The role of topography, climate, soil and the surrounding matrix in the distribution of Veredas wetlands in central Brazil

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Abstract  Wetlands are among the most important ecosystems in the world in terms of endemic biodiversity, carbon storage and hydrological process. Veredas wetlands are distributed across the Brazilian savanna (i.e. Cerrado biome) and are permanently protected areas. Veredas wetlands have a hydromorphic soil, providing water to the main rivers of central Brazil and allowing the occurrence of several endemic species of plants and animals. Although recent studies on biotic and abiotic characteristics have been conducted in several areas of Veredas, the studies are local and there is a lack of information about large-scale patterns. Here we used remote sensing data to explore the role of climate, soil, topography and surrounding matrix explaining Veredas occurrence in the Triângulo Mineiro and Alto Paranáiba (TMAP), a mesoregion of the State of Minas Gerais, Southeastern Brazil. Veredas were more frequent in the western region of TMAP, in areas with lower altitudes, temperature and precipitation seasonality, soil cation exchange capacity, silt and sand content, and slope. Moreover, farming was the most frequent land use in areas surrounding Veredas. Veredas are associated with recharging of the water table and water flow that maintains rivers in the Upper Paraná River water basin. We trust the present assessment will be of help for the development of conservation strategies and biodiversity studies.

Graphical abstract  Research questions, data processing, statistical analysis and illustration of the outputs generated.

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Introduction

Wetlands are ecosystems linked to water availability, covering more than 12 million km² worldwide (Zedler and Kercher 2005). These areas provide important ecosystem services, maintaining environmental quality in terms of biodiversity, carbon sequestration and the water supply in river basins (Engelhardt and Ritchie 2001; Mitsch et al. 2012; Clarkson et al. 2013; Honda and Durigan 2016). Wetlands have lost at least 50% of their natural area since the early 20th century, mainly due to the use of their water by human activities (Davidson 2017). In light of the anthropic abuse of these environments, the Ramsar Convention was drafted in 1971 and was signed by 170 countries to protect a total area of more than 250 million hectares of wetlands (Ramsar 2020). These formations include a wide range of vegetation types, from wet grasslands to wet forests (Burton 2009; Junk et al. 2014; Durigan et al. 2022). Globally, the distribution of wetlands is linked to water content (i.e. both groundwater and soil water contents) due to the elevation of the water table (Hu et al. 2017). Thus, factors such as the carbon cycle budget, topography and precipitation are important to understand wetland occurrence due to high soil water levels in permanently wet soils (Hu et al. 2017).

Brazil has the largest wetland area in the world, accounting for more than 10% of this type of vegetation (ca. 27 million ha) (Ramsar 2020). Federal laws have been formulated to protect these ecosystems, including the Native Vegetation Protection Law (NVPL) (Brazil 2012; Brancalion et al. 2016), which aims to protect the Veredas, a specific type of wetland formation. Veredas are the most important wetland ecosystems in the Cerrado biome of central Brazil due to their large occurrence and unique features and biodiversity (Boaventura...
2007). Among other attributes, the NVPL determines a marginal strip to be protected, with a minimum width of 50 m from the maximum water-table elevation. The Veredas are characterized by a hydromorphic soil and water-table elevation above ground (Boaventura 2007; Ferreira 2008), and in general (but not obligatorily) have a dominance of the Buriti palm (Mauritia flexuosa) associated with a high diversity and endemism of grassy, herbaceous and/or shrubby species (Araújo et al. 2002; Boaventura 2007; Ribeiro and Walter 2008). Veredas are mainly associated with geomorphological features, being distributed in narrow areas along the streamflow (Boaventura 2007). Veredas are of ecological importance, including their unique biodiversity (Silva et al. 2018; Pimenta and Vilela 2021) and hydrological importance in supplying the main Brazilian rivers (Brock et al. 1999). Because of these characteristics, the Veredas represent areas of permanent protection according to Brazilian law (Brazil 2012). However, these environments and their respective surrounding matrices are under intense anthropic activity (Oliveira et al. 2020). Agriculture expansion, soil drainage and pasture are among the several negative management practices that lead to soil leaching, erosion and silting, and that can cause biodiversity losses in Vereda, in both the surrounding matrix and upstream to these areas (Boaventura 2007; de Sousa et al. 2011; Gonçalves et al. 2021). Additionally, there is a lack of studies concerning the land use of Veredas and their surrounding areas. Even though this vegetation type is under legal protection, landowners still use it as a resource of water and grasses for grazing (Oliveira et al. 2020). The use of the surrounding matrix changes the patterns of water percolation through the soil and can cause woody plant encroachment (Guimarães et al. 2017; Ramos et al. 2006), leading to changes in Veredas vegetation structure (Gonçalves et al. 2021).

Veredas differ according to diverse attributes such as lithological classification, soil type, soil granulometry, organic matter content, and vegetation types (Araújo et al. 2002; Ramos et al. 2006; Oliveira et al. 2009a). Some studies suggested that climatic characteristics are associated with the distribution patterns of different vegetation types (Castro et al. 1999; Ratter et al. 2003). In addition, several studies have reported edaphic variables affecting the savanna dynamics on a large scale (Cuni-Sanchez et al. 2016; Tietjen 2016; Venter et al. 2018). However, although Veredas are such an important environment, no studies have focused on their wetland distribution across a wide geographical range.

Some local studies have been conducted on Veredas focusing on plant community (Fagundes and Ferreira 2016; Silva et al. 2016; Bijos et al. 2017; Santos et al. 2018), animal biodiversity (Pereira and Calado 2017; Rodrigues et al. 2018; Fonseca et al. 2018) and abiotic attributes (Borges et al. 2016; Nascimento et al. 2018; Pereira and Figueiredo 2018; Faxina et al. 2019; Rosolen et al. 2019). Moreover, there is evidence suggesting that Veredas can vary from one region to another when it comes to land cover (de Sousa et al. 2011; Rosolen et al. 2015; Sousa et al. 2015), geomorphological surface (Ramos et al. 2006, 2014), plant community (Araújo et al. 2002; Silva et al. 2016), and even fire occurrence (Araújo et al. 2013; Borges et al. 2016). These findings were based on studies of scattered areas of Triângulo Mineiro and Alto Paranaíba (TMAP), the region where Veredas are most studied in the Cerrado on a local scale. Nevertheless, large-scale studies taking into account data from the Veredas are needed to understand their structure and dynamics, and the predominant abiotic characteristics of such areas.

TMAP is one of the regions with a high cover of Veredas in Brazil, comprising 90,545 km². Here we investigated the role of climate, topography, soil properties and surrounding matrix in explaining the distribution of the Veredas in the TMAP region. This region has heterogeneous characteristics concerning climate, topography, hydrological conditions, and land cover. However, Veredas are well delimited by relief and hydrography, and for conceptual and methodological purposes we considered Veredas as defined by Boaventura (2007). The TMAP region is an area of confluence of water basins which form the Paraná River, one of the most important basins in South America both in ecological and economic terms. We aimed to answer the following questions: (I) How are the Veredas distributed in TMAP? Our objective when asking this question is to visualize the pattern of Veredas occurrence in thematic maps. (II) Which are the main drivers of Veredas distribution in TMAP? Based on the definition of Veredas and their characterization by local studies, we hypothesized that their occurrence is related to areas with higher precipitation, clay soil, organic matter and nutrient availability, and lower slope and altitude. (III) Which are the predominant land cover types of Veredas and
their surrounding matrices? Our objective was to provide novel land-cover data for the quantification of Veredas occurrence in TMAP. We hypothesized that both Veredas and adjacent areas would be mostly composed of natural formations (e.g. savanna and forest) rather than anthropic ones (e.g. farming and urban infrastructure).

Methods

Study area

TMAP is a region of Minas Gerais state (Fig. 1) in the Cerrado domain (Azevedo 2019) harboring a diversity of fauna and flora (Drummond et al. 2005). According to the Köppen–Geiger Climate Classification (Alvares et al. 2013), based on climatic similarities (i.e. rainfall, and temperature patterns over the years), the TMAP region can be divided into three climate zones: Aw (tropical zone with dry winter), Cwa (humid subtropical zone with dry winter and hot summer), and Cwb (humid subtropical zone with dry winter and temperate summer).

Data collection and processing

To obtain the Veredas records for the entire region we downloaded georeferenced Veredas polygons provided for each city included in TMAP by the CAR (Cadastro Ambiental Rural—Rural
Environmental Registry) database (Brazil 2012). All data were downloaded between July and October 2020. We made field incursions around Uberlândia/MG (the largest city in TMAP) and determined if the Veredas presence was also recorded in the CAR dataset, GlobCover30, MapBiomas, and Esa Global Land Cover. In this sense, CAR was the most complete dataset since the other sources failed to show as many Veredas records as CAR. This is a remote sensing imagery platform created by the Brazilian Government as a mandatory public electronic registration site to control environmental information of rural properties regarding the situation of permanently protected areas (PPA) (e.g. gallery forest, riparian forest and wetlands, including Veredas) for environmental and economic planning. The CAR database is updated by technicians hired by landowners, the data are submitted to the Brazilian government, and each delimitation of the areas is their responsibility. Analyses concerning the accuracy of the CAR database were not the aim of the present report; however, different studies have been conducted in order to understand how the limitations are identified in the CAR database (Gontijo et al. 2019; Oliveira et al. 2020; Santos 2018).

We preprocessed the georeferenced polygons of each Vereda by merging all of them into a single unit. We corrected sliver polygons (i.e. small areas of spatial overlays with different features) and deleted the overlapping polygons. For this process, we created a topology in a feature dataset with the Veredas polygons and used it to identify the topology errors based on the rules created, i.e., excluding every sliver polygon and overlapping polygons. We then merged the overlapping polygon into another polygon and we revalidated the topology to ensure that the edition was successful (adapted to ArcGIS from Kukulska et al. 2018). This processing was performed due to the limitation of accuracy from the CAR dataset, since each landowner is required to upload his Veredas polygons into the government system, which might use different ways to delineate this type of vegetation, e.g. Garmin® GPS and GPS total station.

After compiling all Veredas records, we selected Veredas polygons with at least 1 km perimeter to set the minimum area that could be identified by our abiotic variables. To standardize our datasets, we based them on the Veredas presence for the Köppen’s climate classification with a smaller sample size, which was Cwb, for a total of 227 records. After establishing this minimum, we created a balanced sampling design by randomly selecting 454 points for each Köppen’s climate classification, 227 of which had the presence of Veredas and 227 had no Veredas (Graphical abstract). Our aim here was to show the Veredas differences from other vegetation types, whether savanna, forest or others. To delimit the Veredas absent polygons, we calculated the mean area of the 227 Veredas present per climate type and used this area to perform a buffer around each Veredas absent point. All statistical analyses were performed considering only the randomized areas.

To characterize the abiotic factors of the Veredas we created climatic, edaphic, and topographic maps. For the climatic maps, we used the Köppen–Geiger Climate Classification (Alvares et al. 2013) regarding variables such as average annual temperature (°C), annual rainfall precipitation during the driest quarter (mm), precipitation during the wettest quarter (mm) and precipitation seasonality (coefficient of variation—CV). Temperature seasonality data (CV) were extracted from WorldClim (Fick and Hijmans 2017) at 30 arc-seconds resolution (~1000 m). We extracted edaphic data including cation exchange capacity (cmol+ kg−1), clay (%), silt (%), sand (%), soil organic carbon (g kg−1) contents, soil pH, and organic carbon stock (ton ha−1) using SoilGrids™ database (Hengl et al. 2017) at 8 arc-second resolution (~250 m). Topographic altitude (m) and slope (°) data were downloaded from the Shuttle Radar Topography Mission (SRTM) at 1 arc-second resolution (~30 m) (NASA and NGA 2000) (Graphical abstract). All datasets used were chosen by consulting the literature and considering the most accurate spatial data.

To extract the average values of all variables for each Vereda, raster images from SoilGrids™ and WorldClim were converted to points and a spatial join/overlap with the Veredas of the TMAP region was used as a target. To standardize our data, we resampled all variables at 30 arc-second resolution (~1000 m) using a cubic convolution algorithm (Keys 1981) and for data processing we used ArcGIS® 10.5 (ESRI 2019).

**Veredas land cover**

We used the database from MapBiomas v. 4.1 (Souza et al. 2020) to evaluate the Veredas land cover and the
surrounding matrix (i.e. areas of a 50 m buffer around Veredas). This platform employs a machine-learning algorithm using mosaics from the Landsat program with time intervals defined according to the variation of the phenology of the plant types in order to improve land cover characterization (Azevedo 2019). The buffer of 50 m from the Veredas polygon limits was used to extract the values of land cover within each Vereda. We chose these values based on the Native Vegetation Protection Law (NVPL) which establishes that, in order to be conserved, the Veredas PPAs have to be accompanied by a marginal strip of a minimum width of 50 m established from the permanently wet and damp soil (Brazil 2012). This approach allowed us to characterize and compare not only the first 50 m of the Veredas but also the land cover of the respective surrounding areas. To determine the values of the land cover of the surrounding areas we excluded the area of the Veredas and characterized the land cover by converting the MapBiomas raster to georeferenced polygons, which permitted us to aggregate the classifications into the five categories available: forest formation, savanna formation, farming, urban infrastructure, and water coverage. We point out that Veredas are a specific type of vegetation which might involve different land uses classified into the five categories of MapBiomas. Image processing was conducted using ArcGIS® 10.5 in this and all previous topics (ESRI 2019).

Statistical analysis

To evaluate the main drivers of the Veredas distribution, we extracted the mean values of climatic, edaphic, and topographic variables for each area described previously using the R-package FactoMineR version 1.39 (Husson et al. 2017) and submitted them to principal component analysis (PCA). This procedure allowed us to reduce dimensionality, to evaluate associations between variables, and to visually detect the most contributive ones. We used a correlation matrix because our variables were on different scales (Abdi and Williams 2010). To normalize the data we used logarithmic transformations of cation exchange capacity, carbon stock, carbon content and mean slope (adding 0.1 to this due to zeros). The presence/absence of Veredas according to each climate classification was treated as a supplementary variable in order to draw ellipses visually showing the difference between groups.

To determine whether the abiotic local factors differed according to the presence/absence of Veredas, climate type (Aw, Cwa or Cwb) and the interaction term we performed a two-way Permutational Multivariate Analysis of Variance (PERMANOVA; 10,000 iterations) based on a Euclidean distance using the R-package vegan version 2.5-6 (Oksanen et al. 2019). We first checked for multicollinearity among the predictor variables by assessing their variance inflation factors (VIFs) using the R-package usdm version 1.1.18 (Naimi 2017) and successively removing variables with the highest VIFs until all were < 3 (as suggested by Zuur et al. 2010). After removing the sand content, precipitation during the wettest month, elevation, precipitation seasonality, carbon stock, mean temperature and clay content variables (in this order), all remaining VIFs were ≤ 2.21. We conducted a post-hoc multilevel pairwise analysis with Bonferroni correction using the R-package pairwiseAdonis version 0.3 (Martinez Arbizu 2018).

Differences in the aforementioned abiotic variables according to the same fixed effects (Veredas presence/absence, climate type and the interaction term) were assessed separately by analysis of variance (ANOVA) for each variable, keeping the logarithm corrections previously used for some variables. However, since some variables were proportional (i.e. clay, sand, and silt contents and mean slope), we employed a generalized linear model (GLM, in the R-package glmmTMB) adjusting a beta distribution, which is appropriate for this kind of data (Stroup 2012). We calculated proportions by dividing values by their theoretical maximum. Thus, clay, sand and silt contents were divided by 100, and the mean slope by 90°. We still added a constant of 0.0001 to run the model because the beta distribution does not allow values equal to 0.

The significance of the models was determined by the F and \( \chi^2 \) tests for ANOVAs and GLMs, respectively, adjusting a type II sum of squares in the R-package car (Fox and Weisberg 2020). The fit of the models was checked visually using the QQ plot of residuals and the plot of residuals vs. predicted values by simulating the residuals 250 times in the R-package DHARMA (Hartig 2020). Post-hoc analyses were conducted using Tukey-adjusted comparisons in the R-package emmeans version (Lenth et al. 2020). Since we were interested in differences between areas
with and without Veredas within each climate type, we conducted contrasts conditioning on the latter.

Finally, we employed a chi-square test to determine the predominant land cover types in Veredas and also in their surrounding matrices in the TMAP region. After finding a significant result, we ran separate chi-squared goodness of fit tests for each vegetation type. We used the `p.adjust` function in the R stats package to apply the false discovery rate adjustment to p-values (Benjamini and Hochberg 1995) and to avoid type I error. All statistical analyses were conducted using R software version 3.6.0 (R. Core Team 2019).

### Results

#### Abiotic characteristics of Veredas

The Triângulo Mineiro and Alto Paranaíba (TMAP) region contain 6782 Veredas covering 765.4 km² out of a total area of 90,545 km². We found that the distribution of Veredas was variable across the studied area. They appeared to be concentrated in two clusters, the major one located in the western area of the TMAP region and the second located in the northwestern area of the same region (Fig. 2a).

Climatic, edaphic, and topographic variables were associated with Veredas occurrence within the TMAP region. The variation in such factors suggests that specific conditions may be required for, or are related to the occurrence of Veredas and the establishment of their typical vegetation type. The Aw climate is the most common in the TMAP region, occupying 44,521 km² of the total area and occurring throughout the western region (Fig. 2b). The eastern region is dominated by Cwa (21,713 km²), which transits to Cwb (24,311 km²), more common in the extreme east. Climate type thus seems to be related to Veredas distribution (Fig. 2b). The Veredas area with the Aw climate was 4808 km², followed by 825 km² in the area with the Cwa climate and 340 km² in the area with the Cwb climate.

![Fig. 2 Veredas and climate in Triângulo Mineiro and Alto Paranaíba (TMAP). a Veredas distribution map, and b Köppen–Geiger climate classification of the TMAP region](image)
The following climatic variables occur in the Veredas areas within the TMAP: a mean temperature of 19.38 °C (± SD ± 7.75 °C) (Fig. 3a) and a mean annual precipitation of 1255.70 mm (± 508.13 mm) (Fig. 3b). The topographic variables revealed that the Veredas of the TMAP are located at a mean altitude of 549.93 m (± 263.14 m) (Fig. 3c) with a mean slope of 0.25° (± 0.20°) (Fig. 3d). Finally, the edaphic variables show that the area under study has a mean carbon content of 8.37 g kg⁻¹ (± 4.32 g kg⁻¹) (Fig. 3e), a mean carbon stock of 46.05 ton ha⁻¹ (± 19.43 ton ha⁻¹) (Fig. 3f), a mean cation exchange capacity of 5.47 cmol⁺ kg⁻¹ (± 2.66 cmol⁺ kg⁻¹) (Fig. 3g), a mean clay content of 29.93% (± 13.54%) (Fig. 3h), a mean pH of 4.65 (± 1.85) (Fig. 3i), a mean sand content of 44.60% (± 19.64%) (Fig. 3j), and a mean silt content of 11.78% (± 5.30%) (Fig. 3k).

Factors explaining Veredas distribution

When analyzing the relationships among these variables, we found that the first PC axis explained 45.13% of data variance while the second PC axis explained 14.30% and the third explained 11.50% (PC1 + PC2 + PC3 = 70.93%) (Fig. 4). The main variables explaining PC1 were precipitation during the wettest quarter (explaining 12.09% of PC1), elevation (11.55%), soil sand content (11.43%), mean annual temperature (10.77%), soil clay content (10.77%), and mean annual precipitation (9.22%).
The main variables explaining PC2 were soil cation exchange capacity (25.38% of PC2), soil carbon content (16.71%), soil pH (12.95%), and soil carbon stock (12.41%). The main variables explaining PC3 were precipitation during the driest quarter (34.11%) and seasonal precipitation (29.16%). By visualizing the biplot (Fig. 4), we found that areas with the presence of *Veredas* showed a high overlap with areas with the absence of *Veredas* in each respective climate (Fig. 4). This corroborates the nonsignificant effects of the presence/absence of *Veredas* according to the abiotic variables in the Euclidean space (PERMANOVA: pseudo-$F_{1,594} = 2.88; p=0.085$). In the PCA, the ellipses of the Aw climate were located at one extreme of the biplot and were related to higher values of precipitation during the driest quarter, seasonal temperature, mean temperature, pH, and sand content. At the other extreme of the biplot, we found that Cwb climate was related to higher elevation, soil clay content, mean annual precipitation, mean precipitation during the wettest quarter, and seasonal precipitation. Cwa was located in the middle of the biplot with intermediate values when compared to the other two climate types. This arrangement is in agreement with that found in the areas of occurrence of each climate type (Fig. 2a). Similarly, we found a significant effect of climate type in the PERMANOVA (pseudo-$F_{2,594} = 361.39; p<0.001; R^2 = 0.54$; Fig. 4), with all climate types being different from each other ($p<0.05$ in all pairwise contrasts). We also found a significant effect according to the interaction term (pseudo-$F_{2,594} = 10.11; p<0.001; R^2 = 0.02$; Fig. 4), although it explained a much smaller amount of variance. In post-hoc tests, we did not find differences when comparing Aw with *Veredas* vs. Aw without *Veredas* and also when comparing Cwb with vs. Cwb without *Veredas*. All other pairwise comparisons were significant.

Considering the separate tests for each variable, we found that mean annual precipitation showed significant differences according to the Köppen climate classification (Table 1). The mean annual precipitation in
the Cwb climate was 2.61% higher than in Cwa and 10.79% higher than in Aw. The mean annual precipitation in Cwa was 7.97% higher than in Aw (Table 1).

Although Veredas occurrence did not show differences, the interaction term indicated differences when contrasting the presence vs. absence of Veredas in Aw (p = 0.007) and Cwa (p < 0.001) (Table 1). Mean precipitation was 1.54% higher in areas with no Veredas in Aw and 1.89% higher in areas with Veredas in Cwa (Table 1).

Mean annual temperature differed between climate classifications, with Aw being 2.62 °C and 1.37 °C higher than Cwa and Cwb, respectively, and Cwa being 1.25 °C higher than Cwb (Table 1). We did not find any significant effect concerning the interaction term (Table 1). This result shows that annual temperature is one factor that can be a driver of Veredas presence since higher temperatures can be linked to this vegetation type.

Precipitation during the driest quarter differed according to Veredas occurrence, being 7.55% higher where Veredas were present (Table 1). The interaction term, considering climate types, i.e., Aw, Cwa and Cwb, and Veredas occurrence, was also significant, with Cwa (p < 0.001) being 24.68% higher for areas with the presence of Veredas (Table 1). This result shows that precipitation is one of the factors that can drive the presence of Veredas, with higher precipitation during the driest months being linked to this occurrence.

During the wettest quarter, precipitation differed according to the occurrence of Veredas, being 0.82% higher where Veredas were absent (Table 1). There were no significant effects regarding the interaction term (Table 1), showing that precipitation during the wettest months was not linked to the presence of Veredas in each classification type, so that higher levels of precipitation during the wettest months were not a factor regarding the occurrence of Veredas.

Areas with Veredas had 1.61% higher precipitation seasonality than areas without this vegetation (Table 1). The interaction term was also significant, with Cwa (p < 0.001) showing 3.98% higher values for areas without Veredas (Table 1). This result shows that Veredas mainly occur in areas with lower differences in precipitation between seasons, indicating that the presence of Veredas may be linked to lower

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Table 1  Possible environmental drivers of Veredas

| Variable                        | Climate | Cwa | Cwb | Cwa | Cwb | Aw | Climate | Cwa | Cwb | Aw | Interaction |
|---------------------------------|---------|-----|-----|-----|-----|----|---------|-----|-----|----|-------------|
| **Descriptive (mean ± SD)**     |         |     |     |     |     |    |         |     |     |    |             |
| Mean precipitation (mm)         | 1436.11 ± 82.29* | 1550.60 ± 46.42* | 1591.10 ± 38.59* | 1528.59 ± 90.80* | 1523.28 ± 85.54* | 383.11 | < 0.001 | 1.25 | 0.26 | 9.59 | < 0.001 |
| Mean temperature (°C)           | 22.76 ± 0.50* | 21.39 ± 0.51* | 20.14 ± 0.52* | 21.53 ± 1.14 | 21.32 ± 1.22 | 1374.82 | < 0.001 | 25.66 | < 0.001 | 0.56 | 0.57 |
| Precipitation of driest quarter (mm) | 51.65 ± 9.35* | 44.17 ± 15.42* | 41.73 ± 12.09* | 47.31 ± 13.12 | 43.99 ± 12.95 | 31.34 | < 0.001 | 11.12 | < 0.001 | 13.14 | < 0.001 |
| Precipitation of wettest quarter (mm) | 790.57 ± 38.73* | 797.45 ± 23.62* | 825.64 ± 18.72* | 781.32 ± 49.4 | 787.89 ± 48.02 | 650.05 | < 0.001 | 7.94 | 0.05 | 4.07 | 0.02 |
| Precipitation seasonality (CV)  | 79.08 ± 2.77* | 81.98 ± 4.52* | 82.83 ± 3.61* | 80.65 ± 3.75 | 81.95 ± 4.09 | 62.89 | < 0.001 | 20.59 | < 0.001 | 14.21 | < 0.001 |
| Temperature seasonality (SD*100) | 184.35 ± 9.03* | 166.64 ± 10.03* | 172.35 ± 13.44* | 171.73 ± 13.53 | 177.17 ± 12.47 | 154.12 | < 0.001 | 41.82 | < 0.001 | 22.60 | < 0.001 |

Results from linear models applied to the abiotic variables to test the effects of climate type, of Veredas presence/absence or the interaction term. Shaded cells indicate specific tests of our hypotheses. Asterisks (*) indicate variables with log correction applied. Different superscript letters in climate type levels indicate significant differences at the 0.05 level. F and χ² (in italic) statistics refer to ANOVAs and GLMS with beta distribution, respectively.
ranges of precipitation, which keeps the soil wet throughout the year.

Temperature seasonality was 2.80% higher where Veredas were absent (Table 1). The interaction term indicated differences in Cwa (p < 0.001) and Cwb (p < 0.001), where temperature seasonality was 5.55% and 6.59% higher in the absence of Veredas, respectively (Table 1). This result shows that Veredas mainly occur in areas with lower differences in temperature between seasons, indicating that the presence of this vegetation may be linked to lower temperature ranges, which are also important by keeping the soil wet throughout the year.

Neither the presence/absence of Veredas nor the interaction term had significant effects regarding the carbon content of the soil (Table 1), showing that this variable was not linked to the presence of Veredas in our study area.

Similarly, carbon stock had no significant effects regarding the presence/absence of Veredas or the interaction (Table 1), again showing that this variable was not linked to the presence of Veredas in our study area.

Cation exchange capacity was 8.83% higher in areas with the absence of Veredas than in areas with the presence of this vegetation (Table 1), with no significant effect according to the interaction term (Table 1). Thus, according to our results, lower cation exchange capacity may be linked to the presence of Veredas.

Clay content did not differ according to the presence/absence of Veredas (Table 1). Regarding the interaction term, we found that clay content was 10.97% higher where Veredas were absent in the Aw climate (p < 0.001) (Table 1). Thus, according to our results, lower soil clay content may be linked to the presence of Veredas in some regions (here, Aw climate classification).

Although we did not find effects on pH according to the presence/absence of Veredas, the interaction term was significant, with pH being 0.50% higher in the absence of Veredas for the Aw climate (p = 0.04) (Table 1). Thus, lower soil pH may be linked to the presence of Veredas in some regions (here, Aw climate classification).

Sand content was 3.06% higher when Veredas were present. The interaction term results indicated a difference within Aw (p < 0.001), where sand content was 9.76% higher in the presence of Veredas (Table 1). Thus, higher soil sand content may be linked to the presence of Veredas in some regions (here, Aw climate classification).

Silt content was 6.73% higher in the absence of Veredas (Table 1). According to the interaction term, we found that in Aw (p < 0.001) and Cwa (p < 0.001) silt content was 10.77% and 9.52% higher, respectively, where Veredas were present (Table 1). Thus, higher soil silt content may be linked to the presence of Veredas in some regions (here, Aw and Cwa climate classifications).

Regarding altitude, areas with the absence of Veredas were 2.03% higher (Table 1). The interaction term was not significant (Table 1). Veredas can occur
at different altitudes, although in general their presence may be linked to lower altitudes.

Slope also showed significant differences in the occurrence of Veredas, being 16.67% higher where Veredas were absent (Table 1). Considering the interaction term, we found a significant effect within Cwb, where slope was 15.26% lower in the presence of Veredas than in the absence of this vegetation (Table 1). Slope indicates that Veredas are more prone to occur in flat areas, considering that their occurrence is linked to the bottom of a valley (Boaventura 2007).

Veredas land cover

Concerning the land cover in Veredas, farming was the most representative activity (41.5%), followed by forest and savanna formations (35.2% and 22.6%, respectively) (Fig. 5). Urban infrastructure (0.1%) and water coverage (0.6%) represented the smallest proportions. Accordingly, in areas surrounding Veredas, farming also represented most of the land cover (65.2%), followed by savanna (18.4%) and forest formations (12.8%). Urban infrastructure (1.3%) and water coverage (2.4%) represented the smallest proportions.

Land cover percentages differed between Veredas and the surrounding areas ($\chi^2 = 14.99$, df=4, $p = 0.005$, Fig. 5). Pairwise tests showed that farming areas were larger in surrounding areas than within Veredas ($\chi^2 = 5.43$, df=1, $p = 0.049$) and forests were larger within Veredas than in surrounding areas ($\chi^2 = 5.45$, df=1, $p = 0.049$). We did not find significant differences concerning savanna formation, urban infrastructure or water coverage (all $p > 0.05$).

Discussion

In this study, we showed that Veredas in the Triângulo Mineiro and Alto Paranaíba (TMAP) are concentrated in the west of the region, where the Aw climate prevails. The occurrence of Veredas is negatively associated with altitude, temperature and precipitation seasonality, cation exchange capacity, silt content, altitude and slope, and positively associated with sand content. Moreover, the assessment of Veredas’ land cover showed that even with the current policies for wetland management in Brazil, farming is the predominant land use/land cover in areas of Veredas. Moreover, the high proportion of forest formation within Veredas indicates woody plant encroachment (WPE) (i.e. the progressive increase in tree cover in natural open vegetation areas). Since Veredas areas are associated with water recharging and provisioning, we hope that our findings can stimulate the development of conservation strategies and further studies. Below, we discuss in detail our findings and their consequences.

Abiotic characteristics explaining Veredas distribution

The floristic, geologic and hydrologic attributes of Veredas in the TMAP region have been extensively studied for decades, focusing on local approaches (Araújo et al. 2002; Guimarães et al. 2002; Oliveira et al. 2009a; Resende et al. 2013; Fagundes and Ferreira 2016; Nascimento et al. 2018; Pereira and Figueiredo 2018). However, studies dealing with a general overview of Veredas distribution and their correlates are still lacking. Despite the small proportion of Veredas area in the TMAP region (0.008%), they are still the most important resource for water stocking and availability for wildlife and human activities. This is especially important during the dry season when the water table regulates the flow of surface water downgrades (Ramos et al. 2006; Nascimento et al. 2018). According to our results, climatic, edaphic, and topographic characteristics are notably different between the eastern and western areas of the TMAP. Abiotic variables contributed to the occurrence of Veredas and their distribution differences in the region. This process of water movement is key to maintaining the emergence and recharging of the water table and supplying the rivers of central Brazil that flow to other parts of the country (Honda and Durigan 2016). Additionally, the area between rivers (i.e. the inside area of basins) functions as a recharging region providing storage and slowing the water flow from the basins (Mokadem et al. 2018; Costa et al. 2019; Achu et al. 2020).

The western TMAP region, with the highest distribution of Veredas, is dominated by the Aw climate, a tropical type with two well delimited tropical seasons (dry winter and wet summer), which is widespread in Neotropical savannas (Sarmiento and Montaço...
from other areas where Veredas were absent were carbon stock and carbon content. These variables have been reported to be higher as a result of the type of vegetation found in Veredas compared with other areas (Bernoux et al. 2002) since the accumulation of soil organic matter is higher in wetlands than in other vegetation types (Sahrawat 2003). However, the results indicated that the soil carbon stock and content of Veredas were similar to those of areas in which Veredas were absent. This may be explained by factors associated with the changes in carbon content in the soil, such as WPE, waterlog-restricted above versus below ground biomass accumulation, and fire frequency (Fidelis and Fernanda 2013; Neil and Kerrylee 2014).

The eastern TMAP region is characterized by rugged topography with high altitude, while the western area shows the opposite, with almost a plateau with lower altitude and where the distribution of Veredas is higher. The altitude of the eastern region may have enabled water drainage from the eastern to the western TMAP, where the slope is reduced. This represents an ideal condition for water emergence and waterlogging. Thus, the occurrence of Veredas may be a consequence of this process. Topographic variables were expected to be the most important factors of Veredas distribution since outcroppings of the water table determine the existence of this physiognomy (Ribeiro and Walter 2008; Augustin et al. 2009). As expected, altitude and slope were lower in Veredas areas, since this environment is associated with the emergence of groundwater, which naturally occurs in flat lowland areas.

Our results showed that the existence of Veredas is determined by the three groups of variables examined, i.e. climatic, edaphic, and topographic factors, and also by the related occurrence of different climate types. The different climate types in Veredas may lead to subclasses of this particular vegetation, resulting in a range of hydrological and abiotic variables (Malthby and Barker 2009; LePage 2011) within the TMAP region. Altogether, our data indicate a pattern of Veredas distribution throughout the range of the TMAP region. This is especially important in a climate change scenario where Cerrado temperature increases and precipitation decreases (Vose et al. 2005; Strassburg et al. 2017; Hofmann et al. 2021). Thus, Veredas tend to become drier, groundwater tends to decrease the flow of the rivers from central

Veredas are known for their distinct soil properties, displaying high levels of organic carbon, low soil granulometry, and permanently wet soil (de Sousa et al. 2011; Wantzen et al. 2012). Concerning the edaphic variables, carbon content, carbon stock, cation exchange capacity, and clay and silt contents show an overall pattern of higher values in the eastern area of the TMAP, while pH and sand content have higher values in the opposite area. This pattern of edaphic characteristics highlights the heterogeneity throughout the range of the study area, and the existence of Veredas is possibly driven by these variables. Sand content was higher in Veredas areas, while cation exchange capacity and silt content were lower. The soil characteristics of Veredas were expected to be different from other Cerrado areas since they are under different conditions (i.e. permanently flooded) and support typical vegetation linked to particular soil characteristics (Ramos et al. 2006). These differences are reported here in several variables, such as higher sand content and lower cation exchange capacity for Veredas, indicating that these areas are more prone to losing nutrients and organic matter by leaching (Johnston 1991; Davis et al. 2006). Moreover, the edaphic properties that we expected to be different

1975; Beck et al. 2005). This climate zone has precipitation and temperature patterns suitable for the development of Veredas’ typical flora (e.g. Mauritia flexuosa (Urrego et al. 2016). Here we show that higher precipitation associated with topographic variables (i.e. lower altitude and slope) is related to Veredas distribution across climate types (i.e. higher densities in Aw), also when comparing areas with Veredas present to those in which they are absent. This makes sense since these conditions probably help to maintain the area permanently wet and avoid WPE, positively affecting the survival of shrub-herbaceous and grass species. During the driest quarter (i.e. during the dry season), precipitation was higher where there were Veredas, while precipitation during the wettest quarter (i.e. during the wet season), precipitation seasonality, and temperature seasonality were lower in Veredas areas. This demonstrates that the climate seasonality pattern is one of the most important factors determining the occurrence of Veredas over a large geographical area like the TMAP, which is in agreement with the maintenance of permanently wet soils, releasing water during the dry season and recharging during the rainy season (Jasechko et al. 2014).

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Brazil and WPE tends to increase, leading to the loss of this important environment.

Veredas land cover

*Veredas* shelter more natural formations (i.e. forest and savanna) than their surrounding counterparts. However, even with the protection of these areas by Brazilian law, we found that more than 40% of the total *Veredas* area is currently used for farming. The indiscriminate use of wetlands is an international issue (King et al. 2021), and in Brazil it can be explained by the stimulus to *commodities* production since the 1970s (Pereira 2012). In addition to the agricultural expansion, during the military dictatorship, the Brazilian government promoted the use of wetlands, including Veredas, in a disastrous program “*Provárzeas Nacional*” (Brazil 1981), which was supported by farmers and even by a few researchers (Reis and Rassini 1985). More recently, as the demand for irrigation water increased, the *Veredas* soil began to be drained, becoming non-hydromorphic and facilitating WPE and vegetation changes (Venter et al. 2018; Borghetti et al. 2019). Farming is the most common land cover in both areas, *Veredas* and the surrounding matrix, showing that this vegetation type is threatened, even more considering that most of the natural land cover within *Veredas* is also dominated by forest formation.

We found that farming, forest formation, and urban infrastructure, a non-typical land cover for this ecosystem, accounted for more than 80% of *Veredas*’ land cover. Savanna is usually the most representative land cover of *Veredas* due to its specific formation associated with herbaceous-shrubby species and/or grassland formations (Boaventura 2007; Ribeiro and Walter 2008). However, *Veredas* were found to contain more forest formation than savanna, indicating that these ecosystems may be experiencing a process of WPE, as described for several areas in the Cerrado biome (Rosan et al. 2019; Gonçalves et al. 2021). These land use results are problematic for *Veredas* conservation since human-mediated drainage of groundwater turns the hydromorphic soil into drier ground, boosting the species turnover. The typical *Vereda* herbaceous-shrubby species adapted to year-round hydromorphic soils are progressively replaced by woody species with higher transpiration potential, accelerating even more soil desiccation (Knoop and Walker 1985; Drew 1997; Osawa et al. 2020). In the long term, this dynamic behavior reduces both plant taxonomic and functional diversity (Brock et al. 1999; Honda and Durigan 2016) since *Veredas* with permanently flooded soil have higher species diversity (Oliveira et al. 2009a). Thus, due to their importance, the conservation of *Veredas* and overall wetlands has been stressed in several reports (Singh et al. 2019; Oliveira et al. 2020; Otte et al. 2021).

Comparatively, the surrounding matrix areas are even in worse conditions. We have refuted our hypothesis of higher coverage of natural formations in *Veredas* environments. Although the NVPL postulates the conservation of such environments, we found that farming alone comprised 65% of the total surrounding area. It is known that recharge of the water table level is based on the water percolating through the soil, which requires native vegetation (Jasechko et al. 2014). Without it, the soil becomes drier and leaching brings particulate matter into *Veredas* areas, causing siltation (Zedler and Kercher 2005). The presence of forest formations in the surrounding areas (18%) represents another problem since plants from this formation have high transpiration and reduce soil water content (van Auken 2009; Neil and Kerrylee 2014). Thus, our results highlight that we may expect a progressive reduction of *Veredas* areas, at least in the TMAP region since most land cover types both within *Veredas* and the surrounding matrix do not contribute to water conservation.

**Conclusion**

The conservation of *Veredas* depends on understanding their characteristics and dynamics. Although *Veredas* are considered to be wetlands, they have specific hydrological biotic and abiotic settings, differing in general from other wetlands due to their particular flora. The TMAP region has a heterogeneous range of abiotic factors that drive the distribution of *Veredas*. Our study is the first to take a general approach to these environments over a wide geographical area. Since little attention has been paid to large-scale assessments so far, we provide an important basis for further studies, especially those related to *Veredas* management and conservation. Our results highlight that the favorable environments for *Veredas* occurrence are linked to several climatic, edaphic
and topographic variables, with soil carbon content and carbon stock being the only variables that do not influence the occurrence of Veredas in our study area. In addition, we report that farming and forest formation are the most common land covers for both Veredas and the surrounding matrix, representing a source of concern. This is valuable information for Veredas management since these areas are supposed to be conserved by law, although the presence of anthropic activities and woody plant encroachment shows that the protection of such vegetation types is compromised. Also, Veredas conservation and the consequences of desiccation may be particularly important in the TMAP region, which involves the confluence of water basins that form the Paraná River and have been intensely used for hydroelectric power. We call attention to the great threat to the conservation of such environments posed by human activities both within the Veredas and their respective surrounding matrix (e.g., pasture, agriculture, and urbanization). The information provided here about the soil characteristics and the general land cover of the Veredas can help the government, NGO and other entities to develop conservation strategies and biodiversity studies regarding land management and Veredas restoration plans. Our suggestion for future wide-scale research on Veredas is divided into two main categories: identification of the areas of their possible occurrence and assessment of their conservation status based on the role of climatic, edaphic, topographic and surrounding matrices in the entire Cerrado biome. Furthermore, complementary studies assessing WPE over time and space in Veredas will be important to evaluate vegetation dynamics in this environment.

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Data availability Data are all derived from public sources.

Code availability N/A.

Declarations None.

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