboveground stocks, while diverging in others, such as belowground stocks. In CAR, higher total biomass was driven by the greater contribution of belowground biomass, reflected in a BGB/AGWB ratio > 1 (1.95), whereas in CSS this ratio was below 1 (0.90). This pattern suggests distinct functional strategies between the vegetation types, with greater biomass allocation to belowground structures in CAR.

The root-to-wood ratio observed in CAR approaches values typically reported for global shrublands and grasslands [24], whereas CSS showed values closer to those reported for tropical savannas [24], CSS in Minas Gerais [18], and São Paulo [79]. These results reinforce that dense shrub formations can store substantial amounts of biomass when the belowground compartment is considered, challenging the perception of lower structural importance of non-forest ecosystems [15,80–82].

The model results reinforce this pattern by indicating that different biomass components respond differently to the spatial gradient. While AGWB was influenced only by the regional effect, with no significant differences between vegetation types, BGB responded to both the regional gradient and vegetation physiognomy. This result suggests that variation in belowground biomass was more sensitive to vegetation structure than aboveground biomass, indicating that belowground biomass allocation processes are more strongly associated with functional differences between CSS and CAR, as well as with spatial variation at the regional scale.

In addition, the strong concentration of roots in the upper soil layers may also be associated with higher nutrient availability, although still limited, as well as greater biological activity in this zone of the soil profile, as widely observed in tropical ecosystems [83]. Although CAR showed higher BGB throughout the entire soil profile, the lack of a significant interaction between vegetation type and soil depth indicates that both systems share a similar pattern of vertical root distribution. Thus, the observed differences relate to the magnitude of the stock, particularly in the surface layers, rather than to differences in its distribution along the sampled soil profile (1 m).

Another relevant factor is the higher stem density in CAR, which may intensify root overlap and increase root concentration in the upper soil layers [84]. This effect may be further enhanced by the high occurrence of lianas reported for this physiognomy [28], contributing to greater belowground structural complexity. These factors suggest that root dominance in CAR may result from the interaction between edaphic constraints (nutrients and water) and the structural organization of the community.

Regarding soil texture, although both vegetation types shared similar textural classes, soils under CAR showed, on average, higher clay content compared with CSS, a condition that may favor the retention of water and nutrients in the soil [85]. However, the substantial overlap among the observed textural classes suggests that soil texture alone was not sufficient to explain differences in biomass allocation patterns. This interpretation is supported by the model results, in which clay content did not show a significant effect on

most biomass components across vegetation types, with the exception of necromass, which is discussed below.

Necromass was the only compartment associated with soil texture, showing a negative relationship with clay content. A possible explanation is that more clay-rich soils favor greater water retention and decomposer activity, thereby accelerating the decomposition of dead organic matter [86]. However, this effect should be interpreted with caution due to its relatively small magnitude and the absence of similar effects in the other biomass compartments, and high spatial heterogeneity.

Regarding litter, its higher contribution in CAR may be associated with the deciduous character of this vegetation [28,30] and the climatic seasonality of the semi-arid region, where leaf shedding occurs in a concentrated manner during the dry season, resulting in marked pulses of litter deposition [87,88]. However, this component should also be interpreted with caution, as sampling intensity was limited to a single quadrat per plot, which is a common approach but may not fully capture spatial variability.

Although this factor was not directly assessed in the present study, another key driver of biomass stocks is the high fire frequency in the Cerrado domain, which may promote greater investment in belowground structures in savanna and shrub formations [89]. Because belowground biomass is less affected by fire than aboveground biomass [90], allocation to belowground compartments represents an important adaptive strategy in environments with frequent fire regimes [91].

These results reinforce the importance of including multiple biomass compartments, particularly belowground biomass, in biomass and carbon stock estimates. The exclusion of roots can lead to substantial underestimation, especially in formations such as CAR, where belowground biomass dominated the total stock. This is particularly relevant given that Carrasco is often regarded as a vegetation type of lower structural importance.

However, comparisons among studies are still limited by important methodological differences. These include differences in diameter inclusion criteria (diameter at breast height—DBH; basal diameter—Db) and minimum threshold values (2, 3, or 5 cm) [92,93], which can result in non-comparable estimates among studies. In addition, the scarcity of region-specific allometric equations and the difficulty of direct biomass measurements introduce additional sources of uncertainty.

These limitations also extend to necromass, litter [94,95], and roots [96]. In the case of roots, methodological variability is particularly relevant, including differences in sampling depth, collection methods, and definitions of fine and coarse root classes. Although fine roots have traditionally been defined as <2 mm, this definition has been questioned by evidence of variation among species and environments [97,98]. In this study, the decision not to restrict diameter classes aimed to minimize arbitrariness and more comprehensively capture the belowground contribution, considering the applied methodology.

In addition, litter and necromass estimates were based on point sampling, as was root sampling using soil trenches, which may introduce uncertainties associated with the spatial heterogeneity of these compartments. This limitation should be considered when interpreting the results, particularly in highly heterogeneous ecosystems such as tropical systems [99].

Finally, the findings highlight the need to expand knowledge on shrub formations in the Brazilian semi-arid region and to develop more standardized methodological protocols for biomass quantification, particularly for belowground components, in order to reduce uncertainties and improve comparability among studies at regional and global scales.

5. Conclusions

This study reinforces the floristic and structural differences between the CSS and CAR physiognomies, which were reflected in similar aboveground biomass allocation patterns but distinct belowground patterns. The results also demonstrate that estimates based solely on aboveground biomass tend to substantially underestimate total biomass stocks in semi-arid transitional vegetation, as other components, such as belowground biomass, represent a significant portion of this pool.

Therefore, this highlights the importance of including these often neglected non-forest vegetation formations in biomass inventories and climate mitigation strategies. In addition, the conservation of these physiognomies should be prioritized, given their relevant role in maintaining biodiversity and carbon storage, particularly in semi-arid regions.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d18060348/s1, Table S1: Descriptive measures of total and compartmental biomass stocks in Cerrado *sensu stricto* (CSS) and Carrasco (CAR) areas in the North and Northwest regions of Minas Gerais, Brazil; Table S2: Estimated coefficients of generalized linear models (GLMs) assessing the effects of vegetation type, region, and clay content on biomass components in Cerrado *sensu stricto* (CSS) and Carrasco (CAR) areas in northern and northwestern Minas Gerais, Brazil; Table S3: Results of the generalized linear mixed model (GLMM) assessing the effects of vegetation type, soil depth, and their interaction on belowground biomass (BGB) in Cerrado *sensu stricto* (CSS) and Carrasco (CAR) areas in northern and northwestern Minas Gerais, Brazil; Figure S1: Residual diagnostics generated using the DHARMa package for the gamma GLM used to address the research question on the effects of vegetation type, spatial gradient, and soil texture on total biomass (TB); Figure S2: Residual diagnostics generated using the DHARMa package for the gamma GLM used to address the research question on the effects of vegetation type, spatial gradient, and soil texture on aboveground biomass (AGB); Figure S3: Residual diagnostics generated using the DHARMa package for the Gamma GLM used to address the research question on the effects of vegetation type, spatial gradient, and soil texture on aboveground woody biomass (AGWB); Figure S4: Residual diagnostics generated using the DHARMa package for the gamma GLM used to address the research question on the effects of vegetation type, spatial gradient, and soil texture on litter; Figure S5: Residual diagnostics generated using the DHARMa package for the tweedie GLM used to address the research question on the effects of vegetation type, spatial gradient, and soil texture on necromass; Figure S6: Residual diagnostics generated using the DHARMa package for the gamma GLM used to address the research question on the effects of vegetation type, spatial gradient, and soil texture on belowground biomass (BGB); Figure S7: Residual diagnostics generated using the DHARMa package for the gamma GLMM used to address the research question on the interaction between vegetation type and soil layers on belowground biomass (BGB), with plot included as a random effect.

Author Contributions: Conceptualization, K.N.O., E.P.M. and A.O.S.; methodology, K.N.O., E.P.M. and A.O.S.; investigation, K.N.O., E.P.M. and A.O.S.; data curation, K.N.O., M.S.M. and A.O.S.; formal analysis, K.N.O., E.P.M., A.O.S., G.B.d.A., A.V.R. and E.A.T.M.; visualization, K.N.O., E.P.M., A.O.S., G.B.d.A., A.V.R. and E.A.T.M.; writing—original draft preparation, K.N.O., M.S.M., J.A.d.S. and E.P.M.; writing—review and editing, all authors; project administration, A.O.S.; funding acquisition, A.O.S. and D.M.S. All authors have read and agreed to the published version of the manuscript.

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Abbreviations

The following abbreviations are used in this manuscript:

CSS	Cerrado *sensu stricto*
CAR	Carrasco
TB	Total biomass (AGWB, necromass, litter, and BGB)
AGB	Aboveground biomass (AGWB, necromass, and litter)
AGWB	Aboveground woody biomass
BGB	Belowground biomass

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