



Vegetation structure and edaphic factors in *veredas* reflect different conservation status in these threatened areas



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ABSTRACT

Background: In Cerrado humid areas, *veredas* are considered as hygrophilous communities, marked by the presence of the *Mauritia flexuosa* palm tree emerging in the wetter zones. Changes in *veredas* ecosystems due to drought and changes in the water table, which represent important areas for biodiversity maintenance in the Brazilian cerrado, can lead to the emergence of new landscapes and ecosystems. Assuming that the *veredas* are changed in species composition due to anthropogenic factors, in this study, we evaluated the flora composition and described the current vegetation profile of two *veredas* under different disturbances levels that are located in the north of Minas Gerais State, Brazil.

Results: Altogether, 2,268 individuals of 91 species belonging to 36 families were recorded. Our results demonstrated that the studied *veredas* were floristically different in terms of the arboreous-shrubby species composition, richness, and diversity. Despite the hygrophilous forest formations and open areas in the two *veredas* present typical species from these environments (same species with high importance values), the drought in the water table caused an expansion of Cerrado species in the open areas and in the hygrophilous forest. Furthermore, in the hygrophilous forest there was an increase in the abundance of species that occur in less saturated soils.

Conclusion: Our results demonstrate that the studied *veredas* are changing in species composition due to anthropogenic factors which leads to the drought of these formations (water balance effect). These anthropogenic effects cause a modification with the expansion and increase in the abundance of typical species of other areas of Cerrado and resistant to less saturated soils, leading to the *veredas* collapse. Finally, future studies should investigate other *veredas* on a broader scale to detect changes in the water table that lead to a consequent change in vegetation structure. In this way, we will have support for the conscientious management and conservation of these areas that represent equilibrium places for the Cerrado biome.

1. Background

The Cerrado has a complex mosaic of distinct phytophysionomies,

with savanna and forest formations. In Cerrado humid areas, *veredas* are considered as hygrophilous communities, marked by the presence of the *Mauritia flexuosa* L.f. (buriti) palm tree emerging in the wetter zones

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(Araújo et al., 2002; Ribeiro and Walter, 2008; Oliveira et al., 2009; Ávila et al., 2016). *Veredas* communities occupy hydromorphic soils, gleys, and organic turfs (Gleysols and Histosols), and are associated with relatively shallow water tables (Ramos et al., 2006; IUSS Working Group WRB, 2015; Bijos et al., 2017). *Veredas* emerge from wet patches in the soil that are established by variations in the topography and alternation of layers of soil with distinct levels of permeability (Oliveira et al., 2009; Neves et al., 2015; Bijos et al., 2017). The vegetation is formed of a continuous herbaceous-shrubby layer and the gradient between more and less wet zones determines the variations in species composition (Araújo et al., 2002; Guimarães et al., 2002; Oliveira et al., 2009; Resende et al., 2013; Nunes et al., 2015). Thus, the herbaceous/shrubby component predominates in open areas and more humid soil, and the tree component occurs close to the water table expansion region (hygrophilous forests), in soil that is usually permanently saturated (Araújo et al., 2002; Oliveira et al., 2009; Nunes et al., 2015).

Studies in *veredas* are needed to fill the gaps in information about fauna, flora, ecology, hydrology, among others inherent to any ecosystem, in order to assess their impacts, when their biotic and abiotic functions are altered (Meirelles et al., 2004; Ávila et al., 2016). The factors that are contributing to the mischaracterization of *veredas* are dams, with flooding and vegetation suppression, construction of unplanned roads, promoting the siltation of *veredas* courses, soil compaction mainly by cattle trampling, use of its floodplains as natural roads and the opening of roads with the use heavy machinery (Guimarães et al., 2002; Brasil et al., 2021). Furthermore, climate change and fires (Bond and Wilgen, 1996) have been a great threat in the process of degradation of the *veredas*. Associated with climate change that causes drier years (with low rainfall), more warmer periods (Oliveira et al., 2017; Hofmann et al., 2021) and deforestation in these areas, the water balance is affected causing changes in hydrological processes and leading to drought of these areas in Cerrado (Oliveira et al., 2014, 2015, 2017). In addition, little attention has been paid to the consequences of climate change, land use and land cover on groundwater recharge. Furthermore, hypotheses have been proposed that groundwater levels may determine vegetation density and diversity (Orellana et al., 2012; Rossatto et al., 2012; Villalobos-Vega et al., 2014). The decrease in the level of the water table that causes the *veredas* drought indicates that it is the main impact causing modification of this formation (Ávila et al., 2016).

These ecosystems are losing their vegetation originality. Open areas are more exposed to anthropogenic changes and their species are the most susceptible to environmental changes (Araújo et al., 2002; Oliveira et al., 2009). Further studies on the composition, richness, and diversity of plant species in *veredas* communities are essential for understanding relevant ecological processes and also for developing appropriate conservation policies (Junk et al., 2014; Rosolen et al., 2015; Neves et al., 2015; Bijos et al., 2017). Changes in *veredas* ecosystems, which represent important areas for the biodiversity maintenance in the Brazilian Cerrado, can lead to the emergence of new landscapes and ecosystems. These modified *veredas* may represent systems that differ in composition and/or function from present and past systems as a consequence of changing species distributions, environmental alteration through climate and land use change and shifting values about nature and ecosystems (Harris et al., 2006; Root and Schneider, 2006). Thus, this formation has been losing its original characterization where common species in *veredas* are being replaced by species from other arboreal formations in Cerrado (Ávila et al., 2021).

Assuming that the *veredas* are undergoing changes in species composition due to anthropogenic factors and climate change which leads to the drought of these formations (water balance effect), in this study, we evaluated the flora composition and described the current vegetation profile of two *veredas* under different levels of disturbances that are located in the north of Minas Gerais State, Brazil. We evaluated the species composition in the open areas and in the hygrophilous forests in the two *veredas* and verified whether the difference in species composition was influenced by soil fertility and acidity. We expected

that: a) higher levels of disturbances (drought of these formations with water balance effect), affecting wood community differentiating the vegetation profile and species composition between the two *veredas*; b) soil fertility influences abundance, richness and diversity of species positively in these areas, and soil acidity negatively; c) the *vereda* with high water balance disturbance will have its open area more similar to other cerrado (savanna) vegetation types and its hygrophilous forest with a different species composition from the more conserved *vereda* (due drought of these formation). Thus, the results of species composition presented here will bring information about the modification of these ecosystems and the emergence of new possibly fragile ecosystems, susceptible to greater effects of climate change.

2. Methods

2.1. Study areas

We collected data in two Conservation Units: Área de Proteção Ambiental do Rio Pandeiros (APA Rio Pandeiros) and Parque Estadual Veredas do Peruaçu (PEVP). The two areas are located in the north of the Minas Gerais State. Almescla *vereda* (15°20'54.9" S; 44°53'84.5" W), in the APA Rio Pandeiros, is located in the municipality of Bonito de Minas, and the Peruaçu *vereda* (15°01'10.5" S; 44°42'15.3" W), in the PEVP, in the municipality of Cônego Marinho (Fig. 1). The region has a Aw type tropical climate according to Köppen's classification, with dry winter and average annual temperature of 22.2–22.7 °C, and rainfall ranging from 1,008 to 1,073 mm, respectively (Alvares et al., 2013; Azevedo et al., 2014). During the study period the two areas did not show differences in mean temperature and total precipitation (see Supplementary Material Fig. S1, $P > 0.05$, $F = 2.70$, $df = 138$). The soil in the region is considered dystrophic and sandy (Nunes et al., 2015), classified as Hystosols (IUSS Working Group WRB, 2015). The vegetation in the study area is represented by Cerrado and Caatinga transition phytogeographies, culminating in a mosaic of riparian and dry forests, savanna, and palm swamps - *veredas* (Menino et al., 2012; Ávila et al., 2021). All study sites are characterized by high and threatened biodiversity (Myers et al., 2000), and specifically the areas of *veredas* in the region are in the process of drought, with loss of springs (according to reports from residents and visual observations) and its landscape shows various anthropic activities, such as raising domestic animals, farming, grazing, harvesting wood and burning (Ávila et al., 2021). However, it is still possible to observe the presence of water above soil from the groundwater in some locals, and the vegetation presents a typical structure of hygrophilous environments, with the presence of two main zones (open areas, and hygrophilous forest). The Peruaçu *vereda* presents drought at an advanced stage, with loss of springs and retraction of the upper portion of the river (42 km). Furthermore, according to reports from the residents, the *vereda* has burnt sections, with high tree mortality leading to a change in landscape. This is evidenced due to changes in the vegetation composition at various points along its course and the approximation and invasion of typical cerrado species.

2.2. Vegetation sampling

For sampling the plant community in the studied areas, the plot method was used (Mueller-Dombois and Ellenberg, 1974). For a better characterization of the *veredas* sampled, these are defined in two zones linked to topography and soil drainage: hygrophilous forest and open area. In the Almescla *vereda*, the plots allocated were distributed in two transects parallel to the watercourse. In the transect one defined as the hygrophilous forest, 30 plots of 10 m × 20 m with a distance of 150 m between plots were distributed along the transect. The arboreal-shrubby individuals within these plots with DBH ≥ 5 cm (diameter at breast height – measured 1.30 m above ground level) had their height estimated and were identified and marked with numbered aluminum plates. Furthermore, within each of the 10 m × 20 m plots, smaller plots with a

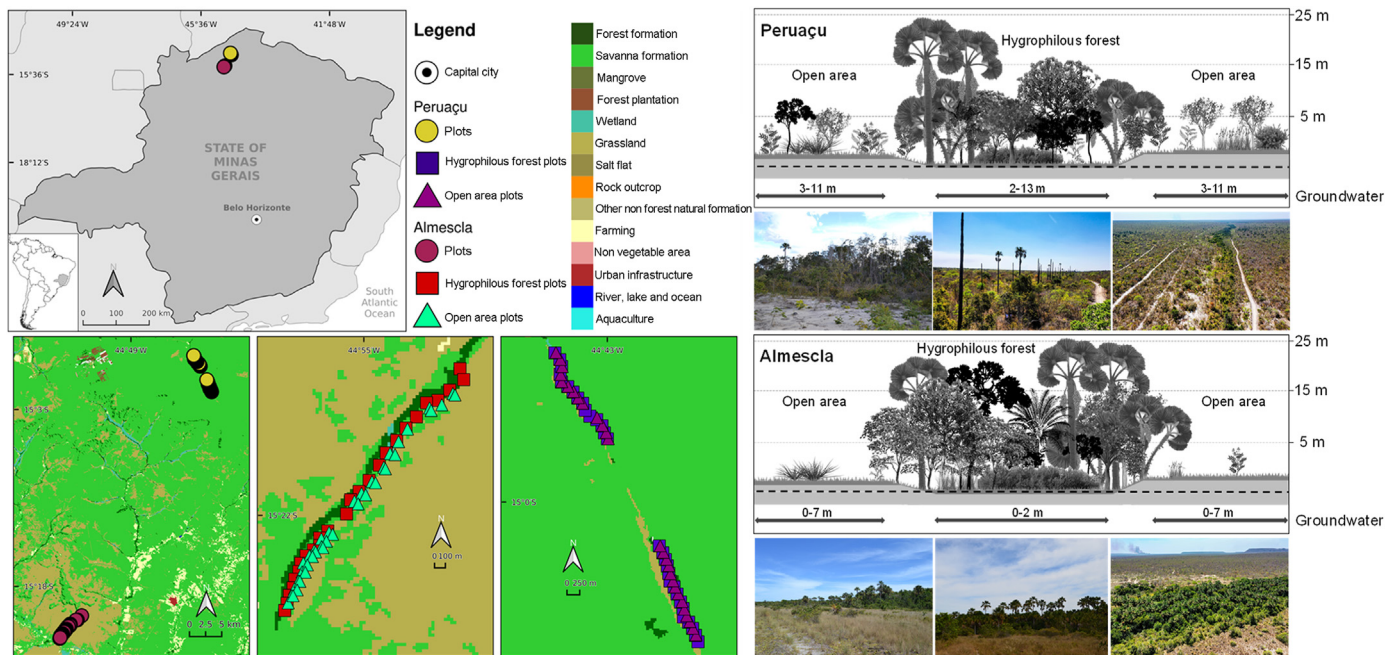


Fig. 1. Location of the studied *veredas*, distribution of sampled plots, photographs, illustrations, and vegetation profile description of the Peruaçu and Almescla *veredas*. The photographs and illustrations show the open areas and the hygrophilous forest with the level of the groundwater and the height of the plant species. The data for the map construction were obtained from the Mapbiomas platform (Souza et al., 2020).

dimension of 5 m × 5 m were delimited for sampling the arboreal-shrubby individuals from the lower strata and/or juveniles. Thus, in these subplots all arboreal-shrubby individuals with DBH ≥ 3 cm had their height estimated, registered, and numbered with aluminum plates. In relation to the zone defined as the open area, two transects 20 m apart were allocated. In these transects, 38 plots of 10 m × 20 m were demarcated, 150 m between plots, arranged in parallel with the plots marked in the hygrophilous forest. All shrub-tree individuals at DBS (diameter at the base of the stem) ≥ 5 cm were marked with aluminum plates, measured and identified. Likewise, sub-plots of 5 m × 5 m were plotted within the plots for sampling the shrub-sub-shrub individuals. Thus, all individuals with DBS ≥ 3 cm were marked, identified and measured.

The procedure applied to the second area of study, the *vereda* Peruaçu, was similar to that described in the *vereda* Almescla. However, there were changes in some methods due to the advanced stage of drought in this ecosystem. Thus, in the transect defined as hygrophilous forest, 30 plots of 10 m × 20 m and 5 m × 5 m were also allocated along with the subplots. However, there was no division in two transects in the open area as occurred in the Almescla. Thus, only one transect was established along the open area with 27 plots of 20 m × 10 m along with the subplots.

To delineate the plots, a compass and measuring tape were used, and to demarcate them, PVC pipes were positioned at each plot vertex and their limits were marked with sisal wire. The individual's identification was carried out in the field, given prior species knowledge, and through collected material (vegetative or reproductive) for identification through specialized literature, sent to specialists or comparison with existing material. Vouchers for all plant species were collected, identified, and deposited in the Montes Claros Herbarium (MCMG), of the Universidade Estadual de Montes Claros (UNIMONTES), and the Norte Mineiro Herbarium (ICA-UFGM) of the Universidade Federal de Minas Gerais (UFMG). The family names followed the Angiosperm Phylogeny Group (APG, 2016), and species names were confirmed in the Plant list database (<http://www.theplantlist.org/>) and updated/corrected whenever necessary.

2.3. Groundwater level measurement

In addition to visual confirmation, the groundwater level (charged and uncharged) was measured in both *veredas* considering the open and hygrophilous areas over 20 months (July/2019 to August/2021). Measurements were not performed in November and December 2020 and January, March, April and June 2021 due to logistical issues. The water table was measured using three monitoring wells distributed along the two *veredas* studied. The wells were allocated and drilled at the ends of the transects. The perforations were carried out using a semi-mechanized auger. The holes were lined with tubes and the drilling depths exceeded the water table by approximately 2 m. The water table measurements were performed using an HS electronic water level meter (hydrosupplies, mode: ASNA-30).

2.4. Soil variables

Composite soil samples of 500 g from the topsoil (0–20 cm depth) were collected in all plots to evaluate the effect of soil variables on the species composition and structure. The soil texture (proportions of coarse sand (CS), fine sand (FS), silt, and clay) and the chemical variables [water pH (pH), Calcium Chloride pH (CaCl₂ pH), phosphorus (PMehlic), potassium (K), calcium (Ca), magnesium (Mg), aluminum (Al), hydrogen and aluminum (H + Al), effective cation exchange capacity (t), base saturation (V), aluminum saturation (m)] of each composite sample were performed at the Laboratory for Soil Analysis at the Institute of Agricultural Sciences (Universidade Federal de Minas Gerais) according to Teixeira et al. (2017).

2.5. Data analysis

We calculated the phytosociological parameters: absolute and relative density, dominance and frequency, and importance value (Mueller-Dombois and Ellenberg, 1974). All phytosociological parameters were conducted in R (Development Core Team, 2021), and the code created to perform the analysis is available on the GitHub (<https://github>

ub.com/GustavoHeringer/phytosociology; Heringer et al., 2020). We estimated the sampling completeness for each sampled area by computing the Chao 1 species richness estimator (Chao, 1984; Colwell and Coddington, 1994) using the iNEXT package (Hsieh et al., 2014) in R (Development Core Team, 2021). With the same package, we also plotted rarefaction and extrapolation curves (Hsieh et al., 2014). The Shannon diversity index (H') and Bray-Curtis dissimilarity (Magurran, 2011) were calculated in the R program (Development Core Team, 2021).

To assess the differences in species composition, first Nonmetric Multidimensional Scaling (NMDS) was calculated using the Bray-Curtis dissimilarity distance between species (Legendre and Legendre, 1998). The records contain combinations of continuous numerical data and we used the abundance of individuals in the plots for each species. The distance is always a number between 0 (identical) and 1 (maximally dissimilar) (Legendre and Legendre, 1998). The resulting dissimilarity matrix was used for computing the NMDS ordination with the function `metaMDS` in the `vegan` package in R, which identifies a stable solution using several random starts with smaller stress values (Borcard et al., 2011; Oksanen et al., 2016). In our analysis, we set the number of random starts as 2000, and examined whether solutions with two or three dimensions best describe the data. The optimal number of dimensions was two because the stress remained with acceptable value (Borcard et al., 2011). Finally, using the species-plot matrix at all sampled sites, we calculated a modularity analysis derived from ecological network theory. This analysis has the possibility to verify the affinity of some species for the areas and plots sampled. Thus, if certain plots occupy the same module, it means that these plots have a high species overlap showing greater similarity in species composition. We evaluate how the different plots differ in species composition using Modularity indices that quantify the prevalence of species within subsets of plots in the community and was calculated using the `DIRTLPAwb` + algorithm (Beckett, 2016) using the `computeModules` function in `Bipartite` package (Dormann et al., 2008). In addition to using the raw modularity, we used the Patefield null model, which fixes the matrix size and the marginal totals, which is species richness and species observation, while shuffling occurrence randomly (Patefield, 1981). We consider the modularity and consequent separation of the plots in the different modules to be significant if the observed value was greater than those generated by the null model.

To investigate the relation with the soil variables and the plots and *veredas* formations, principal component analysis (PCA) was performed with all soil variables. We use the first and second principal components (principal component 1 and principal component 2) resulting from the PCA as a generalized index that synthesizes the information of the soil variables. We calculated the PCA analysis using the “FactoMineR” package” (Husson et al., 2016) in R (Development Core Team, 2021).

We evaluated the association between plots in the open areas and hygrophilous forests in the two *veredas* in the modular network. We conducted the Chi-square test to contrast the proportion of plots in the different areas sampled across the modules. We then illustrated the proportion/contribution of each area to each module graphically using Pearson residuals from the Chi-square test with the `corrplot` package in R (Wei and Simko, 2017). Then, we fitted Linear Models with a Poisson distribution, tanking richness, Shannon diversity index (H') and abundance as the predictor's variables and areas as response variables - fixed factors. We also fitted Linear Models with a Poisson distribution, taking PCA analysis axes for soil and NMDS as the predictor's variables and species richness, abundance and Shannon diversity index (H') as response variables - fixed factors (Zuur et al., 2009). All statistical analyses were conducted in R (Development Core Team, 2021).

3. Results

Altogether, 2,268 individuals of 91 species belonging to 36 families were recorded (Table S1). The family Fabaceae was the most represented (17 species), followed by Melastomataceae (nine), Malpighiaceae and

Vochysiaceae with seven species each. In the hygrophilous forests, Peruaçu presented 43 species, while Almescla had 37 species. For open areas, Peruaçu 26 species and Almescla 32 species. Thus, all sampled areas differed in terms of species richness ($F = 6.87$; $p < 0.001$), diversity ($F = 2.40$; $p = 0.05$), and abundance in the plots ($F = 11.46$; $p < 0.0001$; Figs. 1 and 2).

In the sampled areas, the species varied in their importance value (IV), being in the Peruaçu hygrophilous forest *Tapirira guianensis* Aubl. (Anacardiaceae), *Xylopia emarginata* Mart. (Annonaceae), *Cecropia pachystachya* Trécul (Urticaceae) and the palm *Mauritiella armata* (Mart.) Burret (Arecaceae) the species with the highest IV values. In the Almescla hygrophilous forest, *Tapirira guianensis* Aubl. (Anacardiaceae), *Mauritia flexuosa* L. f. (Arecaceae), *Mauritiella armata* (Mart.) Burret and *Cecropia pachystachya* Trécul (Urticaceae) had the highest IV values. In this way, almost all the species are repeated in the two areas in relation to their importance value, except for *Xylopia emarginata* being a species with higher importance value only in the *vereda* Almescla (Table S1).

In relation to the open areas, in Peruaçu *Stryphnodendron adstringens* (Mart.) Coville (Fabaceae), *Tachigali subvelutina* (Benth.) Oliveira-Filho (Fabaceae), *Senna cana* (Nees & Mart.) H.S. Irwin & Barneby (Fabaceae) and *Macairea radula* (Bonpl.) DC. (Melastomataceae) had the highest IV values, and *Byrsonima pachyphylla* A. Juss. (Malpighiaceae), *Xylopia aromatica* (Lam.) Mart. (Annonaceae), *Macairea radula* (Bonpl.) DC. (Melastomataceae) and *Curatella americana* L. (Dilleniaceae) were the species with the highest VI values in the Almescla open areas (Table S1). The rarefaction curve for the hygrophilous forest areas exhibited a tendency toward stabilization. However, for open areas, the rarefaction curves did not stabilize, as in these areas there are few tree species compared to hygrophilous forest (Fig. 2).

We identified that the groundwater level differs between the two *veredas* ($p < 0.0001$; $F = 128.5$; $df = 0.62$). In Almescla, the groundwater presents variations in the charged and uncharged levels due to variation in precipitation, showing still normal conditions. However, for the Peruaçu, the groundwater level is in deficit (see Supplementary Material Fig. S2). In the chemical soil analyses, the first PCA axis contained 31.4% of the variation, and the second comprised 28.7%. The values that contributed most to the variation and had the highest positive correlation with the first axis were m%, Al, H + Al, Clay, Sand, Silt and Mg (Fig. 3a-d). In addition, the first axis had high pH values (negative coordinates in PC1) and high H + Al values (positive coordinates in PC1; Fig. 3c). Therefore, we consider the first PCA axis as a soil acidity gradient. The second axis of the PCA showed a positive correlation with sand, Mg and V % and negatively correlated with H + Al, P, K, Al, silt, Ca, pH and V%, considered in the soil PCA a fertility gradient, which the positive coordinates comprise the most fertile soils (Fig. 3d).

Thus, the first axis of the PCA (soil acidity gradient) explained the variation in richness, abundance and diversity of species in the open areas of Peruaçu and Almescla (richness: $F = 5.53$, $r = 0.13$, $p = 0.02$; abundance: $F = 9.81$, $r = 0.17$, $p = 0.003$; Shannon index: $F = 3.88$, $r = 0.10$, $p = 0.05$; Table 1), but it was not related to richness, abundance and diversity in the hygrophilous forest (richness: $F = 3.33$, $r = 0.10$, $p = 0.07$; abundance: $F = 3.29$, $r = 0.10$, $p = 0.07$; Shannon index: $F = 2.95$, $r = 0.10$, $p = 0.09$). The second axis of the PCA (fertility gradient) was related to richness and abundance of open areas, but not to species diversity (richness: $F = 5.53$, $r = 0.13$, $p = 0.04$; abundance: $F = 12.04$, $r = 0.20$, $p = 0.001$; Shannon index: $F = 3.88$, $r = 0.10$, $p = 0.14$). In addition, the second axis of the PCA did not show a relation for the hygrophilous forest with any of the response variables analysed (richness: $F = 0.01$, $r = 0.01$, $p = 0.92$; abundance: $F = 2.62$, $r = 0.20$, $p = 0.11$; Shannon index: $F = 0.44$, $r = 0.01$, $p = 0.51$; Table 1).

The NMDS of the species composition had a stress value of 0.10 and identified a difference in species composition and dissimilarity between the sampled areas (Fig. 4a-b). Thus, the open areas and hygrophilous forest plots differed in relation to their species composition in Almescla and Peruaçu. That way, the first axis of the NMDS analysis was correlated with the richness and abundance of species in the open areas, but not

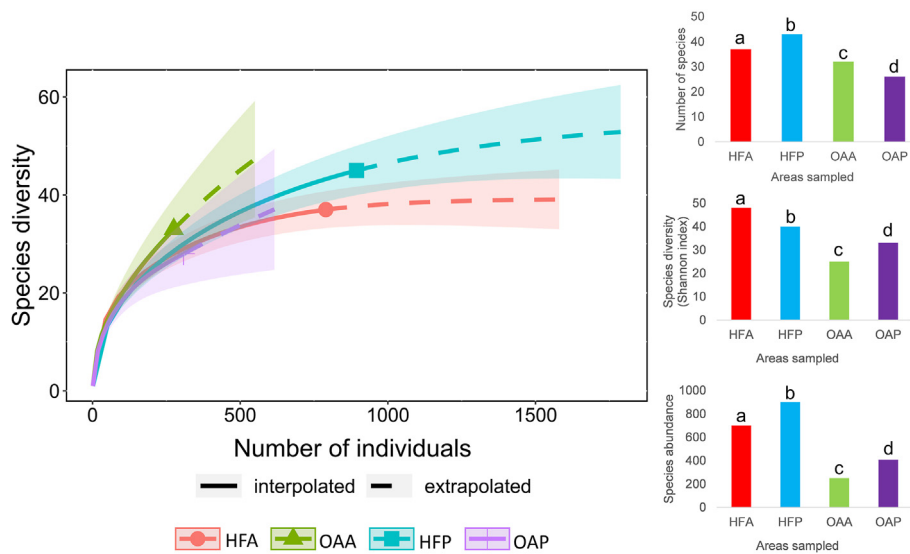


Fig. 2. Rarefaction and extrapolation curve using the Chao 1 estimator of species richness and sampling effort calculated as the ratio of observed and estimated species richness for the sampled areas (Peruaçu and Almescla *veredas*) and richness, Shannon index and abundance comparisons between areas. HFA = hygrophilous forest Almescla; HFP = hygrophilous forest Peruaçu; OAA = Open area Almescla; OAP = Open area Peruaçu.

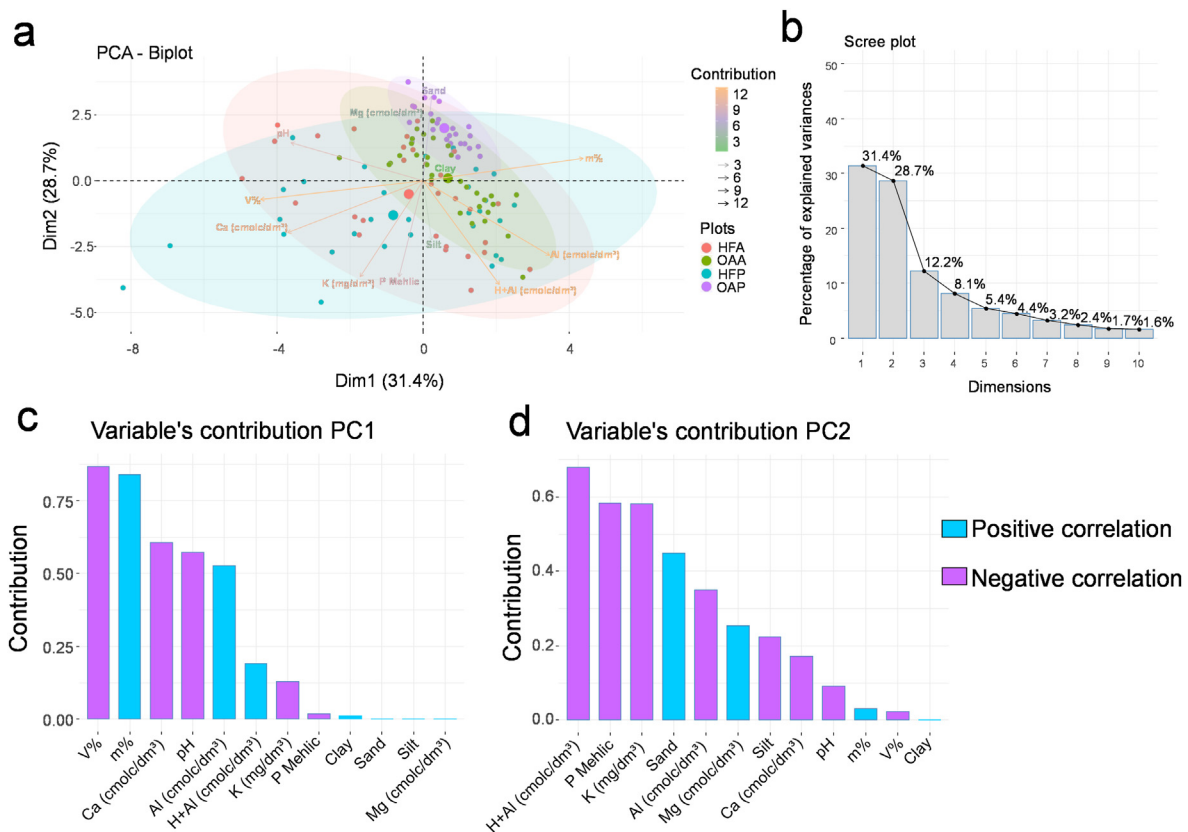


Fig. 3. Principal component analysis (PCA) from soil data (a) and scree plot showing the percentage of explained variances in each dimension (b). Contribution and Pearson correlations of the soil variables to the variances of first (c) and second PCA dimensions (d). HFA = hygrophilous forest Almescla; HFP = hygrophilous forest Peruaçu; OAA = Open area Almescla; OAP = Open area Peruaçu.

with the species diversity (richness: $F = 6.21$, $r = 0.11$, $p = 0.02$; abundance: $F = 140.50$, $r = 0.76$, $p < 0.0001$; Shannon index: $F = 1.15$, $r = 0.03$, $p = 0.29$; Table 1). Regards the hygrophilous forest, the first axis of the NMDS was related to species richness and abundance but not with diversity of species (richness: $F = 5.64$, $r = 0.20$, $p = 0.02$; abundance: $F =$

143.70 , $r = 0.71$, $p < 0.001$; Shannon index: $F = 0.15$, $r = 0.02$, $p = 0.70$). On the other hand, axis 2 only for the abundance of species, was related to open areas (richness: $F = 0.58$, $r = 0.01$, $p = 0.45$; abundance: $F = 4.44$, $r = 0.10$, $p = 0.04$; Shannon index: $F = 0.05$, $r = 0.02$, $p = 0.83$), and for hygrophilous forest, none of the response variables analysed

Table 1

Results from Generalized Linear Models testing the effect of soil variables and NMDS results in richness, abundance, and species diversity in the *vereda* Peruaçu and Almescla.

Response	Predictors	Open area					Hygrophilous forest				
		<i>t</i>	df	<i>F</i>	<i>r</i>	<i>p</i> value	<i>t</i>	df	<i>F</i>	<i>r</i>	<i>p</i> value
Richness	PC1 (soil acidity gradient)	2.35	43	5.53	0.13	0.02	-1.83	58	3.33	0.10	0.07
	PC2 (fertility gradient)	2.10	43	4.41	0.10	0.04	0.10	58	0.01	0.01	0.92
	MDS1	2.49	43	6.21	0.11	0.02	-2.38	58	5.64	0.20	0.02
Abundance	MDS2	-0.76	43	0.58	0.01	0.45	0.37	58	0.14	0.14	0.70
	PC1 (soil acidity gradient)	3.13	43	9.81	0.17	0.003	-1.81	58	3.29	0.10	0.07
	PC2 (fertility gradient)	3.47	43	12.04	0.20	0.001	1.62	58	2.62	0.20	0.11
Shannon index	MDS1	11.85	43	140.50	0.76	<0.001	-11.99	58	143.70	0.71	<0.001
	MDS2	2.11	43	4.44	0.10	0.04	-0.15	58	0.03	0.20	0.87
	PC1 (soil acidity gradient)	1.97	43	3.88	0.10	0.05	-1.72	58	2.95	0.10	0.09
Shannon index	PC2 (fertility gradient)	1.49	43	2.21	0.10	0.14	-0.66	58	0.44	0.01	0.51
	MDS1	1.07	43	1.15	0.03	0.29	0.38	58	0.15	0.02	0.70
	MDS2	-0.21	43	0.05	0.02	0.83	0.23	58	0.05	0.03	0.82

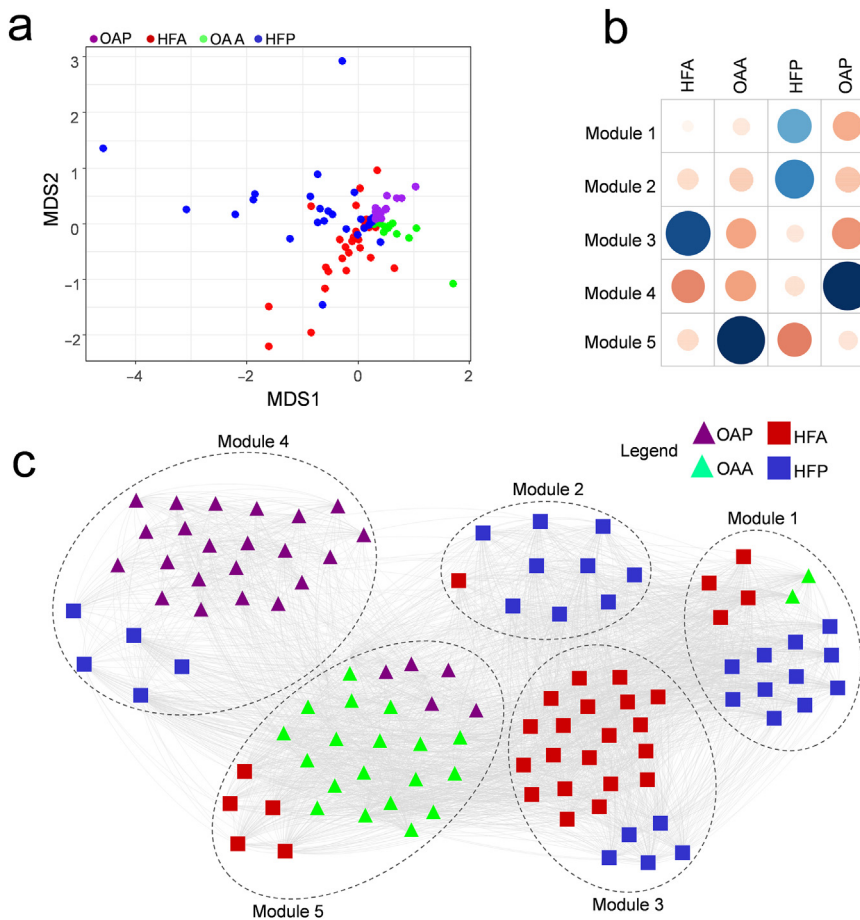


Fig. 4. NMDS results for the plots and areas sampled in the two *veredas* (a); correlation plot showing the association power of the plots composition and the five detected modules in the modularity analysis (b). Blue circles indicate a positive association, expressed by positive Pearson residual values, while red circles indicate a negative association, or negative Pearson residual values; network combining the plots recovered from the two *veredas*. The modular network structure (c), discriminating the open areas and hygrophilous forests distribution. Each module is delimited by circles with dotted lines. The lines connecting the different sampled areas mean that these sites share plant species with each other. Thus, the greater the number of shared species, the greater the number of connections. HFA = hygrophilous forest Almescla; HFP = hygrophilous forest Peruaçu; OAA = Open area Almescla; OAP = Open area Peruaçu. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

showed a significant relationship with the second axis of the NMDS (richness: $F = 0.14, r = 0.14, p = 0.70$; abundance: $F = 0.03, r = 0.20, p = 0.87$; Shannon index: $F = 0.05, r = 0.03, p = 0.82$; Table 1).

This difference in species composition was consolidated by modularity analysis, which was significant ($Q = 0.52$; delta $Q = 0.48$; Fig. 4c–d) and identified 5 modules. Some of the modules included plots from more than one area (Fig. 4c), but in general, the plots of the same area tend to occupy the same module, showing a definition in the species composition between the different modules ($\chi^2 = 158.55, df = 12, p < 0.0001$; Fig. 4c). For instance, modules 1 and 2 were strongly associated with Peruaçu hygrophilous forest plots, module 3 with Almescla hygrophilous forest plots, module 4 with open areas Peruaçu and module 5 with open areas of Almescla plots (Fig. 4c).

4. Discussion

Our results showed that the studied *veredas* were floristically contrasting in terms of the arboreous-shrubby species composition, richness, and diversity. These results have already been reported for the tree stratum when comparing different sites of Cerrado sensu stricto, possibly in response to the interactions among climate, altitude, and soil fertility (Oliveira-Filho et al., 1989; Ratter et al., 2003; Silva et al., 2006). In addition, our results demonstrate that open areas are more likely to vary in species richness, abundance and diversity due to changes in soil acidity and fertility.

The studied *veredas* were relatively rich in tree species when compared with the other palm swamps (Guimarães et al., 2002; Resende

et al., 2013) and other phytophysiognomies dominated by herbaceous-shrubby vegetation, such as moist grasslands (Munhoz and Felfili, 2008). Differently, the species richness was lower than that found in other phytophysiognomies of the Brazilian savannas, such as dry shrub-grassland (Munhoz and Felfili, 2006), possibly due to differences in water content, physical and chemical properties of the soil, and other biotic factors (Bijos et al., 2017). The herbaceous-shrubby layer is a principal component of humid ecosystems, although at the sites where they occur there are diverse, characteristic, and exclusive flora that include a predominance of typical species morphologically and physiologically adapted to survival in saturated environments (Blom, 1999).

However, the high richness of tree species draws attention to an expansion of species from the Cerrado in the open areas of the studied *veredas*, which leads to a mischaracterization of this formation. This expansion of species from the Cerrado may be due to the open area's drainage, which allows for a decrease in species adapted to this condition and the emergence of tree species arising from Cerrado. This can be reinforced by the vegetation profile of the Peruaçu open areas, which has a wide distribution of larger shrub and arboreal species. *Stryphnodendron adstringens*, *Tachigali subvelutina* and *Senna cana* trees are characteristic species of cerrado areas that had high importance values in the open areas of *vereda* Peruaçu. In the *vereda* Almescla, despite the species being more characteristic in open areas in the *veredas*, such as Melastomataceae and Malpighiaceae (*Byrsonima pachyphylla* and *Macaírea radula*), *Curatella americana* has already been expanding its individuals in open areas. This reflects the warning for conservation strategies. Regarding the hygrophilous forest areas, despite the specific characteristics and the greater abundance of tree species compared to the open areas, the results found here show divergence in relation to the composition of tree species between the two *veredas*. This is reinforced by the more advanced drought in the Peruaçu *vereda*, indicating possible future changes in this forest formation. Thus, an expansion of species typical of less saturated environments or a tendency towards a monodominance of species more resistant to changes in the level of the water table (*vereda* drought) will also occur in these areas of hygrophilous forest (Orellana et al., 2012; Rossatto et al., 2012; Villalobos-Vega et al., 2014; Oliveira et al., 2017). The presence of species common in drier areas such as *Astronium fraxinifolium* Schott, *Senegalia langsdorffii* (Benth.) Seigler & Ebinger, *Guarea kunthiana* A. Juss. and *Guarea macrophylla* Vahl already indicates the effect of drying on these forest areas.

The Brazilian Cerrado includes forest, savanna, and grassland formations, so that both forest and savanna communities experience the same climate regime (Ribeiro and Walter, 2008). Soil moisture and fertility levels, as well as geographic proximity, are also important factors contributing to species distributions in those environments (Silva Júnior et al., 2001). Swamp forests, as well as palm swamps, are humid formations within the Cerrado biome, with different surrounding plant communities that will influence their species compositions (Teixeira and Assis, 2011; Menino et al., 2012; Ávila et al., 2016). Thus, in relation the edaphic factors, like the flood, the greater availability of nutrients is generally related to lower species richness and a higher number of individuals (Huston, 1980; Enright et al., 1994; Slik et al., 2010; Ávila et al., 2016). A higher nutrient availability allows faster growth with more biomass accumulation and more individuals, which can trigger exclusive competition leading to reduced species richness (Enright et al., 1994). Despite the negative relationship between species richness and soil fertility in large part of the studies, soil fertility can positively or negatively affect richness and dominance of species (Dupré et al., 2002). This may explain the fact that open areas have a higher incidence of certain species of Melastomataceae and Malpighiaceae, for example.

According to the Brazilian environmental legislation, *veredas* forests are situated in "Areas of Permanent Preservation" and their suppression could only occur in special cases (Kurtz et al., 2013, 2015). Unfortunately, this has not always been enforced, which led to the destruction of a large portion of these forests in Brazil. Swamp forests are a very fragile vegetation (Scarano et al., 1998; Kurtz et al., 2013, 2014), and

particularly sensitive to changes in the flooding regime. When these changes occur due to human activity and become permanent, in addition to rapid degradation, the forests show no natural recovery (Scarano et al., 1998; Kurtz et al., 2014). However, external factors are responsible for changes in these formations. With the effect of climate change that causes drying years (with low rainfall), more warmer periods (Oliveira et al., 2017; Hofmann et al., 2021), the water balance is affected by changes in hydrological processes and leading to drought of these areas in the Cerrado, this process being the main responsible for the modification of these formations. In addition to these changes, it is evident that land use and land cover change in different physiognomies of the undisturbed closed has the potential to modify the groundwater recharge dynamics. These impacts on recharge will depend on the extent of the change in closed physiognomies or cropland expansion areas. Thus, the patterns and aspects discussed above are important to guide the future efforts of conservation and management of *veredas* remnants in and the restoration of disturbed areas. Furthermore, these results make clear the change in the structure of the vegetation in these *veredas*.

5. Conclusions

Thus, assuming that *veredas* are changed in species composition possibly due to local anthropogenic factors which leads to the drought of these formations (water balance effect), we demonstrated that the studied *veredas* were floristically different in terms of the arboreous-shrubby species composition, richness, and diversity. These differences are mainly due to local scale effects that cause drier and warmer periods and to the expansion of the drought in these formations. These anthropogenic effects cause a vegetation modification with the expansion and increase in the abundance of species typical of other areas of Cerrado and resistant to less saturated soils, leading to the collapse of the *veredas*. Finally, future studies should investigate other *veredas* on a broader scale to detect changes in the water table that lead to a consequent change in vegetation structure. In this way, we will have subsidies for the conscientious management and conservation of these areas that represent equilibrium places for the Cerrado biome.

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Competing interests

The authors declare no competing financial interests.

Author contributions

YRFN, IFPA and WVN conducted the conception and design of the work. YRFN, IFPA, OSO, LAF, RSF and WVN conducted data collection. RSF and RMS proceeded identification of the species. CSS conducted statistical analysis and draft of the work. All the authors read and approved the final manuscript.

Availability of data and materials

The authors confirm that if the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository and the data DOI will be included at the end of the article.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Appendix A. Supplementary data

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