

Brazilian Deciduous Tropical Forest enclaves: floristic, structural and environmental variations

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Abstract Several theories have been proposed to explain the raised richness and diversity of species in native tropical forests, with an emphasis on those that invoke the niche characteristics. In the present study, we sample the woody vegetation in four enclaves of Deciduous Forests and investigate whether environmental variables can explain the floristic and structural differences among the sampled fragments. The studied areas are located the “Cerrado” biome core zone and in “Cerrado”–Atlantic Forest and “Cerrado–Caatinga” transition zones. The woody vegetation (diameter at breast height—DBH ≥ 5 cm) was sampled in 100 plots of 20 × 20 m, 25 plots in each enclaves. The investigated environmental variables were chemical and textural properties of the soil, rockiness, declivity and altitude. We found significant differences for the floristic variables (richness, diversity), among all the environmental variables, as well as for the density, height and for the DBH first class. We noticed

strong influence of the environmental variables, and the nutrients availability, texture, soil acidity and the land relief are the most responsible for the floristic-cultural difference. We propose that the gradient existence of rainfall has influenced the edaphic characteristics, creating variations in the habitats, which may have favored the arrival and establishment of different species in each study area and the distinctive development of the woody vegetation at the enclaves to the Deciduous Forest.

Keywords Disturbing history · Fragments · Habitats · Vegetation contacts · Woody vegetation

Introduction

The tropical forests are geographically distributed near the equator line, and it is more specifically located between the Tropic of Cancer and the Tropic of Capricorn, between the latitudes 23.5°N and 23.5°S (Whitmore 1990). Those forests are recognized for their high richness and diversity of species, and several theories have been proposed to explain this pattern (Waide et al. 1999; Chown et al. 2003). Most of those theories are related to the high environmental heterogeneity (Wilson 2000; Kolb and Diekmann 2004). Thus, it is supposed that the spatial distribution of the species and the structure of the woody vegetation in tropical forests are related to the discontinuous distribution of biotic and abiotic factors along the space (Ricklefs 1977; Denslow 1980; Shmida and Wilson 1985) and of its complex chain of interactions.

Historical and biogeographical aspects are also fundamental to determine the distribution standards and vegetation structuration in the entire world (Kellman and Tackaberry 1997). However, this relation is difficult to

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measure. On the other hand, the local environmental variables, because of its ease to measure, are commonly most investigated mainly the association with composition and structure of the regional communities, especially the ones from edaphic order (fertility, pH, texture and water availability) and climatic order (rainfall and temperature) (Oliveira Filho et al. 1994; Oliveira Filho and Fontes 2000; Fagundes et al. 2007; Gonzaga et al. 2008; Machado et al. 2008; Apgaua et al. 2014; Neves et al. 2015).

The contribution of environmental variables to the distribution of species changes considerably in space, among vegetation types (Oliveira Filho and Fontes 2000) and in the same physiognomy, especially when it occurs in a wide geographical distribution, as in the Brazilian Deciduous Seasonal Forests (Santos et al. 2012). Because the vegetation is present in great extension in Brazil (Rizzini 1977; Ribeiro and Walter 2008) and in the form of enclaves along the “Cerrado”, Atlantic Forest and Amazon rainforest, in general distributed over limestone outcrops (Rizzini 1977) is submitted to a large environmental amplitude like the variation in the edaphic conditions (Fagundes et al. 2007) and climatic conditions (Santos et al. 2007), for example. The Neotropical Dry Forests have high diversity (alpha), high endemism and high species turnover (beta diversity) (Dryflor et al. 2016), but are highly threatened by human activities and have few protected areas (Miles et al. 2006).

Thus, we investigate the differences in chemical and textural properties of the soil, rockiness, declivity and altitude and we evaluate their relationships with the structural variables, and also the richness, the diversity, the equability and the rarity of species of the woody vegetation in four Deciduous Forest enclaves, located in the core zone of the “Cerrado” biome, in the “Cerrado”–Atlantic Forest transition zone and in the “Cerrado–Caatinga”. We evaluated the hypothesis that there are differences in the floristic and structural composition among the studied enclaves and that such differences in Deciduous Forests are the reflection of local abiotic factors.

Materials and methods

We sampled four fragments of the Deciduous Forest spread in four enclaves of this phytogeography located in the core zone of the “Cerrado” biome (Paracatu, Minas Gerais; from now on denominated CE), in the “Cerrado”–Atlantic Forest transition zone (Arcos, Minas Gerais; denominated ZTMA) and two in the “Cerrado–Caatinga” (Peruaçu, Minas Gerais and Coribe, Bahia; denominated ZTCA 1 and ZTCA 2, respectively). Thus, the geographical extension of the work comprises the coordinates 13°29′–20°17′S and 44°14′ and 46°49′W (Fig. 1; Table 1).

To sample the woody vegetation, we divided each fragment in 20-m wide strips, perpendicular to the land declivity, and subdivided those strips into plots of 20 × 20 m. Then, we randomly selected the sampling lines and then the plots in the lines. Thus, to each fragment, we randomly selected 25 plots, which totalized one hectare of sampling area. We inventoried all of the tree individuals which had the diameter at breast height (DBH) ≥ 5 cm, except dead individuals, lianas and climbers. Individuals with multiple stems were measured when the square root of the sum of the perimeters was >15.71 cm (square root of the sum of the diameters’ squares), which implies an equivalent basal area (Moro and Martins 2011).

To perform chemical, physical and textural analyses of the soil, we collected five simple samples which result in soil compound samplings (0–20 cm deep) in all the plots (Rodrigues et al. 2007). To analyze the samplings, we used the EMBRAPA Protocol (EMBRAPA 1997).

We had a rocky coverage percentage on the surface of the plots by means of the adapted method of Braun Blanquet (1979). The evaluation consisted in the assignment of nominal values: 0 = absence of superficial rocks; 1 = 0–25%; 2 = 26%; 3 = 51–75%; and 4 = 76–100%.

We evaluated the declivity of the land by measuring the inclination of the microtopography in each plots with the help of the hypsometer (Oliveira Filho et al. 1998; Espírito Santo et al. 2002). We measured the microtopography from the central line sight of each plots, and basing on their vertices, we calculated the declivity, obtained by the difference between maximum and minimum elevation.

The richness and diversity of tree species in the four enclaves were evaluated by the following parameters: number of species, Shannon diversity (H) and evenness (J) (Brower and Zar 1984) (see Gonzaga et al. 2013). The species richness was compared among the enclaves through rarefaction curves (Gotelli and Colwell 2001) using the PAST program (Hammer et al. 2001) and 1000 randomisations, besides that the diversity was compared by means of diversity profiles, Obtained from the Rényi exponential series (Hill 1973). With this analysis, it was possible to compare both richness and fairness of species in each enclave, and the arbitrary choice of diversity index is not necessary (Melo 2008). The rarity of the species in each enclave is used as a criterion for numerical rarity of the species that had only one individual per hectare (Rabinowitz 1981).

We performed Kruskal–Wallis test (Zar 1996) to compare the possible differences in soil variables in relief, hypsometric quota and structural descriptors of vegetation parameters (total minimum and maximum diameter class density and basal area and height) between the enclaves. For variables that showed significant differences was applied, retrospectively, the Dunn test (Zar 1996). We



Fig. 1 Location of the Deciduous Forest enclaves sampled in different Brazilian phytogeographical domains with detail of biomes (*light gray*) “Caatinga”; (*medium gray*) “Cerrado”; (*dark gray*) Atlantic Forest. CE Core zone of the “Cerrado” biome, ZTMA “Cerrado”–Atlantic Forest transition zone and ZTCA 1 and ZTCA 2 = “Cerrado–Caatinga” transition zone. See description of the areas in Table 1

Table 1 Geographical and environmental information in the Deciduous Forest enclaves. CE Core zone of the “Cerrado” biome, ZTMA “Cerrado” transition Zone–Atlantic Forest and ZTCA 1 and ZTCA 2 = “Cerrado” Zone–“Caatinga” transition. See location of areas shown in Fig. 1

	ZTMA	CE	ZTCA 1	ZTCA 2
Latitude (S)	20°17′	17°13′	14°54′	13°29′
Longitude (W)	45°37′	46°49′	44°22′	44°14′
Altitude (m)	819	626	696	533
Area (ha)	100	100	200	50
Climate (Köppen)	Cwa	Aw	Aw	Aw
Annual average temperature (°C)	20.7	22.0	26.3	24.4
Annual average rainfall (mm)	1600	1350	947	900
Dry months ^a (months/year)	3	3	5	5
Karst region	Bambuí Group	Bambuí Group	Bambuí Group	Bambuí Group
Soil types	Litholic Neosols	Litholic Neosols	Litholic Neosols	Litholic Neosols

^a Considered dry months those with rainfall below 30 mm (AYOADE 2010)

process and analyze the BioEstat software version 5.0 (Ayres et al. 2007) and adopted as a criterion of significance $P \leq 0.05$. For the frequency distribution of individuals, calculate diameter classes and used constant

intervals of 5.0 cm diameter class (5–10, 10–15, 15–20 and >20 cm).

In order to check the formation of clusters according to the similarity in floristic and structural composition of the

enclaves, we have used classification by TWINSpan (two-way indicator species analysis) (Kent and Coker 1992). To do so, we prepared an array of quantitative data (density) of species in enclaves, using the following cutoff levels 0, 1, 2, 4, 8, 16, 32, 64 and 128. Consider satisfactory eigenvalues above 0.5 because this limit produces strong divisions and significant ecological significance (Kent and Coker 1992). We have processed the TWINSpan analysis with the use of PC-ORD software version 6.0 for Windows (McCune and Mefford 2011).

Results

The physical properties of the soils among the enclaves were significantly different (Kruskal–Wallis; $P < 0.001$) (Table 2). ZTCA 1 has presented soils characteristics better drained, with high levels of sand and low levels of clay, statistically different from the other enclaves (Table 2). In opposite position, we recorded in ZTMA the highest values of clay and lower values of sand, both significantly different from the other areas (Table 2).

In relation to the acidity of the soil, we have had a higher pH in ZTCA that was considered the most neutral within the four enclaves (7.78 ± 0.27), which statistically differed it from the others. However, all of the other enclaves showed tendency to the neutral acidity ($\text{pH} \approx 7$) and did not differed significantly (Table 2). If considering the potential soil acidity ($H + Al$), ZTMA was the one that showed significantly superior values, considering the most acid enclave, while the others showed intermediary to neutral values ($>3.0 \text{ cmolc dm}^{-3}$) and did not differed statistically (Table 2).

Basing on variables that summarize the availability of nutrients in the soils, we observed that ZTCA 2 and CE showed higher levels of Ca, SB, V, CTC and Na, all statistically similar between the two enclaves. In addition to these variables, ZTCA 2 showed significantly higher values for potassium (K: $0.51 \pm 0.2 \text{ mg dm}^{-3}$) (Table 2). This situation was similar to that recorded in CE which also showed significantly higher values for phosphorus (P: $524.44 \pm 397.02 \text{ mg dm}^{-3}$) and organic matter (OM: $124.54 \pm 64.33 \text{ dag kg}^{-1}$). In summary, ZTCA 1 showed fertility levels ranging from intermediate to low, while ZTMA presented only magnesium with high levels (Table 2).

Table 2 Environmental variables evaluated in 100 plots of the Deciduous Forest enclaves

Environmental	ZTMA	CE	ZTCA 1	ZTCA 2	Kruskal–Wallis	
					F	P
Physical properties of soils						
Sand (g Kg^{-1})	343 ± 103.21^c	504 ± 13.84^b	686 ± 39.58^a	485 ± 40.82^b	1,406.666	***
Silt (g Kg^{-1})	254 ± 52.38^a	246 ± 13.84^a	114 ± 22.91^b	231 ± 49.62^a	725.023	***
Clay (g Kg^{-1})	415 ± 96.82^a	250 ± 0.00^b	200 ± 21.65^c	286 ± 47.91^b	695.267	***
Chemical properties of soils						
pH in H_2O	6.99 ± 0.87^b	7.17 ± 0.49^b	6.85 ± 0.25^b	7.78 ± 0.27^a	150.723	***
P (mg Dm^{-3})	8.97 ± 6.15^b	524.44 ± 397.02^a	12.28 ± 12.23^b	141.2 ± 42.57^b	370.136	***
K^+ (mg dm^{-3})	0.16 ± 0.07^c	0.28 ± 0.06^b	0.21 ± 0.06^{bc}	0.51 ± 0.2^a	475.809	***
Ca^{++} (cmolc dm^{-3})	0.44 ± 0.2^c	18.48 ± 6.23^a	4.83 ± 1.39^b	20.08 ± 5.58^a	1,334.453	***
Mg^{++} (cmolc dm^{-3})	3.37 ± 0.92^a	3.02 ± 0.94^a	0.73 ± 0.31^c	1.98 ± 0.46^b	693.939	***
SB (cmolc dm^{-3})	4.13 ± 1.05^b	21.93 ± 7.18^a	5.82 ± 1.66^b	22.59 ± 5.89^a	1,110.823	***
V (%)	54.88 ± 19.51^c	88.84 ± 5.65^a	67.84 ± 7.09^b	92.24 ± 1.61^a	673.879	***
$H + Al$ (cmolc Dm^{-3})	3.9 ± 2.6^a	2.4 ± 0.57^b	2.64 ± 0.28^b	1.83 ± 0.15^b	105.894	***
Effective CEC (cmolc Dm^{-3})	7.98 ± 1.8^b	24.33 ± 6.7^a	8.44 ± 1.62^b	24.6 ± 5.92^a	1,027.604	***
Potential CEC (cmolc Dm^{-3})	0.11 ± 0.08^b	0.15 ± 0.06^{ab}	0.05 ± 0.02^c	0.19 ± 0.03^a	276.266	***
Organic Matter (dag Kg^{-1})	90.36 ± 45.23^b	124.54 ± 64.33^a	39.11 ± 8.01^c	69.96 ± 13.77^b	199.867	***
Cover rock (%)	25.92 ± 33.65^b	46.08 ± 34.46^{ab}	46.8 ± 29.92^{ab}	68.50 ± 27.27^a	130.995	***
Relief						
Altitude (m)	819.6 ± 29.12^a	626.24 ± 23.39^c	696.64 ± 9.37^b	533 ± 25.76^d	6,797.656	***
Slope (m)	3.75 ± 2.52^b	3.58 ± 2.32^b	5.42 ± 4.11^b	19.04 ± 6.52^a	778.805	***

CE Core zone of the “Cerrado” biome, ZTMA “Cerrado”–Atlantic Forest transition zone and ZTCA 1 and ZTCA 2 = “Cerrado–Caatinga” transition zone. The values are averages \pm standard deviation of 25 samples of each enclave. The Kruskal–Wallis test indicated that significant differences ($P < 0.05$) and averages followed by the same letter do not differ by the Dunn test ($P < 0.05$). *** $P < 0.001$, NS not significant, SB sum of bases, V base saturation, $H + Al$ potential acidity, CEC cation exchange capacity

The highest rock coverage was found in ZTCA 2 ($68.50 \pm 27.27\%$) and the lowest in ZTMA ($25.92 \pm 33.65\%$) and was the only ones that differed significantly in relation to other fragments (Table 2). The enclaves with higher proportion of rock cover were considered to have the lowest availability and depth of the soil, and thus, ZTCA 2 showed more shallow soils, while soils ZTMA be deeper (Table 2).

The altitudes ranged from 819.6 ± 29.12 m in the ZTMA to 533 ± 25.76 m in ZTCA 2 and were statistically different between all the enclaves (Table 2). Regarding the slope, ZTCA 2 only differentiated for showing the highest slope (19.04 ± 6.52 m), almost four to five times greater than the value recorded in other enclaves (Table 2).

The rarefaction curves (Fig. 2) showed higher potential richness in species for ZTCA 1 and CE. On the other hand, ZTCA 2 was the enclave with the lowest number of species. Except between CE and ZTCA1, the other curves showed significant differences by analysis of the confidence intervals (95%) of the curves. However, for clarity the confidence intervals are not shown in the curves of stress collector (Fig. 2).

Considering the diversity profile of the parameter $\alpha = 0$, where diversity is equal to the number of species in the sample, the largest enclaves of richness were CE (65 species) and ZTCA1 (64), which did not differ; however, ZTMA (46) and ZTCA (43) have differed that were also significantly different from each other (Fig. 3). As for α tending to 1, where diversity value is equivalent to the Shannon diversity (Euler number's base), all enclaves differed significantly, following the gradient from highest to lowest diversity ZTCA 1—CE—ZTMA—ZTCA 2, similar to that observed for the index of Pielou (Table 3). The same pattern occurred for $\alpha = 2$, where the value is the inverse of Simpson index and higher values of α , in

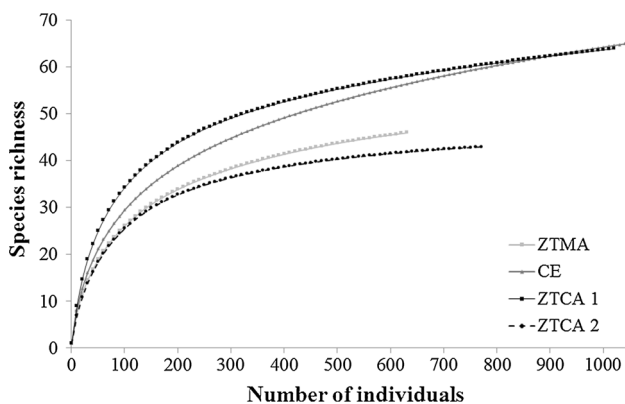


Fig. 2 Rarefaction curves of tree species richness in relation to the number of individuals recorded in the Deciduous Forest enclaves. *CE* Core zone of the “Cerrado” biome, *ZTMA* “Cerrado”—Atlantic Forest transition zone and *ZTCA 1* and *ZTCA 2* = “Cerrado—Caatinga” transition zone

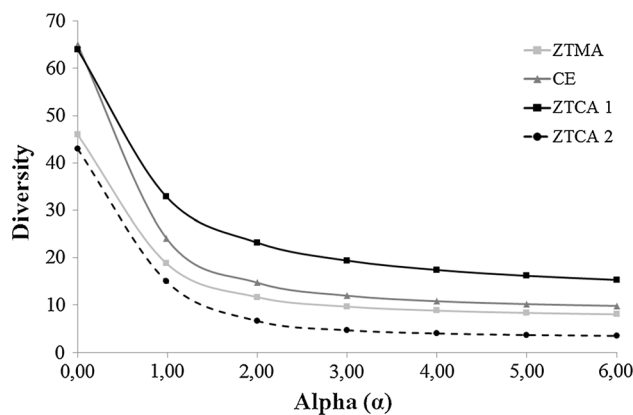


Fig. 3 Profiles diversity of tree species sampled in Deciduous Forest enclaves. *CE* Core zone of the “Cerrado” biome, *ZTMA* “Cerrado”—Atlantic Forest transition zone and *ZTCA 1* and *ZTCA 2* = “Cerrado—Caatinga” transition zone. When $\alpha = 0$, the diversity is expressed by the richness or the number of species in the sample; $\alpha \rightarrow 1$, it is equivalent to the Shannon diversity (Naperian base); $\alpha = 2$, it is the inverse of the Simpson index ($1/D$)

other words, those that evaluate only equability and despise evenness and species richness (Fig. 3). Considering the infrequency of species, a pattern similar to the previously found by following the gradient CE (27% of rare species)—ZTCA 1 (20%)—ZTMA (19%)—ZTCA 2 (16%).

In all, 3,504 individuals were sampled in the four enclaves. The densities were significantly lower in ZTMA (635 ind ha^{-1}) and ZTCA 2 (778 ind ha^{-1}) and higher in ZTCA 1 ($1,046 \text{ ind ha}^{-1}$) and CE ($1,045 \text{ ind ha}^{-1}$) (Table 3). No significant differences were observed in terms of basal area due to the high internal variation in the enclaves, which ranged from $15.98 \pm 5.90 \text{ m}^2 \text{ ha}^{-1}$ (ZTCA 1) to $26.29 \pm 30.17 \text{ m}^2 \text{ ha}^{-1}$ (ZTCA 2) (Table 3). In terms of heights, significant differences were found with ZTMA recording the lowest average peak height (15.28 ± 1.57 m) and the highest average value of minimum height (5.1 ± 1.63 m), whereas in CE there was the highest average maximum height (20.44 ± 3.3 m) (Table 3). ZTCA 2 was the enclave with the highest biomass (34% of total sample) and one of lower abundance (22%) (Table 3).

Comparisons among the four enclaves allowed to detect statistical differences in the total number of individuals, as well as the height (maximum and minimum) (Table 3). However, the basal area differed significantly among the areas ($P > 0.05$). The CE and ZTCA 1 enclaves had higher values of total density and were statistically similar among themselves and different from the other areas (Table 3). The maximum total heights of trees in the sampled differed statistically (Table 3). CE showed the highest average value of maximum height (20.44 ± 3.3 m), while ZTMA recorded the lowest maximum height 15.28 ± 1.57 m. For the minimum height, it is noticed that ZTMA had the

Table 3 Structural variables of 100 plots of the deciduous forest enclaves

	ZTMA	CE	ZTCA 1	ZTCA 2	Kruskal–Wallis	
					F	P
Species richness	46	65	64	43		
Shannon diversity (H)	2.91	3.17	3.48	2.69		
Pielou index (J)	0.76	0.76	0.83	0.71		
Number of rare species ($n = 1$)	9	18	13	7		
Tree density (ind ha ⁻¹)						
DBH 5–10 cm (all classes)	635 ± 231.39 ^b	1 046 ± 67.41 ^a	1 045 ± 37.5 ^a	778 ± 192.07 ^b	114.191	***
DBH 5–10 cm	254 ± 151.67 ^c	630 ± 372.84 ^a	614 ± 176.2 ^b	509.38 ± 214.53 ^c	14.377	***
DBH 10–15 cm	153 ± 108.57	219 ± 140.73	197 ± 90.23	192 ± 94.57	1.5494	ns
DBH 15–20 cm	89 ± 65.38	90 ± 65.75	110 ± 59.95	67 ± 55.3	2.024	ns
DBH > 20 cm	139 ± 68.50	107 ± 73.43	124 ± 72.70	103 ± 53.68	1.502	ns
Basal area (m ² ha ⁻¹)	17.52 ± 7.30	17.7 ± 9.49	15.98 ± 5.90	26.29 ± 30.17	20.100	ns
Height (m)						
Maximum height	15.28 ± 1.57 ^c	20.44 ± 3.30 ^a	18.12 ± 3.50 ^{ab}	15.84 ± 4.06 ^{b, c}	132.274	***
Minimum height	5.10 ± 1.63 ^a	3.05 ± 1.06 ^b	3.27 ± 0.70 ^b	3.39 ± 0.66 ^b	157.257	***

CE Core zone of the “Cerrado” biome, ZTMA “Cerrado”–Atlantic Forest transition zone and ZTCA 1 and ZTCA 2 = “Cerrado–Caatinga” transition zone. Except for the richness, diversity, evenness and rarity of tree species are presented for the total sample of each enclave, and other values are ± standard deviations of 25 plots sampled in each enclave. The Kruskal–Wallis test indicated that significant differences ($P < 0.05$) and averages followed by the same letter do not differ by the Dunn test ($P < 0.05$). *** $P < 0.001$ and ns not significant

highest value (5.10 ± 1.63 m), and this was significantly different from the others (Table 3).

The frequency distributions in the diameter classes in all the enclaves showed high concentration of individuals in the smaller classes and marked decrease toward the largest ones, characterized as negative exponential distribution or reverse— J (Fig. 4). The first two classes (5–20 cm), when added together, accounted for over 64% of sampled individuals, which emphasizes the importance of these classes in the structure of woody vegetation of the enclaves. The

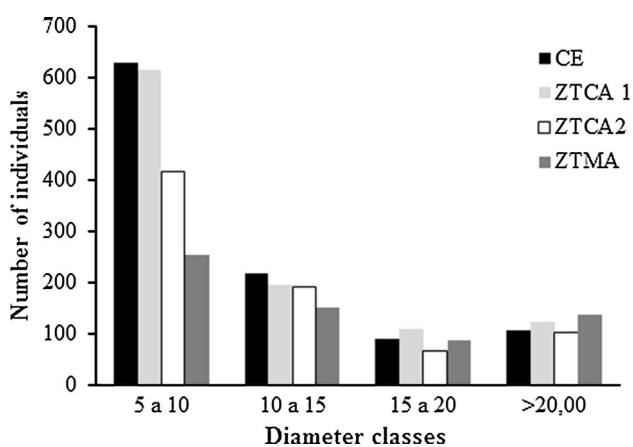


Fig. 4 Distribution in diameter classes of tree individuals (DBH ≥ 5 cm) sampled in Deciduous Forest enclaves. CE Zone core of the “Cerrado” biome, ZTMA “Cerrado”–Atlantic Forest transition zone and ZTCA 1 and ZTCA 2 = “Cerrado–Caatinga” transition zone

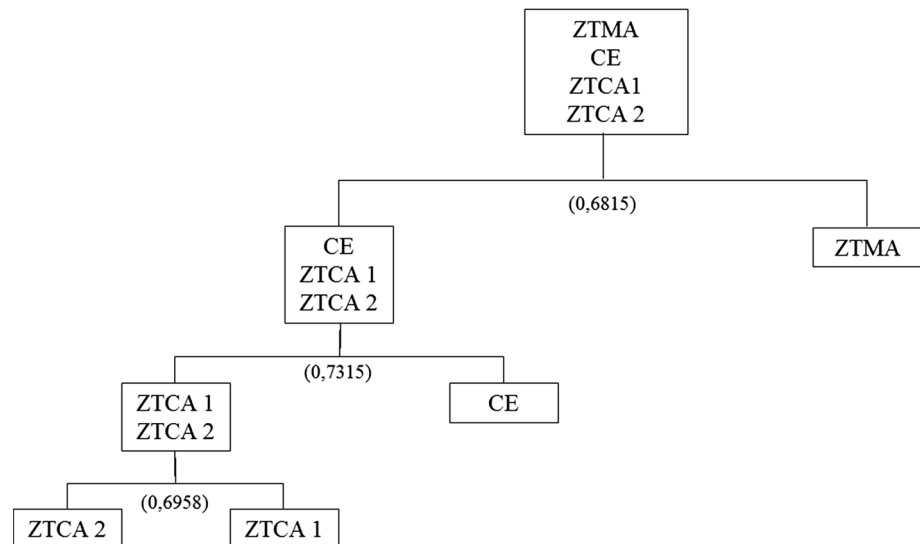
comparison of the distribution of frequencies in diameter classes adopted in the four enclaves has shown statistical differences only for the first class (5–10 cm of DBH). Thus, CE, ZTCA1 and ZTCA2 showed high concentration of individuals in the initial class and are considered statistically similar, while ZTMA density was lower in this class, and the difference between this and the others was significant (Table 3).

The analysis classification by TWINSPLAN has shown strong divisions in all the levels, with values higher than 0.68 (Fig. 5). That suggests that the four investigated enclaves had strong floristic-structural differentiation, since according to Felfili et al. (2011) values over 0.3 characterize the distinction among the species. On the first division (eigenvalue: 0.6815), the ZTMA enclave was separated from the other areas (Fig. 5), while on the second hierarchic level (eigenvalue: 0.7315) the ZTCA 2 and ZTCA 1 were grouped and the CE area was separated. And on the last group divisions (eigenvalue: 0.6958), the ZTCA 2 and ZTCA 1 enclaves were separated.

Discussion

The variations in edaphic and geomorphological factors were determinants in the characterization of woody vegetation in the Deciduous Forests enclaves. The abiotic factors commonly related to the structure and dynamics of tropical forests are solar radiation and availability of water

Fig. 5 Classification of the enclaves Deciduous Forest generated by TWINSpan, based on the tree species density ($DBH \geq 5$ cm). CE Zone core of the “Cerrado” biome, ZTMA “Cerrado”–Atlantic Forest transition zone and ZTCA 1 and ZTCA 2 = “Cerrado–Caatinga” transition zone



and mineral nutrients in soils (Hugget 1995). The importance of each one differs significantly among the terrestrial biomass or even within a similar physiognomy, especially when this is inserted in form of enclaves in different vegetation matrices, as is the case of the FED. The Dry Forest occurs on fertile soils where the rainfall is less than 1,800 mm per year (Dryflor et al. 2016). Here we found that except for the solar radiation that we did not evaluate, the fertility, texture, acidity and relief were the main responsible for floristic-structural differentiation in the enclaves of Deciduous Forests.

When we consider that the particle size distribution, expressed by soil texture, is the characteristic that best describes the water retention capacity of the soil (Beutler et al. 2002; Fernandes and Corá 2004), we assumed that ZTMA showed large ability to water storage, with higher levels of clay. Moreover, ZTCA 1 has shown the highest values of sand, thus the lower water holding capacity. Relationship between the texture and water retention capacity of the soil occurs as a result of the relationship between macro and micropores, respectively, soils with higher levels of sand and clay (Paiva et al. 2000). Thus, besides the availability of nutrients in the soil, which naturally tends to be high in the FED, the availability of water in the soil was also important in the distribution of vegetation.

Just as the physical properties of soils, the decrease in rainfall toward $ZTMA > CE > ZTCA 1 > ZTCA 2$, also exerted influence on soil water availability. Similar pattern was also observed in the Brazilian semiarid region (Rodal et al. 2008), where they found that physiognomic changes are common along the rainfall gradient and that the seasonality is as important as the total precipitation and the number of dry months per year. Thus, our results corroborate the assertion that Deciduous Seasonal Forests are

associated with a strong seasonal rainfall regime (Murphy and Lugo 1986; Gentry 1995), where it is assumed that the water storage capacity of each locality presents a preponderance in the distribution of species (Rizzini 1977).

In addition, we observed the action of the full set of rainfall and soil properties also influenced the species distribution and structure of woody vegetation in the seasonal Dry Forests. After all, it is expected that, the more it is pronounced and the less their capacity to resist the water stress is, the more it decreases (Andrade et al. 2009). In this case, the environmental characteristics, whether of the soil or climate nature, can be the difference that allow or restrict the arrival and the establishment and development of species in each locality.

Although the studied fragments are located on the same type of geological origin material derived from limestone “Grupo Bambuí” (Iglesias and Uhlein 2009), the differences in the physical properties of the soils also may have influenced the chemical characteristics. The texture of the soil also acts in nutritional availability, since clay particles are derived from weathering of larger fractions, and although they are more resistant, they have lower nutrient reserves in its constitution than the material from which they came from.

Regarding this, the relationship of texture and nutritional availability soil can be established once ZTMA, area of higher concentration of clay, had the lowest fertility. However, the remnants with higher nutritional availability (CE and ZTCA 2) showed lower levels of clay. Thus, it was noticed that, as well as for precipitation, there is also an increasing gradient of fertility in the following sequence: $ZTMA < ZTCA1 < CE < ZTCA 2$. Nevertheless, one should notice that all the areas had levels of basis saturation (V) greater than 50%, which indicates the existence of eutrophic soils (Embrapa 1999), that is, with high

levels of nutrients, moderate to high pH and low aluminum content, which are characteristic of the environments with occurrence of FED (Pennington et al. 2000; Prado 2000).

The differences between structural vegetations parameters probably reflected the relationship with the environmental conditions imposed on her. Factors such as climate, physical composition and chemical properties of soil and relief are important in the distribution and structure of forest formations (Oliveira Filho et al. 1994, 1998; Oliveira Filho and Fontes 2000), reflecting mainly in the horizontal and vertical communities' stratification (Fagundes et al. 2007). Works performed in Brazilian Deciduous Forests find relationship between vegetation and soil characteristics, most of them related to soil nutrient availability (Fagundes et al. 2007; Santos et al. 2012). This relationship directly influences the height, density and biomass of these communities (Sampaio et al. 1981) which reinforces our hypothesis that abiotic factors govern the vegetation structural patterns of the Deciduous Forest enclaves.

Limitations associated with fertility recorded in the ZTMA, as well as the history of disturbances, may also have influenced the patterns described in the vegetation. Several studies indicate that previous events may affect vegetation development (Oliveira Filho et al. 1997; Kennard et al. 2002; Fagundes et al. 2007). Signals of degrading events were observed inside the fragment in ZTMA, and that may have influenced the vegetation structure due to, for example, competition for exotic species that would limit both the germination and the development of the tree individuals. This would explain the low density and basal area recorded in this fragment. In general, Dry Forest is in a critical conservation state, because so little of it is no disturbed and of the remnant areas little is protected (Miles et al. 2006). Thus, we believe that both the environmental conditions, especially those related to nutrient availability and acidity of the soil, and the history of disturbance in the area resulted in lower density and height of vegetation sampled in ZTMA.

We assume that the texture and acidity of soils were responsible for the floristic separation of ZTMA from the other enclaves and this possessed soils with higher clay content and higher pH and potential acidity ($H + Al$), and other areas more neutral soils pH having low-to-intermediate clay contents. Variations in clay and soil pH were also responsible for the distinction of areas Deciduous Forests of southeastern Brazil (Oliveira Filho et al. 2001). Thus, we found that differences between environmental variables besides influencing the vegetation structure also influenced the separation of FED in floristic terms.

We attribute the floristic separation between CE and other fragments due to the influence of relief, rockiness and organic matter, since CE presented planer surface, soils with higher organic matter content and lower concentration

of rocks, than the other areas, similar to that found by others studies (Fagundes et al. 2007). While the separation of ZTCA 1 and ZTCA 2 we associate to the differences in the availability of nutrients and once more the texture and rockiness. ZTCA 2 presented more fertile soils, with higher percentage of sand and high concentration of rocks. Others authors (Oliveira Filho et al. 1994, 1998) also observed that fertility variables and the rocky concentration exerted a strong influence on the distinction of seasonal environments. In fact, the floristic variation of dry forest species is also explained by environmental conditions (Neves et al. 2015).

When we take as a basis the model of succession for Seasonal Forests in the Atlantic Forest (Machado and Oliveira Filho 2010), we can infer from the large number of individuals and low basal area that ZTCA 1 would be the initial phase of construction with degradation. Thus, in forests where degradation evidences remain, even in restructure processes are in progress, it is possible to observe the characteristics of environments that are in the stage of degradation, such as reduced basal area (Machado and Oliveira Filho 2010). Actually, in general, in mature forests, a major number of trees with higher basal areas are observed, while those at early stages of regeneration form large densification of thin trees (Parthasarathy 1999).

The size structure of the tree individuals, represented by a greater number of individuals in the smaller classes indicated that communities are self-regenerative, the *J-Reverse*-type distributions, can characterize community stock, that is, presenting considerable abundance in the natural regeneration of individuals available for the establishment of individuals. This is typical of stable tropical forests, which do not exhibit large disturbances and composition in different species that create permanent seedling bank. However, most forests known as native forests with inverted exponential distribution do not present a balanced distribution, but tend to converge to that standard (Harper 1977).

The differences in vertical stratification observed allowed us to infer that ZTCA 2, CE and ZTCA 1 are more compartmentalized due to the larger amplitudes between the Brazilian minimum and maximum values shown for these areas, which resulted in greater diversification of strata. Well-stratified forests have high diversity and differentiation of ecological niches and comprise most flora and fauna diversity in different vertical strata, in the same plant community (Hunter Júnior 1990). Thus, the most plausible explanation for the observed differences in the vertical stratification is its relationship with the environmental and historical factors. For example, the fertility of soils which limits the development of the individuals, or even the selective cutting larger species that may have influenced both the structure of the studied remnants and their floral compositions (Emmerich 1990).

We conclude that the floristic, structural and environmental variations observed allowed us to assume our initial hypothesis that the chemical and textural properties of the soil rockiness, declivity and altitude have influenced in the composition, and structure of the woody vegetation in the Deciduous Forests enclaves as true, which has reflected in the identification of environmental-floral-structural gradient in the studied fragments.

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