



UNIVERSIDADE DE BRASÍLIA
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

TAXONOMIC AND PHYLOGENETIC DIVERSITY OF HERBACEOUS-SHRUB
SPECIES IN *VEREDAS* (BRAZILIAN SAVANNA PALM SWAMPS) AND
FACTORS THAT DETERMINE THEIR COMPOSITION AND DISTRIBUTION



Vereda dos Ingleses, Chapada dos Veadeiros, GO

Picture: Natália Bijos

Natália Rodrigues Bijos

Brasília - DF, 2024



UNIVERSIDADE DE BRASÍLIA
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

TAXONOMIC AND PHYLOGENETIC DIVERSITY OF HERBACEOUS-SHRUB
SPECIES IN *VEREDAS* (BRAZILIAN SAVANNA PALM SWAMPS) AND
FACTORS THAT DETERMINE THEIR COMPOSITION AND DISTRIBUTION

Natália Rodrigues Bijos

Tese de Doutorado apresentada ao programa de
Pós-Graduação em Ecologia da Universidade de
Brasília como critério para obtenção do título de
Doutor em Ecologia

Orientadora: Dra. Cássia Beatriz Rodrigues Munhoz

Brasília - DF, junho de 2024

AGRADECIMENTOS

À minha orientadora, professora e amiga, Dra. Cássia B. R. Munhoz, por ter me apresentado ao universo das veredas, 15 anos atrás, durante a graduação e seguir me orientando até hoje, sempre confiando, me incentivando, me desafiando e contribuindo para a construção do meu potencial como pesquisadora. Agradeço a amizade, as aventuras vividas no campo, o apoio, os conselhos, por me apontar na direção certa e pela convivência dentro e fora da vida acadêmica. Mesmo com as dificuldades vividas, sempre que possível, estava disposta a ajudar quem precisasse. Gratidão por estar ao meu lado, me auxiliando em todas as etapas deste trabalho.

À minha família (mãe, pai, Elaine, Cecília, Ana Clara), agradeço por terem acompanhado todo meu processo na pós-graduação, sempre me incentivando, me apoiando e confiando que eu entregaria um ótimo trabalho.

À minha família afetiva (Katia, Telma, Joca, Dona Fátima, Eliel, Catarina e Malu), por terem me acolhido com carinho e amor, pela convivência tranquila, risadas, descontrações, conselhos valiosos, incentivos, confiança e muita paciência ao longo dessa minha jornada.

Aos meus gatos (Floriano, Olívia, Oliver, Gregório, Orlando, Maria Vanúbia e Ronilson (*in memoriam*), por serem sempre carinhosos e me lembrarem o quanto é saudável fazer uma pausa de vez em quando e apenas apreciar a simplicidade do momento presente.

Aos mestres e à comunidade Zen Budista, cujos ensinamentos me auxiliam a manter minha mente saudável, meus pés no chão e focar no momento presente.

Ao Dr. Eliel de Jesus Amaral, pela amizade, paciência, ajuda nos campos, revisão do texto e por aceitar fazer parte da minha família.

À MSc. Mariana Rabello, pela amizade, acolhimento, confiança, paciência e pelo auxílio na revisão do texto.

À Valéria Bastos, pela amizade e confiança, por me ouvir, acompanhar minha jornada nesse doutorado e sempre torcer pelo meu sucesso, e por se importar e proteger as riquezas naturais do Cerrado na RPPN Recanto do Arco-íris.

Aos queridos taxonomistas, pelas valiosas identificações botânicas: Dra. Adriana L. R. Oliveira, Eriocaulaceae; Dr. João Bringel, Asteraceae; e Dr. Jair E. Q. Faria, diversas famílias.

Às professoras, técnicas e alunos do Departamento de Botânica e herbário UB da UnB, pelas trocas valiosas, ensinamentos, conversas, por toda a ajuda e pelos momentos de descontração.

Às gerências do ICMBio responsáveis pelas Unidades de Conservação, aos donos das propriedades privadas e a todos os auxiliares de campo que permitiram que esta pesquisa se concretizasse.

Aos membros da minha banca de qualificação de doutorado, que revisaram cuidadosamente meu trabalho, deram valiosas contribuições e me apontaram na direção certa para que eu entregasse uma pesquisa de qualidade: Dr. Leandro Maracahipes, Dr. Marcelo Moro e Dra. Mercedes Bustamante.

Aos professores do Programa de Pós-Graduação em Ecologia, por seus valiosos ensinamentos e experiências, que foram fundamentais para a construção do meu conhecimento sobre ecologia ao longo do doutorado.

À Universidade de Brasília e ao Programa de Pós-Graduação em Ecologia, por me aceitar como aluna de doutorado e por disponibilizarem recursos financeiros que possibilitaram a aquisição de materiais de pesquisa e viagens ao campo.

À secretaria da Pós-Graduação do Instituto de Ciências Biológicas, por todo cuidado e agilidade com meus requerimentos administrativos.

À CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior), pela bolsa de estudos, que permitiu que eu me dedicasse exclusivamente a esta pesquisa.

Por fim, agradeço aos membros da banca, Dr. Marcelo Moro, Dra. Ingrid Horák-Terra e Dr. Augusto Franco, por aceitarem o convite para avaliar o presente estudo.

SUMMARY

RESUMO	6
ABSTRACT	8
INTRODUCTION	10
CHAPTER 1 – Soil texture and fertility determine the beta diversity of plant species in <i>veredas</i> in Central Brazil.....	38
CHAPTER 2 – Stochastic processes influencing beta diversity of herbaceous-shrub species in <i>veredas</i> in Central Brazil.....	81
CHAPTER 3 – Phylogenetic diversity and evolutionary processes of herbaceous-shrub species in <i>veredas</i> (Brazilian palm swamp) in Central Brazil.....	118
CONCLUSION	155
APPENDIX	158

RESUMO

Diversidade taxonômica e filogenética de espécies herbáceo-arbustivas em veredas e fatores que determinam sua composição e distribuição

As veredas são fisionomias de savana úmida caracterizadas como um complexo vegetacional no qual um estrato herbáceo-arbustivo predomina na paisagem e a palmeira *Mauritia flexuosa* L. está distribuída em sua zona mais úmida. Sua vegetação se desenvolve sobre solos saturados e é cercada por uma matriz de Cerrado sobre solos bem drenados. O objetivo deste trabalho é avaliar como processos ecológicos e evolutivos afetam a diversidade alfa e beta taxonômica e filogenética de espécies herbáceo-arbustivas em veredas, e identificar o processo estruturador (baseado na teoria neutra ou de nicho) que influencia essas comunidades. Para isso, utilizei os dados de ocorrência e de cobertura de 560 espécies herbáceas, subarbustivas e arbustivas disponíveis para 21 veredas (315 transectos de 10 m) no Brasil central, juntamente com suas coordenadas geográficas, 12 variáveis de solo e 14 variáveis bioclimáticas. A partir disso, avaliei a diversidade de espécies nas veredas, verifiquei a influência das variáveis do solo sobre a composição e diversidade das espécies, calculei os índices de diversidade beta taxonômica (DBT), avaliei a correlação de fatores edáficos, climáticos e espaciais com a composição de espécies. Por fim, construí uma árvore filogenética com as espécies de vereda e testei a relação entre a diversidade alfa filogenética e as variáveis ambientais, e ainda examinei os efeitos das distâncias do solo, climática e espacial na diversidade beta filogenética (DBF). Os resultados mostraram que a proporção de espécies exclusivas nas veredas variou de 4 a 38%, indicando que a distribuição de espécies nas comunidades é semelhante a um mosaico. Os solos das veredas são ácidos, com altos níveis de alumínio, matéria orgânica e areia, mas baixos níveis de fósforo, magnésio e cálcio. O fósforo do

solo, o pH, a matéria orgânica, a saturação por cátions e a proporção de areia foram importantes para entender a composição de espécies (86% da variação) e a riqueza de espécies (63%) nas veredas. Observei que as veredas com alta diversidade florística tem solos de baixa fertilidade. Em geral, as diversidades alfa e beta foram altas e houve diferenças significativas nos atributos dos solos das veredas. Além disso, considerando a DBT, verifiquei que as comunidades de plantas foram mais influenciadas pela substituição espacial das espécies (*turnover*) do que pelo aninhamento de espécies (*nestedness*), com preditores espaciais explicando melhor sua composição e distribuição. As variáveis ambientais que influenciam a DBT das veredas são saturação por cátions, pH, areia, temperatura e precipitação. Por fim, essas descobertas revelaram um padrão de distribuição de agrupamento filogenético nas veredas, refletindo a influência de filtros ambientais. As matrizes de distância geográfica, climática e do solo foram mutuamente importantes para explicar significativamente a variação na DBF e no componente de substituição de espécies. Em resumo, considerando a DBT, processos ligados a teoria neutra, atuam na formação de comunidades de vereda. Por outro lado, tanto o agrupamento filogenético quanto a dispersão filogenética atuam na flora das veredas, indicando que o efeito combinado dos processos de nicho e estocásticos influencia a DBF dessas comunidades distintas.

Palavras-chave: áreas úmidas, Cerrado, variáveis ambientais e espaciais, filobetadiversidade, limitação de dispersão, processos estocásticos e determinísticos

ABSTRACT

Veredas (Brazilian palm swamps) are wet savanna physiognomies characterized as a vegetational complex in which an herbaceous-shrub layer dominates the landscape and the *Mauritia flexuosa* L. palm tree is distributed in its wetter zone. Their vegetation grows over saturated soils, embedded in a Cerrado savanna matrix over well drained soils. Here I aim to assess how ecological and evolutionary processes affect the taxonomic and phylogenetic alpha and beta diversities of herbaceous-shrub species in *veredas*, and to identify the structuring process (based on neutral or niche theory) that influences these communities. To accomplish that I used the occurrence and cover data of 560 herbaceous, subshrub, and shrub species available for 21 *vereda* sites (315 10-m transects) in central Brazil, together with their geographic coordinates, 12 soil attributes, and 14 bioclimatic variables. From this, I assessed the species diversity in the *veredas*, verified the influence of soil variables on species composition and diversity, calculated the taxonomic β -diversity (TBD) indices of the *veredas*, and evaluated the correlation of soil, climatic and spatial factors with the species composition. Finally, I constructed a phylogenetic tree with the *vereda* plant species and tested the relationship between phylogenetic alpha diversity and environmental variables, and examined the effects of soil, climatic, and spatial distances on phylogenetic β -diversity (PBD). My results showed that the proportion of exclusive species in the *veredas* ranged from 4 to 38%, indicating that species distribution in the communities is mosaic-like. *Vereda* soils were acidic, with high levels of aluminum, organic matter, and sand, but low levels of phosphorus, magnesium, and calcium. Soil phosphorus, pH, organic matter, cation saturation, and sand proportion were important in understanding species composition (86% of the variation) and species richness (63%) in *veredas*. I observed that *veredas* with high floristic diversity have low

fertility soils. Overall, alpha and beta diversities were high in the studied sites and there were significant differences in the soil properties of the *veredas*. Furthermore, regarding the TBD, I found that the plant communities were more influenced by the spatial turnover of species than by nestedness, with spatial predictors better explaining their composition and distribution. The most important environmental variables influencing the TBD of *veredas* are cation saturation, pH, sand, temperature and precipitation. Finally, my findings revealed a pattern of phylogenetic clustering distribution in the *veredas*, reflecting the potential role of environmental filtering. Geographic, climatic, and soil distance matrices were mutually important to significantly explain the variance in PBD and in the turnover component. In summary, considering the TBD, processes related to the neutral theory act in the formation of *vereda* communities. On the other hand, both phylogenetic clustering and phylogenetic dispersal act on the flora of *veredas*, indicating that the combined effect of niche and stochastic processes influences the PBD of these distinguished communities.

Keywords: wetlands, Cerrado, environmental and spatial variables, phylobetadiversity, dispersal limitation, stochastic and deterministic processes

INTRODUCTION

An understanding of the processes that shape the structure of biological communities in space and time is a fundamental aspect of community ecology. The organization of communities is the result of complex processes that describe how organisms colonize and persist in a habitat. These processes are determined by a series of factors, which may be combined or not, such as environmental filters, species interactions, species spatial distribution, dispersal capacity, stochasticity, and speciation (Keddy 1992; Kraft et al. 2015). Two theories have been proposed to explain how communities are assembled: the neutral theory (Hubbell 2001) and the niche theory (Grinnell 1917; Tilman 2004).

The neutral theory of biodiversity and biogeography postulates that all individuals within a community are ecologically equivalent in terms of their probability of generating descendants, migrating, dying, and undergoing speciation (Hubbell 2001). In accordance with Hubbell's (2001) neutral theory, the structure of a community can be modeled exclusively by random events of dispersal, migration, speciation, and extinction. Dispersal and speciation increase the diversity of communities, while extinction reduces it. Additionally, this theory presents a rule related to the limitation of resources, which states that a population cannot increase in abundance if there is no decrease in the number of individuals from another population in the community. This rule also applies to stochastic processes, as they cause variations in the occurrence and abundance of species (Hubbell 2001).

In contrast to Hubbell's neutral theory, niche theory postulates that for an organism to occur in a given location, it must pass through biotic and abiotic filters (Grinnell 1917; Tilman 2004). For this to occur, the organism must possess suitable morphological, functional, and physiological characteristics that allow it to survive and evolve successfully (Grinnell 1917; Tilman 2004). Niche related processes are influenced by

fluctuations in temperature, precipitation, and edaphic factors, as well as interactions with other species, including parasitism, competition, and predation (Grinnell 1917; Tilman 2004).

Although each proposal is theoretically sound, it is probable that the processes determining communities are related to both theories, involving both the ecological fitness of the species and stochastic events (Chase & Myers 2011). At different points in the evolutionary history of communities, they may have been continuously affected by both niche processes and neutral processes, which acted to contribute in different proportions to their formation (Gravel et al. 2006; Leibold & McPeck 2006).

To comprehend the way evolutionary processes impact communities, it is essential to understand the impact of environmental filters on vegetation (Toledo et al. 2012). Altitude (Chun & Lee 2018) and climatic factors such as temperature, precipitation, and seasonality (Lehmann et al. 2014; Šímová et al. 2018) are effective predictors of plant species composition and distribution at the regional and continental scales. In contrast, soil characteristics can influence plant communities at both regional (Pennington et al. 2017; Yi et al. 2020) and local scales (Jakubka et al. 2017; Souza et al. 2021).

The integration of a phylogenetic approach to the study offers the potential to elucidate the ecological and evolutionary processes regulating the coexistence of species in greater detail (Vamosi et al. 2009; Yi et al. 2020). Phylogenetic community structure describes the phylogenetic relationships of species within and across communities (Cavender-Bares et al. 2009). An examination of how environmental and geographical factors affect the phylogenetic diversity of communities may reveal the mechanisms responsible for community assembly (Webb et al. 2002; Cavender-Bares et al. 2009; Mayfield & Levine 2010).

Some studies have indicated that high phylogenetic diversity among coexisting species may suggest phylogenetic overdispersion, which is often driven by competition for divergent traits (Webb et al. 2002; Li et al. 2014). Conversely, habitat filtering can cause phylogenetic clustering, especially when there is phylogenetic niche conservatism (Wiens & Graham 2005). If phylogenetic diversity matches a random null model, community assembly may be stochastic and related to neutral theory (Webb et al. 2002; Cavender-Bares et al. 2009). However, the interplay between species trait evolution, habitat filtering, and competition is complex and not fully explained by any single mechanism (Gerhold et al. 2015; Kraft et al. 2015).

The Cerrado (Brazilian savanna) is considered the richest savanna on the planet (Kier et al. 2005) summing a total of 14,067 plant species (Brazil Flora Group 2015; Flora e Funga do Brasil 2022). The structure and organization of the vegetation in the Cerrado are influenced by a number of factors, including climate (Silva et al. 2008; Horák-Terra et al. 2022b), latitude (Eiten 1972), distinctions in relief, soil and water table depth, soil factors (Reatto et al. 2008), water availability (Lima & Silva 2008), fire frequency (Hoffmann et al. 2012) and anthropogenic disturbances (e.g. burning and land use changes) (Rodrigues et al. 2022; Hofmann et al. 2023; Salmona et al. 2023). The extensive area of the Cerrado encompasses all these environmental variations, which have occurred over millions of years resulting in the diversification of its flora into a vegetation mosaic that includes forest, savanna, and grassland formations (Ribeiro & Walter 2008).

Veredas are Brazilian savanna palm swamps that occur along river borders and swamped sites within the Cerrado dominion (Fig. 1). These ecosystems are found on poorly drained, permanently waterlogged, or seasonally waterlogged soils during the rainy season (Durigan et al. 2022) (Fig. 2). They are commonly found in shallow valleys or flat terrain, where they may occur in poorly defined drainage lines, near springs, or

bordering gallery forests (Ribeiro & Walter 2008). *Veredas* are distinguished by the presence of an extensive and dense herbaceous-shrub stratum, with *Mauritia flexuosa* L. (*buriti*) palms distributed in the most saturated portions of the soil (Ribeiro & Walter 2008). They are found on hydromorphic soils, such as *Organossolos* and *Gleissolos* (Ramos et al. 2006; Ramos et al. 2014; Horák-Terra et al. 2022a). Furthermore, the soils of these ecosystems exhibit elevated levels of organic matter, iron, and aluminum, accompanied by low levels of calcium, magnesium, and phosphorus, and a medium level of acidity (Ramos et al. 2014; Horák-Terra et al. 2022a).









Figure 1. Pictures of the veredas at: (A) Nova Xavantina, in the state of Mato Grosso; (B) Mosteiro Eisho-Ji, at Pirenópolis in Goiás; (C) Grande Sertão Veredas National Park, in Minas Gerais; (D) Jardim de Maitreya, in Chapada dos Veadeiros National Park in Goiás; (E) Serra Geral do Tocantins Ecological Station, in Tocantins; and (F) Linda Serra de Topázios Private Natural Heritage Reserve, in Goiás



Figure 2. Vereda at Posse, in Goiás State, showing the saturated soil with shallow water table, the *M. flexuosa* palms and the herbaceous vegetation

Veredas are defined as vegetational complexes, with their flora being organized based on three soil moisture zones (border, middle, and core), which are linked to drainage and topography (Eiten 1972). The core zone, which has permanently saturated soil, is characterized by the presence of buritis, a few trees, and a high density of shrubs. The middle zone, which is seasonally wet, is dominated by herbaceous and subshrub vegetation. The border zone, with better soil drainage, is dominated by herbaceous-shrub species (Araújo et al. 2002). The presence of moisture zones in this ecosystem indicates that it is ecologically dependent on water in the soil, and that the structure of its vegetation, especially the herbaceous-shrub layer, is determined by this gradient (Resende et al. 2013). The vegetation of *veredas* is mainly composed of herbaceous plants (Fig. 3) from the families Poaceae, Cyperaceae, Xyridaceae, and Eriocaulaceae, as well as subshrubs and shrubs of the families Melastomataceae, Asteraceae, and Rubiaceae, with the outstanding presence of the palm *M. flexuosa*, which is widespread in this type of habitat (Resende et al. 2013; Ramos et al. 2014; Bijos et al. 2017; Arantes et al. 2019). It's worth to mention that *veredas* exhibit high beta diversity between different localities within the Cerrado (Bijos et al. 2017). Although *veredas* are one of the habitats of the Cerrado dominion, they exhibit low floristic similarity with the surrounding vegetation types (Silva et al. 2018).



(B)









(G)





Figure 3. Some of the herbaceous plants that occur in *veredas*: (A) *Abolboda poarchon* Seub.; (B) *Axonopus brasiliensis* (Spreng.) Kuhlm.; (C) *Bulbostylis jacobinae* (Steud.) Lindm.; (D) *Cephalostemon angustatus* Malme; (E) *Echinolaena inflexa* (Poir.) Chase; (F) *Paepalanthus elongatus* (Bong.) Körn.; (G) *Rhynchospora globosa* (Kunth) Roem. & Schult.; (H) *Xyris paradisiaca* Wand.

Wetlands, such as *veredas*, provide several important ecosystem services. They maintain the hydrological system (Pousa et al. 2019), harbor a diverse range of taxonomic groups and endemic species (Durigan et al. 2022), facilitate the filtering and storage of freshwater (Horák-Terra et al. 2022a), and act as a carbon sink in organic soils (Beer et

al. in press). In addition, these ecosystems play an essential role in groundwater recharge during dry seasons and in regulating the moisture availability in the atmosphere through evapotranspiration processes (Pousa et al. 2019). However, despite the significant ecological importance of wetlands, the existing legislation does not adequately protect these open, non-forest ecosystems (Rosolen et al. 2015; Durigan et al. 2022; Moreira et al. 2015). Climate change and anthropogenic threats, including habitat degradation, groundwater drainage, pollution, and woody species encroachment are already significantly impacting Cerrado wetlands (Rodrigues et al. 2022; Salmona et al. 2023; Trindade et al. 2024) (Fig. 4). Future projections indicate that the current deforestation rates will lead to a reduction of water flow in over 90% of Cerrado watersheds (Salmona et al. 2023). Furthermore, the reduced rainfall in the Cerrado region, resulting from changes in atmospheric circulation and evapotranspiration (Hofmann et al. 2023), will accelerate the irreversible degradation of wetlands. Wetlands, such as *veredas*, depend on precipitation to replenish groundwater and maintain high water table levels (Laio et al. 2009). This, in turn, affects the complexity of the vegetation.





Figure 4. (A) An anthropized burned *vereda* with burning signs on the *M. flexuosa*, and (B) a burned *vereda* within a national park, with dead *M. flexuosa* palms

To date, no studies have been conducted that examine the relationship between environmental variables and the taxonomic and phylogenetic diversity and distribution of herbaceous-shrub species in *veredas* at a regional scale. Most studies on *veredas* have been conducted at the local level (Gonçalves et al. 2022) or have focused on floristic (Araújo et al. 2002) and phytosociological aspects (Resende et al. 2013; Ramos et al. 2014; Bijos et al. 2017; Arantes et al. 2019), soil anthropogenic impacts (Horák-Terra et al. 2022a), or paleoenvironmental reconstruction (Horák-Terra et al. 2022b) and soil descriptive aspects (Ramos et al. 2006; Sousa et al. 2015; Horák-Terra et al. 2022a).

The comprehension of the assemblages of herbaceous plant communities permits the verification of the interrelationship between species and the evolutionary effect on them (Massante et al. 2019; Yi et al. 2020). Understanding vegetation-environment relationships is of paramount importance for the effective conservation and maintenance of biodiversity and for making predictions about vegetation responses to environmental changes in the future (Engelbrecht et al. 2007; Toledo et al. 2012). The incorporation of phylogenetic information will enhance my knowledge of the evolution, diversity, and ecology of *veredas*. Moreover, it will facilitate the prediction of changes in community

diversity and dynamics, including species turnover and extinction, especially in the context of rapid climate change (Lean & Maclaurin 2016).

In this context, my objective is to assess the impact of ecological and evolutionary processes on the taxonomic and phylogenetic alpha and beta diversities of herbaceous-shrub species in *veredas* and to identify the structuring process (based on neutral or niche theory) that influences these communities (Fig. 5).

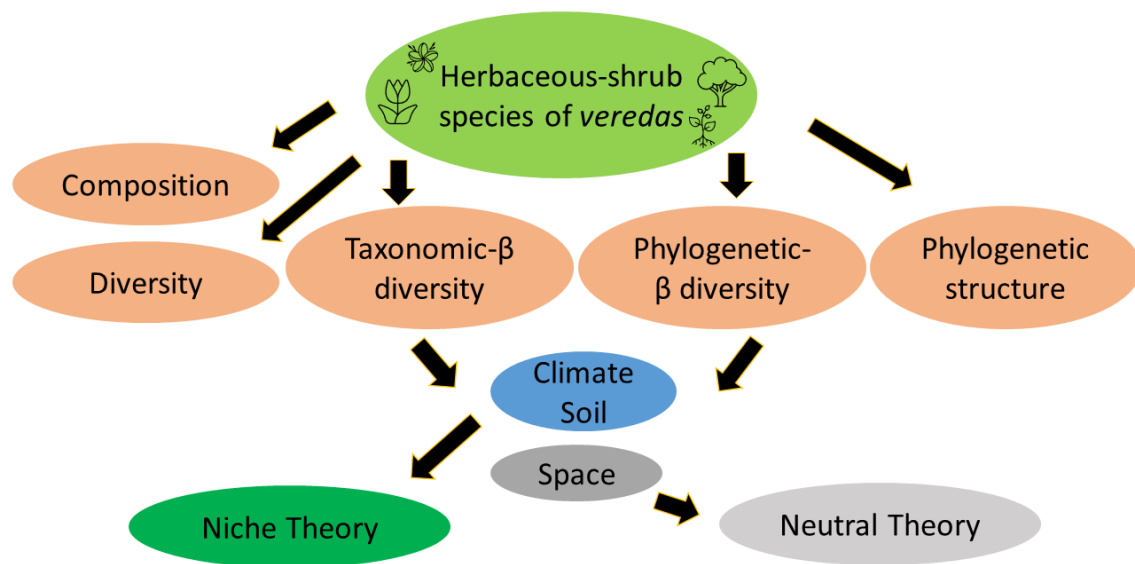


Figure 5. In this study I sought to understand the composition and diversity of herbaceous-shrub species in *veredas*, what their phylogenetic structure is like, what filters influence beta taxonomic and phylogenetic diversity, whether they are environmental (climate and soil attributes) or spatial, and what theory explains these processes, whether it is the Niche Theory or the Neutral Theory

Considering the aforementioned topics, this study has been divided into three chapters:

Chapter 1: “Soil texture and fertility determine the beta diversity of plant species in *veredas* in Central Brazil”, whose aim is: to investigate the relationships between the distribution and composition of herbaceous-shrub species and soil properties in the *veredas* of Central Brazil.

Chapter 2: “Stochastic processes influencing beta diversity of herbaceous-shrub species in *veredas* in Central Brazil”, whose aim is: to ascertain whether the structuring processes influencing the taxonomic beta diversity of plants in *veredas* are based on the neutral or niche theory.

Chapter 3: “Phylogenetic diversity and evolutionary processes of herbaceous-shrub species in *veredas* (Brazilian palm swamp) in Central Brazil”, whose aim is: to determine whether the phylogenetic β -diversity of herbaceous-shrub species in *veredas* is driven by niche-related evolutionary processes or neutral processes.

References

- Arantes ACV, Damasceno-Junior GA, Pott V J, Moreira SN, Pott A. 2019. Seasonal diversity of vegetation structure of veredas, Mato Grosso do Sul, Brazil. *Oecologia Australis* 23(4):799-811. <https://doi.org/10.4257/oeco.2019.2304.07>
- Araújo GM, Barbosa AAA, Arantes AA, Amaral AF. 2002. Composição florística de veredas no município de Uberlândia, MG. *Revista Brasileira de Botânica* 25:475-493. <https://doi.org/10.1590/S0100-84042002012000012>
- Beer F, Munhoz CBR, Couwenberg J, Horák-Terra I, Bijos NR, Fonseca LMG, Wantzen KM. in press. Peatlands in the Brazilian Cerrado: insights into knowledge, status and research needs. *Perspect. in Ecol. and Conserv.*
- Bijos NR, Eugênio CUO, Mello TRB, Souza GF, Munhoz CBR. 2017. Plant species composition, richness, and diversity in the palm swamps (*veredas*) of Central Brazil. *Flora* 236–237:94-99. <http://dx.doi.org/10.1016/j.flora.2017.10.002>
- Brazil Flora Group. 2015. Growing knowledge: an overview of Seed Plant diversity in Brazil. *Rodriguésia* 66(4):1085–1113. <https://doi.org/10.1590/2175-7860201566411>
- Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW. 2009. The merging of community ecology and phylogenetic biology. *Ecol. Lett.* 12:693-715. <https://doi.org/10.1111/j.1461-0248.2009.01314.x>
- Chase JM, Myers JA. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. – *Philosophical Transactions of the Royal Society B* 366:2351-2363. <https://doi.org/10.1098/rstb.2011.0063>
- Chun JH, Lee CB. 2018. Partitioning the regional and local drivers of phylogenetic and functional diversity along temperate elevational gradients on an East Asian peninsula. *Scientific reports* 8(1):2853. <https://doi.org/10.1038/s41598-018-21266-4>

- Eiten G. 1972. The Cerrado vegetation of Brazil. *The Botanical Review* 38:201-341.
<https://doi.org/10.1007/BF02859158>
- Engelbrecht BM, Comita LS, Condit R, Kursar TA, Tyree MT, Turner BL, Hubbell SP. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*. 447:80–82. <https://doi.org/10.1038/nature05747>
- Flora e Funga do Brasil 2022. Jardim Botânico do Rio de Janeiro.
<http://floradobrasil.jbrj.gov.br/>.
- Gerhold P, Cahill JF, Winter M, Bartish IV, Prinzing A. 2015. Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Funct. Ecol.* 29:600-614. <https://doi.org/10.1111/1365-2435.12425>.
- Gonçalves RVS, Cardoso JCF, Oliveira PE *et al.* 2022. The role of topography, climate, soil and the surrounding matrix in the distribution of Veredas wetlands in central Brazil. *Wetlands Ecol Manage* 30:1261–1279. <https://doi.org/10.1007/s11273-022-09895-z>
- Gravel D, Canham CD, Beaudet M, Messier C. 2006. Reconciling niche and neutrality: the continuum hypothesis. *Ecology Letters* 9:399-409.
<https://doi.org/10.1111/j.1461-0248.2006.00884.x>
- Grinnell J. 1917. The niche-relationships of the California Thrasher. *The Auk* 34(4):427-433. <https://doi.org/10.2307/4072271>
- Hofmann GS, Silva RC, Weber EJ, Barbosa AA, Oliveira, LFB, Alves RJV, Hasenack H, Schossler V, Aquino FE, Cardoso MF. 2023. Changes in atmospheric circulation and evapotranspiration are reducing rainfall in the Brazilian Cerrado. *Sci. Rep.* 13: 11236. <https://doi.org/10.1038/s41598-023-38174-x>
- Hoffmann WA, Geiger EL, Gotsch SG, Rossatto DR, Silva LCR, Lau OL, Haridasan M, Franco AC. 2012. Ecological thresholds at the savanna-forest boundary: how plant

- traits, resources and fire govern the distribution of tropical biomes. *Ecology letters* 15(7):759-768. <https://doi.org/10.1111/j.1461-0248.2012.01789.x>
- Horák-Terra I, Terra FS, Lopes AKA, Dobbss LB, Fontana A, Silva AC, Vidal-Torrado P. 2022a. Soil characterization and drainage effects in a savanna palm swamp (vereda) of an agricultural area from Central Brazil. *Rev. Bras. Ciênc. Solo.* 46:e0210065. <https://doi.org/10.36783/18069657rbc20210065>
- Horák-Terra I, Trindade RNR, Terra FS, Silva AC, De Camargo PB, Viana CBO, Vidal-Torrado P. 2022b. Soil processes and properties related to the genesis and evolution of a Pleistocene savanna palm swamp (vereda) in central Brazil. *Geoderma* 410:115671. <https://doi.org/10.1016/j.geoderma.2021.115671>.
- Hubbell SP. 2001. *The unified neutral theory of biodiversity and biogeography* (MPB-32). Princeton University Press.
- Jakubka D, Lessmeister A, Hahn K, Traore S, Schumann K, Thiombiano A, Bernhardt-Römermann M. 2017. Effects of climate, habitat and land use on the cover and diversity of the savanna herbaceous layer in Burkina Faso, West Africa. *Folia Geobotanica* 52:129-142. <https://doi.org/10.1007/s12224-017-9289-9>
- Keddy PA. 1992. Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* 3:157-164. <https://doi.org/10.2307/3235676>
- Kier G, Mutke J, Dinerstein E, Ricketts TH, Küper W, Kreft H, Barthlott W. 2005. Global patterns of plant diversity and floristic knowledge. *Journal of Biogeography* 32(7):1107-1116. <https://doi.org/10.1111/j.1365-2699.2005.01272.x>
- Kraft NJB, Adler PB, Godoy O, James EC, Fuller S, Levine JM. 2015. Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology* 29:592-599. <https://doi.org/10.1111/1365-2435.12345>

- Laio F, Tamea S, Ridolfi L, D'Odorico P, Rodriguez-Iturbe I. 2009. Ecohydrology of groundwater-dependent ecosystems: 1. Stochastic water table dynamics. *Water Resour. Res.* 45, W05419. <https://doi.org/10.1029/2008WR007292>
- Lean C, Maclaurin J. 2016. The Value of Phylogenetic Diversity. in: Pellens R, Grandcolas P. (eds), *Biodiversity Conservation and Phylogenetic Systematics. Topics in Biodiversity and Conservation*, vol 14. Springer, Cham. https://doi.org/10.1007/978-3-319-22461-9_2.
- Lehmann CER, Anderson TM, Sankaran M, *et al.* 2014. Savanna vegetation-fire-climate relationships differ among continents. *Science* 343(6170):548-552. <https://doi.org/10.1126/science.1247355>
- Leibold MA, McPeck MA. 2006. Coexistence of the niche and neutral perspective in community ecology. *Ecology* 87(6):1399-1410. [https://doi.org/10.1890/0012-9658\(2006\)87\[1399:COTNAN\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1399:COTNAN]2.0.CO;2)
- Li XH, Zhu XX, Niu Y, Sun H. 2014. Phylogenetic clustering and overdispersion for alpine plants along elevational gradient in the Hengduan Mountains Region, southwest China. *J. Syst. Evol.* 52:280-288. <https://doi.org/10.1111/jse.12027>.
- Lima JEFW, Silva E. 2008. Recursos Hídricos do Bioma Cerrado: importância e situação. In Sano SM, Almeida SP, Ribeiro JF. (eds) *Cerrado: ecologia e flora*. Planaltina, Embrapa. p. 89-106.
- Liu W, Yang J, Sun J, Li X. 2016. Species turnover of wetland vegetation in northeastern China: Disentangling the relative effects of geographic distance, climate, and hydro-geomorphology. *Flora - Morphology, Distribution, Functional Ecology of Plants* 220:1-7. <https://doi.org/10.1016/j.flora.2016.01.005>

- Massante JC, Götzenberger L, Takkis K, *et al.* 2019. Contrasting latitudinal patterns in phylogenetic diversity between woody and herbaceous communities. *Scientific reports* 9:7917. <https://doi.org/10.1038/s41598-019-42827-1>
- Mayfield MM, Levine JM. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13:1085-1093. <https://doi.org/10.1111/j.1461-0248.2010.01509.x>
- Moreira SN, Eisenlohr PV, Pott A, Pott VJ, Oliveira-Filho AT. 2015. Similar vegetation structure in protected and non-protected wetlands in Central Brazil: conservation significance. *Environ. Conserv. J.* 42:356–362. <https://doi.org/10.1017/S0376892915000107>
- Pennington VE, Palmquist KA, Bradford JB, *et al.* 2017. Climate and soil texture influence patterns of forb species richness and composition in big sagebrush plant communities across their spatial extent in the western U.S. *Plant Ecology* 218:957-970. <https://doi.org/10.1007/s11258-017-0743-9>
- Pousa R, Costa MH, Pimenta FM, Fontes VC, De Brito VFA, Castro M. 2019. Climate Change and Intense Irrigation Growth in Western Bahia, Brazil: The Urgent Need for Hydroclimatic Monitoring. *Water.* 11(5):933. <https://doi.org/10.3390/w11050933>
- Ramos MVV, Curi N, Motta PEFD, Vitorino ACT, Ferreira MM, Silva MLN. 2006. Veredas do Triângulo Mineiro: Solos, água e uso. *Ciência e Agrotecnologia* 30(2):283-293. <https://doi.org/10.1590/S1413-70542006000200014>
- Ramos MVV, Haridasan M, Araújo GM. 2014. Caracterização dos solos e da estrutura fitossociológica da vegetação de Veredas da Chapada no Triângulo Mineiro. *Fronteiras: Journal of Social, Technological and Environmental Science* 3(2):180-210. <https://doi.org/10.21664/2238-8869.2014v3i2.p180-210>

- Reatto A, Correia JR, Spera ST, Martins ES. 2008. Solos do bioma Cerrado: aspectos pedológicos. In Sano SM, Almeida SP, Ribeiro JF. (eds) Cerrado: ecologia e flora. Planaltina, Embrapa. p. 107-149.
- Resende ILDM, Chaves LJ, Rizzo JA. 2013. Floristic and phytosociological analysis of palm swamps in the central part of the Brazilian savanna. *Acta Botanica Brasilica* 27:205-225. <https://doi.org/10.1590/S0102-33062013000100020>
- Ribeiro JF, Walter BMT. 2008. As principais fitofisionomias do bioma Cerrado. In Sano SM, Almeida SP, Ribeiro JF. (eds) Cerrado: ecologia e flora. Planaltina, Embrapa. p. 151-212
- Rodrigues AA, Macedo MN, Silvério DV, Maracahipes L, Coe MT, Brando PM, Shimbo JZ, Rajão R, Soares-Filho B, Bustamante MMC. 2022. Cerrado deforestation threatens regional climate and water availability for agriculture and ecosystems. *Glob. Chang. Biol.* 28:6807–6822. <https://doi.org/10.1111/gcb.16386>
- Rosolen V, de Oliveira DA, Bueno GT. 2015. Vereda and Murundu wetlands and changes in Brazilian environmental laws: challenges to conservation. *Wetl. Ecol. Manag.* 23:285–292. <https://doi.org/10.1007/s11273-014-9380-4>
- Salmona YB, Matricardi EAT, Skole DL, Silva JFA, Coelho Filho ODA, Pedlowski MA, Sampaio JM, Castrillon LCR, Brandão RA, Silva ALD. 2023. A worrying future for river flows in the Brazilian Cerrado provoked by land use and climate changes. *Sustainability.* 15:4251. <https://doi.org/10.3390/su15054251>
- Silva DP, Amaral AG, Bijos NR, Munhoz CBR. 2018. Is the herb-shrub composition of *veredas* (Brazilian palm swamps) distinguishable? *Acta Botanica Brasilica* 32:47–54. <https://doi.org/10.1590/0102-33062017abb0209>

- Silva FAM, Assad ED, Evangelista BA. 2008. Caracterização climática do bioma Cerrado. In Sano SM, Almeida SP, Ribeiro JF. (eds) Cerrado: ecologia e flora. Planaltina, Embrapa. p. 69-88.
- Šímová I, Violle C, Svenning JC, *et al.* 2018. Spatial patterns and climate relationships of major plant traits in the New World differ between woody and herbaceous species. *Journal of Biogeography* 45(4):895-916. <https://doi.org/10.1111/jbi.13171>
- Sousa RFD, Brasil EPF, Figueiredo CCD, Leandro WM. 2015. Soil organic matter fractions in preserved and disturbed wetlands of the cerrado biome. *Revista Brasileira Ciência do Solo* 39(1):222-231. <https://doi.org/10.1590/01000683rbc20150048>
- Souza GF, Almeida RF, Bijos NR, Fagg CW, Munhoz CBR. 2021. Herbaceous-shrub species composition, diversity and soil attributes in moist grassland, shrub grassland and savanna in Central Brazil. *Brazilian Journal of Botany* 44:227-238. <https://doi.org/10.1007/s40415-020-00672-x>
- Tilman D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences of the United States of America* 101:10854-10861. <https://doi.org/10.1073/pnas.0403458101>
- Toledo M, Peña-Claros M, Bongers F, *et al.* 2012. Distribution patterns of tropical woody species in response to climatic and edaphic gradients. *Journal of Ecology* 100:253-263. <https://doi.org/10.1111/j.1365-2745.2011.01890.x>
- Trindade VL, Ferreira MC, Costa LS, Amaral EJ, Bustamante MMC, Munhoz CBR. 2024. The effect of woody encroachment on taxonomic and functional diversity and soil properties in Cerrado wetlands. *Flora*. 152524. <https://doi.org/10.1016/j.flora.2024.152524>

- Vamosi SM, Heard SB, Vamosi JC, Webb CO. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology* 18:572-92. <https://doi.org/10.1111/j.1365-294X.2008.04001.x>
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ. 2002. Phylogenies and community ecology. *Annual Review of Ecology, Evolution and Systematics* 33:475-505. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150448>
- Wiens JJ, Graham CH. 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Evol. Syst.* 36:519–539. <https://doi.org/10.1146/annurev.ecolsys.36.102803.095431>
- Yi S, Wu P, Bai F, Zhou D, Peng X, Zhang W, Guo W. 2020. Environmental Filtering Drives Plant Community Assembly Processes in the Riparian Marsh of Downstream Yellow River, China. *Wetlands* 40(2):287-298. <https://doi.org/10.1007/s13157-019-01182-7>

CHAPTER 1

Soil texture and fertility determine the beta diversity of plant species in *veredas* in Central Brazil

Chapter published: Bijos NR, Silva DP, Munhoz CBR (2023). Soil texture and fertility determine the beta diversity of plant species in *veredas* in Central Brazil. *Plant and Soil*. 492:241–259. <https://doi.org/10.1007/s11104-023-06168-3>

Abstract

Understanding the correlation between soil properties, species composition and diversity in *veredas* (Brazilian savanna palm swamps) can provide insights for managing this unique and endangered environment. We evaluated the relationships between the distribution and composition of herbaceous, subshrub, and shrub species and soil physicochemical properties of 21 *vereda* sites (315 10-m transects) in Central Brazil. Our results showed high floristic alpha and beta diversity in the studied sites and significant differences in soil properties of the *veredas*. The proportion of exclusive species in the *veredas* ranged from 4% to 38%, indicating that the plant species distribution in the *veredas* is mosaic-like. *Vereda* soils were acidic, with high levels of aluminum, organic matter, and sand, but low levels of phosphorus, magnesium, and calcium. Soil phosphorus, pH, organic matter, cation saturation, and sand proportion were important in understanding *veredas*' species composition (86% of the variation) and species richness (63%). Phosphorus and pH were positively correlated with species richness, whereas organic matter was negatively correlated. Organic matter, cation saturation, and sand were negatively correlated with compositional similarity, but phosphorus was positively

correlated. *Veredas* with high floristic diversity had low fertility soils. The studied *veredas* showed significant differences in soil properties, with some variables being key drivers in assembling significantly diverse herbaceous-shrub communities in these wetland islands surrounded by a dry matrix of the Cerrado savanna.

Keywords: wetlands, herbaceous-shrub, palm swamp, Cerrado, niche, soil-vegetation relationship

Introduction

Plants in a community need to overcome the barriers imposed by abiotic and biotic factors to survive (Cornwell et al. 2009). To understand the ecological processes that sustain plant species diversity (Mckane et al. 2002) and patterns of vegetation structure (Grime and Pierce 2012), it is necessary to recognize the essential resources used by plants in their habitats (Higgins et al. 2011). The coexistence of many plant species in communities where environmental filters shape the composition and structure of vegetation may indicate the presence of niche partitioning, which demonstrates diversification in resource use by plants (Higgins et al. 2011; Rossatto et al. 2014). Variations in soil properties are strong environmental filters that influence the composition of plant communities (Langan et al. 2017). This is because of the differential responses of plant species to variations in soil texture (Ruggiero et al. 2002; Medinski et al. 2010; Huang and Hartemink 2020), amount of available water (Medinski et al. 2010; Ribeiro et al. 2021), nutrient availability (Mota et al. 2018; Souza et al. 2021; Amaral et al. 2022), and soil pH (Medinski et al. 2010; Viani et al. 2014; Amaral et al. 2022).

Veredas (Brazilian savanna palm swamps) are one of the habitats found in the Cerrado (Brazilian savanna), and are characterized by wet, poorly drained, permanently waterlogged, or seasonally waterlogged soils during the rainy season (Durigan et al.

2022). They are commonly found in shallow valleys or flat terrains, where they may occur in poorly defined drainage lines, near springs, or bordering gallery forests (Ribeiro and Walter 2008). The fluctuation of the water table height is important for both the edaphic factors and the flora community composition (Nunes et al. 2022; Nogueira et al. 2022; Horák-Terra et al. 2022). *Veredas* can generally be subdivided into three zones, considering their moisture gradient: border, middle, and core (Eiten 1994). The border is surrounded by slightly elevated areas with dry and well-drained soils, and a typical savanna (*cerrado*) vegetation; then, the vegetation progressively transitions from typical *cerrado* on the drier upland towards the seasonally wet grassland on the lower region of the valley, which is predominantly composed by a continuous herbaceous and shrub stratum. The middle is periodically saturated with water and presents an herbaceous and subshrub vegetation. The core is the lower region of the terrain; it is composed of a permanent wet grassland (herbaceous and shrub stratum) and a strip of *buritis* (*Mauritia flexuosa* L.f.) with an occasional shrub layer underneath them. The transitions of the zones can be sudden or gradual. The soils of the *veredas* are hydromorphic, classified as Histosols and Gleysols (EMBRAPA 2006; Ramos et al. 2006; Ramos et al. 2014). These soils are generally moderately acidic, with high levels of aluminum, organic matter, and iron and low levels of phosphorus, magnesium, and calcium (Ramos et al. 2014). Because of the characteristic topography and soil drainage of the *veredas*, the soil moisture gradient is correlated with differences in chemical properties (Ramos et al. 2006; Ramos et al. 2014), thus favoring the occurrence of microhabitats, leading to variations in flora composition and richness at the same location (Araújo et al. 2002; Oliveira et al. 2009; Resende et al. 2013). These differences may be associated with water table level seasonality, distinct sediment deposition, or anthropogenic interference (Oliveira et al. 2009; Rosolen et al. 2015; Arantes et al. 2019).

Veredas play an essential role in the ecosystem by conserving the hydrological system (Queiroz 2015) and contributing to biodiversity by harboring several taxonomic groups and endemic species (Sousa et al. 2013; Bijos et al. 2017; Nogueira et al. 2022). They also provide many ecosystem services, such as the storage of large amounts of carbon in the soil (Sousa et al. 2015), water (Lima and Silva 2008), traditional farming families (Schmidt et al. 2011), and raw materials for crafts, fibers, and fruits for traditional communities (Sampaio et al. 2008). The herbaceous and shrub flora of *veredas* is distinct from that of other surrounding Cerrado vegetation types (Silva et al. 2018). Nevertheless, floristic heterogeneity occurs both within (Araújo et al. 2002) and between *veredas* from different localities (Resende et al. 2013; Bijos et al. 2017; Nogueira et al. 2022). When comparing *veredas* from different areas, the heterogeneity is significantly high, as the communities exhibit a large proportion of exclusive herbaceous and shrub species despite the differences in their diversity and floristic composition (Bijos et al. 2017; Silva et al. 2018, Nogueira et al. 2022).

Although some studies have evaluated the flora (Araújo et al. 2002; Bijos et al. 2017; Silva et al. 2018; Arantes et al. 2019) and soil properties of *veredas* (Ramos et al. 2006; Ramos et al. 2014; Sousa et al. 2015; Nogueira et al. 2022; Nunes et al. 2022), there is a knowledge gap regarding the correlations between the distribution, composition, and diversity of herbaceous and shrub species, and soil properties of these communities at a regional scale. Research on other Cerrado formations has demonstrated that at regional or local scales several factors, such as the presence of soil aggregates, nutrients, amount of exchangeable aluminum, water availability, and soil drainage, can directly or indirectly influence plant diversity and habitat heterogeneity (Ribeiro et al. 2021; Lira-Martins et al. 2022). In addition, soil texture (Lira-Martins et al. 2022), water table depth (Ribeiro et al. 2021), topographical relief (Oliveira-Filho et al. 1989), fire frequency (Veenendaal

et al. 2018), and anthropogenic disturbance (Ribeiro and Walter 2008; Veenendaal et al. 2018) also affect the floristic composition of plant communities.

To understand the species distribution patterns of *veredas* and determine the main soil properties driving the formation of these communities, we aimed to investigate the relationships between the distribution and composition of herbaceous and shrub species and soil properties in the *veredas* of Central Brazil, covering more than 7° of latitude and 9° of longitude. Thus, we addressed the following questions: (1) Do herbaceous and shrub species composition and diversity vary significantly among *veredas*? (2) Are the composition and diversity of plants in *veredas* related to soil properties? (3) Which are the most important soil variables that influence species composition and diversity of plants in *veredas* on a regional scale? In this work, it is hypothesized that physicochemical soil properties exhibit a significant relationship with distinct plant species composition and diversity of *veredas*. Since the soils of *veredas* have low phosphorus content and pH, but high organic matter content (Ramos et al. 2014), we also hypothesized that phosphorus and pH are positively correlated with the floristic diversity of *veredas*, but that organic matter content is negatively correlated.

Materials and methods

Study area

The present study was conducted in 21 *veredas* from national parks or preserved private lands of Central Brazil. *Veredas* were distributed in six Brazilian states, ranging between 10-17° S, 43-52° W (Fig. 1). The phytosociological sampling data of nine *veredas* were published by Bijos et al. (2017), soil and phytosociological data of three *veredas* were published by Nogueira et al. (2022), and nine were included in the present study. According to the Köppen classification system, the climate of the study areas was Aw,

which is described as tropical seasonal with a rainy summer (October to April) and a dry winter (May to September) (Alvares et al. 2013). The soil types found in the study areas are classified as Gleysols (Ramos et al. 2014), characterized as hydromorphic and poorly drained, which contain poorly decomposed organic material under a grayish layer (Reatto et al. 2008). The predominant soil classes in the regions of the *veredas* include dystrophic Red Ferralsols, dystrophic Leptsols, dystrophic Haplic Cambisols, and Orthic Arenosols (Santos et al. 2011) (Table S1). Study sites were located over four hydrographic regions: Tocantins-Araguaia, Paraná, São Francisco, and Atlântico Leste (National Water and Sanitation Agency, ANA, 2021) (Table S2).

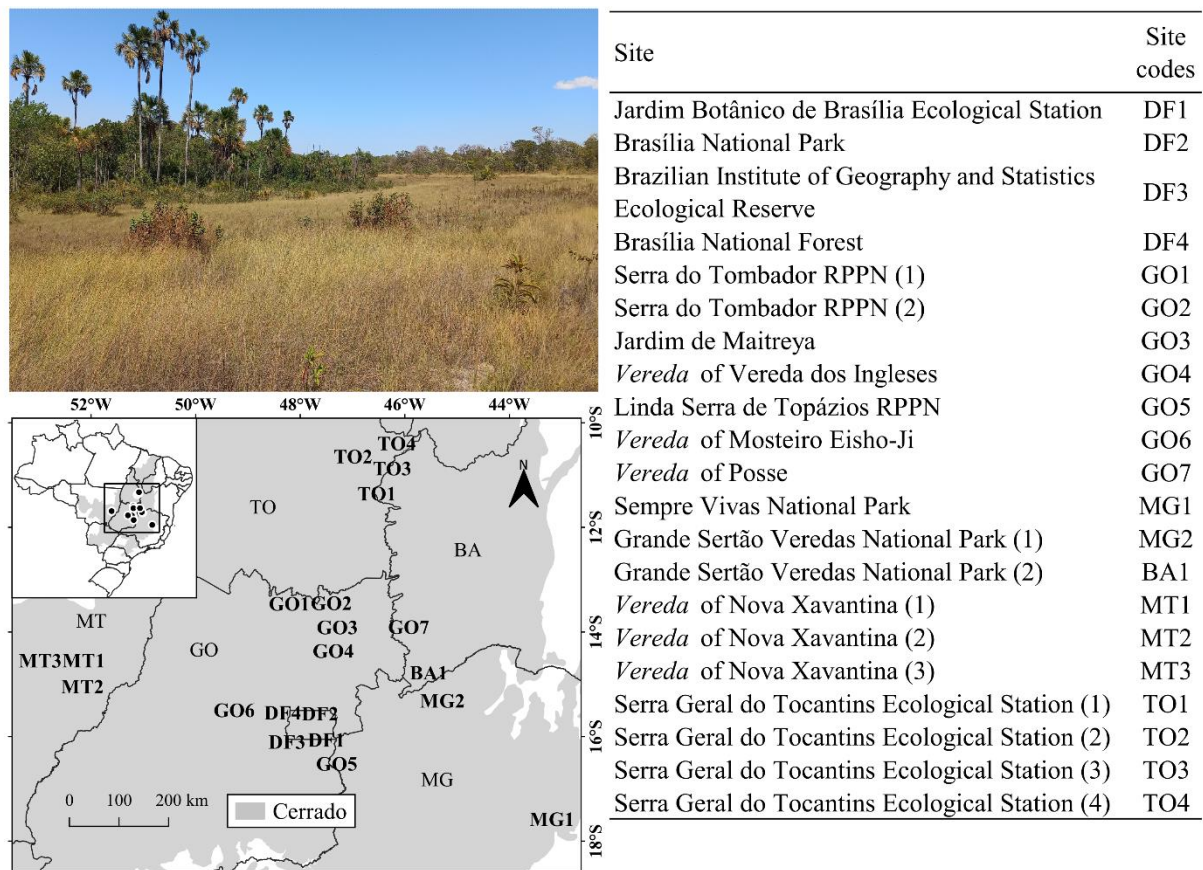


Fig. 1 Map of the 21 *vereda* study sites and a photo of the *vereda* GO7. RPPN = Private Natural Heritage Reserve, DF = Distrito Federal, GO = Goiás, MG = Minas Gerais, BA = Bahia, TO = Tocantins, and MT = Mato Grosso

Vegetation and Soil Sampling

Vegetation sampling was conducted during the rainy season (November to May), as the chances of sampling a larger number of species in their reproductive stage are greater in this period (Munhoz and Felfili 2006). In each *vereda*, sampling of herbaceous, subshrub, and shrub species was conducted in 15 transects of 10 m each (sample units), from the *M. flexuosa* line to the border of the *vereda* with the *cerrado*. The distribution of the transects were randomly stratified, with five transects in each of the three previously described zones of the *veredas*: border, middle, and core. To determine the horizontal linear cover and species composition, we applied the line intersection method (Canfield 1941; Munhoz and Araújo 2011). Thus, using a millimeter tape, we recorded the length of all herbaceous, subshrub, and shrub individuals that touched or crossed the tape, covering the base and clump of plants, or perpendicular projections of leaves intercepted by the line (Cummings and Smith 2000). We calculated the absolute cover (AC) and relative cover (RC), according to the methods described by Munhoz and Felfili (2006). We considered the AC value to be the sum of species horizontal projections on the sampling units. To determine the RC of each *vereda*, we divided the AC value of each species by the sum of the AC of all species and multiplied it by 100. Species were identified by comparison with herbarium (University of Brasília, UB) specimens, consultation with experts, and specialized literature, including the ‘Flora e Funga do Brasil’ platform and speciesLink. The collected botanical material was deposited in the UB herbarium and the Brazilian Institute of Geography and Statistics (IBGE) herbarium. The botanical nomenclature of the families was determined according to APG IV (Angiosperm Phylogeny Group IV) and that of the species according to the project ‘Flora e Funga do Brasil’ 2022 (Flora e Funga do Brasil 2022). The species, family, and author names were checked using the ‘flora’ package (Carvalho 2020) of the R program (version 4.2.2; R

Core Team 2022), which contains all the accepted botanical names and synonyms available in 'Flora e Funga do Brasil' (2020). Although *M. flexuosa*, a characteristic palm tree of *veredas*, was present in all the study sites, we did not include this species and trees in our analysis because their cover represents less than 10% of the vegetation, and in the middle and border zones they are absent (Ribeiro and Water 2008).

We collected soil samples in each 10 m transect from a depth of 0-20 cm. Samples were collected 1 m from the center point of each sampling unit. The physical and chemical properties of the soil were analyzed to determine the relative contents of sand, clay, and silt; pH (CaCl_2 0.01 mol L⁻¹); aluminum (Al^{3+}); calcium (Ca^{2+}); magnesium (Mg^{2+}); potassium (K^+); phosphorus (P); organic matter (OM); cation saturation (V); and cation exchange capacity (CEC). Soil texture (sand, clay, and silt content) was determined using the densimetric method of Bouyoucos, and the percentage of organic matter was quantified using the Walkley–Black method ($\% \text{ organic C} \times 1.724$). Cations Ca^{2+} , Mg^{2+} , and Al^{3+} were extracted using a 1 mol L⁻¹ KCl solution, and K^+ and P were extracted with Mehlich-1 solution (0.0125 mol L⁻¹ H_2SO_4 + 0.05 mol L⁻¹ HCl). Potential cation exchange capacity (CEC) was estimated according to the equation ($T = \text{Ca}^{2+} + \text{Mg}^{2+} + \text{K}^+ + \text{H}^+ + \text{Al}^{3+}$). Cation saturation (V) by $\{V = [(\text{Ca}^{2+} + \text{Mg}^{2+} + \text{K}^+)/\text{CEC}] \times 100\}$. Soil physicochemical properties were analyzed according to the Embrapa protocol (2017).

Data analysis

We wanted to understand how different soil properties affected species richness and species cover of the *veredas* and whether there were significant dissimilarities between the herbaceous and shrub species compositions in the *veredas*. Additionally, we wanted to understand whether the *veredas* significantly differed in terms of their soil properties.

To assess species diversity in the *veredas*, we used the Shannon–Wiener index (H'), Simpson's dominance index (D), and Pielou's evenness index (J'), with species cover data as a measure of abundance, which were calculated using the ‘diversity’ function of the ‘vegan’ package (Oksanen et al. 2022).

To verify the floristic relationship among different *veredas*, we applied the hierarchical cluster analysis (Borcard et al. 2011), using species AC data by site. We calculated the distance matrix using the Bray–Curtis dissimilarity index, then applied the ‘hclust’ function using the ‘average’ method, which calculates the lowest distance (or highest similarity) between clusters before merging (Legendre and Legendre 2012). We selected the ‘average’ (UPGMA; Unweighted Pair-Groups Method using Arithmetic Averages) clustering model based on the cophenetic correlation value, a coefficient that measures the goodness-of-fit between matrices. The clustering method that produces the highest cophenetic correlation may be the one that provides the best clustering model for the distance matrix (Legendre and Legendre 2012). We used the gap statistic method (Tibshirani et al. 2001) to determine the appropriate number of clusters present in the dataset by applying the ‘clusGap’ and the ‘fviz_gap_stat’ functions of the ‘cluster’ (Maechler et al. 2022) and ‘factoextra’ (Kassambara and Mundt 2020) packages, respectively. According to the gap statistic method, the optimal number of clusters present in the dataset was three, leading us to use it in all further analysis. (Fig. S1).

To order the areas in a multidimensional space while accounting for spatial autocorrelation, we used the adjusted principal coordinate analysis (aPCoA; Shi 2021), employing the presence and absence data and species AC data in the analysis. For the presence and absence analysis, we used Jaccard's similarity coefficient, and for the AC analysis, we employed the Bray–Curtis coefficient (Borcard et al. 2011). Ordination analysis was performed using the ‘aPCoA’ function of the ‘aPCoA’ package (Shi 2021).

To check whether there was a significant difference between the species composition of the communities and to identify the distinctions or separations between the emerged groups, we performed a permutational multivariate analysis of variance (PERMANOVA) using the ‘adonis’ function of the ‘vegan’ package (Oksanen et al. 2022), with 999 permutations.

To identify indicator species significantly associated with each cluster group, we performed the indicator species analysis (Dufrêne and Legendre 1997) using the ‘multipatt’ function of the ‘indicspecies’ package (De Cáceres and Legendre 2009). A total of 999 permutations were performed to test species significance using the Monte Carlo test. Species were considered indicators if $p \leq 0.05$ and the indicator value (IndVal) $\geq 25\%$ (Dufrêne and Legendre 1997).

The Kruskal–Wallis rank sum test (Borcard et al. 2011) was used between the *veredas* and groups formed in the cluster analysis to assess the significant differences in each soil variable. We applied the ‘kruskal.test’ function on the soil data and later the ‘pairwise.wilcox.test’ function to assess which pairs of *veredas* or groups were significantly distinct with regard to the soil variable. Prior to the test, we verified that the assumptions of normality and homoscedasticity of the residuals were satisfied.

We used canonical correspondence analysis (CCA; Legendre and Legendre 2012) to examine the correlation between the soil physicochemical properties and flora composition of the communities. We used the AC matrix of species and soil data in the analysis and applied the ‘cca’ function from the ‘vegan’ package (Oksanen et al. 2022). CCA is used to explain species-environment and environment-area relationships, even when species distributions are skewed, samples are taken from unusual sampling designs, and environmental variables are highly self-correlated (ter Braak and Šmilauer 2012). The statistical validity of CCA, its axes, and the soil variables were assessed using the

Monte Carlo permutation test ($\alpha = 0.05$; Borcard et al. 2011) with 999 permutations. Prior to CCA, we checked for multicollinearity among the soil variables using Pearson correlation analysis. We retained the variables that exhibited values of $|r| < 0.7$ and were ecologically important for the study areas.

To understand how soil physicochemical properties affect changes in richness and species cover, we used regression models. To better represent species cover, we used PCoA (principal coordinate analysis) eigenvectors from axis one as the response variable, and the soil variables selected from the Pearson correlation (V, OM, P, pH, and sand) (Table S3) as predictors, for which we applied a linear model (LM). We also ran a generalized linear model (GLM) with a 'poisson' distribution log link function to understand how soil V, OM, P, pH, and sand affected changes in species richness. We selected the best model by applying a backward selection for the predictor variables (V, OM, P, pH, and sand) until only significant variables remained in the model. We analyzed and validated the models according to the recommendations by Zuur et al. (2009).

We tested for spatial autocorrelation in species richness and species composition, and in the residuals from the regression models (GLM and LM) using Moran's I correlograms. This enabled us to evaluate whether geographically close sites were similar concerning species richness and composition and to check for the residual independence assumption of regression models. For species richness, both correlograms, based on raw data and on residuals from GLM, did not show a significant autocorrelation ($p > 0.05$ after Bonferroni's correction). To apply Moran's I correlogram to species cover data and presence/absence data, we used the coordinate points of the first axis of each PCoA, respectively. For presence/absence data, the correlogram based on the first axis of the PCoA showed a significant positive autocorrelation at the first distance class (Moran's I = 0.96, $p < 0.001$ after Bonferroni's correction), as well as for species cover data (Moran's

$I = 0.82$, $p < 0.001$ after Bonferroni's correction). The correlogram based on residuals from LM showed a significant negative autocorrelation in the third distance class (Moran's $I = -0.45$, $p = 0.01$ after Bonferroni's correction). Thus, we generated distance-based Moran eigenvector maps (MEM; Dray et al. 2006) and performed a global test on the residuals from LM against all MEM variables (Blanchet et al. 2008). Neither positive nor negative eigenvectors were significant (positive MEMs: $p = 0.37$; negative MEMs: $p = 0.96$) in the global test, indicating that the spatial autocorrelation in model residuals was not strong and that it was not necessary to add spatial variables to the LM. The PCoA was performed using the 'cmdscale' function of the 'vegan' package (Oksanen et al. 2022), while for the Moran's I analyses, we used the function 'correlog' of the 'pgirmess' package (Giraudoux 2022), and for the generation of MEM variables we used the function 'mem.select' of the 'adespatial' package (Dray et al. 2022). We also tested for the presence of spatial autocorrelation in each soil variable using Moran's I correlogram, by applying 'Moran.I' function of the 'ape' package (Paradis and Schliep 2019) and corrected the p -value using Bonferroni correction.

All analyses were performed using the R program (version 4.2.2; R Core Team 2022). We considered a 5% significance level in all statistical tests.

Results

Vegetation composition and diversity

A total of 560 plant species, belonging to 220 genera and 69 families, were sampled (Table S4). The families with the highest numbers of species were Poaceae (16.96%), Cyperaceae (10.36%), Asteraceae (9.46%), Melastomataceae (6.96%), Xyridaceae (6.96%), and Eriocaulaceae (5.89%). The number of plant species per *vereda* ranged from 33 to 124, while the proportion of exclusive species ranged from 4% to 38% (Table 1).

Only *Paspalum lineare* Trin. was present in all the *veredas*. *Rhynchospora globosa* (Kunth) Roem. & Schult. occurred in 20 areas but was not recorded in MG2 (Table S4). The species with the highest relative coverages were *P. lineare*, *R. globosa* and *Trachypogon spicatus* (L.f.) Kuntze. *P. lineare* was most abundant in the *veredas* GO6 and GO1, *T. spicatus* in MG2 and GO7, and *R. globosa* in MG1 and MT3 (Table S4). The most abundant species in the *veredas* varied greatly, with GO4 and GO5 having a greater number of species (Table S4), indicating high evenness (Table 1). The *veredas* with few highly dominant species in the communities were DF1, GO1, GO6, MG2, and MT3 (Table S4). The *veredas* with most of their total relative cover concentrated in a few species were DF1, GO1, GO6, MG2, and BA1 (Table S4), which was corroborated by the low evenness values (Table 1). The Shannon diversity values differed from the species richness values of the *veredas* (Table 1). The Simpson's index varied from 0.78 to 0.98, and the evenness was high for most areas, with higher values for GO4 and GO5 and lower for GO6 (Table 1). Based on the diversity indices, we can consider the *veredas* GO4 and GO5 as the most diverse, and BA1 and GO1 as the least diverse (Table 1).

Table 1. Richness and diversity of herbaceous and shrub species in the *veredas*. The site codes are described in Fig. 1

Site	Number of species	Number of exclusive species	Shannon index (H')	Simpson index (D')	Pielou evenness index (J')
DF1	48	4	2.31	0.85	0.60
DF2	80	11	2.94	0.88	0.67
DF3	98	17	3.13	0.92	0.68
DF4	77	10	2.93	0.89	0.68
GO1	40	10	1.98	0.78	0.54
GO2	58	11	2.50	0.86	0.61
GO3	71	15	2.79	0.90	0.65
GO4	106	37	3.72	0.95	0.80
GO5	124	26	4.15	0.98	0.86
GO6	86	33	2.17	0.78	0.49
GO7	72	21	2.49	0.78	0.58
MG1	54	12	2.36	0.84	0.59

MG2	69	21	2.39	0.79	0.56
BA1	33	4	2.09	0.80	0.60
TO1	50	6	2.95	0.93	0.75
TO2	58	4	2.67	0.87	0.66
TO3	58	4	2.83	0.91	0.70
TO4	45	2	2.54	0.88	0.67
MT1	75	14	2.63	0.87	0.61
MT2	73	15	2.99	0.92	0.70
MT3	70	14	2.51	0.82	0.59

The cluster dendrogram (Fig. 2) and PCoA of species cover (Fig. 3a, axis 1) showed a marked division between the *veredas* located in Tocantins, Minas Gerais, and Bahia in the northeast and eastern Cerrado, and Goiás and Distrito Federal in the central region. The PCoA second axis and dendrogram demonstrated that the *veredas* of Mato Grosso (MT1, MT2 and MT3) and MG1 were different from GO7, BA1, and MG2 (Figs. 2 and 3a) in terms of species cover. The dendrogram shows a formation of smaller groups between *vereda* pairs, such as in GO7 and MG2, GO1 and GO2, and GO3 and DF2 (Fig. 2). Groups of *veredas* were slightly separated in the presence/absence PCoA analysis (Fig. 3c); the *veredas* from Mato Grosso showed significant differences from the other *veredas* in axis 2; meanwhile, most of the *veredas* from Tocantins were found to be distinct from the others in axis1 (Fig. 3c); finally, the *veredas* from Group 1 were only partially differentiated from the other *veredas*, indicating some overlap with other groups (Fig. 3c). The PCoA showed a similar pattern to the cluster analysis, representing the compositional differences among the *veredas*, both in relation to species cover and presence and absence (Figs. 2 and 3). After we removed the effect of spatial location using aPCoA, the separation of the *veredas* in three major groups became less apparent, considering species cover (Fig. 3a and 3b) and presence/absence (Fig. 3c and 3d), showing that the species composition dataset is affected by the location. The PERMANOVA test demonstrated significant differences in species composition between

different *veredas* ($F = 9.72$; $R^2 = 0.398$; $p = 0.001$) and between the three major groups formed in the cluster analysis ($F = 27.77$; $R^2 = 0.151$; $p = 0.001$).

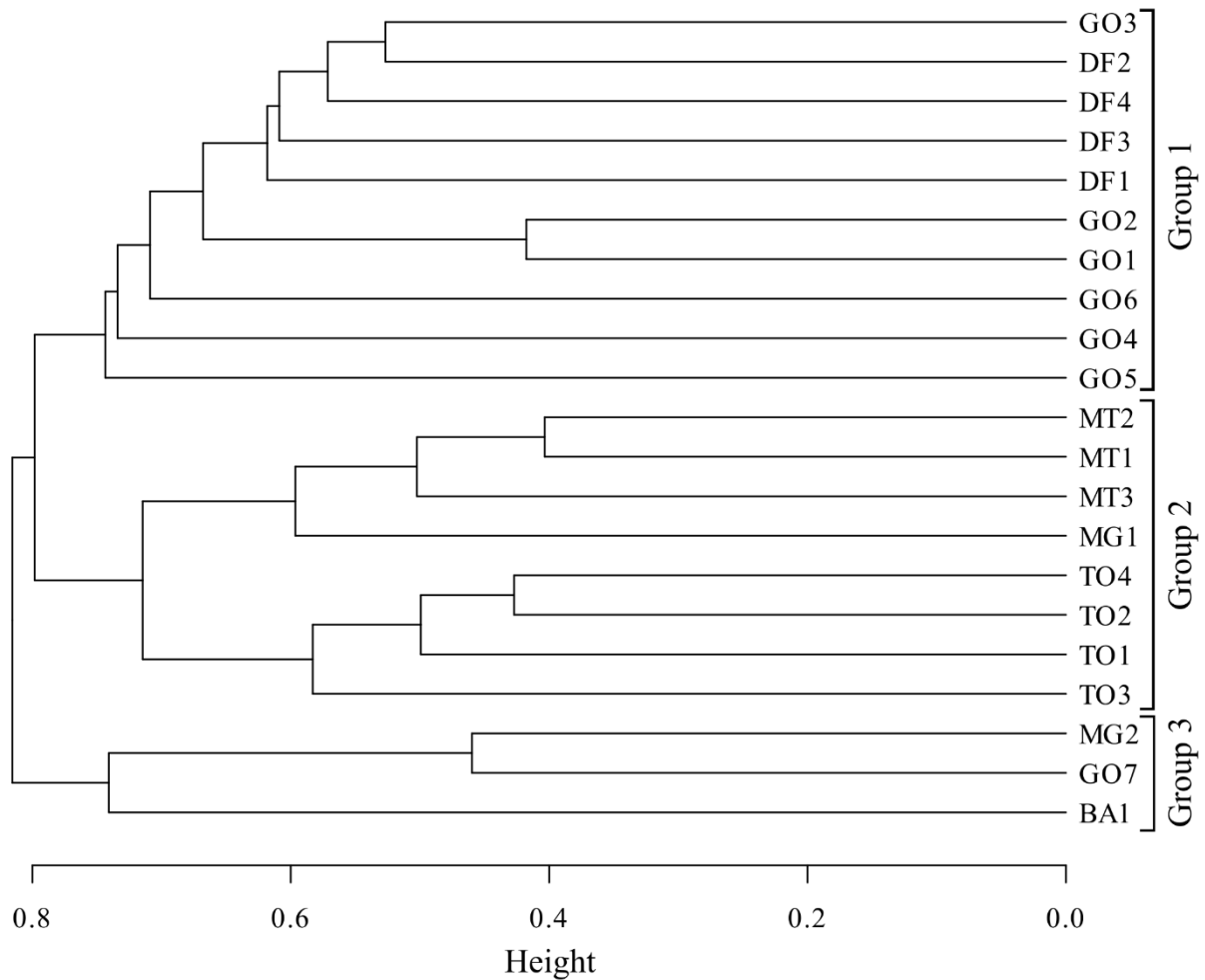


Fig. 2 Dendrogram of floristic similarity between different *veredas* using Bray–Curtis dissimilarity and ‘average’ (cophenetic coefficient = 0.78) linkage method. The keys highlight the separation between the groups of *veredas* located in Central Cerrado and northeast and east Cerrado, and the thick black lines highlight the groups of *veredas* that showed similarity. The site codes are described in Fig. 1

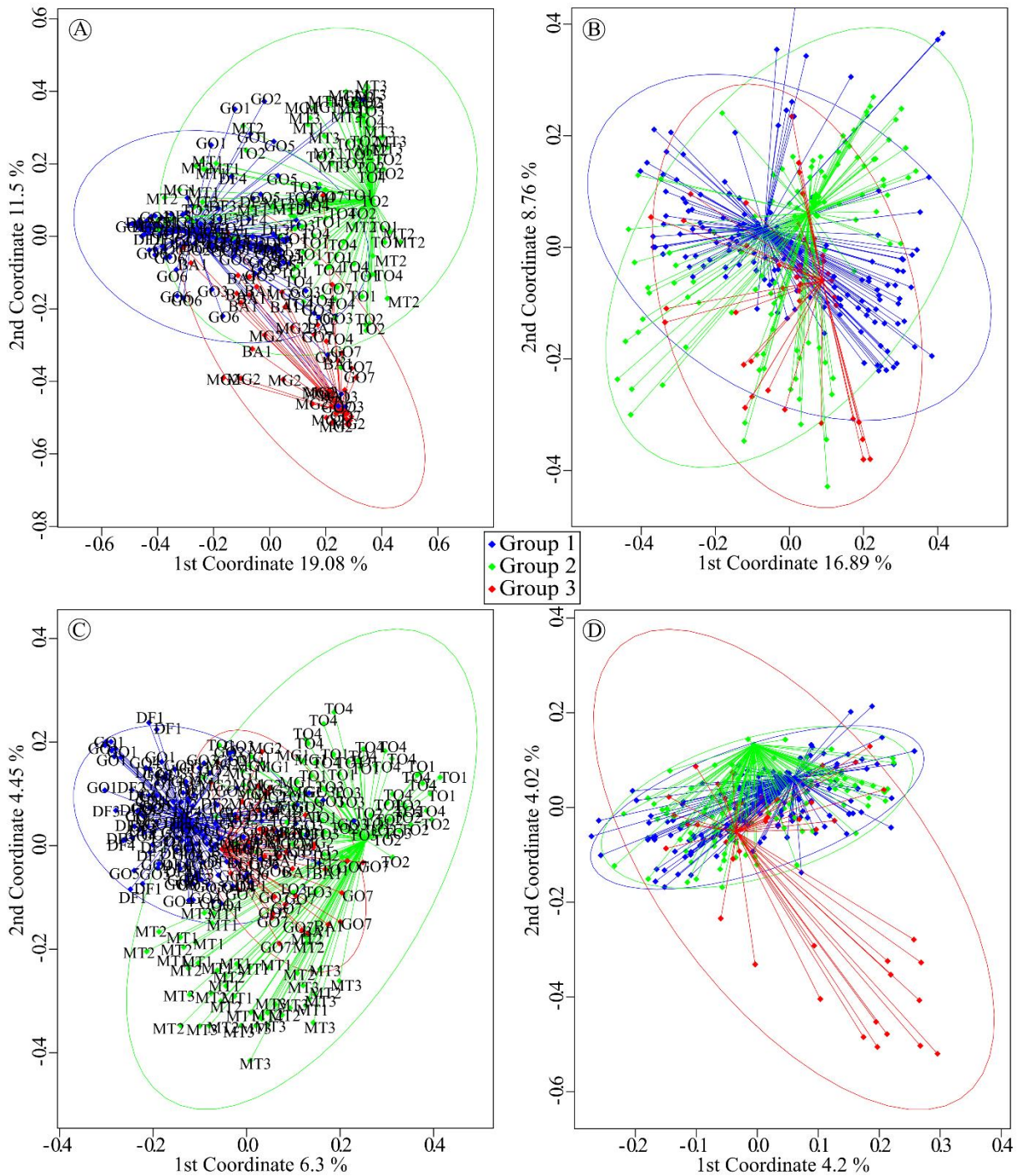


Fig. 3 Original PCoA ordination diagram (A and C) showing floristic relationship in the studied *veredas* and covariate adjusted PCoA (B and D) colored by the main groups formed in the hierarchical cluster analysis (Groups 1, 2 and 3). (A and B) Analysis diagram generated from species cover data and (C and D) with presence/absence data. The ellipses represent 95% intervals around the centroid of the *vereda* groups. The site codes are described in Fig. 1

The most representative indicator species were from group 3 (BA1, GO7, and MG2), which had 15 species, and included *Borreria poaya* (A.St-Hil.) DC, *Palhinhaea cernua* (L.) Franco & Vasc, and *Macairea radula* (Bonpl.) DC (Table 2). Group 2 alone had one indicator species and was more meaningful when combined with group 3, thereby represented the following species: *T. spicatus* (L.f.) Kuntze and *Trichantheium cyanescens* (Nees ex Trin.) Zuloaga & Morrone (Table 2). Group 1 included five indicator species, the most significant one being *Scleria leptostachya* Kunth (Table 2). Groups 1 and 3 combined were represented by two species, *Andropogon virgatus* Desv. and *Axonopus brasiliensis* (Spreng.) Kuhlm.

Table 2. Relative frequency values (0-100%) of indicator species per cluster group. Gray filled values indicates the cluster groups in which species were selected as indicators. Species order follows decreasing IndVal. The site codes are described in Fig. 1

Family / Species	IndVal	p	Group / Vereda																					
			1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	3	3	3
			DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	MG1	MT1	MT2	MT3	TO1	TO2	TO3	TO4	BA1	GO7	MG2	
Rubiaceae																								
<i>Borreria poaya</i> (A.St.-Hil.) DC.	1.000	0.001	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.037	0.074	0.00007
Lycopodiaceae																								
<i>Palhinhaea cernua</i> (L.) Franco & Vasc.	1.000	0.001	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.111	0.587	0.00744
Melastomataceae																								
<i>Macairea radula</i> (Bonpl.) DC.	0.953	0.001	-	-	0.439	-	-	-	-	-	-	0.007	-	-	0.609	-	-	-	-	-	-	1.566	1.305	0.00730
Cyperaceae																								
<i>Scleria leptostachya</i> Kunth	0.944	0.001	0.483	0.448	0.736	2.952	-	0.106	2.090	1.588	2.013	0.099	-	0.023	0.042	0.020	-	-	-	-	-	-	-	
Poaceae																								
<i>Trachypogon spicatus</i> (L.f.) Kuntze	0.933	0.004	-	0.182	-	-	-	0.254	16.361	-	1.112	3.582	-	0.589	8.883	2.550	11.209	12.291	7.292	20.414	15.582	44.075	0.40015	
<i>Axonopus brasiliensis</i> (Spreng.) Kuhlm.	0.904	0.049	0.521	4.714	-	2.510	0.100	0.157	0.484	0.093	0.025	6.259	-	0.092	0.042	0.328	-	-	-	0.088	-	1.585	0.00409	
<i>Andropogon virgatus</i> Desv.	0.880	0.050	2.749	11.594	7.417	4.316	14.441	1.220	11.692	6.662	6.014	-	0.658	-	-	-	5.916	-	-	0.637	0.103	0.229	0.02445	
Xyridaceae																								
<i>Xyris jupicai</i> Rich.	0.837	0.020	0.458	-	-	-	0.023	0.004	-	-	0.033	-	-	-	-	-	-	-	-	-	-	0.111	0.218	0.00011
Poaceae																								
<i>Oedochloa procurrens</i> (Nees ex Trin.) C.Silva & R.P.Oliveira	0.830	0.023	-	1.787	0.142	-	0.187	4.803	1.754	2.020	1.042	-	-	-	-	-	-	0.018	-	0.080	-	-	-	
Asteraceae																								
<i>Chrysolea desertorum</i> (Mart. ex DC.) Dematt.	0.816	0.020	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.023	0.00215
Cyperaceae																								
<i>Scleria reticularis</i> Michx. ex Willd.	0.816	0.020	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.043	0.00106
Eriocaulaceae																								

Family / Species	IndVal	p	Group / Vereda																					
			1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	3	3	3
			DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	MG1	MT1	MT2	MT3	TO1	TO2	TO3	TO4	BA1	GO7	MG2	
<i>Syngonanthus helminthorrhizus</i> (Mart. ex Körn.) Ruhland	0.816	0.009	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.161	0.085	-
Lentibulariaceae																								
<i>Utricularia hispida</i> Lam.	0.808	0.013	-	-	-	0.009	-	-	-	-	-	-	0.004	-	-	-	-	-	-	-	-	-	0.144	0.00029
Euphorbiaceae																								
<i>Euphorbia potentilloides</i> Boiss.	0.797	0.017	-	0.034	-	0.093	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.035	0.00598
Poaceae																								
<i>Paspalum trichostomum</i> Hack.	0.789	0.009	-	-	-	-	-	3.274	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7.347	0.05076
<i>Trichantheium cyanescens</i> (Nees ex Trin.) Zuloaga & Morrone	0.785	0.038	-	-	-	-	-	-	-	-	-	0.124	0.124	0.413	0.141	-	0.996	0.062	0.313	-	-	-	-	0.00208
Xyridaceae																								
<i>Xyris asperula</i> Mart.	0.782	0.014	-	0.114	-	-	0	0.004	-	-	-	0.039	-	-	-	-	-	-	-	-	-	0.173	-	0.00325
Droseraceae																								
<i>Drosera montana</i> A.St.-Hil.	0.775	0.032	-	0.068	-	0.009	-	-	0.061	0.453	0.689	0.004	-	-	-	-	-	-	-	-	-	-	-	-
Malpighiaceae																								
<i>Byrsonima umbellata</i> Mart. ex A.Juss.	0.769	0.020	-	-	-	-	-	-	-	-	-	-	-	0.290	-	-	-	-	-	-	-	-	0.427	0.00412
Poaceae																								
<i>Paspalum multicaule</i> Poir.	0.766	0.013	-	-	-	-	-	-	-	-	0.784	-	-	-	-	0.160	-	-	-	-	-	-	1.053	0.00923
Rapateaceae																								
<i>Cephalostemon angustatus</i> Malme	0.749	0.016	-	-	-	-	-	-	-	-	-	-	-	0.883	1.253	0.028	-	-	-	-	-	2.102	2.428	-
Euphorbiaceae																								
<i>Microstachys bidentata</i> (Mart.& Zucc.) Esser	0.707	0.045	0.046	-	-	-	-	0.004	-	0.085	-	-	-	-	-	-	-	-	0.586	-	-	0.280	0.00569	
Melastomataceae																								
<i>Chaetogastra gracilis</i> (Bonpl.) DC.	0.707	0.046	0.261	0.608	-	0.196	-	-	-	0.464	0.158	-	-	-	-	-	-	-	-	-	-	-	-	-
Asteraceae																								
<i>Riencourtia oblongifolia</i> Gardner	0.707	0.049	0.008	-	0.581	1.057	-	-	0.297	-	0.843	-	-	-	-	-	-	-	-	-	-	-	-	-

		Group / Vereda																					
		1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	3	3	3
Family / Species	IndVal	<i>p</i>	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	MG1	MT1	MT2	MT3	TO1	TO2	TO3	TO4	BA1	GO7	MG2
Eriocaulaceae																							
<i>Paepalanthus chiquitensis</i>																							
Herzog	0.707	0.050	-	-	-	-	-	-	-	-	-	-	-	-	0.229	0.381	0.232	-	0.151	-	-	-	-

Overall, *veredas* had acidic soils with high levels of aluminum and organic matter and low levels of phosphorus, magnesium, and calcium (Table S5). The average proportion of sand in the *veredas* was higher than that of clay and silt (Table S5). *Veredas* of DF and GO1 had higher clay levels than other groups; higher levels of organic matter were recorded for DF1, DF3, DF4, GO7, MG1, and BA1; *veredas* of Mato Grosso, TO1, and GO7 had a higher proportion of cation saturation (V), while BA1 and MG1 had lower cation saturation; and the amount of phosphorus was higher in GO5 and lower in DF2 than in others (Table S5).

The *veredas* clearly differed in regional soil classes (Table S1). Soil classes for group 2 and 3 had predominantly plain relief sandy soils (Orthic Arenosols), and *veredas* from group 1 were distributed in regions with three different soil classes (Table S1). Soil variables were significantly different between the *veredas* as well as between the three groups formed by the cluster analysis (Table S6). However, in groups 1 and 2, Al, OM and pH were not significantly different, and in groups 2 and 3, Ca, Mg, K, and soil textures did not differ significantly. CEC, phosphorus, and cation saturation were significantly different in all groups. Moran's I correlogram based on raw soil data showed significant spatial autocorrelation for the following variables Al (Moran's I = 0.27, $p = 0.04$ after Bonferroni's correction), K (Moran's I = 0.33, $p = 0.02$ after Bonferroni's correction), pH (Moran's I = 0.37, $p = 0.02$ after Bonferroni's correction), V (Moran's I = 0.50, $p = 0.001$ after Bonferroni's correction), CTC (Moran's I = 0.28, $p = 0.04$ after Bonferroni's correction), sand (Moran's I = 0.25, $p = 0.04$ after Bonferroni's correction), silt (Moran's I = 0.31, $p = 0.01$ after Bonferroni's correction), clay (Moran's I = 0.30, $p = 0.01$ after Bonferroni's correction), indicating that the spatial location is affecting the variables. Thus, some of the variables did not show a significant autocorrelation: OM, Mg and P ($p > 0.05$ after Bonferroni's correction).

Soil-vegetation interactions

The soil variables retained after Pearson correlation were sand, pH, phosphorus, V, and OM. The total amount of variation explained by the CCA was 30.2%. The first four axes accounted for 27% of the variation in soil variables, with 8.60% of the variation explained by axis 1, 7.40% by axis 2, 5.84% by axis 3, and 4.73% by axis 4 (Table 3). The Monte Carlo test (Table 3) indicated that the relationship between species composition and soil properties of the *veredas* was significant ($p = 0.002$), but only for axis 1 ($p = 0.012$). The soil variables most closely associated with the *veredas* composition were cation saturation ($p = 0.001$), organic matter ($p = 0.007$), and pH ($p = 0.003$) (Table 4). The strongest correlation with CCA axis 1 was observed for sand (negative) (Table 4). CCA axis 2 was highly correlated with pH (positive), cation saturation (positive), and organic matter (negative), and CCA axis 3 showed strong correlation for phosphorus (positive) (Table 4). The distribution of the *veredas* in the CCA was similar to both the dendrogram and the PCoA, with axis 1 showing clear separation between the *veredas* of Mato Grosso, Tocantins, Minas Gerais, BA1, and GO7 and those of Distrito Federal and Goiás (Fig. 4). The first axis showed a positive correlation with phosphorus and pH and a negative correlation with cation saturation, organic matter, and sand; the second axis showed a negative correlation with organic matter and sand, and a positive correlation with cation saturation, pH, and phosphorus (Fig. 4).

Table 3. Summary of canonical correspondence analysis (CCA) and Monte Carlo permutation test ($\alpha = 0.05$) of plant species cover and soil properties of the *veredas*

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.485	0.417	0.329	0.267
Proportion explained (%)	8.601	7.406	5.840	4.739
Cumulative proportion	8.601	16.003	21.840	26.582
<i>F</i> and (<i>p</i>) axes values	1.847 (0.012)	1.590 (0.126)	1.254 (0.527)	1.018 (0.771)
<i>F</i> and (<i>p</i>) CCA values	1.295 (0.002)			

Table 4. Intraset correlation of soil variables with the first three axes of CCA and *F* and *p*-values estimated by permutation test ($\alpha = 0.05$) of plant species cover and soil properties of the *veredas*. Values in bold are significant at $p < 0.05$

Soil variables	Axis 1	Axis 2	Axis 3	<i>F</i> and (<i>p</i> -values)
Phosphorus	0.54334	0.48176	0.68753	1.190 (0.157)
Cation saturation	-0.49374	0.76005	0.42255	1.586 (0.001)
Organic Matter	-0.33659	-0.7284	-0.59678	1.445 (0.007)
pH (CaCl ₂)	0.34136	0.87442	-0.34477	1.419 (0.003)
Sand	-0.72072	-0.43411	0.54047	0.837 (0.767)

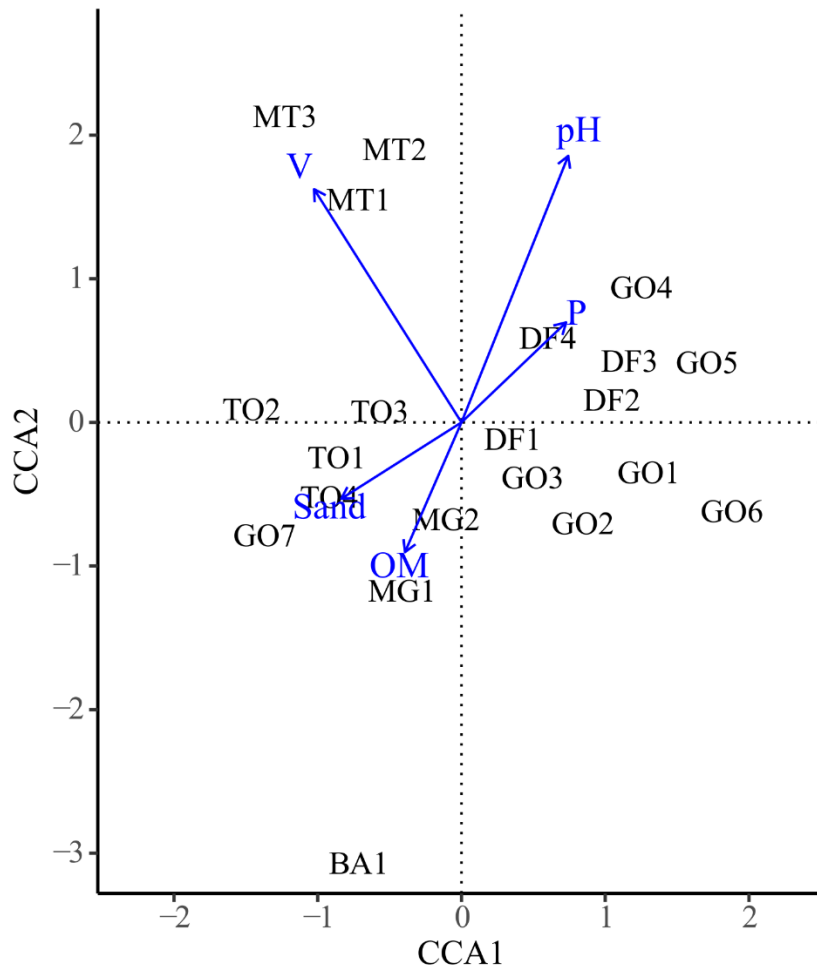


Fig. 4 Ordination diagram obtained by canonical correspondence analysis (CCA) of the 21 *veredas* and soil variables on the first two axes, based on species cover data. Total amount of variation explained: 30.2%. Variation explained by axes 1 and 2 were 8.6%, and 7.4%, respectively. OM = organic matter, V = cation saturation, P = phosphorus. The site codes are described in Fig. 1

The results of the GLM showed that phosphorus, organic matter, and pH were significant predictors of species richness (Table 5). Phosphorus and pH were positively correlated with species richness, whereas organic matter was negatively correlated (Table 5). For compositional similarity (PCoA1 scores), organic matter, cation saturation, and sand were negatively correlated, whereas phosphorus was positively correlated (Table 5). The selected soil predictors accounted for 86% ($R^2 = 0.86$) and 63.49% (pseudo-

R-squared = 63.49) of the variation in species composition and species richness, respectively.

Table 5. Significant soil predictors of herbaceous and shrub composition of the *veredas*. Values under PCoA1 (species dissimilarity) represent the *t value* and its respective *p*-value ($\alpha = 0.05$) of linear model (LM) between the first axis of PCoA and soil variables. Values under species richness represent the *z value* and its respective *p*-value ($\alpha = 0.05$) of generalized linear model (GLM) between species richness and soil variables

	LM		GLM	
	PCoA1 <i>t value</i>	<i>p</i>	Species richness <i>z value</i>	<i>p</i>
(Intercept)	-7.941	<0.0001	5.419	<0.0001
Cation saturation	8.811	<0.0001	–	–
Sand	5.646	<0.0001	–	–
Organic Matter	5.843	<0.0001	-2.245	0.0250
Phosphorus	-6.510	<0.0001	7.868	<0.0001
pH (CaCl ₂)	–	–	3.785	0.00015

Discussion

The *veredas* showed major variations in species composition and diversity and shared only one common species, *Paspalum lineare* Trin., which is one of the most widespread species, with its distribution ranging from Mexico to northeastern Argentina (Zuloaga et al. 2004). Overall, the number of exclusive species in all *veredas* was similar to the total number of species recorded for each *vereda*, and the number of unique species was higher in the *veredas* that exhibited higher species richness. A low number of shared species have also been reported in other studies involving *veredas* (Araújo et al. 2002; Resende et al. 2013). For herbaceous and shrub species in other vegetation types, the similarities among sites are also low (Mendes et al. 2012; Amaral et al. 2022).

The studied *veredas* varied in altitude, temperature, and precipitation (Table S5), because of their broad spatial distribution. The occurrence of *veredas* can be influenced

by climatic, edaphic, and topographic variables (Gonçalves et al. 2022). The most diverse *veredas* (GO4 and GO5) are in the mountainous regions of Chapada dos Veadeiros (GO4) and Topázios Range (GO5), two areas in higher altitudes (above 1,000 m), with cooler temperatures (mean min 15 / max 26 °C), and with high species richness and endemism (Simon and Proença and 2000; Proença et al. 2000; Vidal et al. 2019). Geographic barriers can limit species dispersal, restricting their occurrence to a specific region. The *veredas* located in the mountainous regions of Chapada dos Veadeiros (GO3, GO4), Topázios Range (GO5), and the Espinhaço Range (MG1) contained high-altitude endemic plant species from the families Eriocaulaceae and Xyridaceae (Giulietti et al. 1987; Munhoz and Proença 1998; Proença et al. 2000). The dispersal of these species is limited by lower temperatures and differentiated soil factors, such as the abundance of rocky soils, which are all characteristic of high-altitude areas (Giulietti et al. 1987; Stannard 1995). On the other hand, one of the least diverse *veredas*, with the lowest Shannon (H') value and low evenness, was found in Serra do Tombador (GO1), northeastern Goiás, on the edge of Chapada dos Veadeiros at a lower altitude (below 1,000 m). The Cerrado vegetation surrounding the *vereda* GO1 in northeastern Goiás is known for having a predominance of mesotrophic species, with records of low number of woody species (Ratter et al. 2003). As previously observed for the Cerrado species, the species distribution of the *veredas* is also mosaic-like (Felfili et al. 2004; Felfili et al. 2008), especially since they are restricted to hydromorphic soils and surrounded by vegetation on well-drained soils.

The PCoA and cluster analysis supported the high variation in species composition demonstrated by our results. The ordination showed that species occurrence was more similar than species cover in the groups of *veredas* formed by the cluster analysis. The *veredas* from the cluster groups were closely distributed in the ordination and each group was distanced from one another. When excluding the effect of space on species

composition, the adjusted PCoA analysis did not reveal any clear separation among groups. This is because spatial autocorrelation, which can create patterns of similarity or dissimilarity, was no longer a factor in the analysis. Group 1 and 2 contained five and one indicator species, respectively (Table 2), confirming that high heterogeneity existed in the areas. Two indicator species were common between groups 2 and 3. Group 3 contained 15 indicator species with an IndVal > 72%, higher than the other groups. The cluster analysis at the third level of the divisions completely agreed with the Cerrado ecoregion zoning proposed by Sano et al. (2019), except for MG1, which is isolated in the Jequitinhonha ecoregion. The species composition of MG1 was distinct compared with that of the other *veredas*, probably because the site region, i.e., the south of the Espinhaço Range, is influenced by neighboring sites of high-altitude southeastern grasslands with many records of plant endemism (Giulietti and Pirani 1988; Echternacht et al. 2011).

Studies evaluating the distribution of trees (Sano et al. 2019) and herbaceous and shrub (Amaral et al. 2017) species in Cerrado have described floristic ecoregions, i.e., a geographically defined assemblage of natural communities with similar environmental conditions (Dinerstein et al. 1995), which are associated with soil, geomorphology, climate, altitude, vegetation, and plant species data. In the Brazilian Planalto Central ecoregion, the altitudinal gradient creates important centers of endemism for diverse species (Simon and Proença 2000; Vidal et al. 2019), including herbaceous and shrub flora (Amaral et al. 2017; Sano et al. 2019). Group 1 is entirely distributed in the Planalto Central ecoregion, which is near the center of the Cerrado, known to be a hotspot of biological diversity and where our richest *veredas* were located (GO5, GO4, DF3; Table 1). Additionally, the location of these *veredas* leaves them far from neighboring biomes, which can also explain the greater local richness (Françoso et al. 2016). The Araguaia Tocantins ecoregion encompasses practically all the *veredas* from group 2 (MG1 is an

exception) and it is in a hydrographic region with the same name. Few endemic and exclusive species are registered from this ecoregion (Arruda 2003; Sano et al. 2019; Vidal et al. 2019), which is supported by our results as well, especially for the *veredas* in the Tocantins state, which have the lowest incidences of exclusive species. The *veredas* from group 3 (GO7, MG2, and BA1) were entirely located in the Chapadão do São Francisco ecoregion, where the soil drainage capacity and slope of the terrain are very low (Arruda 2003), characteristics that are associated with the occurrence of hydromorphic soils and *veredas*. The rate of species endemism in this ecoregion is intermediate when compared to the other ecoregions (Sano et al. 2019), which corresponds to our results for the *veredas* in group 3.

CCA analysis showed that soil organic matter, cation saturation, and pH were good predictors of species cover. As expected, *veredas* from Tocantins state (TO) and from group 3 were correlated with sand, since the sites are in a region of orthic Arenosols, which are deep soils with a sandy or sandy loam texture composed essentially of quartz (Reatto et al. 2008). Cation saturation was an important driver of species cover for the *veredas*, indicating high levels of this attribute at the Mato Grosso sites. The increase in cation saturation and sand proportion was negatively correlated with compositional similarity. Some studies have acknowledged cation saturation (Mota et al. 2018; Souza et al. 2021) and soil texture (Ruggiero et al. 2002; Amaral et al. 2022; Lira-Martins et al. 2022) as important factors associated with the flora communities in Cerrado. In other savannas, higher levels of sand can indicate higher richness of herbaceous and shrub vegetation (Medinski et al. 2010). High sand content (> 50%) decreases soil capacity to retain or release cations or anions, soil organic carbon and cation saturation (Huang and Hartemink 2020), thus reducing soil fertility in the *veredas*. Also, the low percentage of soil cation saturation in the *veredas* was probably limited by the acidic soils, which

contains acid cation aluminum, limiting plant growth and nutrient cation absorption (Weil and Brady 2016). Although the fertility is low, waterlogged sandy soils makes the soil structure softer and suitable for root growth and shoot emergence (Huang and Hartemink 2020).

The increase in soil phosphorus content was positively correlated with overall species richness and compositional similarity, whereas organic matter negatively correlated with them. Nogueira et al. (2022) also found significant interactions between phosphorus and species richness and relative cover in *veredas*. Phosphorus is a vital nutrient responsible for photosynthesis, transformation of sugars and starches, energy transfer, nutrient movement within plants, and efficient root growth (Weil and Brady 2016). Regarding organic matter, the hydromorphic soil of the *veredas* is responsible for the accumulation of organic materials in the early stages of decomposition because the poor aeration conditions of the soil reduce the humification process and increase the C:N ratio (Sousa et al. 2015). Although the soil organic matter content at the *veredas* is high, the humus derived from the oxidation of this element is slowly produced and less available, which, combined with the low pH levels, makes the soil nutrient-poor (Sousa et al. 2015). These conditions restrict species occurrence, allowing only specialized species to survive (Weil and Brady 2016). A strong negative correlation of soil organic matter accumulation on herbaceous and shrub species richness has also been observed in other Cerrado vegetation types (Xavier et al. 2019; Souza et al. 2021).

Richness was positively correlated with an increase in pH. pH was a good predictor for some of the *veredas* with the highest species numbers, such as those in Distrito Federal (DF2, DF3, DF4), Chapada dos Veadeiros (GO4), and Topázios Range (GO5). Plant communities in wetlands present a higher number of species with higher soil pH levels (Xiaolong et al. 2014). Extreme levels of soil pH can influence plant distribution, not only

directly, but also by affecting the mineralization of soil organic matter and the availability of nutrients (Medinski et al. 2010; Viani et al. 2014). The soils of the *veredas* presented low pH, and the H⁺ ions remained high, which can hinder the absorption of essential nutrients by the plants (Ellis and Mellor 1995), therefore reducing the chances for species to colonize a habitat under such harsh conditions.

Soil water saturation and soil nutrients can limit plant establishment, once low nutrient content and water saturation create a strong environmental pressure that might perform a more rigorous species filtering (Viani et al. 2014; Lira-Martins et al. 2022). Typically, the soils of the *veredas* presents a non-uniform distribution of moisture due to variation in the water table fluctuation (Hórak-Terra et al. 2022), which creates high patchiness in the soil moisture gradient, and may also promote plant species richness and variation in species composition in the communities (Araújo et al. 2002; Oliveira et al. 2009; Resende et al. 2013). The water table depth of the *vereda* increases from the core zone to the border zone and its levels can oscillate influenced by the rainy and dry season of the Cerrado. During the dry season, when the water table level is lowered, especially at the border of the *vereda* (the core zone is always wet), surface soil horizons become exposed and unsaturated, intensifying the organic matter decomposition, and changing nutrient availability in the soil (Hórak-Terra et al. 2022). During the rainy season, suspended soil particles (Ca, Mg, Na, Fe, Mn, and Al) can be removed by the rain from the border and accumulate in the lower parts of the *vereda* (Ramos et al. 2014). Also, the core zone of the *veredas* present higher proportions of accumulated organic matter (Hórak-Terra et al. 2022), because soil-pore spaces of wet regions are predominantly filled by water (Ramos et al. 2014), which slows down the humification of organic residues (Sousa et al. 2015).

The studied *veredas* showed significant differences in soil properties and species composition which were driven by specific soil filters, such as cation saturation, organic matter, phosphorus, sand proportion, and pH. These results are key to understanding how different these environments are, in comparison to other vegetation types within and outside the Cerrado, how they function and are relevant for decision making to efficiently protect fragile wetlands such as *veredas*, especially under imminent global environmental changes and anthropogenic interference. The increasing conversion of native vegetation to cultivated pasturelands, along with the excessive use of center-pivot irrigation systems for agriculture, has reduced water availability in important ecoregions of the Cerrado (Planalto Central, Chapadão do São Francisco, and Jequitinhonha) (Rodrigues et al. 2022), negatively impacting the soil organic carbon stock and water holding capacity of the *veredas* (Horák-Terra et al. 2022). As a result, the flora of the *veredas* is highly endangered, and these areas are considered a high-priority for conservation efforts, including the creation of new conservation units (Amaral et al. 2017; Sano et al. 2019). We hope that this study can provide new insights into this topic, with practical consequences for restoration programs concerning the management and recovery of degraded areas, as well as the conservation of natural areas.

References

- Alvares CA, Stape JL, Sentelhas PC, de Moraes Gonçalves JL, Sparovek G (2013) Köppen's climate classification map for Brazil. *Meteorol Z* 22:711–728. <https://doi.org/10.1127/0941-2948/2013/0507>
- Amaral AG, Bijos NR, Moser P, Munhoz CBR (2022) Spatially structured soil properties and climate explain distribution patterns of herbaceous-shrub species in the Cerrado. *Plant Ecol* 223:85–97. <https://doi.org/10.1007/s11258-021-01193-7>

- Amaral AG, Munhoz CB, Walter BM, Aguirre-Gutiérrez J, Raes N (2017) Richness pattern and phytogeography of the Cerrado's herb-shrub flora and implications for conservation. *J Veg Sci* 28:848–858. <https://doi.org/10.1111/jvs.12541>
- ANA – Agência Nacional de Águas e Saneamento Básico (2021) Regiões Hidrográficas. Available via: <https://dadosabertos.ana.gov.br>. Accessed 26 Aug 2021
- Arantes ACV, Damasceno-Junior GA, Pott V J, Moreira SN, Pott A (2019) Seasonal diversity of vegetation structure of *veredas*, Mato Grosso do Sul, Brazil. *Oecol Aust* 23:799–811. <https://doi.org/10.4257/oeco.2019.2304.07>
- Araújo GM, Barbosa AAA, Arantes AA, Amaral AF (2002) Composição florística de *veredas* no município de Uberlândia, MG. *Braz J Bot* 25:475–493. <https://doi.org/10.1590/S0100-84042002012000012>
- Arruda MB (2003) Representatividade ecológica com base na biogeografia de biomas e ecorregiões continentais do Brasil. O caso do bioma Cerrado. Ph.D. Dissertation. Universidade de Brasília, Brasília
- Bijos NR, Eugênio CUO, Mello TRB, Souza GF, Munhoz CBR (2017) Plant species composition, richness, and diversity in the palm swamps (*veredas*) of Central Brazil. *Flora* 236–237:94–99. <http://dx.doi.org/10.1016/j.flora.2017.10.002>
- Blanchet FG, Legendre P, Borcard D (2008) Forward selection of explanatory variables. *Ecology* 89:2623–2632. <https://doi.org/10.1890/07-0986.1>
- Borcard D, Gillet F, Legendre P (2011) Numerical ecology with R. Springer, New York
- Canfield R (1941) Application of line interception in sampling range vegetation. *J Forest* 39:388–394. <https://doi.org/10.1093/jof/39.4.388>
- Carvalho G (2020) flora: Tools for Interacting with the Brazilian Flora 2020. R package version 0.3.4. <https://CRAN.R-project.org/package=flora>

- Cavender-Bares J, Kozak KH, Fine PV (2009) The merging of community ecology and phylogenetic biology. *Ecol Lett* 12:693–715. <https://doi.org/10.1111/j.1461-0248.2009.01314.x>
- Chen RF, Zhang FL, Zhang QM, Sun QB, Dong XY, Shen RF (2011) Aluminium-phosphorus interactions in plants growing on acid soils: does phosphorus always alleviate aluminium toxicity? *J Sci Food Agric* 92:995–1000. <https://doi.org/10.1002/jsfa.4566>.
- Cornwell WK, Ackerly DD (2009) Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecol Monogr* 79:109–26. <https://doi.org/10.1890/07-1134.1>
- Cummings J, Smith D (2000) The line-intercept method: a tool for introductory plant ecology laboratories. In: Karcher SJ (ed) *Tested studies for laboratory teaching. Proceedings of the 22nd workshop/conference of the association for biology laboratory education (ABLE), South Carolina*, pp 234-246
- De Cáceres M, Legendre P (2009) Associations between species and groups of sites: Indices and statistical inference. *Ecology* 90:3566–3574. <https://doi.org/10.1890/08-1823.1>
- Dinerstein E, Olson D, Graham D, Primm S, Bookbinder M, Ledec G (1995) Una evaluación del estado de conservación de las eco-regiones terrestres de América Latina y el Caribe. WWF, Washington, DC Available via: <http://documentos.bancomundial.org/curated/es/917091468269687252/Una-evaluacion-del-estadode-conservacion-de-las-ecoregiones-terrestres-de-America-Latina-y-el-Caribe>.
- Accessed 18 Jul 2022
- Dray S, Bauman D, Blanchet G, Borcard D, Clappe S, Guenard G, Jombart T, Larocque G, Legendre P, Madi N, Wagner HH (2022) *adespatial*: multivariate multiscale

- spatial analysis. R package version 0.3-20. <https://CRAN.R-project.org/package=adespatial>
- Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol Model* 196:483–493. <https://doi.org/10.1016/j.ecolmodel.2006.02.015>
- Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol Monogr* 67:345–366. [https://doi.org/10.1890/0012-9615\(1997\)067\[0345:SAAIST\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2)
- Durigan G, Munhoz CB, Zakia MJB et al (2022) Cerrado wetlands: multiple ecosystems deserving legal protection as a unique and irreplaceable treasure. *Perspectives in Ecology and Conservation*.
- Echternacht L, Trovó M, Oliveira CT, Pirani JR (2011) Areas of endemism in the Espinhaço Range in Minas Gerais, Brazil. *Flora* 206:782–791. <https://doi.org/10.1016/j.flora.2011.04.003>
- Eiten G (1994) Vegetação do Cerrado. In: Pinto MN (ed) *Cerrado: caracterização, ocupação e perspectivas*, UnB/SEMATEC, Brasília, DF, pp 17-73
- Ellis S, Mellor A (1995) *Soils and environment*. Routledge, New York
- EMBRAPA - Empresa Brasileira de Pesquisa Agropecuária (2006) *Centro Nacional de Pesquisa de Solos. Sistema brasileiro de classificação de solos*, 2nd edn. Rio de Janeiro
- EMBRAPA - Empresa Brasileira de Pesquisa Agropecuária (2017) *Manual de métodos de análise de solo*. Embrapa, Brasília. *Pesquisa de Solos. Sistema brasileiro de classificação de solos*, 2nd edn. Rio de Janeiro
- Felfili JM, Felfili MC, Nogueira PE, Silva JF, Farinas MR, Silva Junior MC, Rezende AV, Fagg CW (2008) Padrões fitogeográficos e sua relação com sistemas de terra no

- bioma Cerrado. In: Sano SM, Almeida SP, Ribeiro JF (eds) Cerrado: Ecologia e Flora, Embrapa Cerrados, Brasília, DF, pp 213-228
- Felfili JM, Silva Júnior MC, Sevilha AC, Fagg CW, Teles Walter BM, Nogueira PE, Rezende AV (2004) Diversity, floristic and structural patterns of cerrado vegetation in Central Brazil. *Plant Ecol* 175:37–46. <https://doi.org/10.1023/B:VEGE.0000048090.07022.02>
- Flora e Funga do Brasil (2022) Jardim Botânico do Rio de Janeiro. <https://reflora.jbrj.gov.br/reflora/>. Available via: <http://floradobrasil.jbrj.gov.br/>. Accessed 20 Sep 2022
- Françoso RD, Haidar RF, Machado RB (2016) Tree species of South America central savanna: endemism, marginal areas and the relationship with other biomes. *Acta Bot Bras* 30:1–9. <https://doi.org/10.1590/0102-33062015abb0244>
- Giraudoux P (2022) *pgirmess*: spatial analysis and data mining for field ecologists. R package version 2.0.0. <https://CRAN.R-project.org/package=pgirmess>
- Giulietti AM, Menezes NL, Pirani JR, Meguro M, Wanderley MGL (1987) Flora da Serra do Cipó, Minas Gerais: Caracterização e lista das espécies. *Bol Bot Universidade de São Paulo* 9:1–151
- Giulietti AM, Pirani JR (1988) Patterns of geographic distribution of some plant species from Espinhaço Range, Minas Gerais and Bahia, Brazil. In: Vanzolini P, Heyer WR (eds) *Proceedings of a Workshop on Neotropical Distribution Patterns*. Academia Brasileira de Ciências, Rio de Janeiro, pp 39-69
- Gonçalves RVS, Cardoso JCF, Oliveira PE et al. (2022) The role of topography, climate, soil and the surrounding matrix in the distribution of *Veredas* wetlands in central Brazil. *Wetlands Ecol Manage* 30:1261–1279. <https://doi.org/10.1007/s11273-022-09895-z>

- Grime JP, Pierce S (2012) The evolutionary strategies that shape ecosystems. Wiley-Blackwell, Chichester
- Huang J, Hartemink AE (2020) Soil and environmental issues in sandy soils. *Earth-Science Rev*, 208:103295. <https://doi.org/10.1016/j.earscirev.2020.103295>
- Higgins SI, Delgado-Cartay MD, February FC, Combrink IJ (2011) Is there a temporal niche separation in the leaf phenology of savanna trees and grasses? *J Biogeogr* 38:2165–2175. <https://doi.org/10.1111/j.1365-2699.2011.02549.x>
- Horák-Terra I, Terra F da S, Lopes AKA (2022) Soil characterization and drainage effects in a savanna palm swamp (*vereda*) of an agricultural area from Central Brazil. *Rev Bras Ciênc Solo* 46:e0210065. <https://doi.org/10.36783/18069657rbc20210065>
- Kassambara A, Mundt F (2020) factoextra: Extract and Visualize the Results of Multivariate Data Analyses. R package version 1.0.7 <https://CRAN.R-project.org/package=factoextra>
- Langan L, Higgins SI, Scheiter S (2017) Climate-biomes, pedo-biomes or pyro-biomes: which world view explains the tropical forest – savanna boundary in South America? *J Biogeogr* 44(10):2319-2330. <https://doi.org/10.1111/jbi.13018>
- Legendre P, Legendre L (2012) Numerical Ecology. Elsevier, Amsterdam. pp 512-519
- Lima JEFW, Silva EM (2008) Recursos hídricos do bioma Cerrado: importância e situação. In: Sano SM, Almeida SP, Ribeiro JF (eds) Cerrado: ecologia e flora. Embrapa, Planaltina, DF, pp 89-106
- Lira-Martins D, Nascimento DL, Abrahão A et al (2022) Soil properties and geomorphic processes influence vegetation composition, structure, and function in the Cerrado Domain. *Plant Soil* 476:549–588. <https://doi.org/10.1007/s11104-022-05517-y>

- Maechler M, Rousseeuw P, Struyf A, Hubert M, Hornik K (2022) cluster: Cluster Analysis Basics and Extensions. R package version 2.1.4 <https://CRAN.R-project.org/package=cluster>
- Mckane, RB, Jonhson LC, Shaver GR et al (2002) Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nat* 415:68–71. <https://doi.org/10.1038/415068a>
- Medinski TV, Mills AJ, Esler KJ, Schmiedel U, Jürgens N (2010) Do soil properties constrain species richness? Insights from boundary line analysis across several biomes in southwestern Africa. *J Arid Env* 74(9):1052–1060. <https://doi.org/10.1016/j.jaridenv.2010.03.004>
- Mendes MRDA, Munhoz CBR, Silva Júnior MCD, Castro AAJF (2012) Vegetation and soil relationship in moist grassland in the National Park of Sete Cidades, Piauí, Brazil. *Rodriguésia* 63:971–984. <https://doi.org/10.1590/S2175-78602012000400014>
- Mota GS, Luz GR, Mota NM, Coutinho ES, Veloso MDDM, Fernandes GW, Nunes YRF (2018) Changes in species composition, vegetation structure, and life forms along an altitudinal gradient of rupestrian grasslands in south-eastern Brazil. *Flora* 238:32–42. <https://doi.org/10.1016/j.flora.2017.03.010>
- Munhoz CBR, Araújo GM (2011) Métodos de Amostragem do estrato herbáceo-subarbustivo. In: Felfili JM, Eisenlohr PV, Melo MMRF, Andrade LA, Neto JAAM, editores. *Fitossociologia no Brasil: Métodos e Estudos de Casos*. Universidade Federal de Viçosa, Viçosa, pp 213-230
- Munhoz CBR, Felfili JM (2006) Fitossociologia do estrato herbáceo-subarbustivo de uma área de campo sujo no Distrito Federal, Brasil. *Acta Bot Bras* 20:671–685. <https://doi.org/10.1590/S0102-33062006000300017>

- Munhoz CBR, Proença C (1998) Composição florística do município de Alto Paraíso de Goiás na Chapada dos Veadeiros. *Bol. Herb. Ezechias Paulo Heringer* 3:102–150
- Nogueira EV, Bijos NR, Trindade VL, Heusi GP, Togni PH, Munhoz CBR (2022) Differences in soil properties influence floristic changes in the Veredas of the Brazilian Cerrado. *Braz J Bot* 45(2):763–774. <https://doi.org/10.1007/s40415-022-00795-3>
- Nunes YRF, Souza CS, de Azevedo IFP, de Oliveira OS, Frazão LA, Fonseca RS et al (2022) Vegetation structure and edaphic factors in *veredas* reflect different conservation status in these threatened areas. *For Ecosyst* 9:100036. <https://doi.org/10.1016/j.fecs.2022.100036>
- Oksanen J, Simpson G, Blanchet FG et al (2022) Vegan: community ecology package. R package version 2.6-4 <https://CRAN.R-project.org/package=vegan>
- Oliveira-Filho AT, Shepherd GJ, Martins FR, Stubblebine WH (1989) Environmental factors affecting physiognomic and floristic variation in an area of cerrado in central Brazil. *Journal of Tropical Ecology* 5(4):413–431. <https://doi.org/10.1017/S0266467400003862>
- Oliveira GC, Araújo GM, Barbosa AAA (2009) Florística e zonação de espécies vegetais em *veredas* no Triângulo Mineiro, Brasil. *Rodriguésia* 60:1077–1085. <https://doi.org/10.1590/2175-7860200960417>
- Paradis E, Schliep K (2019) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35:526–528
- Proença C, Oliveira RS, Silva AP (2000) Flores e Frutos do Cerrado. Universidade de Brasília, Brasília

- Queiroz ML (2015) Nascentes, *veredas* e áreas úmidas. Revisão conceitual e metodologia de caracterização e determinação: estudo de caso na Estação Ecológica de Águas Emendadas - Distrito Federal. Master's thesis, Universidade de Brasília, Brasília
- Ramos MVV, Curi N, Motta PEFD, Vitorino ACT, Ferreira MM, Silva MLN (2006) *Veredas* do Triângulo Mineiro: Solos, água e uso. *Cien e Agrotecnol* 30(2):283–293. <https://doi.org/10.1590/S1413-70542006000200014>
- Ramos MVV, Haridasan M, Araújo GM (2014) Caracterização dos solos e da estrutura fitossociológica da vegetação de *Veredas* da Chapada no Triângulo Mineiro. *Front: J Soc, Technol Environ Sci* 3(2):180–210. <https://doi.org/10.21664/2238-8869.2014v3i2.p180-210>
- Ratter JA, Bridgewater S, Ribeiro JF (2003) Analysis of the floristic composition of the Brazilian Cerrado vegetation III: comparison of the woody vegetation of 376 areas. *Edinb. J Bot* 60: 57–109. <https://doi.org/10.1017/S0960428603000064>
- R Core Team (2022) R version 4.2.2: a language and environment for statistical computing. R Found. Stat. computing. R Found Stat. Comput, Vienna, Austria. Available at: <http://www.R-project.org/>
- Reatto A, Correia JR, Spera ST, Martins ES (2008) Solos do bioma Cerrado: aspectos pedológicos. In: Sano SM, Almeida SP, Ribeiro JF (eds) *Cerrado: ecologia e flora*. Planaltina, Embrapa, pp 107-149
- Resende ILDM, Chaves LJ, Rizzo JA (2013) Floristic and phytosociological analysis of palm swamps in the central part of the Brazilian savanna. *Acta Bot Bras* 27:205–225. <https://doi.org/10.1590/S0102-33062013000100020>
- Ribeiro JF, Walter BMT (2008) As principais fitofisionomias do bioma Cerrado. In: Sano SM, Almeida SP, Ribeiro JF (eds) *Cerrado: ecologia e flora*. Embrapa, Planaltina, pp 151-212

- Ribeiro JW, Pilon NA, Rossatto DR, Durigan G, Kolb RM (2021) The distinct roles of water table depth and soil properties in controlling alternative woodland-grassland states in the Cerrado. *Oecol* 195(3):641–653. <https://doi.org/10.1007/s00442-021-04869-z>
- Rodrigues AA, Macedo MN, Silvério DV et al. (2022) Cerrado deforestation threatens regional climate and water availability for agriculture and ecosystems. *Global Change Biology*, 28(22):6807-6822
- Rosolen V, de Oliveira DA, Bueno GT (2015) *Vereda* and Murundu wetlands and changes in Brazilian environmental laws: challenges to conservation. *Wetl Ecol Manag* 23:285–292. <https://doi.org/10.1007/s11273-014-9380-4>
- Rossatto DR, Silva LCR, Sternberg LSL, Franco AC (2014) Do woody and herbaceous species compete for soil water across topographic gradients? Evidence for niche partitioning in a Neotropical savanna. *South Afr J Bot* 91:14–18. <https://doi.org/10.1016/j.sajb.2013.11.011>
- Ruggiero PGC, Batalha MA, Pivello VR, Meirelles ST (2002) Soil-vegetation relationships in cerrado (Brazilian savanna) and semideciduous forest, Southeastern Brazil. *Plant Ecol* 160(1):1–16. <https://doi.org/10.1023/A:1015819219386>
- Sampaio MB, Schmidt IB, Figueiredo IB (2008) Harvesting Effects and Population Ecology of the Buriti Palm (*Mauritia flexuosa* L. f., Arecaceae) in the Jalapão Region, Central Brazil. *Econ Bot* 62(2):171–181. <https://doi.org/10.1007/s12231-008-9017-8>
- Sano EE, Rodrigues AA, Martins ES et al (2019) Cerrado ecoregions: A spatial framework to assess and prioritize Brazilian savanna environmental diversity for conservation. *J Environ Manage* 232:818–828

- Santos HG, Carvalho Junior W, Dart RO et al (2011) O novo mapa de solos do Brasil: legenda atualizada. Embrapa Solos, Rio de Janeiro
- Schmidt IB, Mandle L, Ticktin T, Gaoue OG (2011) What do matrix population models reveal about the sustainability of non-timber forest product harvest? *J Appl Ecol* 48:815–826. <https://doi.org/10.1111/j.1365-2664.2011.01999.x>
- Shi Y (2021) aPCoA: Covariate Adjusted PCoA Plot. R package version 1.3. <https://CRAN.R-project.org/package=aPCoA>.
- Silva DP, Amaral AG, Bijos NR, Munhoz CBR (2018) Is the herb-shrub composition of *veredas* (Brazilian palm swamps) distinguishable? *Acta Bot Bras* 32:47–54. <https://doi.org/10.1590/0102-33062017abb0209>
- Simon MF, Proença C (2000) Phytogeographic patterns of mimosa (Mimosoideae, Leguminosae) in the Cerrado biome of Brazil: an indicator genus of high-altitude centers of endemism? *Biol Conserv* 96:279–296. [https://doi.org/10.1016/S0006-3207\(00\)00085-9](https://doi.org/10.1016/S0006-3207(00)00085-9)
- Sousa FDR, Elmoor-Loureiro LMA, Galvão LM (2013) Cladocerans (Crustacea, Anomopoda and Ctenopoda) from Cerrado of central Brazil: inventory of phytophilous community in natural wetlands. *Biota Neotropica* 13(3):222–229. <https://doi.org/10.1590/S1676-06032013000300025>
- Sousa RFD, Brasil EPF, Figueiredo CCD, Leandro WM (2015) Soil organic matter fractions in preserved and disturbed wetlands of the cerrado biome. *Rev Bras Cien Solo* 39(1):222–231. <https://doi.org/10.1590/01000683rbc20150048>
- Souza GF, Almeida RF, Bijos NR, Fagg CW, Munhoz CBR (2021) Herbaceous-shrub species composition, diversity and soil attributes in moist grassland, shrub grassland and savanna in Central Brazil. *Braz J Bot* 44:227–238. <https://doi.org/10.1007/s40415-020-00672-x>

- Stannard BL (1995) *Flora of the Pico das Almas – Chapada Diamantina, Bahia Brazil*.
Royal Botanic Gardens, Kew
- ter Braak CJF, Smilauer P (2012) *Canoco reference manual and user's guide: software for ordination, version 5.0*. Microcomputer Power
- Tibshirani R, Walther G, Hastie T (2001) Estimating the number of clusters in a data set via the gap statistic. *J R Statist Soc Ser B (Statist Methodol)* 63:411–423
- Veenendaal EM, Torello-Raventos M, Miranda HS et al (2018) On the relationship between fire regime and vegetation structure in the tropics. *New Phytol* 218:153–166. <https://doi.org/10.1111/nph.14940>
- Viani RAG, Rodrigues RR, Dawson TE et al (2014) Soil pH accounts for differences in species distribution and leaf nutrient concentrations of Brazilian woodland savannah and seasonally dry forest species. *Perspect Plant Ecol Evol Syst* 16:64–74
- Vidal JDD, de Souza AP, Koch I (2019) Impacts of landscape composition, marginality of distribution, soil fertility and climatic stability on the patterns of woody plant endemism in the Cerrado. *Glob Ecol Biogeogr* 28:904–916
- Weil RR, Brady NC (2016) *The nature and properties of soils*. Pearson, Edinburgh Gate, Harlow, United Kingdom
- Xavier R, Leite MB, Dexter K et al (2019) Differential effects of soil waterlogging on herbaceous and woody plant communities in a Neotropical savanna. *Oecologia* 190:471–483. <https://doi.org/10.1007/s00442-019-04423-y>
- Xiaolong W, Jingyi H, Ligang X, Rongrong W, Yuwei C (2014) Soil characteristics in relation to vegetation communities in the wetlands of Poyang Lake, China. *Wetlands* 34:829–839 <https://doi.org/10.1007/s13157-014-0546-x>

Zuloaga FO, Pensiero J, Morrone O (2004) Systematics of *Paspalum* Group Notata (Poaceae-Panicoideae-Paniceae). Syst Bot Monogr 71:1–75.

<https://doi.org/10.2307/25027926>

Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York

CHAPTER 2

Stochastic processes influencing beta diversity of herbaceous-shrub species in *veredas* in Central Brazil

Abstract

Veredas are complex grassland-savanna formations assembled over waterlogged saturated soils, surrounded by vegetation types that grow on non-flooded, well-drained soils. Despite their apparent physiognomic similarity, some share less than 62% of their flora with other *veredas* and less than 20% with other vegetation types. To identify the structuring process (based on the neutral or niche theory) influencing the *veredas*, I evaluated the contribution of soil, climate, and spatial variables on the composition and distribution of their herbaceous-shrub species in Central Brazil. I assessed soil attributes, bioclimatic factors, and spatial variables and evaluated the influence of these factors on taxonomic beta diversity using transformation-based Redundancy Analysis and variation partitioning. My findings indicate that: (1) plant communities are more influenced by the spatial turnover of species than by nestedness; (2) spatial predictors better explain the composition and distribution of the flora in the *veredas*; (3) the most important environmental variables were cation saturation, mean temperature of the coldest quarter, precipitation of the coldest quarter, pH, annual precipitation, sand, and temperature seasonality; and finally, (4) stochastic processes, probably related to dispersal limitation, are influencing the formation of *vereda* communities.

Keywords: wetlands, Cerrado, herbaceous-shrub species, environmental and spatial factors, beta diversity, dispersal limitation

Introduction

The organization of communities involves complex processes that describe how organisms colonize and persist in a habitat, determined by a series of factors, combined or not, such as environmental filters, species interactions, species spatial distribution, dispersal capacity, stochasticity, and speciation (Keddy, 1992; Kraft et al., 2015). Niche theory (Grinnell, 1917; Tilman, 2004), explains community structuring by emphasizing the importance of deterministic processes based on ecological niche differentiation, suggesting that organisms occur in a community because they have passed through environmental filters, shaped by variations in environmental conditions (e.g. precipitation, temperature, and soil) and interactions with other species (e.g. mutualism, competition, predation, and parasitism) over time. On the other hand, the neutral theory predicts that all the species in the community are ecologically equivalent and have the same demographic rates (birth, death, dispersal, and speciation rates), hence the community will be structured based on stochastic processes (e.g. ecological drift, random events, and dispersal limitations) (Hubbell, 2001).

The relative importance of each theory in explaining community organization is controversial and continually debated (HilleRisLambers et al., 2012; Martorell and Freckleton, 2014; Leibold et al., 2019; Arim et al., 2023). The importance of deterministic and stochastic processes can vary depending on the horizontal scale studied (Gravel et al., 2006; Chase, 2014; Leibold et al., 2019), the taxa assessed (Legendre et al., 2009; Schmera et al., 2018), among ecosystems (Hubbell, 2001; Myers et al., 2013) and among plant life forms (Liu et al., 2016). At local scale, microhabitat environmental conditions, soil characteristics and competition for resources play a dominant role in shaping plant communities (Gravel et al., 2006; Chase, 2014). As the scale increases, the influence of stochastic processes becomes more apparent, leading to greater variability in species

composition across different sites (Arim et al., 2023). Factors such as seed dispersal, disturbance and random colonization are the most important predictors (Hubbell, 2001; Martorell and Freckleton, 2014; Arim et al., 2023). Both processes often interact and influence each other, with broad-scale stochastic effects impacting local community dynamics (Leibold et al., 2019). To illustrate, a random event, such as a disturbance, can create opportunities for certain plant species to establish on a site (stochastic process). However, the species that ultimately establish themselves in the disturbed area may depend on the presence of their specific traits and interactions with other species (deterministic process) (Leibold et al., 2019). Furthermore, the dependence of biodiversity on environmental predictors is not always linear and the contribution of some predictors may vary depending on the region studied (Kreft and Jetz, 2007). Therefore, despite the differences between the neutral and niche theories, it is likely that the observed patterns of community formation are explained by the combined effect of the two theories, rather than by a single mechanism (Legendre et al., 2009; Chase and Myers, 2011; Leibold et al., 2019).

Ecosystems with dynamic environments, such as some wetlands that experience recurrent flooding or seasonal fluctuations in the water table depth, are expected to be more susceptible to the impact of stochastic processes (Tamea et al., 2010; Arim et al., 2023). The rate of groundwater recharge is the result of events considered to be random, which represent the stochastic force of the dynamic system. These events include precipitation, interception, infiltration, and redistribution (Laio et al., 2009). Variations in soil water content can influence, among other things, the transport of oxygen into the soil, thus controlling the oxidation-reduction potential in this saturated environment (Colmer and Voesenek, 2009; Tamea et al., 2010). This defines the fate of plant biogeochemical processes, microbial activities, and ultimately ecosystem functions and

services, such as the absorption of heavy metals and pollutants and the carbon sequestration and storage (Mitsch and Gosselink, 2015; Moor et al., 2017).

The composition of vegetation in wetlands is influenced by a number of environmental factors, including the water table depth, the soil's physical and chemical properties, the climate, and the presence of anatomical and morphological adaptations in plants that enable them to survive conditions of soil saturation (anoxia) and extreme pH (Colmer and Voesenek, 2009; Mitsch and Gosselink, 2015; Moor et al., 2017). However, the isolated distribution of certain wetlands can amplify the influence of random events and chance occurrences, due to the restriction of seed and spore dispersal between the isolated patches of wetland and surrounding habitats (MacArthur and Wilson, 1967). Limited gene flow can result in increased genetic drift and demographic stochasticity within the population of isolated wetlands, rendering it more susceptible to random events (MacArthur and Wilson, 1967; Hubbell, 2001). Conversely, the dispersal limitation by isolation can enhance trait selection when only species with a high dispersal capacity are able to reach isolated communities (Ai et al., 2013). It can thus be postulated that the combination of environmental factors influencing niche selection by plants and random events are responsible for shaping plant community composition in humid environments (Tamea et al., 2010; Leibold et al., 2019; Arim et al., 2023).

The Cerrado, is a large Brazilian biogeographical dominion dominated by savanna vegetation. It is renowned for its rich biodiversity and diverse range of environments (Eiten, 1972; Ribeiro and Walter, 2008). The composition and diversity of the vegetation of this domain is determined by a combination of factors that act at different spatial scales. These factors include climate seasonality, soil conditions, relief, soil depth, fire frequency, historical processes, anthropogenic actions, and other biotic factors. (Simon et al., 2009; Werneck, 2011; Françoso et al., 2020). The extensive area of the Cerrado

Dominion encompasses all these environmental variations, which have occurred over millions of years resulting in the diversification of its flora into a vegetation mosaic that is vastly dominated by savannas, but also includes semideciduous and deciduous forests, riverine forests, riverine waterlogged grasslands, typical savannas, and natural grassland formations (Oliveira-Filho and Ratter, 2002; Ribeiro and Walter, 2008; Overbeck et al., 2022). *Veredas* are included in the savanna formations and are mosaics of vegetation on seasonally or permanently waterlogged soils, bordered by formations that generally occur on dry, well-drained soils (Ribeiro and Walter, 2008; Durigan et al., 2022).

Vereda is a vegetational complex (Eiten, 1972), distinguished by a continuous herbaceous-shrub layer and a strip of large-sized *buriti* palms (*Mauritia flexuosa* L.f.) emerging in the most saturated soil zone of the community (Durigan et al., 2022; Bijos et al., 2023). *Veredas* are found on hydromorphic soils, which are classified as *Organossolos* and *Gleissolos* (Ramos et al., 2006; Ramos et al., 2014). The soils of these areas are acidic, exhibiting high levels of aluminum and organic matter, and low availability of nutrients (Ramos et al., 2006; Ramos et al., 2014; Bijos et al., 2023). In *veredas*, there are three distinct moisture zones (border, middle, and core) that are influenced by various factors, including drainage, topography, and the water table depth (Eiten, 1972; Durigan et al., 2022). The border zone is situated on moist, seasonally flooded soils, adjacent to the well-drained, non-waterlogged soil typically with cerrado *sensu stricto* vegetation (typical savanna). The border zone is characterized by a diverse array of herbaceous plants, subshrubs, and shrubs. The middle zone is composed of herbaceous plants and subshrubs and are found in moist, long-term seasonally waterlogged soils. In the core zone, the soil is permanently moist or waterlogged throughout the year, and the vegetation is predominantly herbaceous and shrubby, with the presence of the presence of the large-sized *buriti* palms. The *veredas* are distinguished

by their distinctive herbaceous-shrub flora, exhibiting a relatively low floristic similarity with other Cerrado phytophysiognomies (Silva et al., 2018). Furthermore, there is considerable variability in the composition of herbaceous-shrub species across *vereda* sites, reflecting differences in soil properties (Bijos et al., 2023). This variability is even more pronounced between adjacent sites (Bijos et al., 2023).

Understanding vegetation-environment relationships is crucial for the effective conservation and maintenance of biodiversity and for making predictions about vegetation responses to environmental changes in the future (Engelbrecht et al., 2007; Toledo et al., 2012). Empirical studies have demonstrated that geographical distance is the most significant predictor of species distribution in herbaceous-shrub vegetation in wetlands (Fu et al., 2021; Lários et al., 2017). The joint action of spatial and environmental factors, including climate, hydrogeomorphology, total organic carbon, and anthropogenic alterations, has been identified as the primary determinants of vegetation variation (Andrew et al., 2015; Liu et al., 2016). On the local scale, soil attributes, topography, and water table depth are significant predictors of vegetation (Tsuyuzaki et al., 2004; Dwire et al., 2006).

In this context, I aim to ascertain whether the structuring processes influencing the taxonomic beta diversity of plants in *veredas* are based on neutral or niche theory. I will evaluate the influence of soil, climate, and spatial variables on the composition and distribution of herbaceous-shrub species in these communities. Based on this, I address the following questions: (1) What is the contribution of edaphic, climatic and spatial components to the variation in the composition of herbaceous-shrub species in *veredas*? (2) Which process is responsible for the formation of the herbaceous-shrub vegetation of the *veredas*: processes explained by the niche theory (Grinnell, 1917; Tilman, 2004) or by the neutral theory (Hubbell, 2001)? When evaluating the wetlands regionally, it can

be inferred that regional predictors, such as climate and space, will exhibit a higher percentage of explanation than soil (local predictor) regarding the distribution of species. This is because these predictors are known to control the distribution and diversity of species at regional scales (Andrew et al., 2015; Liu et al., 2016; Chun and Lee, 2018). Furthermore, I anticipate a significant impact on the composition of the flora of *veredas* due to stochastic processes, particularly those caused by dispersal barriers. Ecological isolation can impede the dispersal of species between wetland patches, preventing floristic exchange and influencing the assembly of communities in these areas (Arim et al., 2023). Based on this and considering regional environmental differences and differences in dispersal capacities or distances between *veredas*, I hypothesize that the processes determining the composition and distribution of the flora of these communities will be the combined effect of neutral and niche theory.

Materials and methods

Study areas and vegetation sampling

The cover data of 560 herbaceous-shrub species belonging to 220 genera and 69 botanical families in 21 *vereda* sites were sampled during the rainy season. In each *vereda*, I sampled 15 transects of 10 m each. Each 10 m transect is a sample unit. Five transects were randomly placed in three zones of the *veredas*: border, middle, and core. To determine the horizontal cover and plant species composition, I used the line intersection method (Canfield 1941; Munhoz and Araújo 2011). I recorded the length in cm of all herbaceous, subshrub, and shrub individuals that touched or crossed the tape (Cummings and Smith 2000). The assembled species matrix contains the absolute cover (AC) of each species in each area. The AC is the sum of the horizontal projections of the species in meters in the sampling units of the transects (Munhoz and Felfili 2006). Despite the

presence of *M. flexuosa*, a distinctive palm tree of veredas, in all study sites, this species and its associated trees were excluded from my analysis. This is because their coverage represents less than 10% of the total vegetation, and they are absent in the middle and border zones (Ribeiro and Water, 2008). The species data is available at Bijos et al. (2023) (Appendix, Table S4). The *veredas* are situated in Central Brazil, in conservation units or private properties preserved by the owners, covering a distance range of 10° to 17° latitude (S) and 43° to 52° longitude (W) (Fig. 1). The climate of the areas is classified as Köppen seasonal tropical Aw, with a rainy season in summer occurring from November to April, and a dry season in winter, from May to October (Alvares et al., 2013).

Site/State	Site codes	Number of species	Number of exclusive species
Jardim Botânico de Brasília Ecological Station/DF	DF1	48	4
Brasília National Park/DF	DF2	80	11
Brazilian Institute of Geography and Statistics Ecological Reserve/DF	DF3	98	17
Brasília National Forest/DF	DF4	77	10
Serra do Tombador RPPN (1)/GO	GO1	40	10
Serra do Tombador RPPN (2)/GO	GO2	58	11
Jardim de Maitreya/GO	GO3	71	15
<i>Vereda</i> of Vereda dos Ingleses/GO	GO4	106	37
Linda Serra de Topázios RPPN/GO	GO5	124	26
<i>Vereda</i> of Mosteiro Eisho-Ji/GO	GO6	86	33
<i>Vereda</i> of Posse/GO	GO7	72	21
Sempre Vivas National Park/MG	MG1	54	12
Grande Sertão Veredas National Park (1)/MG	MG2	69	21
Grande Sertão Veredas National Park (2)/BA	BA1	33	4
<i>Vereda</i> of Nova Xavantina (1)/MT	MT1	75	14
<i>Vereda</i> of Nova Xavantina (2)/MT	MT2	73	15
<i>Vereda</i> of Nova Xavantina (3)/MT	MT3	70	14
Serra Geral do Tocantins Ecological Station (1)/TO	TO1	50	6
Serra Geral do Tocantins Ecological Station (2)/TO	TO2	58	4
Serra Geral do Tocantins Ecological Station (3)/TO	TO3	58	4
Serra Geral do Tocantins Ecological Station (4)/TO	TO4	45	2

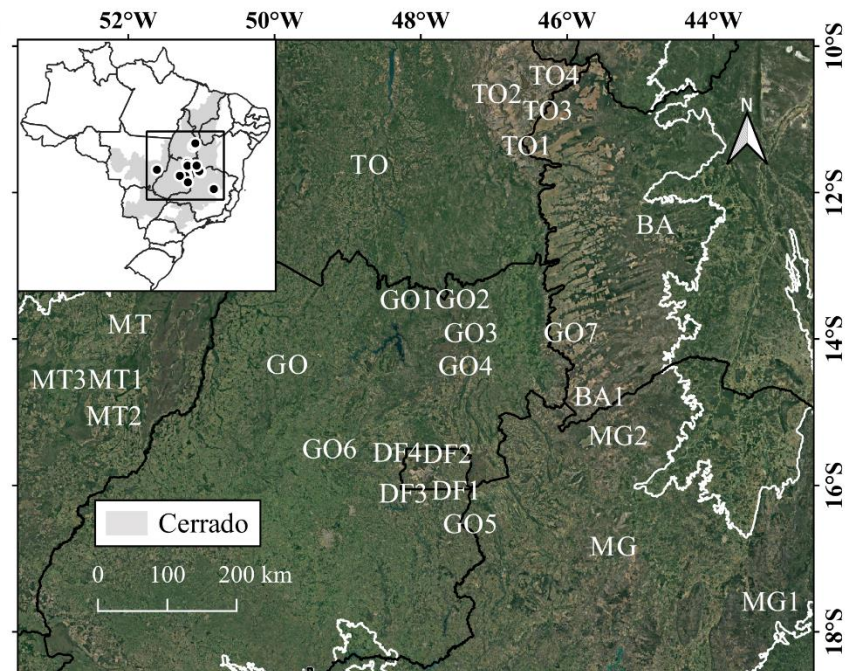


Figure 1 Map illustrating the location, richness, and number of exclusive species observed at the 21 *vereda* sites sampled in Central Brazil. RPPN = Private Natural Heritage Reserve

Environmental and spatial data

The data on the soil physical and chemical properties of the 21 *veredas* were obtained from the work of Bijos et al. (2023), in which surface soil samples (0-20 cm) were collected in the center of each transect. A total of 12 soil variables were utilized in this study. The following soil variables were considered: calcium (Ca), magnesium (Mg), aluminum (Al), potassium (K), cation exchange capacity (CEC), cation saturation (V), phosphorus (P), organic matter (OM), pH, sand, silt, and clay (Appendix, Table S5).

The climate data was obtained using the geographical location information (longitude and latitude) of the areas, using the ArcGIS program. I accessed in the GIS climatic data from the WorldClim 2.0 model (1,000 m spatial resolution; 30 arc-seconds) (Fick and Hijmans, 2017) and acquires the climate variables for each vegetation site corresponding to the coordinates of each site entered in the GIS. A total of 14 bioclimatic variables were utilized in this study. The following bioclimatic variables were considered: BIO1 (annual mean temperature), BIO4 (temperature seasonality), BIO5 (max temperature of the warmest month), BIO8 (mean temperature of the wettest quarter), BIO9 (mean temperature of the driest quarter), BIO10 (mean temperature of the warmest quarter), BIO11 (mean temperature of the coldest quarter), BIO12 (annual precipitation), BIO14 (precipitation of the driest month), BIO15 (precipitation seasonality), BIO16 (precipitation of wettest quarter), BIO17 (precipitation of the driest quarter), BIO18 (precipitation of the warmest quarter) and BIO19 (precipitation of the coldest quarter) (Appendix, Table S7).

Two matrices were assembled, one containing soil variables and the other climate variables. The units of measurement for these variables differed; therefore, they were standardized before analyses, by assuming a zero mean and unit variance, using the 'decostand' function from the 'vegan' package (Oksanen et al., 2022). I investigated the

linear dependencies between the variables by calculating the variance inflation factor (VIF), which quantifies the extent to which the variance of a regression coefficient is inflated in the presence of other explanatory variables (Borcard et al., 2011). Environmental variables exhibiting collinearity with a VIF greater than 10 were progressively excluded using the 'vifcor' function of the 'usdm' package (Naimi, 2014).

Subsequently, forward selection was employed with a double-stop criterion for each matrix (Blanchet et al., 2008), utilizing the 'forward.sel' function from the 'adespatial' package (Dray et al., 2020). The objective of forward selection is to reduce the number of explanatory variables and to make the final environmental model more parsimonious in relation to the species composition data (Blanchet et al., 2008). This selection is only carried out when the global model, which contains non-collinear variables, is significant (Blanchet et al., 2008). The double-stop criterion of Blanchet et al. (2008) stipulates that: (i) The candidate variables must demonstrate a significant effect on the model ($p \leq 0.05$), and (ii) the adjusted R^2 of the explanation of the set of variables must be less than the adjusted R^2 of the global model. The climate variables selected were BIO4 (temperature seasonality), BIO11 (mean temperature of the coldest quarter), BIO12 (annual precipitation), and BIO19 (precipitation of the coldest quarter), while the soil variables were pH and cation saturation. I also included a texture variable (sand) for the soil, because it is ecologically important, as the soils of the studied *veredas* are found in different matrices of *Latossolos* and *Arenossolos* (Santos et al., 2011).

The geographical coordinates of latitude and longitude of the central point of each *vereda* were obtained from Bijos et al. (2023) and were used to produce the spatial filters to be used as explanatory variables, which are based on eigenvector mapping methods, Moran's Eigenvector Maps (MEM; Dray et al., 2006). MEM are orthogonal variables derived from latitude and longitude data obtained from a spatial weighting matrix (SWM;

Bauman et al., 2018). Each MEM value represents a spatial pattern at a given scale (Borcard et al., 2011). There are 21 types of SWM spatial eigenvectors available, depending on the type of pre-defined connectivity adjustment and weighting that is made. In this context, the most suitable SWM was determined by employing the 'listw.candidates' and 'listw.select' functions from the 'adespatial' package (Dray et al., 2019). These functions generated distinct spatial filters and subsequently selected the SWM that yielded the optimal fitting model, defined as the model with the highest adjusted R^2 and $p\text{-value} \leq 0.05$. The significance of the selected variables was tested using a permutation test and the p -value was corrected for multiple testing (Holm correction). The SWM produced five eigenvectors (MEM1, MEM2, MEM4, MEM6, MEM7) with positive values (positive spatial autocorrelation), which were used as spatial predictors in the transformation-based redundancy analysis (tb-RDA) and variation partitioning.

Data analysis

The analyses were conducted using a matrix comprising the structure of the vegetation in each site, represented by absolute cover data (in meters) of the species in each *vereda*. The species were arranged in columns, and the areas were arranged in rows. The absolute cover data were transformed into presence and absence data, which were then used to calculate the β -diversity indices between the areas: β_{sim} ; β_{sor} and β_{sne} (Baselga, 2010). β_{sim} represents Simpson's classic dissimilarity (Simpson, 1949) and shows that changes in species composition are caused purely by turnover. β_{sor} represents the variation in total composition between areas, taking into account patterns of turnover and nestedness. Finally, β_{sne} represents the dissimilarity resulting from nestedness, indicating that changes in communities are due to the addition and removal of species (i.e., an effect of richness). β_{sne} is calculated as the difference between β_{sor} and β_{sim} . The "betapart"

package (Baselga et al., 2023) was used to calculate the β -diversity indices. Additionally, the correlation between the β -diversity indices (β_{sim} , β_{sor} , and β_{sne}) and geographical distance was evaluated using Mantel tests (Baselga, 2010) from the 'vegan' package (Oksanen et al., 2023), with 999 permutations.

To examine the effects of edaphic, climatic, and spatial variables on variation in the composition of *vereda* species, I employed transformation-based redundancy analysis (tbRDA; Legendre and Legendre, 2012). tb-RDA identifies a series of linear combinations of the explanatory variables that best explain the variation in the response matrix. First, we applied the Hellinger transformation to the species cover matrix, as described in Legendre and Legendre (2012). The Hellinger transformation was identified as an optimal approach for analyzing community composition data in a comparative context (Legendre and Legendre 2012). The Hellinger transformation entails the conversion of site-by-species data into relative values per site. This is achieved by dividing each value by the site sum and then taking the square root of the resulting values. Subsequently, the tb-RDA was executed using the Hellinger-transformed cover matrix, the spatial variables (selected MEMs), and the environmental variables retained after the VIF and forward selection analyses. To facilitate visual interpretation of the results, a graph was constructed with the tb-RDA results. To assess the significance of the analysis, of the axes, and the individual tb-RDA variables, I conducted a Monte Carlo permutation test with 999 permutations. Furthermore, Holm's correction for multiple tests was applied to the p-values. The 'vegan' package (Oksanen et al., 2020) was employed for the tb-RDA procedure. In addition, the importance of each predictor variable was evaluated, considering the inter-set correlations and the main axes of tb-RDA.

I calculated the variation partitioning based on redundancy analysis to assess the contribution of edaphic, climatic, and spatial predictors to the variation in the composition

of *vereda* species. The matrices containing the variables selected in the forward selection were utilized. The following contributions were considered: (a) pure soil, (b) pure climate, (c) pure space, (d) shared contribution of soil and climate, (e) shared contribution of climate and space, (f) shared contribution of soil and space, (g) shared contribution of soil, climate, and space, and (h) residuals (Legendre and Legendre, 2012). The analysis was conducted using the 'varpart' function from the 'vegan' package (Oksanen et al., 2020). The percentage of variation attributed to each fraction was accessed by the adjusted-R², the significance of each fraction was assessed by Monte Carlo permutation tests, and p-values were corrected using Holm's correction (Legendre and Legendre, 2012). To facilitate the interpretation of the variation partitioning results, a Venn diagram was constructed.

All analyses were conducted using the R programming language (version 4.2.2; R Core Team, 2022). All statistical tests were conducted with a significance level of 5%.

Results

The result of the β -diversity analysis between the *veredas* showed a high value for β_{sor} (0.925), indicating high floristic dissimilarity between the areas, followed by a high value for β_{sim} (0.904), indicating high species turnover and lower similarity. The value of β_{sne} (nestedness) was the lowest (0.021), compared to β_{sim} and β_{sor} , suggesting that the floristic dissimilarity between the *veredas* was not because of the increase and disappearance of species (nestedness), but due to species turnover across sites. The Mantel test showed that there was a significant correlation between β_{sim} ($r = 0.39$; $p < 0.001$) and β_{sor} ($r = 0.40$; $p < 0.001$) and geographical distance, but not for β_{sne} ($r = 0.14$; $p = 0.870$).

Effects of soil, climate, and space on the floristic composition of veredas

Redundancy analysis significantly explained the variation in species composition determined by soil, climate, and spatial variables (adjusted $R^2 = 35\%$; $F = 1.90$; $p = 0.012$). The first, second and third axes explained 14.9% ($F = 4.57$; $p = 0.012$), 12.6% ($F = 3.87$; $p = 0.012$) and 10.4% ($F = 3.21$; $p = 0.020$) of the canonical variation in species composition, respectively (Table 2). The overall inertia was 0.61. The most important predictors on axis 1 were BIO11 (mean temperature of coldest quarter), MEM2 and sand (Fig. 2; Table 3). These variables separated the *veredas* in the north (TO1, TO2, TO3 and TO4) and west of the Cerrado (MT1, MT2 and MT3) from the *veredas* in the central Cerrado (except BA1, GO7 and MG2). Axis 2 showed the following main variables: MEM1, BIO4 (temperature seasonality), pH, MEM2 and cation saturation, which seemed to influence the separation of the *veredas* in the western Cerrado from the others (Fig. 2; Table 3). Axis 3 was most strongly associated with BIO12 (annual precipitation), MEM1, MEM7 and MEM4 (Table 3). These predictors seem to determine the separation of the *veredas* in the north, center-south (except GO5) and southeast of the Cerrado (including GO1 and GO2) from the other *veredas*. The overall correlation values between species composition and environmental and spatial variables were high, with 97.1% on axis 1 of the tb-RDA, 97.4% on axis 2 and 98.2% on axis 3.

Table 2. Transformation-based redundancy analysis (tb-RDA) and Monte Carlo permutation test ($\alpha = 0.05$) of species composition and environmental and spatial predictors of veredas

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.090	0.076	0.063
Proportion explained (%)	0.149	0.126	0.104
Cumulative proportion	0.149	0.274	0.379

	Axis 1	Axis 2	Axis 3
<i>F</i> and (<i>p</i>) axes values	4.574 (0.012)	3.871 (0.012)	3.208 (0.020)
Adj. R squared; <i>F</i> and (<i>p</i>) RDA values	0.350; 1.90 (0.012)		

Table 3. Interset correlation between the selected environmental and spatial predictors and the scores on the first three axes of the tb-RDA, with *F* and *p* values estimated by the permutation test after Holm's correction ($\alpha = 0.05$). The values in bold represent the variables most highly correlated with each axis

Predictors	Axis 1	Axis 2	Axis 3	<i>F</i> and (<i>p</i>)
Cation saturation	-0.494	0.477	-0.148	1.464 (0.660)
pH	0.361	0.577	0.075	1.227 (1.000)
Sand	-0.561	-0.231	-0.077	1.152 (1.000)
Temperature seasonality (BIO4)	0.028	0.585	-0.278	0.958 (1.000)
Mean temperature of coldest quarter (BIO11)	-0.779	-0.044	0.193	1.252 (1.000)
Annual precipitation (BIO12)	0.483	0.042	-0.569	1.208 (1.000)
Precipitation of coldest quarter (BIO19)	0.498	0.314	0.148	1.244 (1.000)
MEM1	0.243	0.646	-0.521	1.378 (0.963)
MEM2	-0.727	0.515	0.128	1.336 (1.000)
MEM4	0.451	0.367	0.431	2.002 (0.096)
MEM6	0.201	0.050	-0.392	1.816 (1.000)
MEM7	-0.244	-0.276	-0.504	1.281 (0.198)

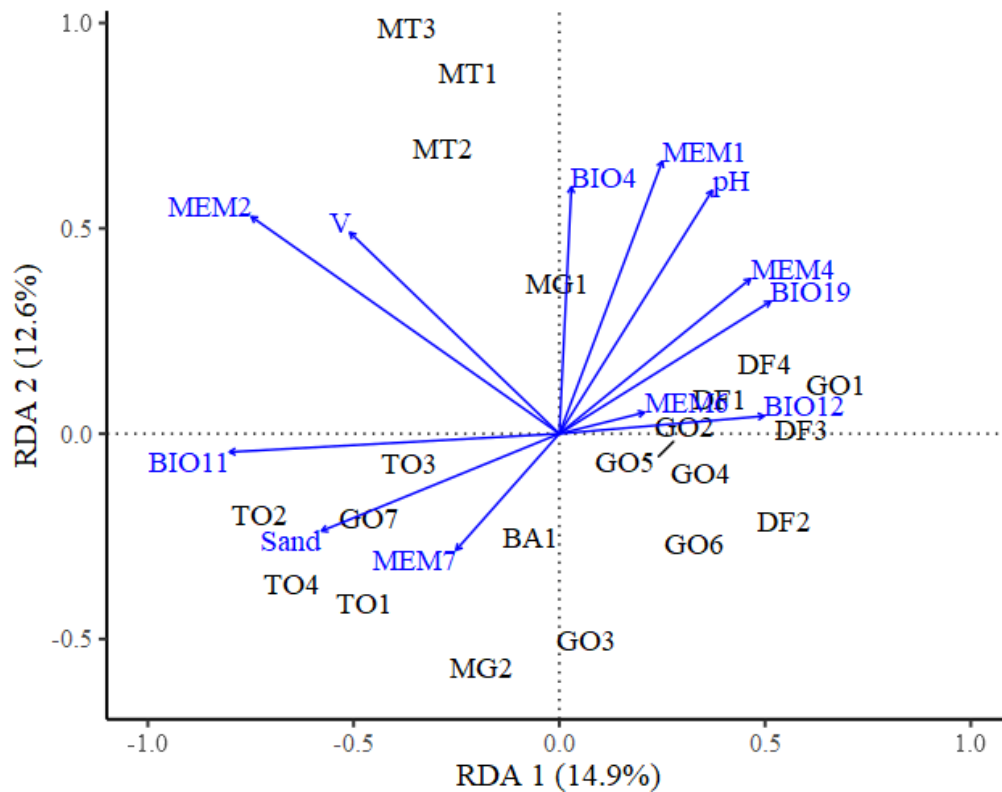


Figure 2 Transformation-based redundancy analysis (tb-RDA) of the herbaceous-shrub species composition of the *veredas*, showing the explanatory proportions of axes 1 and 2, the soil, climate and space variables, and the codes of the 21 *veredas*. V = cation saturation; Sand = sand; BIO4 = temperature seasonality; BIO11 = mean temperature of coldest quarter; BIO12 = annual precipitation; BIO19 = precipitation of coldest quarter; MEM1, MEM2, and MEM4 = fine-scale spatial variables; MEM6 and MEM7 = medium-scale spatial variables. The site codes are described in Figure 1

Variation partitioning with soil, climate, and spatial variables showed that space alone explained most of the variation in species composition with 12% of the explanation (fraction c; $R^2_{adj} = 0.12$; Fig. 3), although the percentage of residues showed high variation with 65% (fraction h; $R^2_{adj} = 0.65$; Fig. 3). The next highest explanations were for all components combined (fraction g; $R^2_{adj} = 0.07$; Fig. 3) and for climate alone (fraction b; $R^2_{adj} = 0.07$; Fig. 3). Finally, climate and space combined explained 6% of

the variation (fraction e; $R^2_{adj} = 0.06$; Fig. 3) and soil alone explained 5% (fraction a; $R^2_{adj} = 0.05$; Fig. 3). Soil and climate combined (fraction d) and soil-space combined (fraction f) showed negative values.

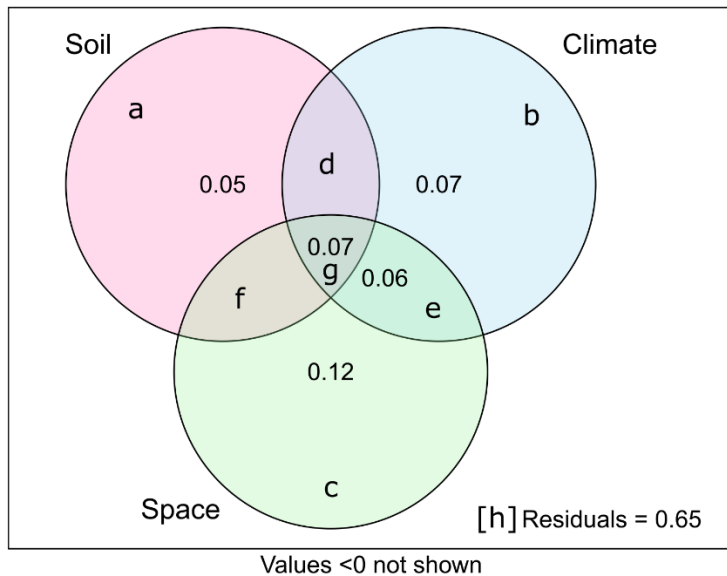


Figure 3 Venn diagram showing the proportion of explanations for each factor and for the combined factors. Results with negative values are not shown. The letters indicate the fractions of the variation partitioning: (a) pure soil, (b) pure climate, (c) pure space, (d) joint contribution of soil and climate, (e) joint contribution of climate and space, (f) joint contribution of soil and space, (g) joint contribution of soil, climate and space, and (h) residuals

Discussion

In this study, I used data on herbaceous-shrub species cover in *veredas* to investigate how environmental and spatial predictors influence plant composition and diversity in these ecosystems. I found that: (i) the plant community is more influenced by the spatial turnover of species (β_{sim}) than by nestedness across communities (β_{sne}); (ii) spatial predictors were better at explaining the composition and distribution of the flora of

veredas; (iii) the most important environmental variables were cation saturation, mean temperature of coldest quarter, precipitation of coldest quarter, pH, annual precipitation, sand, and temperature seasonality; (iv) stochastic processes, probably related to dispersal limitation, act in the formation of *vereda* communities.

My analyses of the patterns of β -diversity showed high floristic dissimilarity among the *veredas*, especially the spatial turnover of species (β_{sim}), indicating that the nestedness of species (β_{sne}) in the *veredas* is not significant, but the variation in species composition is high. Previous studies have also shown that the contribution of the species turnover component to β -diversity is greater than that of the nestedness component (e.g., Yu et al., 2021). Since my study areas have high floristic richness and high dissimilarity, this indicates low migration propagules between *veredas*, which can be explained by the patchiness in the spatial distribution of these environments on saturated soils in the middle of the predominantly dry cerrado matrix. Dynamic habitats, such as riparian wetlands, have already been shown to correlate with dispersal limitation (Brederveld et al., 2011). The studied *veredas* have a distinct species composition and a high proportion of exclusive species (Bijos et al., 2023). This variation in species composition in humid areas may be because of environmental characteristics that induce the appearance of species adapted to the wet, waterlogged environment (Tsuyuzaki et al., 2004; Dwire et al., 2006; Bijos et al., 2023) or spatial limitations related to geographical distance (Fu et al., 2021; Lários et al., 2017).

Veredas are patches of vegetation on humid soils, surrounded by vegetation on well-drained soils, which vary greatly in altitude, soil properties, temperature, and precipitation (Appendix, Table S5). The variation in these factors creates different micro-habitats for each *vereda*. The micro-habitats have their own characteristics, which influence the set of species best suited to inhabiting that space (Levine and HilleRisLambers, 2009).

Furthermore, the lack of connectivity between *veredas* likely hinders the dispersal of plant species, between different *veredas* in different hydrographic basins, resulting in a notable variation in species composition between communities over a given geographical distance (e.g., Brederveld et al., 2011). The structuring of communities by the processes of species turnover is likely linked to the ecological isolation of habitats and related speciation events, which occurred during the formation of the vegetation types in Cerrado Dominion. During the period of the last ice age, the *M. flexuosa* palm trees characteristic of *veredas* were few but scattered. However, at the beginning of the Holocene, they dispersed due to the increase in temperature and the presence of humidity (Rull and Montoya, 2014). It is known that the existence of *veredas* was only possible after climatic stabilization, with average winter temperatures above 15°C, and with the beginning of fluctuations in humidity levels in the areas (Salgado-Labouriau et al., 1997). Consequently, I postulate that the turnover of community composition may have resulted in the simultaneous loss and gain of species due to immigration-extinction dynamics and environmental filtering based on plant characteristics (Matthews and Whittaker, 2014; Filgueiras et al., 2021).

The results of the variation partitioning and tb-RDA analyses demonstrated that the spatial predictors explained a greater proportion of the variation in β -diversity patterns than the environmental predictors (Fig. 2, Fig. 3 and Table 3). This indicates that stochastic processes were the primary drivers of β -diversity patterns in the herbaceous-shrub species in the *veredas*. My hypothesis was thus invalidated by these findings and my second question was answered. The pure fraction of spatial predictors reflects the influence of neutral processes (Legendre et al., 2009). Spatial structures may originate from species assemblages, primarily due to dispersal limitation; this can give rise to aggregate patterns through neutral mechanisms, as individuals of all species have the same demographic rates (Hubbell, 2001; Borda-de-Água et al., 2007), thereby generating

spatial autocorrelation of species. Moreover, it is crucial to highlight that the majority of the Cerrado's herbaceous-shrub species are autochoric and wind-dispersed (Batalha and Martins, 2004), which may have contributed to the greater explanation of the spatial fraction in my analyses.

The difficulty of connectivity between the *veredas*, as they are separated by the matrix of vegetation on dry soil, hinders the dispersal of species adapted to the humid area in the same region. This creates a barrier to the dispersal of diaspores, which reduces the sharing of species between the *veredas* (Bijos et al., 2023) and between adjacent vegetation on dry soil (Silva et al., 2018). Consequently, the partial isolation of wetlands reduces gene flow, potentially leading to increased genetic drift (which is more pronounced in small populations) and demographic stochasticity within the community, rendering it more susceptible to random events (MacArthur and Wilson, 1967; Hubbell, 2001). Furthermore, *veredas* are ecosystems with dynamic environments, as evidenced by the seasonal fluctuations in the water table depth. This is contingent upon random events, such as precipitation, which renders ecosystems like this more susceptible to the impact of stochastic processes (Laio et al., 2009; Tamea et al., 2010; Arim et al., 2023).

The combined environmental and spatial components, in conjunction with pure climate, were also key determinants in the formation of the *veredas* communities. Studies evaluating the distribution patterns of Cerrado vegetation have indicated that temperature and precipitation are significant predictors of vegetation distribution, both for trees and for herbs and shrubs (Amaral et al., 2017; Françoso et al., 2020; Amaral et al., 2022).

Temperature was found to be a more significant predictor than precipitation, with a stronger correlation observed in the Tocantins region, in the northern Cerrado, and in the Espinhaço Range (MG1) in Minas Gerais, in the eastern portion of the Cerrado Dominion. The region where the *veredas* are in Tocantins is where I recorded some of the highest

temperatures (Appendix, Table S7). The state is renowned for its consistently high temperatures throughout the year, as well as its distinctive woody flora, which includes numerous endemic species and a distinct floristic biogeographical district of the Cerrado (Françoso et al., 2020). In contrast, the Espinhaço Range region is situated within a distinctive mountain range where endemic flora has evolved to thrive in a colder climate and is geographically isolated from other areas (Giulietti et al., 1987). It is postulated that, due to climatic conditions in the past, species that were once more widespread, particularly those adapted to lower temperatures, found refuge in these elevated areas (Antonelli et al., 2010). The lower temperatures and soils with rocks, characteristic of high-altitude regions, can impede the dispersal of plant species (Giulietti et al., 1987; Stannard, 1995).

Precipitation is more strongly correlated with the *veredas* of the central Cerrado plateau than with other regions. Other studies have demonstrated a correlation between precipitation and the distribution of plant species in the central plateau (Amaral et al., 2022). This region is notable for exhibiting high levels of plant richness and endemism (Munhoz and Proença, 1998). The *veredas* in this region were the most diverse and had the highest number of exclusive species (Fig. 1). In this central region, plateaus at altitudes above 900 m are the predominant landform. These plateaus have historically experienced more stable climatic conditions and are predicted to have a higher level of endemic species (Vidal et al., 2019). This is likely due to niche stability, which is caused by the isolation that ancient plant lineages tolerated when establishing themselves in a region with these characteristics (Werneck, 2011). Precipitation is a significant predictor of wetland formation, as it replenishes groundwater reservoirs during the rainy season and controls the variation in the water table depth (Laio et al., 2009). This, in turn, influences soil characteristics (mainly aluminum, iron oxides, acidity and rate of organic

matter decomposition) and defines the conditions that plants will have to endure in order to survive (Moor et al., 2017).

Despite exhibiting the lowest percentage of variation in the variation partitioning model, soil was a key predictor of the composition and diversity of *veredas*. The results indicated that cation saturation was the most influential soil variable, followed by pH and texture. Previous research has highlighted the importance of cation saturation (Mota et al., 2018), pH (Viani et al., 2014; Amaral et al., 2022), and texture (Amaral et al., 2022; Lira-Martins et al., 2022) in influencing the composition of Cerrado flora. Furthermore, phosphorus, pH, organic matter, and sand proportion were found to correlate with species composition and diversity of *veredas* (Bijos et al. 2023). The soils of *veredas* are acidic, with low fertility, and a high sand proportion (Appendix, Table S5), particularly in the northern Cerrado where orthic Arenosols prevail (Reatto et al., 2008; Santos et al., 2011). Soil texture plays a pivotal role in nutrient retention and release (Huang and Hartemink, 2020), while extreme pH levels impact nutrient availability (Viani et al., 2014). The adaptations of plants to these soil conditions contribute to reproductive isolation and high levels of endemism. *Vereda* plants demonstrate resilience in nutrient-limited environments with fluctuating water table depths.

It is crucial to highlight that the majority (65%) of the observed variation in the composition of *vereda* species remained undetermined (fraction [h] in Fig. 3). This high proportion of unexplained variation may indicate the contribution of additional predictors not assessed in this study, such as biological factors (e.g., interactions between species) or spatially structured environmental factors, unmeasured soil and climate variables (Legendre et al., 2009), or variables related to fluctuations in water table depth. It may also indicate the action of stochastic processes related to the neutral theory, which assumes that the formation and dynamics of populations do not depend on the niche or

the habitat, but are mainly determined by ecological drift and the dispersal of species (Legendre et al., 2009; Smith and Lundholm, 2010).

The findings of this research not only advance my understanding of the spatial and environmental filters shaping the *veredas* in the Cerrado, but also provide insights for implementing conservation strategies to minimize local extinctions and maximize species preservation. Dispersal limitation is a dominant factor in *vereda* formation, indicating a need to protect the *veredas*, adjacent natural areas, and ecological corridors enabling species dispersal (Baselga, 2010; Brederveld et al., 2011). Climate change and anthropogenic threats, such as habitat degradation, groundwater drainage, pollution, and woody species encroachment are already significantly impacting Cerrado wetlands (Rodrigues et al., 2022; Trindade et al., 2024). Extinction risks may be higher for temperature-sensitive biota (Strassburg et al., 2017) in high-altitude regions with stable climates and high endemism, such as the central plateau and Espinhaço Range (Giulietti et al., 1987; Munhoz & Proença 1998; Proença et al., 2000; Werneck, 2011). Reduced rainfall in the Cerrado region, resulting from changes in atmospheric circulation and evapotranspiration (Hofmann et al., 2023), could accelerate the irreversible degradation of wetlands. *Veredas* depend on precipitation to replenish groundwater and maintain higher levels of the water table (Laio et al., 2009), which in turn affects the complexity of the vegetation.

I expect that my results will contribute to a better understanding of the mechanisms of plant community formation that influence the maintenance and generation of plant biodiversity in the wetland ecosystem. It is important to note that the conservation of these ecosystems is not just a biological imperative; it is also a commitment to preserving the rich biodiversity and ecosystem services that *veredas* provide to human society and local wildlife. For a deeper understanding of the influence of ecological processes on the

formation of *veredas*, future research should incorporate biological predictors (e.g., species interactions) and environmental predictors (e.g., temporal variation in water table depth and other edaphic variables) into their analysis. To the best of my knowledge, no other published studies have evaluated the stochastic and deterministic processes and turnover of non-tree species in Cerrado wetland vegetation using a variation partitioning approach.

References

- Ai, D., Gravel, D., Chu, C., Wang, G., 2013. Spatial structures of the environment and of dispersal impact species distribution in competitive metacommunities. *PLoS One*. 8, e68927. <https://doi.org/10.1371/journal.pone.0068927>.
- Alvares, C.A., Stape, J.L., Sentelhas, P.C., de Moraes Gonçalves, J.L., Sparovek, G., 2013. Köppen's climate classification map for Brazil. *Meteorol. Z.* 22, 711-728. <https://doi.org/10.1127/0941-2948/2013/0507>
- Amaral, A.G., Munhoz, C.B., Walter, B.M., Aguirre-Gutiérrez, J., Raes, N., 2017. Richness pattern and phytogeography of the Cerrado's herb-shrub flora and implications for conservation. *J. Veg. Sci.* 28, 848–858. <https://doi.org/10.1111/jvs.12541>.
- Amaral, A.G., Bijos, N.R., Moser, P., Munhoz, C.B.R., 2022. Spatially structured soil properties and climate explain distribution patterns of herbaceous-shrub species in the Cerrado. *Plant Ecol.* 223, 85–97. <https://doi.org/10.1007/s11258-021-01193-7>.
- Andrew, S.M., Totland, Ø., Moe, S.R., 2015. Spatial variation in plant species richness and diversity along human disturbance and environmental gradients in a tropical wetland. *Wetl. Ecol. Manag.* 23, 395–404. <https://doi.org/10.1007/s11273-014-9390-2>.

- Antonelli, A., Verola, C.F., Parisod, C., Gustafsson, A.L.S., 2010. Climate cooling promoted the expansion and radiation of a threatened group of South American orchids (Epidendroideae: Laeliinae). *Biol. J. Linn. Soc.* 100, 597–607. <https://doi.org/10.1111/j.1095-8312.2010.01438.x>.
- Arim, M., Pinelli, V., Rodríguez-Tricot, L., Ortiz, E., Illarze, M., Fagúndez-Pachón, C., Borthagaray, A. I., 2023. Chance and necessity in the assembly of plant communities: Stochasticity increases with size, isolation and diversity of temporary ponds. *J. Ecol.* 111, 1641–1655. <https://doi.org/10.1111/1365-2745.14119>.
- Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* 19, 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>.
- Baselga, A., Orme, D., Villegger, S., De Bortoli, J., Leprieur, F., Logez, M., Martinez-Santalla, S., Martin-Devasa, R., Gomez-Rodriguez, C., Crujeiras, R., 2023. betapart: Partitioning Beta Diversity into Turnover and Nestedness Components. R package (version 1.6), <https://CRAN.R-project.org/package=betapart>.
- Batalha, M.A., Martins, F.R., 2004. Reproductive phenology of the Cerrado plant community in Emas National Park (central Brazil). *Aust. J. Bot.* 52, 149–161. <https://doi.org/10.1071/BT03098>.
- Bauman, D., Drouet, T., Fortin, M.J., Dray, S., 2018. Optimizing the choice of a spatial weighting matrix in eigenvector-based methods. *Ecol.* 99, 2159–2166. <https://doi.org/10.1002/ecy.2469>.
- Bijos, N.R., Silva, D.P., Munhoz, C.B.R., 2023. Soil texture and fertility determine the beta diversity of plant species in *veredas* in Central Brazil. *Plant Soil*, 492, 241–259. <https://doi.org/10.1007/s11104-023-06168-3>.

- Blanchet, F.G., Legendre, P., Borcard, D., 2008. Forward selection of explanatory variables. *Ecol.* 89, 2623–2632. <https://doi.org/10.1890/07-0986.1>.
- Borcard, D., Gillet, F., Legendre, P., 2011. *Numerical ecology with R*. New York: Springer.
- Borda-de-Água, L., Hubbell, S.P., He, F., 2007. Scaling biodiversity under neutrality. In: Storch, D., Marquet, P., Brown, J. (Eds.) *Scaling Biodiversity*. Ecological Reviews. Cambridge University Press, Cambridge, pp. 347–375.
- Brederveld, R.J., Jähnig, S.C., Lorenz, A.W., Brunzel, S., Soons, M.B., 2011. Dispersal as a limiting factor in the colonization of restored mountain streams by plants and macroinvertebrates. *J. Appl. Ecol.* 48, 1241–1250. <https://doi.org/10.1111/j.1365-2664.2011.02026.x>.
- Canfield, R., 1941. Application of line interception in sampling range vegetation. *J. Forest* 39, 388–394. <https://doi.org/10.1093/jof/39.4.388>
- Chase, J.M., Myers, J.A., 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philos. Trans. Royal Soc. B.* 366, 2351–2363. <https://doi.org/10.1098/rstb.2011.0063>.
- Chase, J.M., 2014. Spatial scale resolves the niche versus neutral theory debate. *J. Veg. Sci.* 25, 319–322. <https://doi.org/10.1111/jvs.12159>.
- Chun, J.H., Lee, C.B., 2018. Partitioning the regional and local drivers of phylogenetic and functional diversity along temperate elevational gradients on an East Asian peninsula. *Sci. Rep.* 8, 2853. <https://doi.org/10.1038/s41598-018-21266-4>.
- Colmer, T.D., Voeselek, L.A.C.J., 2009. Flooding tolerance: suites of plant traits in variable environments. *Funct. Plant Biol.* 36, 665–681. <https://doi.org/10.1071/FP09144>.

- Cummings J., Smith D., 2000. The line-intercept method: a tool for introductory plant ecology laboratories. In: Karcher, S.J. (ed) Tested studies for laboratory teaching. Proceedings of the 22nd workshop/conference of the association for biology laboratory education (ABLE), South Carolina, pp 234-246
- Dray, S., Legendre, P., Peres-Neto, P.R., 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol. Model.* 196, 483–493. <https://doi.org/10.1016/j.ecolmodel.2006.02.015>.
- Dray, S., Bauman, D., Blanchet, G., Daniel Borcard, D., Clappe, S., Guenard, G., Jombart, T., Larocque, G., Legendre, P., Madi, N., Wagner, H.H., Siberchicot, A., 2019. Adespatial: Multivariate multiscale spatial analysis. R package version 0.3–3. <https://cran.r-project.org/package=adespatial>.
- Durigan, G., Munhoz, C.B., Zakia, M.J.B., Oliveira, R.S., Pilon, N.A., do Valle, R.S.T., Walter, B.M.T., Honda, E.A., Pott, A., 2022. Cerrado wetlands: multiple ecosystems deserving legal protection as a unique and irreplaceable treasure. *Perspect. Eco. Conserv.* 20, 185–196. <https://doi.org/10.1016/j.pecon.2022.06.002>.
- Dwire, K.A., Kauffman, J.B., Baham, J.E., 2006. Plant species distribution in relation to water-table depth and soil redox potential in montane riparian meadows. *Wetl.* 26, 131–146. [https://doi.org/10.1672/0277-5212\(2006\)26\[131:PSDIRT\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2006)26[131:PSDIRT]2.0.CO;2).
- Eiten, G., 1972. The Cerrado vegetation of Brazil. *The Bot. Rev.* 38, 201–341. <https://doi.org/10.1007/BF02859158>.
- Engelbrecht, B.M., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L., Hubbell, S.P., 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature.* 447, 80–82. <https://doi.org/10.1038/nature05747>.

- Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37, 4302–4315. <https://doi.org/10.1002/joc.5086>.
- Filgueiras, B.K.C., Peres, C.A., Melo, F.P.L., Leal, I.R., Tabarelli, M., 2021. Winner–Loser Species Replacements in Human-Modified Landscapes. *Trends Ecol. Evol.* 36, 545–555. <https://doi.org/10.1016/j.tree.2021.02.006>.
- Françoso, R.D., Dexter, K.G., Machado, R.B., Pennington, R.T., Pinto, J.R.R., Brandao, R.A., Ratter, J.A., 2020. Delimiting floristic biogeographic districts in the Cerrado and assessing their conservation status. *Biodivers. Conserv.* 29, 1477–1500. <https://doi.org/10.1007/s10531-019-01819-3>.
- Fu, H., Zhou, Y., Yuan, G., Peng, H., Wu, A., Li, W., Jeppesen, E., 2021. Environmental and spatial drivers for wetland plant communities in a freshwater lake: Reduced coupling of species and functional turnover. *Ecol. Eng.* 159, 106092. <https://doi.org/10.1016/j.ecoleng.2020.106092>.
- Giulietti, A.M., Menezes, N.L., Pirani, J.R., Meguro, M., Wanderley, M.G.L., 1987. Flora da Serra do Cipó, Minas Gerais: Caracterização e lista das espécies. *Bol. Bot. Univ. São Paulo.* 9, 1–151. <https://doi.org/10.11606/issn.2316-9052.v9i0p1-151>.
- Gravel, D., Canham, C.D., Beaudet, M., Messier, C., 2006. Reconciling niche and neutrality: the continuum hypothesis. *Ecol. Lett.* 9, 399–409. <https://doi.org/10.1111/j.1461-0248.2006.00884.x>.
- Grinnell, J., 1917. The niche-relationships of the California Thrasher. *The Auk.* 34, 427–433. <https://doi.org/10.2307/4072271>.
- HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M., Mayfield, M.M., 2012. Rethinking community assembly through the lens of coexistence theory. *Annu. Rev.*

- Ecol. Evol. Syst. 43, 227–248. <https://doi.org/10.1146/annurev-ecolsys-110411-160411>.
- Hofmann, G.S., Silva, R.C., Weber, E.J., Barbosa, A.A., Oliveira, L.F.B., Alves, R.J.V., Hasenack, H., Schossler, V., Aquino, F.E., Cardoso, M.F., 2023. Changes in atmospheric circulation and evapotranspiration are reducing rainfall in the Brazilian Cerrado. *Sci. Rep.* 13, 11236. <https://doi.org/10.1038/s41598-023-38174-x>.
- Huang, J., Hartemink, A.E., 2020. Soil and environmental issues in sandy soils. *Earth-Sci. Rev.* 208, 103295. <https://doi.org/10.1016/j.earscirev.2020.103295>.
- Hubbell, S.P., 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press. Princeton, New Jersey.
- Keddy, P. A., 1992. Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* 3, 157-164. <https://doi.org/10.2307/3235676>.
- Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S., Levine, J.M., 2015. Community assembly, coexistence and the environmental filtering metaphor. *Funct. Ecol.* 29, 592–599. <https://doi.org/10.1111/1365-2435.12345>.
- Kreft, H., Jetz, W., 2007. Global patterns and determinants of vascular plant diversity. *Proc. Natl. Acad. Sci.* 104, 5925-5930. <https://doi.org/10.1073/pnas.0608361104>.
- Laio, F., Tamea, S., Ridolfi, L., D'Odorico, P., Rodriguez-Iturbe, I., 2009. Ecohydrology of groundwater-dependent ecosystems: 1. Stochastic water table dynamics. *Water Resour. Res.* 45, W05419. <https://doi.org/10.1029/2008WR007292>.
- Larios, M.C., da Cunha, C.N., Penha, J., Landeiro, V.L., Pinho, J.B., Aragona, M., Valério, L.M., Strüssmann, C., Marques, M.I., Lourenço, L.S., Chupel, T.F., Fernandes, I.M., 2017. Evidence of cross-taxon congruence in Neotropical wetlands: Importance of environmental and spatial factors. *Glob. Ecol. Conserv.* 12, 108–118. <https://doi.org/10.1016/j.gecco.2017.09.003>.

- Legendre, P., Mi, X., Ren, H., Ma, K., Yu, M., Sun, I.-F., He, F., 2009. Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecol.* 90, 663–674. <https://doi.org/10.1890/07-1880.1>.
- Legendre, P., Legendre, L., 2012. *Numerical Ecology*, third ed. Amsterdam: Elsevier
- Leibold, M.A., Urban, M.C., De Meester, L., Klausmeier, C.A., Vanoverbeke, J., (2019). Regional neutrality evolves through local adaptive niche evolution. *Proc. Natl. Acad. Sci.* 116, 2612-2617. <https://doi.org/10.1073/pnas.1808615116>.
- Levine, J.M., HilleRisLambers, J., 2009. The importance of niches for the maintenance of species diversity. *Nature*, 461, 254–257. <https://doi.org/10.1038/nature08251>.
- Lira-Martins, D., Nascimento, D.L., Abrahão, A., Costa, P.B., D’Angioli, A.M., Valézio, E., Rowland, L., Oliveira, R.S., 2022. Soil properties and geomorphic processes influence vegetation composition, structure, and function in the Cerrado Domain. *Plant Soil.* 476, 549–588. <https://doi.org/10.1007/s11104-022-05517-y>.
- Liu, W., Yang, J., Sun, J., Li, X., 2016. Species turnover of wetland vegetation in northeastern China: Disentangling the relative effects of geographic distance, climate, and hydro-geomorphology. *Flora – Morphol. Distrib. Funct. Ecol. of Plants* 220, 1-7. <https://doi.org/10.1016/j.flora.2016.01.005>.
- MacArthur, R., Wilson, E., 1967. *The Theory of Island Biogeography*. Princeton University Press. Princeton, New Jersey.
- Martorell, C., Freckleton, R.P., 2014. Testing the roles of competition, facilitation and stochasticity on community structure in a species-rich assemblage. *J. Ecol.* 102, 74-85. <https://doi.org/10.1111/1365-2745.12173>.
- Matthews, T.J., Whittaker, R.J., 2014. Neutral theory and the species abundance distribution: recent developments and prospects for unifying niche and neutral perspectives. *Ecol. Evol.* 4, 2263–2277. <https://doi.org/10.1002/ece3.1092>.

- Mitsch, W.J., Gosselink, J.G., 2015. *Wetlands*, fifth ed. Wiley, New York.
- Moor, H., Rydin, H., Hylander, K., Nilsson, M. B., Lindborg, R., Norberg, J., 2017. Towards a trait-based ecology of wetland vegetation. *J. Ecol.* 105, 1623-1635. <https://doi.org/10.1111/1365-2745.12734>.
- Mota, G.S., Luz, G.R., Mota, N.M., Coutinho, E.S., Veloso, M.D.D.M., Fernandes, G.W., Nunes, Y.R.F., 2018. Changes in species composition, vegetation structure, and life forms along an altitudinal gradient of rupestrian grasslands in southeastern Brazil. *Flora*. 238, 32–42. <https://doi.org/10.1016/j.flora.2017.03.010>.
- Munhoz, C.B.R., Araújo, G.M., 2011. Métodos de Amostragem do estrato herbáceo-subarbustivo. In: Felfili, J.M., Eisenlohr, P.V., Melo, M.M.R.F., Andrade, L.A., Neto, J.A.A.M., ed. *Fitossociologia no Brasil: Métodos e Estudos de Casos*. Universidade Federal de Viçosa, Viçosa, pp 213-230
- Munhoz, C.B.R., Felfili, J.M., 2006. Fitossociologia do estrato herbáceo-subarbustivo de uma área de campo sujo no Distrito Federal, Brasil. *Acta Bot. Bras.* 20, 671–685. <https://doi.org/10.1590/S0102-33062006000300017>
- Munhoz, C.B.R., Proença, C., 1998. Composição florística do município de Alto Paraíso de Goiás na Chapada dos Veadeiros. *Bol. Herb. Ezechias Paulo Heringer*. 3, 102–150.
- Myers, J.A., Chase, J.M., Jiménez, I., Jørgensen, P.M., Araujo-Murakami, A., Paniagua-Zambrana, N., Seidel, R., 2013. Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecol. Lett.* 16, 151-157. <https://doi.org/10.1111/ele.12021>.
- Naimi, B., Hamm, N.A.S., Groen, T.A., Skidmore, A.K., Toxopeus, A.G., 2014. “Where is positional uncertainty a problem for species distribution modelling?” *Ecography*. 37, 191-203. <https://doi.org/10.1111/j.1600-0587.2013.00205.x>.

- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J., 2022. Vegan: Community Ecology Package. R package v. 2.6-4 (Version 2.6-4).
- Oliveira-Filho, A.T., Ratter, J.A., 2002. Vegetation physiognomies and woody flora of the Cerrado Biome, in: Oliveira PS, Marquis JR (Eds.), *The Cerrados of Brazil: ecology and natural history of a neotropical savanna*. Columbia University Press, New York, pp. 91-120.
- Overbeck, G.E., Vélez-Martin, E., Menezes, L.S., Anand, M., Baeza, S., Carlucci, M.B., Dechoum, M.S., Durigan, G., Fidelis, A., Guido, A., Moro, M.F., Munhoz, C.B.R., Reginato, M., Rodrigues, R.S., Rosenfield, M.F., Sampaio, A.B., Barbosa da Silva, F.H., Silveira, F.A.O., Sosinski, Ê.E., Staude, I.R., Temperton, V.M., Turchetto, C., Veldman, J.W., Viana, P.L., Zappi, D.C., Müller, S.C, 2022. Placing Brazil's grasslands and savannas on the map of science and conservation. *Perspec. in Plant Ecol., Evol. and Syst.* 56, 125687. <https://doi.org/10.1016/j.ppees.2022.125687>
- Proença, C., Oliveira, R.S., Silva, A.P., 2000. *Flores e Frutos do Cerrado*. Universidade de Brasília, Brasília.
- Ramos, M.V.V., Curi, N., Motta, P.E.F.D., Vitorino, A.C.T., Ferreira, M.M., Silva, M.L.N., 2006. Veredas do Triângulo Mineiro: Solos, água e uso. *Ciênc. e Agrotecnologia.* 30, 283-293. <https://doi.org/10.1590/S1413-70542006000200014>.
- Ramos, M.V.V., Haridasan, M., Araújo, G.M., 2014. Caracterização dos solos e da estrutura fitossociológica da vegetação de Veredas da Chapada no Triângulo

- Mineiro. *Fronteiras: J. of Soc. Technol. Environ. Sci.* 3, 180-210.
<https://doi.org/10.21664/2238-8869.2014v3i2.p180-210>.
- R Core Team. 2022. R version 4.2.2: a language and environment for statistical computing. R Found. Stat. computing. R Found Stat. Comput, Vienna, Austria.
<http://www.R-project.org/>.
- Reatto, A., Correia, J.R., Spera, S.T., Martins, E.S., 2008. Solos do bioma Cerrado: aspectos pedológicos, in: Sano, S.M., Almeida, S.P., Ribeiro, J.F. (Eds.), *Cerrado: ecologia e flora*. Embrapa, Planaltina, pp. 107-149.
- Ribeiro, J.F., Walter, B.M.T., 2008. As principais fitofisionomias do bioma Cerrado, in: Sano, S.M., Almeida, S.P., Ribeiro, J.F. (Eds.), *Cerrado: ecologia e flora*. Embrapa, Planaltina, pp. 151-212.
- Rodrigues, A.A., Macedo, M.N., Silvério, D.V., Maracahipes, L., Coe, M.T., Brando, P.M., Shimbo, J.Z., Rajão, R., Soares-Filho, B., Bustamante, M.M.C., 2022. Cerrado deforestation threatens regional climate and water availability for agriculture and ecosystems. *Glob. Chang. Biol.* 28, 6807–6822. <https://doi.org/10.1111/gcb.16386>.
- Rull, V., Montoya, E., 2014. *Mauritia flexuosa* palm swamp communities: natural or human-made? A palynological study of the Gran Sabana region (northern South America) within a neotropical context. *Quat. Sci. Rev.* 99, 17-33.
<https://doi.org/10.1016/j.quascirev.2014.06.007>
- Salgado-Labouriau, M. L., Casseti, V., Ferraz-Vicentini, K. R., Martin, L., Soubiès, F., Suguio, K., Turcq, B., 1997. Late Quaternary vegetational and climatic changes in cerrado and palm swamp from Central Brazil. *Palaeogeogra. Palaeoclimatol. Palaeoecol.* 128, 215-226. [https://doi.org/10.1016/S0031-0182\(96\)00018-1](https://doi.org/10.1016/S0031-0182(96)00018-1)

- Santos, H.G., Carvalho Junior, W., Dart, R.O., Aglio, M.L.D., Souza, J.S., Pares, J.G., Fontana, A., Martins, A.L.S., Oliveira, A.P., 2011. O novo mapa de solos do Brasil: legenda atualizada. Embrapa Solos, Rio de Janeiro.
- Schmera, D., Árva, D., Boda, P., Bódis, E., Bolgovics, Á., Borics, G., Cserecsa, A., Deák, C., Krasznai, E.A., Lukács, B.A., Mauchart, P., Móra, A., Sály, P., Specziár, A., Süveges, K., Szivák, I., Takács, P., Tóth, M., Várbíró, G., Vojtkó, A.E., Erős, T., 2018. Does isolation influence the relative role of environmental and dispersal-related processes in stream networks? An empirical test of the network position hypothesis using multiple taxa. *Freshw. Biol.* 63, 74-85. <https://doi.org/10.1111/fwb.12973>.
- Silva, D.P., Amaral, A.G., Bijos, N.R., Munhoz, C.B.R., 2018. Is the herb-shrub composition of veredas (Brazilian palm swamps) distinguishable? *Acta Bot. Brasilica* 32, 47–54. <https://doi.org/10.1590/0102-33062017abb0209>.
- Simon, M.F., Grether, R., Queiroz, L.P., Skema, C., Pennington, R.T., Hughes, C.E., 2009. Recent assembly of the cerrado, a neotropical plant diversity hotspot, by in situ evolution of adaptations to fire. *Proc. Natl. Acad. Sci.* 106, 20359-20364. <https://doi.org/10.1073/pnas.0903410106>.
- Smith, T.W., Lundholm, J.T., 2010. Variation partitioning as a tool to distinguish between niche and neutral processes. *Ecography.* 33, 648–655. <https://doi.org/10.1111/j.1600-0587.2009.06105.x>
- Stannard, B.L., 1995. Flora of the Pico das Almas – Chapada Diamantina, Bahia, Brazil. Royal Botanic Gardens, Kew.
- Strassburg, B.B.N., Brooks, T., Feltran-Barbieri, R., Iribarrem, A., Crouzeilles, R., Loyola, R., Balmford, A., Latawiec, A.E., Filho, F.J.B.O., Scaramuzza, C.A.M.,

- Scarano, F.R., Soares-Filho, B., Balmford, A., 2017. Moment of truth for the Cerrado hotspot. *Nat. Ecol. Evol.* 1, 0099. <https://doi.org/10.1038/s41559-017-0099>.
- Tamea, S., Muneeppeerakul, R., Laio, F., Ridolfi, L., Rodriguez-Iturbe, I., 2010. Stochastic description of water table fluctuations in wetlands. *Geophys. Res. Lett.* 37, L06403. <https://doi.org/10.1029/2009GL041633>.
- Tilman, D., 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl. Acad. Sci.* 101, 10854-10861. <https://doi.org/10.1073/pnas.0403458101>.
- Toledo, M., Peña-Claros, M., Bongers, F., Alarcón, A., Balcázar, J., Chuvina, J., Leño, C., Licona, J.C., Poorter, L., 2012. Distribution patterns of tropical woody species in response to climatic and edaphic gradients. *J. Ecol.* 100, 253-263. <https://doi.org/10.1111/j.1365-2745.2011.01890.x>.
- Trindade, V.L., Ferreira, M.C., Costa, L.S., Amaral, E.J., Bustamante, M.M.C., Munhoz, C.B.R., 2024. The effect of woody encroachment on taxonomic and functional diversity and soil properties in Cerrado wetlands. *Flora.* 152524. <https://doi.org/10.1016/j.flora.2024.152524>
- Tsuyuzaki, S., Haraguchi, A., Kanda, F., 2004. Effects of scale-dependent factors on herbaceous vegetation patterns in a wetland, northern Japan. *Ecol. Res.* 19, 349–355. <https://doi.org/10.1111/j.1440-1703.2004.00644.x>.
- Viani, R.A.G., Rodrigues, R.R., Dawson, T.E., Lambers, H., Oliveira, R.S., 2014. Soil pH accounts for differences in species distribution and leaf nutrient concentrations of Brazilian woodland savannah and seasonally dry forest species. *Perspectiv. Plant Ecol. Evol. Syst.* 16, 64–74. <https://doi.org/10.1016/j.ppees.2014.02.001>.
- Vidal, J.D.D., Souza, A.P., Koch, I., 2019. Impacts of landscape composition, marginality of distribution, soil fertility and climatic stability on the patterns of woody plant

endemism in the Cerrado. *Glob. Ecol. Biogeogr.* 28, 904-916.
<https://doi.org/10.1111/geb.12901>.

Werneck, F. P., 2011. The diversification of eastern South American open vegetation biomes: Historical biogeography and perspectives. *Quat. Sci. Rev.* 30, 1630–1648.
<https://doi.org/10.1016/j.quascirev.2011.03.009>.

Yu, C., Fan, C., Zhang, C., Zhao, X., Gadow, K.V., 2021. Decomposing Spatial β -Diversity in the temperate forests of Northeastern China. *Ecol. Evol.* 11, 11362-11372. <https://doi.org/10.1002/ece3.7926>.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in Ecology with R. Springer, New York.

CHAPTER 3

Phylogenetic diversity and evolutionary processes of herbaceous-shrub species in *veredas* (Brazilian palm swamp) in Central Brazil

Abstract

Veredas are a humid vegetation type found in the Cerrado geographical domain, dominated by the Brazilian savannas (cerrado *sensu stricto* vegetation). *Veredas* are a waterlogged ecosystem occurring along small rivers and are characterized by an herbaceous-shrub stratum that is predominant in the landscape, with *Mauritia flexuosa* palms distributed over their wetter zone. It is crucial to investigate the phylogenetic alpha and β -diversity structure of *veredas* (Brazilian palm swamps) and their relationship with environmental and spatial filters to comprehend the unique characteristics of these patches of humid vegetation situated within a cerrado vegetation matrix under well-drained soil. Here, I aim to assess how ecological and evolutionary processes affect the phylogenetic alpha diversity and phylobeta diversity of herbaceous-shrub species in *veredas*. I used the occurrence data of 560 herbaceous-shrub species available for 21 *vereda* sites, together with their geographic coordinates, 12 soil variables and 14 climate variables. I evaluated the relationship between phylogenetic metrics (alpha diversity) and environmental variables using ordinary least square models. I also tested the effects of soil, climate, and spatial factor distances on phylogenetic beta diversity (PBD) using multiple regressions on distance matrices. My results demonstrated a pattern of phylogenetic clustering distribution in the *veredas*, reflecting the potential role of environmental filtering. Phylogenetic metrics are strongly influenced by bioclimatic variables and organic matter. Geographic, climatic, and soil distance matrices were

mutually important in significantly explaining the variance in PBD and in its turnover component. My findings indicate that both phylogenetic clustering and phylogenetic dispersal are influencing the flora of the *veredas*. Furthermore, the joint effect of niche and neutral processes is influencing the phylogenetic structure of the *veredas*.

Keywords: wetlands, herbaceous-shrub flora, phylobetadiversity, phylogenetic clustering, neutral and niche theories

Introduction

Understanding the distribution patterns of organisms in the environment requires knowledge about the ecological processes that act on species within communities (Ricklefs and Schluter, 1993; Cavender-Bares et al., 2009). Two theories have been proposed to explain how communities are assembled: neutral theory and niche theory. Neutral theory, proposed by Hubbell (2001), predicts that spatial variation in communities can be influenced by random events, such as limitations in the dispersal process, ecological drift, death, speciation, and extinction (e.g. catastrophic events or landscape changes). In contrast, niche theory (Grinnell, 1917; Tilman, 2004) emphasizes that a given organism occurs in a location because it has passed through environmental filters, brought about by variations in environmental conditions and by interactions with other species (e.g., competition, predation, and parasitism).

Phylogenetic community structure is the pattern of the phylogenetic relationship of species distribution within and among communities (Cavender-Bares et al., 2009). The association between environmental factors, phylogenetic diversity measures, and genetic interactions among taxa can provide valuable insights into the evolutionary and ecological processes governing plant community organization and species coexistence (Webb, 2000; Webb et al., 2002; Cavender-Bares et al., 2009; Mayfield and Levine,

2010). In general, high phylogenetic diversity in coexisting species indicates that closely related lineages tend not to occur in the same habitat, thus producing phylogenetic overdispersion (Webb et al., 2002; Li et al., 2014). This is the case when competition is intense, which drives selection for divergent traits (Webb et al., 2002; Li et al., 2014). Conversely, the strong occurrence of habitat environmental filtering mechanisms can result in phylogenetic clustering. This phenomenon is particularly evident when phylogenetic niche conservatism occurs, whereby lineages tend to maintain the same niche as their ancestral lineages, with sister species occupying the same niche as their ancestors (Wiens and Graham, 2005). When closely related species from a regional assemblage of species coexist in a local community, phylogenetic clustering is generated, thereby driving selection for organisms with similar traits (Webb et al., 2002; Li et al., 2014). Furthermore, it is important to note that if the observed phylogenetic diversity does not differ from that of a random assembly null model, it can be assumed that phylogenetic structuration processes are stochastic and linked to the neutral theory (Webb et al., 2002; Cavender-Bares et al., 2009). Nevertheless, the connection between phylogenies and ecological patterns requires careful consideration of several factors. The relationships between the evolution of species attributes, habitat filtering, and competition are inherently complex, and there is no single mechanism that fully explains them (Gerhold et al., 2015; Kraft et al., 2015).

An alternative approach, such as the use of phylogenetic beta diversity (phylo β -diversity), allows for the identification of the conditions under which neutral and niche-based processes predominate (Cavender-Bares et al., 2009). Phylo β -diversity measures the shared evolutionary information between assemblages in space and time (Graham and Fine, 2008). Low phylo β -diversity indicates niche conservatism with local speciation, resulting in closely related species occupying the same community (Leprieur et al., 2012).

In contrast, high β -diversity is attributed to the presence of lineages originating from the regional pool of species (Leprieur et al., 2012).

Phylogenetic data can be employed in conjunction with geographic distance and environmental gradients to distinguish between neutral processes, such as dispersal limitation, and niche-based processes, such as environmental filters (Graham and Fine, 2008; Baselga, 2010). However, the underlying processes driving phylo β -diversity patterns can vary, particularly in herbaceous communities. In studies of different herbaceous communities, phylo β -diversity has been found to be correlated with environmental factors (Yi et al., 2020; Zappi et al., 2017; Massante et al., 2023), or in a different context, with dispersal limitation (Jiang et al., 2022), or even by both environmental and geographical distance (Chi et al., 2014; Zheng et al., 2022; Li et al., 2024). These findings underscore the importance of employing β -diversity, in conjunction with the phylogenetic component, to elucidate the underlying mechanisms governing community assembly (Leprieur et al., 2012).

Wetlands are ecosystems situated at the interface between aquatic and terrestrial environments (Junk et al., 2014). They may be continental, natural, permanently or periodically flooded by shallow water, or have waterlogged soils (Junk et al., 2014). They are important at the global ecological level, interacting with fauna, flora, soil, and serving as habitats for specific plant and animal communities adapted to their hydrological dynamics (Junk et al., 2014). Throughout most of human history, wetlands were considered “unproductive land”, justifying their degradation and conversion for agriculture and urbanization (Fluet-Chouinard et al., 2023). A series of disturbances, including drainage, land conversion, and the impacts of climate change, fires, sea level rise, and groundwater extraction, have rendered wetlands one of the most threatened

ecosystems in the world. (van Asselen et al., 2013). The rate of wetland loss is accelerating rapidly (Fluet-Chouinard et al., 2023).

Wetlands in the Brazilian Neotropical savanna provide several important ecosystem services. They maintain the hydrological system (Pousa et al., 2019), harbor numerous taxonomic groups and endemic species (Durigan et al., 2022), filter and store freshwater (Horák-Terra et al., 2022a), and serve as a carbon sink in organic soils (Beer et al., in press). Furthermore, these ecosystems contribute to groundwater recharge during dry seasons and to the moisture availability in the atmosphere through evapotranspiration processes (Pousa et al., 2019). Despite the significant ecological importance of wetlands, future projections indicate that, given the current deforestation rates, more than 90% of watersheds within the Cerrado will experience a reduction in their water flow (Salmona et al., 2023).

Veredas are humid savanna physiognomies, defined by their extensive herbaceous-shrub stratum and the presence of palm trees such as *Mauritia flexuosa* L. distributed over their zone with saturated soil. The vegetation structure of these ecosystems indicates that they are ecologically dependent on the water content of the soil, particularly the herbaceous-shrub stratum (Moreira et al., 2015; Durigan et al., 2022). These environments exhibit floristic differences from the adjacent vegetation, sharing less than 20% of the species with other surrounding vegetation types on well-drained soil (Silva et al., 2018). However, approximately 50% of their herbaceous-shrub flora is shared between different *veredas* (Bijos et al., 2017). Furthermore, the taxonomic β -diversity of *veredas* was found to be correlated with spatial factors, indicating that stochastic processes related to dispersal limitation act on community assembly (chapter 2). *Veredas*, defined as vegetation patches on saturated soil amidst typical cerrado vegetation on well-drained soil (Eiten, 1972), experience a unique set of challenges pertaining to the dispersal

of species within and beyond their boundaries. The differences in water drainage and soil composition between *veredas* and their surroundings present significant obstacles for the adaptation of species.

The study of the phylogenetic distribution of herbaceous-shrub species in wetlands, and the environmental and spatial variables driving this distribution, is scarce in savannas (Xavier et al., 2019). To improve my understanding of the evolution, diversity, and ecology of wetland physiognomies in the Brazilian savanna, it is imperative to elucidate the phylogenetic structure of *vereda* species and its interrelation with environmental variables and the ecological and evolutionary processes that influence it. *Veredas* are under significant threat from anthropogenic disturbances and climate change (Salmona et al., 2023). Furthermore, the legislation in place does not adequately protect these non-forest ecosystems (Rosolen et al., 2015; Durigan et al., 2022; Moreira et al., 2015). Moreover, due to these threats, their vegetation is undergoing significant transformation (Gonçalves et al., 2021; Trindade et al., 2024), necessitating an urgent understanding of their phylogenetic structure. Phylogenetic information will help to comprehend and predict changes in community diversity and dynamics, including species turnover and extinction. This, in turn, could facilitate the prediction of how these will affect ecosystem function (Lean and Maclaurin, 2016). Consequently, knowledge of phylogenetic diversity can serve as a proxy for features of value to human well-being, thereby contributing to the management and restoration of the biota in the context of rapid climate change (Lean and Maclaurin, 2016).

This study aims to determine whether the phylo β -diversity of these communities is driven by niche-related evolutionary processes (Grinnell, 1917; Tilman, 2004) or neutral processes (Hubbell, 2001). Furthermore, it seeks to assess the roles of soil, climate, and spatial factors in shaping the phylogenetic structure of these communities. To this end I

addressed the following questions (1) Are the *veredas* phylogenetically clustered or overdispersed? (2) How do variations among soil and climate filters relate to the phylogenetic structure of *vereda* communities? (3) Does phylo β -diversity differ significantly between the *vereda* sites? (4) How do phylo β -diversity components of the *veredas* relate to climate, soil properties, and spatial predictors? (5) Is the phylogenetic structure of *vereda* herbaceous-shrub species being influenced by processes based on niche theory (Grinnell, 1917; Tilman, 2004) or neutral theory (Hubbell, 2001)? From this, I hypothesize that the degree of phylogenetic clustering (niche processes) will increase as the proximity between the *veredas* grows, due to the greater similarity of environmental filters in nearby areas. At the same time, it is also possible that there is a phylogenetic dispersal limitation of species, considering that the flora of the *veredas* is very different from the adjacent well-drained Cerrado communities (Silva et al., 2018) and different among the *veredas* themselves (Bijos et al., 2017). Therefore, the most likely, and what I hypothesize, is that the joint effect of stochastic and deterministic evolutionary processes influences the phylogenetic structuring and β -diversity of the *veredas*.

Materials and methods

Study areas and vegetation sampling

The vegetation sampling occurred during the rainy season. I sampled the cover data of 560 herbaceous-shrub species, encompassing 220 genera and 69 botanical families across 21 *vereda* sites. In each *vereda*, a total of 150 meters were sampled, which constituted 15 transects of 10 meters each (sample unit). A total of five transects were randomly positioned within three distinct zones of the *veredas*: the border, the middle, and the core. To ascertain the horizontal cover and plant species composition, the line intersection method was employed (Canfield 1941; Munhoz and Araújo 2011). The length in

centimeters of all herbaceous, subshrub, and shrub individuals that crossed or touched the measuring tape was recorded (Cummings and Smith 2000). The data pertaining to the species was employed to calculate the absolute cover (AC) of each species in each area. This data was transformed into the species matrix, which was utilized throughout the study. The AC is defined as the sum of the horizontal projections of the species in meters within the sampling units of the transects (Munhoz and Felfili 2006). Although *M. flexuosa* (a distinctive palm tree of *veredas*) was observed in all *vereda* sites, this species and its associated trees were not sampled in this study. Their coverage represents less than 10% of the total vegetation, and they are absent in the middle and border zones (Ribeiro and Water, 2008). The species data is available in Bijos et al. (2023) and, in this study, in Appendix Table S4).

The *veredas* are distributed between 10-17° S, 43-52° W (Fig. 1). The areas are in a tropical seasonal savanna climate region (Aw), according to the Köppen classification system, with a rainy summer (October to April) and dry winter (May to September) (Alvares et al., 2013). Species names were standardized according to The Plant List (<http://www.theplantlist.org/>) using the R package “U.Taxonstand” (Zhang and Qian, 2023). All taxa identified only at family level were excluded and the synonyms of 41 species were merged with their accepted names before further analysis.

Site/State	Site codes	Number of species	Number of exclusive species
Jardim Botânico de Brasília Ecological Station/DF	DF1	48	4
Brasília National Park/DF	DF2	80	11
Brazilian Institute of Geography and Statistics Ecological Reserve/DF	DF3	98	17
Brasília National Forest/DF	DF4	77	10
Serra do Tombador RPPN (1)/GO	GO1	40	10
Serra do Tombador RPPN (2)/GO	GO2	58	11
Jardim de Maitreya/GO	GO3	71	15
Vereda of Vereda dos Ingleses/GO	GO4	106	37
Linda Serra de Topázios RPPN/GO	GO5	124	26
Vereda of Mosteiro Eisho-Ji/GO	GO6	86	33
Vereda of Posse/GO	GO7	72	21
Sempre Vivas National Park/MG	MG1	54	12
Grande Sertão Veredas National Park (1)/MG	MG2	69	21
Grande Sertão Veredas National Park (2)/BA	BA1	33	4
Vereda of Nova Xavantina (1)/MT	MT1	75	14
Vereda of Nova Xavantina (2)/MT	MT2	73	15
Vereda of Nova Xavantina (3)/MT	MT3	70	14
Serra Geral do Tocantins Ecological Station (1)/TO	TO1	50	6
Serra Geral do Tocantins Ecological Station (2)/TO	TO2	58	4
Serra Geral do Tocantins Ecological Station (3)/TO	TO3	58	4
Serra Geral do Tocantins Ecological Station (4)/TO	TO4	45	2

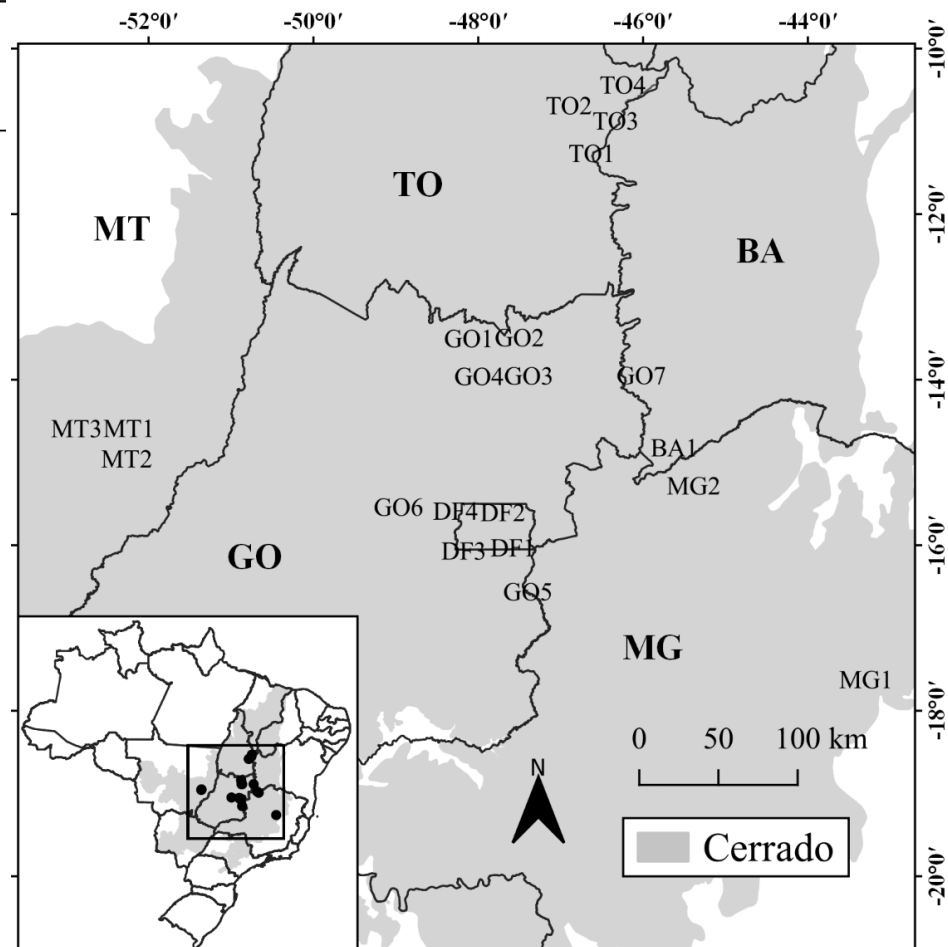


Figure 1 Location of the 21 *vereda* sites sampled in Central Brazil, with their respective species richness and number of exclusive species. RPPN = Private Natural Heritage Reserve

Environmental and spatial data

I collected superficial soil samples from a depth of 0-20 cm at each transect in 21 *veredas* sites, totaling 315 soil samples. The physical and chemical attributes of the soil were analyzed to determine the relative contents of sand, clay, and silt; pH (CaCl_2 0.01 mol L⁻¹); aluminum (Al^{3+}); calcium (Ca^{2+}); magnesium (Mg^{2+}); potassium (K^+); phosphorus (P); organic matter (OM); cation saturation (V); and cation exchange capacity (CEC) (Appendix, Table S5). The percentage of organic matter was determined using the Walkley–Black method ($\% \text{ organic C} \times 1.724$). Soil texture (sand, clay, and silt content) was estimated using the densimetric method of Bouyoucos. Phosphorus and K^+ were extracted with Mehlich-1 solution (0.0125 mol L⁻¹ H_2SO_4 + 0.05 mol L⁻¹ HCl) and cations Ca^{2+} , Mg^{2+} , and Al^{3+} were extracted using a 1 mol L⁻¹ KCl solution. Cation saturation (V) was estimated by $\{V = [(\text{Ca}^{2+} + \text{Mg}^{2+} + \text{K}^+)/\text{CEC}] \times 100\}$. Potential cation exchange capacity (CEC) was estimated according to the equation ($T = \text{Ca}^{2+} + \text{Mg}^{2+} + \text{K}^+ + \text{H}^+ + \text{Al}^{3+}$). Soil physicochemical properties were analyzed according to the Embrapa protocol (2017). These soil data were first published by Bijos et al. (2023).

I obtained the climate data using the geographic location information (longitude and latitude) of the areas, through the Arc-GIS program. Arc-GIS accesses the data previously downloaded from WorldClim v.2.1 database (Fick and Hijmans, 2017) (spatial resolution of 1,000 m; 30 arc-seconds) and acquires the climatic variables corresponding to the informed coordinates. I used 14 bioclimatic variables: BIO1 (Annual Mean Temperature), BIO4 (Temperature Seasonality (standard deviation $\times 100$)), BIO5 (Max Temperature of Warmest Month), BIO8 (Mean Temperature of Wettest Quarter), BIO9 (Mean Temperature of Driest Quarter), BIO10 (Mean Temperature of Warmest Quarter), BIO11 (Mean Temperature of Coldest Quarter), BIO12 (Annual Precipitation), BIO14 (Precipitation of Driest Month), BIO15 (Precipitation Seasonality (Coefficient of

Variation)), BIO16 (Precipitation of Wettest Quarter), BIO17 (Precipitation of Driest Quarter), BIO18 (Precipitation of Warmest Quarter) e BIO19 (Precipitation of Coldest Quarter) (Appendix, Table S7).

The geographical coordinates of latitude and longitude (in decimal degrees) of the center point of each area were recorded using a Garmin GPS (model VISTA HCx) (Appendix, Table S1). Details on how I will use this information to create the spatial explanatory variables are provided below.

Selection of soil and climate variables

As the soil and climate variables are expressed in different measurement units, I standardized the variables prior to analysis, assuming zero mean and unit variance, using the 'decostand' function from the 'vegan' package (Oksanen et al., 2022). Before the analysis, I screened for the multicollinearity among the soil factors and climate factors, separately. Firstly, I calculated Pearson (correlations between the environmental factors), and their variance inflation factors (VIF). Then I discarded the variables that had a coefficient $|r| \geq 0.7$ (Appendix, Tables S3 and S8, for soil and climate, respectively), then calculated the variance inflation factors of the remaining predictors until all variance inflation factors were less than 5 (Dormann et al., 2013, Naimi et al., 2014). The (VIF) procedure exclude the highly correlated variables from the set through a stepwise procedure using the 'vifcor' function of the 'usdm' package (Naimi, 2014). The final set of soil variables included Ca, Al, K, V, P, OM, pH, and sand. And climate variables included BIO4, BIO11, BIO12, BIO18, and BIO19.

Phylogenetic analysis

For the phylogenetic analyses, I constructed a phylogenetic tree to represent the evolutionary relationship between all species in my database. The phylogenetic tree was constructed using an updated version of the most comprehensive phylogeny for plants based on molecular data (Smith and Brown, 2018). I used the function ‘phylo.maker’ from the ‘V.PhyloMaker2’ package (Jin, 2023) to prune the GBOTB.extended.TPL phylogeny to taxa available in my dataset. For taxa in the dataset that were unavailable in the phylogeny, I employed the ‘scenario 3’ approach, which conservatively bind taxa within their parental taxa with dated branch lengths (Qian and Jin, 2016). The procedure resulted in a phylogeny with 540 taxa from 205 genera and 66 families. From the 540 taxa, 152 taxa from the dataset were already present in the GBOTB.extended.TPL phylogeny and 388 taxa were bound to the phylogeny. I resolved the soft polytomies problems of the phylogenetic tree using the ‘multi2di’ function of the ‘geiger’ R package (Pennell et al., 2014) and then used the resulting phylogenetic tree as the reference species pool in subsequent analyses (Appendix, Fig. S2).

Phylogenetic diversity metrics

To estimate the phylogenetic diversity of the herbaceous-shrub communities I applied Faith's phylogenetic diversity index (PD; Faith, 1992). I also evaluated the mean pairwise distance (MPD), which gives more weight to the largest phylogenetic distances between species, and the mean nearest taxon distance (MNTD), which gives more weight to the smallest phylogenetic distances between species (Webb et al., 2008). Since phylogenetic diversity shows a positive correlation with species richness (Tucker and Cadotte, 2013), I compared the PD, MPD, and MNTD values with null models (SES) to keep species richness constant while phylogenetic relationships are being randomized, so that it is possible to compare communities with different species richness. The standardized values

generated values of sesPD, sesMPD, and sesMNTD, which are equivalent to the inverse of the NRI and NTI indices of Webb (2000). The randomization was set for 10.000 runs. To test the significance of the phylogenetic structures, I conducted Student's t-test using the ses.PD, ses.MPD, and ses.MNTD generated. I used the 'picante' package (Kembel et al., 2010) for the analyses.

Phylogenetic beta diversity

To assess differences in lineage composition among the studied *veredas*, considering all species, I calculated phylo β -diversity based on pairwise-site dissimilarity methods (Baselga, 2010). The Sorensen dissimilarity coefficient ($\beta_{\text{sor.phy}}$) was used to calculate total phylo β -diversity and was partitioned into two components based on the phylogenetic tree, $\beta_{\text{sim.phy}}$ and $\beta_{\text{nes.phy}}$. $\beta_{\text{sim.phy}}$ is the Simpson dissimilarity index and quantifies phylo β -diversity due to turnover (or replacement) of branch lengths between sites. $\beta_{\text{nes.phy}}$ quantifies β -diversity resulting from nestedness of branch lengths between sites. $\beta_{\text{sim.phy}}$ and $\beta_{\text{nes.phy}}$ result from two antithetic processes, i.e. branch lengths replacement and branch lengths loss (or gain), respectively (Baselga, 2010). When applied to phylo β -diversity, shared and unique species are replaced with shared and unique branch lengths, respectively (Leprieur et al., 2012). The Sorensen dissimilarity index allows computing the *PhyloSor* index (Bryant et al., 2008), which quantifies the proportion of branch extent shared between two communities: it varies from 0 (all branch lengths shared by the two sites) to 1 (no branch lengths shared by the two sites). Phylo β -diversity calculation was carried out using the function 'phylo.beta.pair' from the 'betapart' package (Baselga et al., 2023).

Contribution of soil, climate, and space to phylogenetic diversity

First, to determine which environmental variables would form the most parsimonious regression models, I applied a selection approach with the lowest Akaike Information Criterion (AIC) values, using the 'stepAIC' function from the 'MASS' package (Venables and Ripley, 2002). All variables in the final models showed a Variance Inflation Factor (VIF) <3. Before model selection, climatic and soil variables were centered and scaled to have zero mean and unit variance to get relative standardized estimates.

To assess the relative importance between the indices of community phylogenetic structure (sesPD, sesMPD and sesMNTD) with environmental predictors (edaphic and climatic), I used Ordinary Least Square models (OLS). I checked for spatial autocorrelation by calculating the Moran's I coefficient in the residuals of models using the function 'Moran.I' in the 'ape' package (Paradis and Schliep, 2019). I found no significant spatial autocorrelation for the response variables (Appendix, Table S9). Pseudo- R^2 was calculated as the square of the correlation between the fitted values from the models and the observed values.

To test the effects of soil factor distance, climate factor distance and spatial factor distance on phylo β -diversity I used multiple regressions on distance matrices (MRM) analysis. MRM entails a multiple regression of a response distance matrix on two or more environmental or spatial distance matrices, each unfolded into a distance vector (Lichstein, 2007). To overcome the problem of lack of independence between paired sites, the significance of the regression coefficients and the coefficients of multiple determination (R^2) was assessed using a permutation test ($n = 999$) (Lichstein, 2007). Total phylo β -diversity ($\beta_{\text{sor.phy}}$), phylogenetic turnover ($\beta_{\text{sim.phy}}$) and nestedness-resultant phylogenetic dissimilarity ($\beta_{\text{nes.phy}}$) were analyzed as response matrices, while soil factor, climate factor and spatial factor matrices were regarded as explanatory distance matrices.

To calculate MRM I used the ‘MRM’ function from the ‘ecodist’ package (Goslee and Urban, 2007).

Data calculation of all statistical analysis was carried out in R software (version 4.2.2; R Core Team, 2022).

Results

The phylogenetic tree generated contains 540 taxa, distributed in 205 genera and 66 families (Appendix, Fig. S2).

The most phylogenetically diverse *veredas* (highest PD) were GO4, GO5, DF3 and GO7. The lowest PD values were for GO1, BA1, TO4 and DF1 (Table 1). The highest MPD value was for GO7, with a less related species composition and greater PD, with an average distance between species of 254.06 million years; and the lowest for TO1, with a more related species composition, with an average distance between species of 195.25 million years (Table 1). The MNTD value was highest for BA1, showing a species composition with an average nearest neighbor distance of 97.22 million years (Table 1). This result indicates that the terminal species are less related (e.g. have more species from different genera). And the MNTD was lower for GO5 (51.48 million years) (Table 1), with more closely related terminal species (e.g. have more species from the same genus). Overall, the standardized phylogenetic diversity metrics sesPD, sesMPD and sesMNTD (Table 1), showed a significant negative mean value, demonstrating that the community is clustered distributed (-1.30, -1.25, -0.90, respectively). At the level of individual sites, DF2, GO1, GO5, MG1, TO1, TO2, and TO4 showed significant phylogenetic clustering (< -1.96) (Table 1), meaning that the phylogenetic distance between the families that make up the communities is lower than expected by chance.

Table 1. Values of the phylogenetic diversity metrics based on species of the 21 *vereda* sites and their respective standardized values. PD = Faith's phylogenetic diversity index, MPD = mean pairwise distance, MNTD = mean nearest taxon distance, sesPD = null model of Faith's phylogenetic diversity index, sesMPD = null model of the mean pairwise distance, sesMNTD = null model of the mean nearest taxon distance. The site codes are described in Figure 1

Phylogenetic diversity metrics						
Sites	PD	MPD	MNTD	sesPD	sesMPD	sesMNTD
BA1	2397.21	243.80	97.22	-0.50	-0.02	0.07
DF1	2496.97	223.43	60.64	-2.31	-1.35	-1.87
DF2	3538.10	224.01	55.01	-2.53	-1.77	-2.08
DF3	4592.11	233.07	60.74	-1.32	-1.12	-1.15
DF4	3998.88	231.44	70.48	-0.97	-1.09	-0.42
GO1	2211.16	209.60	63.40	-2.25	-2.04	-1.79
GO2	3269.52	229.39	73.04	-0.94	-1.05	-0.69
GO3	3652.50	223.86	63.19	-1.31	-1.65	-1.32
GO4	5341.96	242.40	68.36	-0.08	-0.18	0.02
GO5	4903.68	225.49	51.48	-2.67	-2.12	-2.16
GO6	4207.32	244.05	68.76	-0.36	-0.01	-0.61
GO7	4524.28	254.06	93.71	1.15	0.80	1.75
MG1	2779.56	207.56	61.66	-2.09	-2.56	-1.71
MG2	3601.20	244.07	67.76	-1.18	-0.01	-0.91
MT1	4239.58	244.80	83.32	0.23	0.05	0.74
MT2	3805.55	245.57	67.22	-0.88	0.12	-0.92
MT3	3347.64	226.27	59.71	-1.80	-1.43	-1.74
TO1	2518.91	195.25	67.25	-2.48	-3.27	-1.34
TO2	2873.01	199.04	64.66	-2.26	-3.28	-1.39
TO3	3349.94	223.10	76.37	-0.79	-1.53	-0.38
TO4	2465.25	201.39	73.16	-2.02	-2.71	-1.00

The total phylo β -diversity ($\beta_{\text{sor.phy}}$) for the herbaceous-shrub communities of the *veredas* was low (mean \pm SD, 0.498 ± 0.064 , $n = 210$). Turnover component is contributing more to the phylo β -diversity between sites, compared to nestedness component (mean \pm SD, 0.406 ± 0.080 for $\beta_{\text{sim.phy}}$ versus 0.091 ± 0.066 for $\beta_{\text{nes.phy}}$, $n = 210$), as it is shown in both plots (Fig. 2 and 3). This means species are usually being replaced between sites. In particular, turnover was low between some of the *veredas* in

central Cerrado (DF); between the *veredas* in Grande Sertão Veredas National Park; and between two *veredas* in Northern Cerrado (TO).

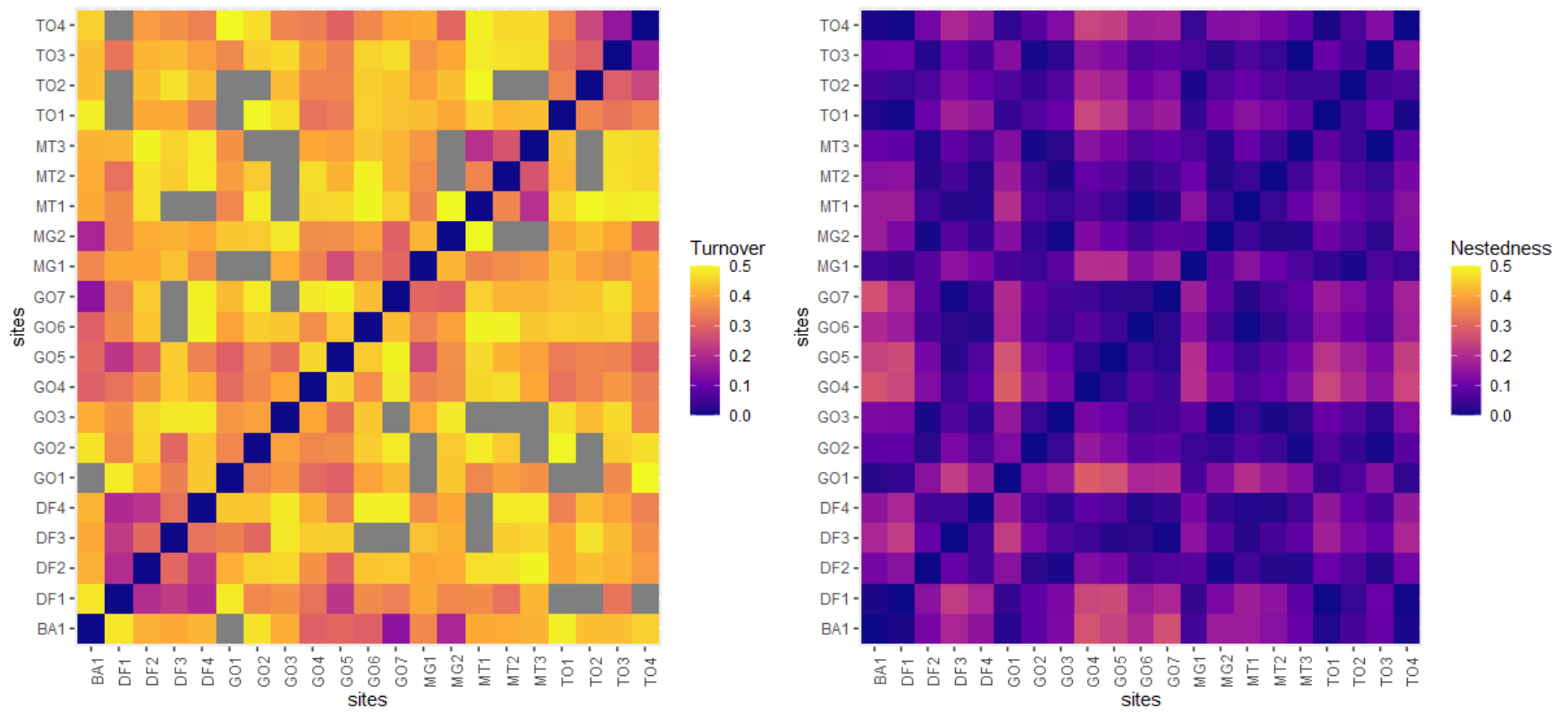


Figure 2 Heatmap showing the contribution of phylo beta-diversity between sites, with the turnover and nestedness components. The site codes are described in Figure 1

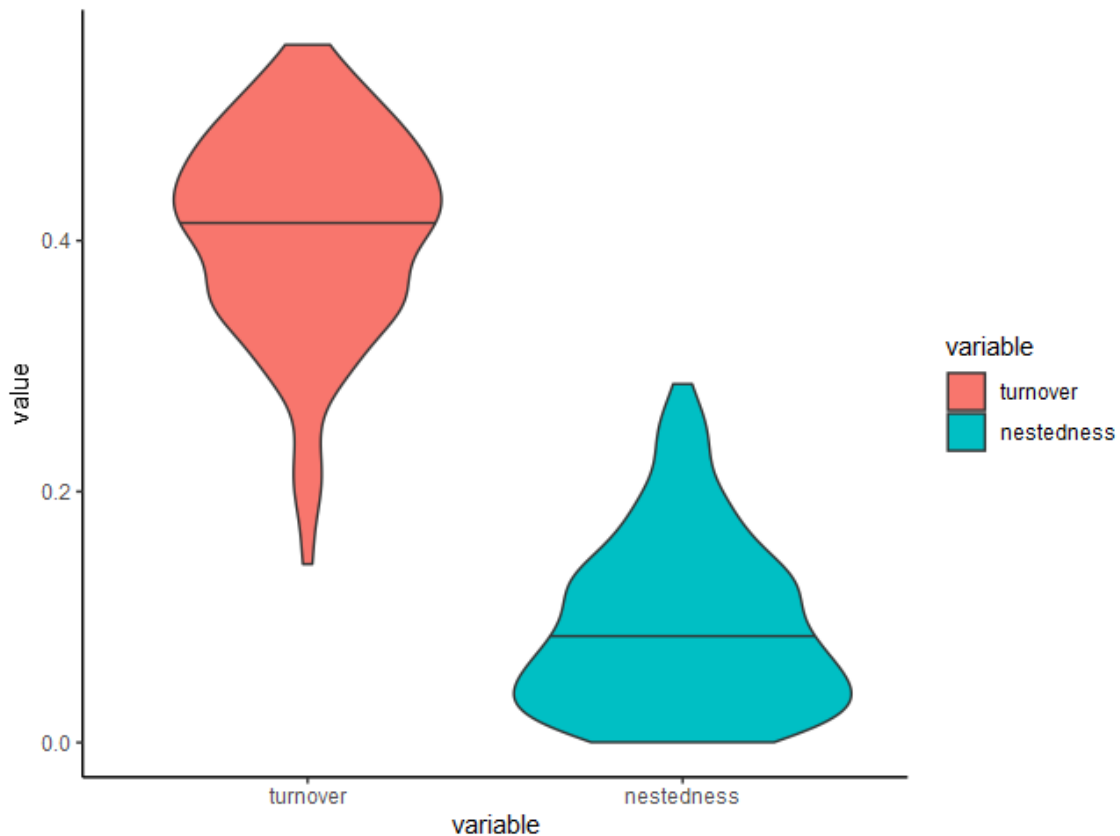


Figure 3 Distribution of turnover and nestedness values, as well as their median

My analysis with the OLS models, showed that the phylogenetic diversity and structure were primarily positively influenced by organic matter and annual precipitation (BIO12) (Fig. 4; Appendix, Tables S10, S11 and S12). After accounting for other variables in the model, mean temperature of the coldest quarter (BIO11) positively correlated with sesPD and sesMNTD (Fig. 4), whereas precipitation of the warmest quarter (BIO18) positively correlated with sesPD (Fig. 4). The Adjusted- R^2 for sesPD was 0.45, whereas sesMPD showed a pseudo- R^2 of 0.41, and sesMNTD of 0.56 (Appendix, Tables S10, S11 and S12).

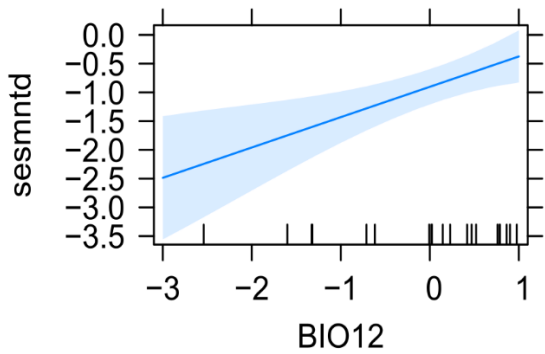
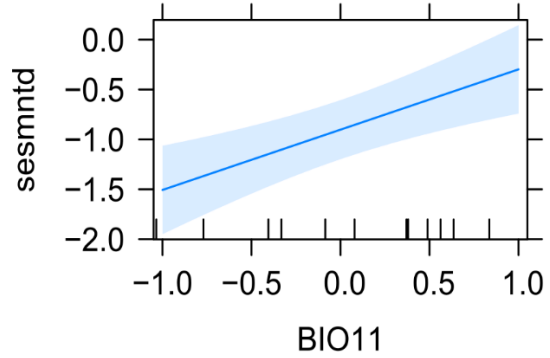
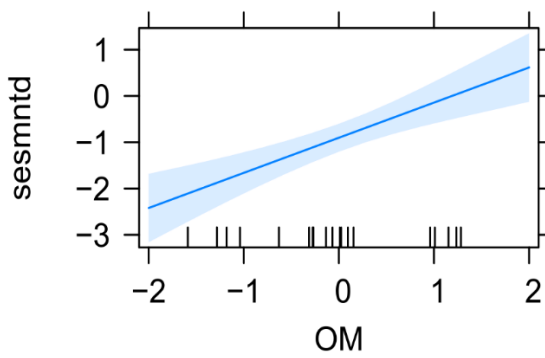
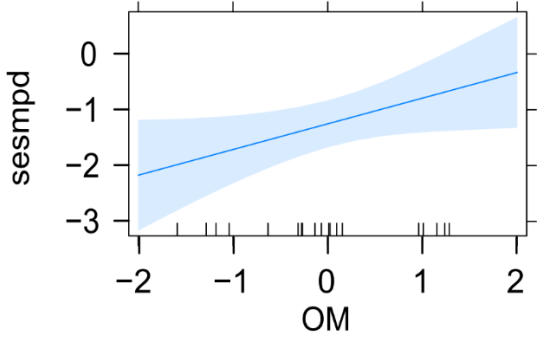
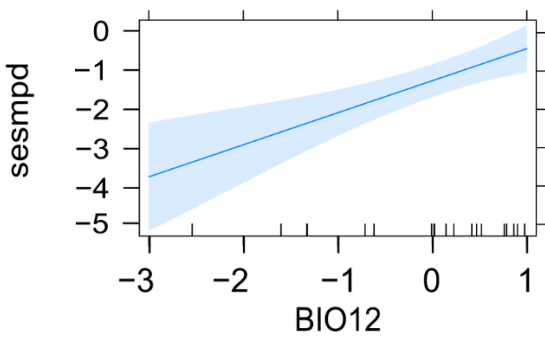
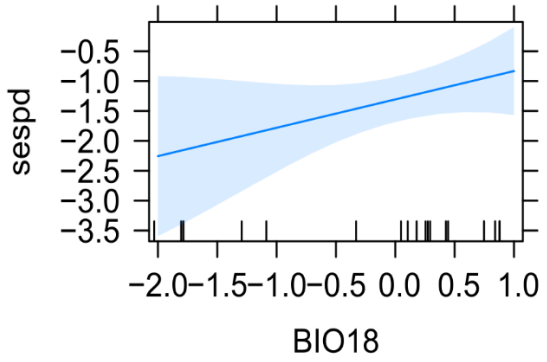
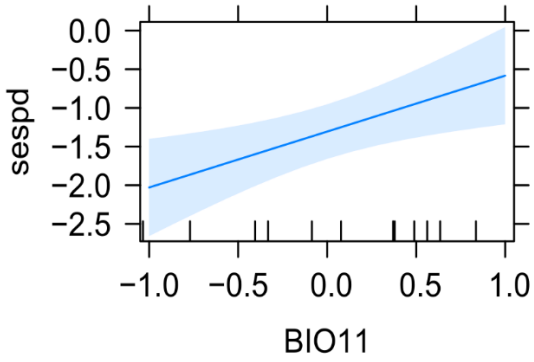
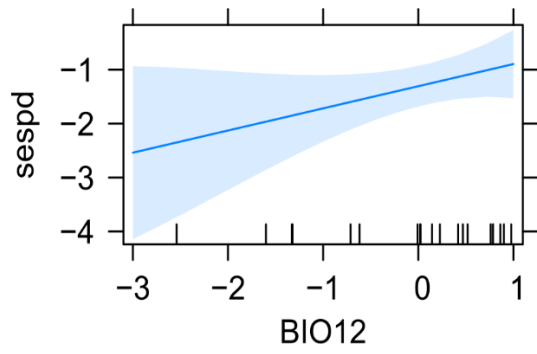
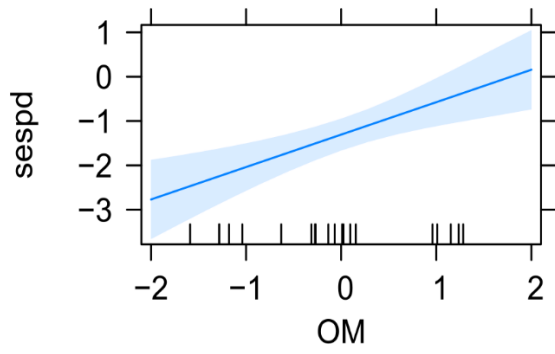


Figure 4 OLS results with sesPD (null model of Faith's phylogenetic diversity index), sesMPD (null model of the mean pairwise distance) and sesMNTD (null model of the mean nearest taxon distance) as response variables and environmental factors as explanatory variables. OM = organic matter; BIO11 = mean temperature of coldest quarter; BIO12 = annual precipitation; BIO18 = precipitation of warmest quarter

Phylo β -diversity ($\beta_{\text{sor.phy}}$) was significantly and mainly associated with the combined effects of geographic, climatic, and soil distance-based variables ($R^2 = 0.149$) (Table 2). They explained much more variance in the turnover ($\beta_{\text{sim.phy}}$) component than in the nestedness ($\beta_{\text{nes.phy}}$) component of phylo β -diversity ($R^2 = 0.128$ versus 0.035). Geographic distance uniquely explained about 0.121 (R^2) of the variance in $\beta_{\text{sor.phy}}$ (Table 2) and explained much less variance in $\beta_{\text{nes.phy}}$ than in $\beta_{\text{sim.phy}}$ ($R^2 = 0.008$ versus 0.127). Climatic distance uniquely explained about 0.082 (R^2) of the variance in $\beta_{\text{sor.phy}}$, 0.060 (R^2) in $\beta_{\text{sim.phy}}$ and 0.001 (R^2) in $\beta_{\text{nes.phy}}$ (Table 2). Soil distance alone for all components and all $\beta_{\text{nes.phy}}$ results were not statistically significant (Table 2).

Table 2. Results of multiple regression on distance matrices (MRM) relating each phylo β -diversity metric to geographic distance, climatic distance, and soil distance. I report the partial standardized regression coefficients for each explanatory distance variable and the coefficient of determination (R^2) of the complete model. Significance was tested using a permutation test (999 permutations): ** $p < 0.001$, * $p < 0.05$, ns $p > 0.05$

	$\beta_{\text{sor.phy}}$	$\beta_{\text{sim.phy}}$	$\beta_{\text{nes.phy}}$
Space + climate + soil	5.764**	0.642*	9.337e-01ns
R^2	0.149**	0.128**	0.035ns
Space + climate	5.489**	0.645**	9.036e-01ns
R^2	0.128**	0.128**	0.011ns
Space + Soil	5.653**	0.639*	9.258e-01ns
R^2	0.141**	0.127**	0.031ns
Soil + climate	0.578*	0.646*	0.932ns
R^2	0.113*	0.061*	0.019ns
Space	5.399**	0.642**	8.976e-01ns
R^2	0.121**	0.127**	0.008ns

Climate	0.545**	0.640*	0.905ns
R ²	0.082**	0.060*	0.001ns
Soil	0.537ns	0.601ns	0.935ns
R ²	0.034ns	0.001ns	0.018ns

Discussion

I found that the communities of *vereda* were phylogenetically clustered, containing more phylogenetically closely related species than expected by chance. Specifically, the phylogenetic distance between the species within these communities was lower than expected by chance. This was not surprising, as Poaceae, Cyperaceae, and Asteraceae are among the largest plant families registered in my study (Appendix, Fig. S2). Phylogenetic clustering suggests the action of strong environmental filters in the communities, indicating that niche conservatism is prevalent (Webb et al., 2002; Cavender-Bares et al., 2009; Wiens and Graham, 2005). In this sense, I believe that the low phylogenetic distance among coexisting species is due to the failure of outsider species (i.e., extant species living in the surrounding vegetation) to arrive and establish in these *veredas*, considering that these habitats are in environmentally stressful ecosystems. In other words, phylogenetic clustering may be acting because outsider species lack the right combination of traits needed to thrive in these unique ecosystems. *Veredas* represent partially isolated patches of vegetation situated on waterlogged soils, surrounded by vegetation on well-drained soils (Eiten, 1972). They exhibit considerable variation in topography, soil characteristics, and regional scale, as well as in altitude, temperature, and precipitation. (Fig. 1; Appendix, Tables S5). The variation of these factors creates different micro-habitats for each *vereda*. These micro-habitats possess their own characteristics that shape the assemblage of species most suited to occupy that niche (Levine and HilleRisLambers, 2009).

Precipitation, temperature, and organic matter were environmental filters driving changes in the phylogeny and diversity of *veredas*. These environmental filters exhibited positive

correlations with all metrics. This finding may be linked to historical environmental conditions that selectively filtered lineages from the regional lineage pool, eventually contributing to local phylogenetic clustering. In the Cerrado, at some point during the LGM, due to the cold and dry climate, *M. flexuosa* palms (characteristic of *veredas*) were scarce and scattered, while grasses were abundant (Behling and Hooghiemstra, 2001). The formation of *veredas* started during the late Pleistocene, with a preponderance of terrestrial plants in a locally stable environment (Horák-Terra et al., 2022b). With increasing temperature and moisture, the grass-dominated savanna changed to grass/shrub savanna in the early Holocene, and later trees began to appear (Behling and Hooghiemstra, 2001). In a transitional phase from 7200 to 5000 ¹⁴C B.P., the expansion of *M. flexuosa* palm swamps began, suggesting an increase in moisture (Behling and Hooghiemstra, 2001; Rull and Montoya, 2014). During the late Holocene, vegetation and climate were similar to present-day conditions, allowing the population of *M. flexuosa* to expand (Behling and Hooghiemstra, 2001) and form the *veredas* as they are known, with a dominant herbaceous-shrub stratum and a strip of *M. flexuosa* in the lower part of the terrain (Horák-Terra et al., 2022b). Therefore, only after climatic stabilization, with average winter temperatures above 15°C and fluctuations in the groundwater levels in the areas, the existence of *veredas* was possible (Salgado-Labouriau et al., 1997).

The low phylo β -diversity ($\beta_{\text{sor.phy}}$) observed among *veredas* suggests low variations in species composition across sites in terms of their evolutionary relationships. My findings indicate that the turnover component ($\beta_{\text{sim.phy}}$) contributed more to the phylo β -diversity between sites compared to the nestedness component ($\beta_{\text{nes.phy}}$). This suggests that dissimilarities in species composition primarily arise from species replacement rather than the gain or loss of species between sites while maintaining the nested structure. The greater contribution of the turnover component over the nestedness component can be attributed to various factors. These include differences in environmental conditions between sites, constraints on dispersal leading

to limited exchange, variations in evolutionary histories, distinctive species interaction networks, anthropogenic factors such as farming, grazing, burning, as well as differences in disturbance regimes like fire occurrence and water table fluctuations (Dobrovolski et al., 2012; Han et al., 2018; Xavier et al., 2019; Qian et al., 2020; Massante and Gerhold, 2020). Considering that the Cerrado remained unglaciated during the LGM, extinctions in the region may have been less severe, potentially enabling a higher persistence of species, the emergence of endemism (Behling and Hooghiemstra, 2001; Werneck, 2011) and facilitating species turnover. In fact, herbaceous communities across different Cerrado vegetation types exhibit turnover along the hydrological gradient, with distinct species adapted for different water table levels (Xavier et al., 2019). Specifically, plant communities in areas with high water table levels, such as *veredas*, tend to comprise specialized species from few evolutionary lineages, showing phylogenetic clustering and low phylogenetic diversity (Xavier et al., 2019). This is expected considering the significant adverse impact of soil water saturation on plant performance and survival in conditions of severe soil anoxia and hypoxia, allowing only specialized species to occur, especially the herbaceous ones (Moor et al., 2017).

For *veredas*, phylo β -diversity, including turnover and nestedness components, was found to be lower than the those observed in the taxonomic β -diversity evaluated in Chapter 2. These findings indicate that β -diversity patterns are primarily characterized by the exchange of phylogenetically close species across space, rather than distant ones (Qian et al., 2020). This can be attributed to the spatial limitations experienced by species, given that *veredas* are wetland patches surrounded by Cerrado vegetation on well-drained soils (Eiten, 1972). Other studies examining regionally distributed communities have also observed a higher taxonomic β -diversity than phylo β -diversity for plant species in North America (Qian et al., 2013), China (Qian et al., 2020), and wetlands in China (Li et al., 2024).

Phylo β -diversity ($\beta_{\text{sor.phy}}$) was significantly and mainly associated with the combined effects of geographic, climatic, and soil distance-based variables. This means that both environmental filtering and dispersal limitation jointly drive the geographic distribution of phylo β -diversity of *vereda*'s plants. Moreover, the $\beta_{\text{sim.phy}}$ component is independent of species richness, and its correlation with all dissimilarity distances indicates that differences in species number may mask differences in phylo β -diversity across assemblages (Baselga, 2010; Leprieur et al., 2012).

Geographic distances play a crucial role in phylo β -diversity as they serve as a proxy for connectivity or isolation between assemblages (Massante and Gerhold, 2020; Qian et al., 2020). On a regional or even local scale, *veredas* are poorly connected; rather, they are partially isolated patches with their herbaceous-shrub species growing on waterlogged soils embedded by vegetation growing on well-drained soils (Eiten, 1972). I hypothesize that these hydrological distinctions limit the colonization of *vereda* species in well-drained habitats and vice versa. Furthermore, the lack of connectivity between *vereda* sites probably hinders the dispersal of plant species, leading to pronounced differences in species composition among communities across geographical distances (Bijos et al., 2023). My findings indicate that clustered communities may result from limited dispersal abilities. Moreover, the presence of closely related species in regions that remained stable throughout the climatically unstable Quaternary period may be attributed to dispersal limitation (Behling and Hooghiemstra, 2001; Werneck, 2011).

The relationship between phylo β -diversity and climatic distance in the MRM analysis suggests that species sorting related to different climatic tolerances conserved across lineages (i.e., phylogenetic niche conservatism; Wiens and Graham, 2005), influenced by geographic distance, likely contributed significantly to the structuring of regional plant assemblages in *veredas*. During the LGM, some regions were indirectly affected by glaciation. These regions

were expected to experience less severe extinctions, allowing a greater number of species to be maintained, thus promoting speciation by isolation of populations, resulting in the occurrence of endemism and species turnover (Baselga, 2010; Werneck, 2011; Dobrovolski et al., 2012). In central Cerrado, where the *veredas* are located, there is evidence of past climatic stability in some regions, especially in regions with elevations above 900 m (Vidal et al., 2019). Niche stability can lead to the isolation of ancient plant lineages and the emergence of new genera and species, contributing to local endemism (Werneck, 2011). In addition, the Late Holocene, saw the end of an arid period and an increase in precipitation towards conditions similar to the present (Werneck, 2011). Increased precipitation may have influenced the formation of the vegetational complex of the *veredas*, by recharging their underground water reservoir, contributing to the water table maintenance (Laio et al., 2009), and providing conditions for specialized plant community to thrive (Nunes et al., 2022; Horák-Terra et al., 2022a; Bijos et al., 2023).

A phylogenetic analysis of 21 *veredas* of the Neotropical savanna in Brazil revealed that herbaceous-shrub species were clustered. This finding suggests that phylogenetically aggregated communities contain more closely related species and may be influenced by environmental filters, particularly given the correlation between climatic and soil factors versus phylogenetic structure and phylo β -diversity. The phenomenon of dispersal limitation also played a significant role in explaining phylo β -diversity. This is because *veredas* have limited interconnectivity with one another and are soil-saturated environments situated near ecosystems that thrive in well-drained soils (Eiten, 1972). Consequently, it can be concluded that the phylo β -diversity of *veredas* is influenced by both deterministic and stochastic processes. Future studies should investigate the functional and phylogenetic diversity of *vereda* species and adjacent dryland species, with a particular focus on the influence of other environmental filters such as hydrological interactions and measures of the water table levels on the phylogenetic

metrics. This approach would provide a more comprehensive understanding of the ecological adaptability of wetland plants.

References

- Alvares, C.A., Stape, J.L., Sentelhas, P.C., de Moraes Gonçalves, J.L., Sparovek, G., 2013. Köppen's climate classification map for Brazil. *Meteorol. Z.* 22,711-728. <https://doi.org/10.1127/0941-2948/2013/0507>.
- Amaral, A.G., Bijos, N.R., Moser, P., Munhoz, C.B.R., 2022. Spatially structured soil properties and climate explain distribution patterns of herbaceous-shrub species in the Cerrado. *Plant Ecol.* 223, 85-97. <https://doi.org/10.1007/s11258-021-01193-7>.
- Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* 19, 134-143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>.
- Baselga, A., Orme, D., Villeger, S., De Bortoli, J., Leprieur, F., Logez, M., Martinez-Santalla, S., Martin-Devasa, R., Gomez-Rodriguez, C., Crujeiras, R., 2023. betapart: Partitioning Beta Diversity into Turnover and Nestedness Components. R package version 1.6.
- Beer, F., Munhoz, C.B.R., Couwenberg, J., Horák-Terra, I., Bijos, N.R., Fonseca, L.M.G., Wantzen, K.M., in press. Peatlands in the Brazilian Cerrado: insights into knowledge, status and research needs. *Perspect. in Ecol. and Conserv.*
- Behling, H., Hooghiemstra, H., 2001. Neotropical savanna environments in space and time: Late Quaternary interhemispheric comparisons, in: Markgraf, V. (Ed.), *Interhemispheric climate linkages*. Academic press, pp. 307-323. <https://doi.org/10.1016/B978-012472670-3/50021-5>.
- Bijos NR, Munhoz CBR. In press. Stochastic processes influencing beta diversity of herbaceous-shrub species in *veredas* in Central Brazil.

- Bijos, N.R., Eugênio, C.U.O., Mello, T.R.B., Souza, G.F., Munhoz, C.B.R., 2017. Plant species composition, richness, and diversity in the palm swamps (*veredas*) of Central Brazil. *Flora*. 236, 94-99. <http://dx.doi.org/10.1016/j.flora.2017.10.002>.
- Bijos, N.R., Silva, D.P., Munhoz, C.B.R., 2023. Soil texture and fertility determine the beta diversity of plant species in *veredas* in Central Brazil. *Plant Soil*. 492, 241–259. <https://doi.org/10.1007/s11104-023-06168-3>.
- Bryant, J.A., Lamanna, C., Morlon, H., Kerkhoff, A.J., Enquist, B.J., Green, J.L., 2008. Microbes on mountainsides: contrasting elevational patterns of bacterial and plant diversity. *Proc. Nat. Acad. Sci.* 105, 11505–11511. <https://doi.org/10.1073/pnas.0801920105>.
- Canfield, R., 1941. Application of line interception in sampling range vegetation. *J. Forest* 39, 388–394. <https://doi.org/10.1093/jof/39.4.388>
- Cavender-Bares, J., Kozak, K.H., Fine, P.V.A., Kembel, S.W., 2009. The merging of community ecology and phylogenetic biology. *Ecol. Lett.* 12, 693-715. <https://doi.org/10.1111/j.1461-0248.2009.01314.x>.
- Chi, X., Tang, Z., Fang, J., 2014. Patterns of phylogenetic beta diversity in China's grasslands in relation to geographical and environmental distance. *Basic Appl. Ecol.* 15, 416–425. <https://doi.org/10.1016/j.baae.2014.07.003>.
- Cummings J., Smith D., 2000. The line-intercept method: a tool for introductory plant ecology laboratories. In: Karcher, S.J. (ed) *Tested studies for laboratory teaching. Proceedings of the 22nd workshop/conference of the association for biology laboratory education (ABLE)*, South Carolina, pp 234-246
- Dobrovolski, R., Melo, A.S., Cassemiro, F.A.S., Diniz-Filho, J.A.F., 2012. Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of

- beta diversity. *Glob. Ecol. Biogeogr.*, 21, 191-197. <https://doi.org/10.1111/j.1466-8238.2011.00671.x>.
- Dormann, C.F., Elith, J., Bacher, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27-46. <https://doi.org/10.1111/j.1600-0587.2012.07348.x>.
- Durigan, G., Munhoz, C. B., Zakia, M. J. B., Oliveira, R. S., Pilon, N. A., do Valle, R. S. T., ... Pott, A., 2022. Cerrado wetlands: multiple ecosystems deserving legal protection as a unique and irreplaceable treasure. *Perspect. ecol. conserv.* 20, 185-196. <https://doi.org/10.1016/j.pecon.2022.06.002>.
- Eiten, G., 1972. The Cerrado vegetation of Brazil. *The Bot. Rev.* 38, 201–341. <https://doi.org/10.1007/BF02859158>.
- EMBRAPA - Empresa Brasileira de Pesquisa Agropecuária (2017) Manual de métodos de análise de solo. Embrapa, Brasília. Pesquisa de Solos. Sistema brasileiro de classificação de solos, 2nd edn. Rio de Janeiro
- Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* 61, 1-10. [https://doi.org/10.1016/0006-3207\(92\)91201-3](https://doi.org/10.1016/0006-3207(92)91201-3).
- Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37, 4302-4315. <https://doi.org/10.1002/joc.5086>.
- Fluet-Chouinard, E., Stocker, B.D., Zhang, Z., ..., McIntyre P.B., 2023. Extensive global wetland loss over the past three centuries. *Nature.* 614, 281–286. <https://doi.org/10.1038/s41586-022-05572-6>.
- Gerhold, P., Cahill, J.F., Winter, M., Bartish, I.V., Prinzing, A., 2015. Phylogenetic patterns are not proxies of community assembly mechanisms (they are far better). *Funct. Ecol.* 29, 600-614. <https://doi.org/10.1111/1365-2435.12425>.

- Gonçalves, R.V.S., Cardoso, J.C., Oliveira, P.E., Oliveira, D.C., 2021. Changes in the Cerrado vegetation structure: insights from more than three decades of ecological succession. *Web. Ecol.* 21,55-64. <https://doi.org/10.5194/we-21-55-2021>.
- Goslee, S.C., Urban, D.L., 2007. The ecodist package for dissimilarity-based analysis of ecological data. *J. Stat. Softw.* 22, 1-19. <https://doi.org/10.18637/jss.v022.i07>.
- Graham, C., Fine, P., 2008. Phylogenetic beta diversity: linking ecological and evolutionary processes across space and time. *Ecol. Lett.* 11, 1265-1277. <https://doi.org/10.1111/j.1461-0248.2008.01256.x>.
- Grinnell, J., 1917. The niche-relationships of the California Thrasher. *The Auk.* 34, 427-433. <https://doi.org/10.2307/4072271>.
- Han, J., Shen, Z., Li, Y., Luo, C., Xu, Q., Yang, K., Zhang, Z., 2018. Beta diversity patterns of post-fire forests in central Yunnan Plateau, southwest China: Disturbances intensify the priority effect in the community assembly. *Front. Plant Sci.* 9, 1000. <https://doi.org/10.3389/fpls.2018.01000>.
- Horák-Terra, I., Terra, F.S., Lopes, A.K.A., 2022a. Soil characterization and drainage effects in a savanna palm swamp (*vereda*) of an agricultural area from Central Brazil. *Ver. Bras. Ciênc. Solo.* 46, e0210065. <https://doi.org/10.36783/18069657rbcs20210065>.
- Horák-Terra, I., Trindade, R.N.R., Terra, F.S., Silva, A.C., De Camargo, P.B., Viana, C.B.O., Vidal-Torrado, P., 2022b. Soil processes and properties related to the genesis and evolution of a Pleistocene savanna palm swamp (*vereda*) in central Brazil. *Geoderma* 410, 115671. <https://doi.org/10.1016/j.geoderma.2021.115671>.
- Hubbell, S.P., 2001. *The unified neutral theory of biodiversity and biogeography (MPB-32)*. Princeton University Press.

- Jiang, L., Hu, D., Wang, H., Lv, G., 2022. Discriminating ecological processes affecting different dimensions of α -and β -diversity in desert plant communities. *Ecol. Evol.*, 12, e8710. <https://doi.org/10.1002/ece3.8710>.
- Jin, Y., 2023. V.PhyloMaker2: Make phylogenetic hypotheses for vascular plants. R package version 0.1.0.
- Junk, W.J., Piedade, M.T.F., Lourival, R., 2014. Brazilian wetlands: their definition, delineation, and classification for research, sustainable management, and protection. *Aquat. Conserv.* 24, 5-22. <https://doi.org/10.1002/aqc.2386>.
- Kembel, S., Cowan, P., Helmus, M., 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26, 1463–1464. <https://doi.org/10.1093/bioinformatics/btq166>.
- Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S., Levine, J.M., 2015. Community assembly, coexistence and the environmental filtering metaphor. *Funct. Ecol.* 29, 592-599. <https://doi.org/10.1111/1365-2435.12345>.
- Laio, F., Tamea, S., Ridolfi, L., D'Odorico, P., Rodriguez-Iturbe, I., 2009. Ecohydrology of groundwater-dependent ecosystems: 1. Stochastic water table dynamics. *Water Resour. Res.* 45, 5. <https://doi.org/10.1029/2008WR007292>.
- Lean, C., Maclaurin, J., 2016. The Value of Phylogenetic Diversity. in: Pellens R, Grandcolas P. (eds), *Biodiversity Conservation and Phylogenetic Systematics. Topics in Biodiversity and Conservation*, vol 14. Springer, Cham. https://doi.org/10.1007/978-3-319-22461-9_2.
- Leprieur, F., Albouy, C., de Bortoli, J., Cowman, P.F., Bellwood, D.R., Mouillot, D., 2012. Quantifying phylogenetic beta diversity: distinguishing between “true” turnover of lineages and phylogenetic diversity gradients. *PLoS ONE.* 7, e42760. <https://doi.org/10.1371/journal.pone.0042760>.
- Levine, J.M., HilleRisLambers, J., 2009. The importance of niches for the maintenance of species diversity. *Nature.* 461, 254-257. <https://doi.org/10.1038/nature08251>.

- Li, X.H., Zhu, X.X., Niu, Y., Sun, H., 2014. Phylogenetic clustering and overdispersion for alpine plants along elevational gradient in the Hengduan Mountains Region, southwest China. *J. Syst. Evol.* 52, 280-8. <https://doi.org/10.1111/jse.12027>.
- Li, Y., Liu, F., Zhou, Y., Liu, X., Wang, Q., 2024. Geographic patterns and environmental correlates of taxonomic, phylogenetic and functional β -diversity of wetland plants in the Qinghai-Tibet Plateau. *Ecol. Indic.* 160, 111889. <https://doi.org/10.1016/j.ecolind.2024.111889>.
- Lichstein, J.W., 2007. Multiple regression on distance matrices: A multivariate spatial analysis tool. *Plant Ecol.* 188, 117–131. <https://doi.org/10.1007/s11258-006-9126-3>.
- Massante, J.C., Gerhold, P., 2020. Environment and evolutionary history depict phylogenetic alpha and beta diversity in the Atlantic coastal white-sand woodlands. *J. Veg. Sci.*, 31, 634-645. <https://doi.org/10.1111/jvs.12900>.
- Massante, J.C., Neri, A.V., Villa, P.M., Fialho, I.F., Pontara, V., Bueno, M., Gastauer, M., 2023. Looking similar but all different: Phylogenetic signature of Brazilian rocky outcrops and the influence of temperature variability on their phylogenetic structure. *J. Ecol.* 111, 1905-1920. <https://doi.org/10.1111/1365-2745.14148>.
- Mayfield, M.M., Levine, J.M., 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol. Lett.* 13, 1085–1093. <https://doi.org/10.1111/j.1461-0248.2010.01509.x>.
- Moor, H., Rydin, H., Hylander, K., Nilsson, M. B., Lindborg, R., Norberg, J., 2017. Towards a trait-based ecology of wetland vegetation. *J. Ecol.* 105, 1623-1635. <https://doi.org/10.1111/1365-2745.12734>.
- Moreira, S.N., Eisenlohr, P.V., Pott, A., Pott, V.J., Oliveira-Filho, A.T., 2015. Similar vegetation structure in protected and non-protected wetlands in Central Brazil:

- conservation significance. *Environ. Conserv. J.* 42, 356–362.
<https://doi.org/10.1017/S0376892915000107>.
- Munhoz, C.B.R., Araújo, G.M., 2011. Métodos de Amostragem do estrato herbáceo-subarbustivo. In: Felfili, J.M., Eisenlohr, P.V., Melo, M.M.R.F., Andrade, L.A., Neto, J.A.A.M., ed. *Fitossociologia no Brasil: Métodos e Estudos de Casos*. Universidade Federal de Viçosa, Viçosa, pp 213-230
- Munhoz, C.B.R., Felfili, J.M., 2006. Fitossociologia do estrato herbáceo-subarbustivo de uma área de campo sujo no Distrito Federal, Brasil. *Acta Bot. Bras.* 20, 671–685.
<https://doi.org/10.1590/S0102-33062006000300017>
- Naimi, B., Hamm, N.A.S., Groen, T.A., Skidmore, A.K., and Toxopeus, A.G., 2014. Where is positional uncertainty a problem for species distribution modelling? *Ecography* 37 (2): 191-203. <https://doi.org/10.1111/j.1600-0587.2013.00205.x>
- Nunes, Y.R.F., Souza, C.S., de Azevedo, I.F.P., de Oliveira, O.S., Frazão, L.A., Fonseca, R.S., 2022. Vegetation structure and edaphic factors in veredas reflect different conservation status in these threatened areas. *For. Ecosyst.* 9, 100036.
<https://doi.org/10.1016/j.fecs.2022.100036>.
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J., 2022. *Vegan: Community Ecology Package*. R package version 2.6-4
- Paradis, E., Schliep, K., 2019. Ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinform.* 35, 526–528.

- Pennell, M.W., Eastman, J.M., Slater, G.J., Brown, J.W., Uyeda, J.C., FitzJohn, R.G., Harmon, L.J., 2014. geiger v2.0: an expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics*, 30, 2216-2218. <https://doi.org/10.1093/bioinformatics/btu181>.
- Pousa, R., Costa, M.H., Pimenta, F.M., Fontes, V.C., De Brito, V.F.A., Castro, M., 2019. Climate Change and Intense Irrigation Growth in Western Bahia, Brazil: The Urgent Need for Hydroclimatic Monitoring. *Water*. 11, 933. <https://doi.org/10.3390/w11050933>.
- Qian, H., Jin, Y., 2016. An updated megaphylogeny of plants, a tool for generating plant phylogenies and an analysis of phylogenetic community structure. *J. Plant. Ecol.* 9, 233–239. <https://doi.org/10.1093/jpe/rtv047>.
- Qian, H., Swenson, N.G., Zhang, J., 2013. Phylogenetic beta diversity of angiosperms in North America. *Glob. Ecol. Biogeogr.* 22, 1152–1161. <https://doi.org/10.1111/geb.12076>.
- R Core Team., 2022. R version 4.2.2: a language and environment for statistical computing. R Found. Stat. computing. R Found Stat. Comput, Vienna, Austria.
- Ricklefs, R.E., Shluter, D., 1993. Species diversity in ecological communities. University of Chicago Press, Chicago, Illinois, USA.
- Rosolen, V., de Oliveira, D.A., Bueno, G.T., 2015. Vereda and Murundu wetlands and changes in Brazilian environmental laws: challenges to conservation. *Wetl. Ecol. Manag.* 23, 285–292. <https://doi.org/10.1007/s11273-014-9380-4>.
- Rull, V., Montoya, E., 2014. *Mauritia flexuosa* palm swamp communities: natural or human-made? A palynological study of the Gran Sabana region (northern South America) within a neotropical context. *Quat. Sci. Rev.* 99, 17-33. <https://doi.org/10.1016/j.quascirev.2014.06.007>.
- Salgado-Labouriau, M.L., Caseti, V., Ferraz-Vicentini, K.R., Martin, L., Soubiès, F., Suguio, K., Turcq, B., 1997. Late Quaternary vegetational and climatic changes in cerrado and palm

- swamp from Central Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 128, 215-226. [https://doi.org/10.1016/S0031-0182\(96\)00018-1](https://doi.org/10.1016/S0031-0182(96)00018-1).
- Salmona, Y.B., Matricardi, E.A.T., Skole, D.L., Silva, J.F.A., Coelho Filho, O.D.A., Pedlowski, M.A., Sampaio, J.M., Castrillon, L.C.R., Brandão, R.A., Silva, A.L.D., 2023. A worrying future for river flows in the Brazilian Cerrado provoked by land use and climate changes. *Sustainability*. 15, 4251. <https://doi.org/10.3390/su15054251>.
- Silva, D.P., Amaral, A.G., Bijos, N.R., Munhoz, C.B.R., 2018. Is the herb-shrub composition of *veredas* (Brazilian palm swamps) distinguishable? *Acta bot. bras.* 32, 47–54. <https://doi.org/10.1590/0102-33062017abb0209>.
- Smith, S.A., Brown, J.W., 2018. Constructing a broadly inclusive seed plant phylogeny. *Am. J. Bot.* 105, 302–314.
- Tilman, D., 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proc. Nat. Acad. Sci.* 101, 10854-10861. <https://doi.org/10.1073/pnas.0403458101>.
- Trindade, V.L., Ferreira, M.C., Costa, L.S., Amaral, E.J., Bustamante, M.M.C., Munhoz, C.B.R., 2024. The effect of woody encroachment on taxonomic and functional diversity and soil properties in Cerrado wetlands. *Flora*. 152524. <https://doi.org/10.1016/j.flora.2024.152524>.
- Tucker, C.M., Cadotte, M.W., 2013. Unifying measures of biodiversity: understanding when richness and phylogenetic diversity should be congruent. *Divers. distrib.* 19, 845-854. <https://doi.org/10.1111/ddi.12087>.
- Van Asselen, S., Verburg, P. H., Vermaat, J. E., Janse, J. H., 2013. Drivers of wetland conversion: a global meta-analysis. *PLoS ONE*. 08, e81292.
- Venables, W.N., Ripley, B. D., 2002. *Modern Applied Statistics with S*. Fourth Edition. Springer, New York. ISBN 0-387-95457-0.

- Vidal, J.D.D., de Souza, A.P., Koch, I., 2019. Impacts of landscape composition, marginality of distribution, soil fertility and climatic stability on the patterns of woody plant endemism in the Cerrado. *Glob. Ecol. Biogeogr.* 28, 904-916. <https://doi.org/10.1111/geb.12901>.
- Webb, C.O., 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *Am. Nat.* 156, 145-155. <https://doi.org/10.1086/303378>.
- Webb, C.O., Ackerly, D.D., Kembel, S.W., 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Version 4.0.1. <http://www.phylodiversity.net/phylocom/>.
- Webb, C.O., Ackerly, D.D., McPeck, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. *Annu. Rev. Ecol. Evol. Syst.* 33, 475-505. <https://doi.org/10.1146/annurev.ev.ecolsys.33.010802.150448>.
- Werneck, F.P., 2011. The diversification of eastern South American open vegetation biomes: Historical biogeography and perspectives. *Quat. Sci. Rev.* 30, 1630–1648. <https://doi.org/10.1016/j.quascirev.2011.03.009>.
- Wiens, J.J., Graham, C.H., 2005. Niche conservatism: Integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Evol. Syst.* 36, 519–539. <https://doi.org/10.1146/annurev.ecolsys.36.102803.095431>.
- Xavier, R.O., Leite, M.B., Dexter, K., Matos, D.M.S., 2019. Differential effects of soil waterlogging on herbaceous and woody plant communities in a Neotropical savanna. *Oecologia*, 190, 471-483. <https://doi.org/10.1007/s00442-019-04423-y>.
- Yi, S., Wu, P., Bai, F., Zhou, D., Peng, X., Zhang, W., Guo, W., 2020. Environmental Filtering Drives Plant Community Assembly Processes in the Riparian Marsh of Downstream Yellow River, China. *Wetlands* 40, 287-298. <https://doi.org/10.1007/s13157-019-01182-7>.

- Zappi, D.C., Moro, M.F., Meagher, T.R., Nic, Lughadha, E., 2017. Plant biodiversity drivers in Brazilian *campos rupestres*: insights from phylogenetic structure. *Front. Plant Sci.* 8, 2141. <https://doi.org/10.3389/fpls.2017.02141>.
- Zhang, J., Qian, H., 2023. U.Taxonstand: An R package for standardizing scientific names of plants and animals. *Plant Divers.* 45, 1-5. <https://doi.org/10.1016/j.pld.2022.09.001>.
- Zheng, J., Arif, M., He, X., Ding, D., Zhang, S., Ni, X., Li, C., 2022. Plant community assembly is jointly shaped by environmental and dispersal filtering along elevation gradients in a semiarid area, China. *Front. Plant Sci.* 13, 1041742. <https://doi.org/10.3389/fpls.2022.1041742>.

CONCLUSIONS

This study provided and organized a database on the occurrence and cover of 560 herbaceous, subshrub, and shrub species across 21 *vereda* sites (315 10-m transects) situated in the Brazilian central region, using information extracted from the literature and new field surveys. The data set includes the species' geographic coordinates, 12 soil physicochemical properties, and 14 bioclimatic variables. The *veredas* exhibit significant differences in species composition and diversity. A closer examination of *veredas* and their soils revealed that specific soil filters, including cation saturation, organic matter, phosphorus, sand proportion, and pH, are significant drivers of *veredas*' species composition. When considering taxonomic beta diversity (TBD), it was found that the plant communities were influenced by the spatial turnover of species, with spatial predictors better explaining their composition and distribution. These findings suggest that dispersal limitation is a dominant factor in the formation of *vereda* communities and that stochastic processes are influencing the TBD of these communities. To the best of my knowledge, no other published studies have evaluated the influence of stochastic and deterministic processes on the TBD of non-tree species in Cerrado wetland vegetation. Furthermore, I generated the first phylogenetic tree for herbaceous-shrub species of *veredas*. The results demonstrated that phylogenetic β -diversity was significantly and predominantly associated with the combined effects of geographic, climatic, and soil distance-based variables. The phylogenetic analysis revealed significant phylogenetic clustering, with the phylogenetic structure of *vereda* species being significantly correlated with environmental filters. The high phylogenetic β -diversity among *veredas*, with significant turnover contribution, indicates substantial spatial variation in community composition in terms of species' evolutionary relationships. This is likely due to the partially isolated nature of *veredas*, which are wetland patches surrounded by Cerrado vegetation on well-drained soils. This could limit species dispersal. Overall, these findings highlight that both deterministic processes, namely

environmental filtering and niche conservatism, as well as stochastic processes like dispersal limitation, drive the phylogenetic diversity patterns of herbaceous-shrub communities in Neotropical savanna wetlands.

The results of this study indicate that each *vereda* has a distinct ecological niche, influenced by differences in soil properties and microclimates, with some *veredas* exhibiting unique characteristics due to their altitude above 1000 meters. Furthermore, the species present in the *veredas* are subject to dispersal limitations due to the limited connectivity between the areas. These factors have resulted in a notable dissimilarity in species composition, with each *vereda* exhibiting a distinctive set of species, including some that are endemic to that particular area.

The findings of this research not only advance my understanding of the spatial and environmental filters shaping the *veredas* in the Cerrado, but also provide insights for implementing conservation strategies to minimize local extinctions and maximize species preservation. The recognition of stochasticity, specifically dispersal limitation, as a dominant component in the formation of these ecosystems implies the consideration of strategies aimed not only at protecting the *veredas*, but also at protecting the adjacent natural environments and the ecological corridors that form possible species dispersal routes (Baselga, 2010; Brederveld et al., 2011). It is crucial to recognize that the conservation of these ecosystems is not just a biological imperative; it is also a commitment to preserving the rich biodiversity and ecosystem services that *veredas* provide to human society and local wildlife. To gain a more comprehensive understanding of the influence of ecological processes on the formation of *veredas*, future research should integrate biological predictors (e.g., species interactions) and environmental predictors (e.g., temporal variation in water table depth and other edaphic variables) into their analysis. Future studies should also investigate the functional and phylogenetic diversity of *vereda* species and adjacent landscape species, with a particular focus

on the influence of other environmental filters such as hydrological interactions and measures of the water table levels on the phylogenetic metrics. This approach would provide a more comprehensive understanding of the ecological adaptability of wetland plants.

References

- Baselga A. 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology Biogeography* 19:134-143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Brederveld, R.J., Jähnig, S.C., Lorenz, A.W., Brunzel, S., Soons, M.B., 2011. Dispersal as a limiting factor in the colonization of restored mountain streams by plants and macroinvertebrates. *J. Appl. Ecol.* 48, 1241-1250. <https://doi.org/10.1111/j.1365-2664.2011.02026.x>.

APPENDIX

Table S1. Soil types found in the region of the 21 *vereda* sites and their respective geographic coordinates in degrees/minutes/seconds. The site codes are described in Fig. 1

Site	Soil types	Longitude (W)	Latitude (S)
DF1	Dystrophic Red Ferralsols	47°51'14.5"	15°53'31.0"
DF2	Dystrophic Red Ferralsols	47°58'37.9"	15°46'48.9"
DF3	Dystrophic Red Ferralsols	47°53'57.2"	15°55'53.5"
DF4	Dystrophic Red Ferralsols	48°04'10.2"	15°45'44.6"
GO1	Dystrophic Leptsols	47°48'45.5"	13°40'39.6"
GO2	Dystrophic Leptsols	47°48'04.2"	13°40'01.7"
GO3	Dystrophic Leptsols	47°41'15.7"	14°07'43.9"
GO4	Dystrophic Leptsols	47°45'49.3"	14°08'09.0"
GO5	Dystrophic Haplic Cambisols	47°41'54.6"	16°44'15.1"
GO6	Dystrophic Haplic Cambisols	48°58'02.6"	15°42'49.1"
GO7	Orthic Arenosols	46°19'22.1"	14°07'25.6"
MG1	Dystrophic Leptsols	43°37'20.0"	17°47'51.7"
MG2	Orthic Arenosols	45°42'52.7"	15°08'38.8"
BA1	Orthic Arenosols	45°54'36.4"	14°59'51.8"
MT1	Orthic Arenosols	52°33'04.4"	14°45'48.2"
MT2	Orthic Arenosols	52°34'37.2"	14°49'04.3"
MT3	Orthic Arenosols	52°33'38.1"	14°45'58.4"
TO1	Orthic Arenosols	46°54'23.7"	11°07'41.1"
TO2	Orthic Arenosols	46°37'04.3"	10°51'49.7"
TO3	Orthic Arenosols	46°36'54.0"	10°52'07.8"
TO4	Orthic Arenosols	46°31'45.0"	10°36'48.5"

Table S2. Hydrographic regions of the 21 *vereda* sites. The site codes are described in Fig. 1

Site	Hydrographic regions
GO1, GO2, GO3, GO4, GO6, GO7, TO1, TO2, TO3, TO4, MT1, MT2, MT3	Tocantins-Araguaia
DF1, DF2, DF3, DF4, GO5	Paraná
MG2, BA1	São Francisco
MG1	Atlântico Leste

Table S3. Pearson's correlation among soil properties ($|r| < 0.7$). Al = aluminum concentration, Ca = calcium, Mg = magnesium, K = potassium, P = phosphorus, OM = organic matter, V = cation saturation, and CEC = cation exchange capacity

	Al	Ca	Mg	K	pH	P	OM	V	CEC	Sand	Silt
Ca	-0.075										
Mg	-0.099	0.704									
K	0.381	-0.019	-0.235								
pH	-0.667	-0.037	0.147	-0.096							
P	-0.052	0.433	0.599	0.289	0.171						
OM	0.248	-0.168	0.036	0.408	-0.348	0.295					
V	-0.258	0.346	0.562	-0.326	0.369	0.251	-0.414				
CEC	0.400	-0.025	-0.169	0.146	-0.719	-0.121	0.571	-0.748			
Sand	0.350	0.181	0.390	-0.255	-0.505	0.143	0.217	0.020	0.305		
Silt	-0.311	-0.199	-0.509	0.364	0.412	-0.188	-0.186	-0.202	-0.183	-0.938	
Clay	-0.281	-0.181	-0.496	0.370	0.396	-0.181	-0.170	-0.191	-0.182	-0.952	0.995

Table S4. Relative Cover (%) of the species sampled in the 21 *vereda* sites. The site codes are described in Fig. 1

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
Acanthaceae																					
<i>Justicia sericographis</i> V.A.W.Graham	-	-	-	-	-	-	-	1.5190	-	-	-	-	-	-	-	-	0.4332	-	-	-	-
<i>Ruellia angustior</i> (Nees) Lindau	-	-	-	-	-	-	-	0.2265	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ruellia incomta</i> (Nees) Lindau	-	-	0.0244	-	-	-	-	0.1332	-	-	-	-	-	-	-	-	-	-	-	-	-
Alstroemeriaceae																					
<i>Alstroemeria longistyla</i> Schenk	-	0.0253	-	0.1024	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amaranthaceae																					
<i>Froelichiella grisea</i> R.E.Fr.	-	-	-	-	-	-	0.1091	0.3571	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Gomphrena</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0381	-
<i>Pfaffia denudata</i> (Moq.) Kuntze	-	-	-	-	-	-	-	0.0160	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pfaffia jubata</i> Mart.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0048	-	-	-	-	-	-
Apiaceae																					
<i>Eryngium ebracteatum</i> Lam.	-	-	-	-	-	0.3769	-	0.1865	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eryngium juncifolium</i> (Urb.) Mathias & Constance	-	-	0.1057	0.0047	-	-	-	-	-	-	-	-	0.6532	-	-	-	-	-	-	-	-
Apocynaceae																					
<i>Mandevilla myriophylla</i> (Taub. ex Ule) Woodson	-	-	-	-	-	-	-	-	-	0.0318	-	-	-	-	-	-	-	-	-	-	-
<i>Mandevilla tenuifolia</i> (J.C.Mikan) Woodson	-	-	-	-	-	-	-	-	-	-	-	-	0.0328	-	-	-	-	-	-	-	-
<i>Minaria cordata</i> (Turcz.) T.U.P.Konno & Rapini	-	0.0169	0.0041	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Nephradenia acerosa</i> Decne.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1837	-	-	-	-	0.0609	-

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Nephradenia</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1338	0.0305	-
<i>Oxypetalum appendiculatum</i> Mart.	-	-	0.1341	0.4935	-	-	-	-	0.3404	-	-	-	-	-	-	-	-	-	-	-	-
<i>Oxypetalum pachygynum</i> Decne.	-	-	-	-	-	0.0805	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Araceae																					
<i>Thaumatococcus daniellii</i> (Mayo) Sakur., Calazans & Mayo	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0242	-	-	-	-	-	-
<i>Thaumatococcus uliginosus</i> (Mayo) Sakur., Calazans & Mayo	-	-	-	0.0745	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Urospatha sagittifolia</i> (Rudge) Schott	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0428	-	-	-	-
<i>Xanthosoma striatipes</i> (Kunth & Bouché) Madison	-	-	-	0.3073	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Asteraceae																					
<i>Achyrocline alata</i> (Kunth) DC.	0.2732	-	1.9548	0.5215	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Achyrocline satyroides</i> (Lam.) DC.	0.2227	-	0.3170	0.6192	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ageratum fastigiatum</i> (Gardner) R.M.King & H.Rob.	-	-	-	-	-	-	-	0.1386	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Aspilia foliacea</i> (Spreng.) Baker	-	0.0591	0.0894	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Aspilia montevidensis</i> (Spreng.) Kuntze	-	-	-	0.1117	-	-	-	0.0773	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Aspilia</i> sp1	-	-	-	-	-	-	-	-	-	0.0566	-	-	-	-	-	-	-	-	-	-	-
Asteraceae sp1	-	-	-	-	-	-	-	-	-	0.0460	-	-	-	-	-	-	-	-	-	-	-
<i>Ayapana amygdalina</i> (Lam.) R.M.King & H.Rob.	-	0.0591	-	-	0.1004	0.1143	-	-	-	0.0071	-	-	-	-	-	-	-	-	-	-	-
<i>Ayapana</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.4930	0.0724	0.0520

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Baccharis reticularia</i> DC.	-	0.2196	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Baccharis retusa</i> DC.	-	-	-	0.0186	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Baccharis tridentata</i> Vahl	-	-	-	0.0093	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Calea elongata</i> (Gardner) Baker	-	-	-	-	0.0319	0.6988	0.0349	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Calea gardneriana</i> Baker	-	-	-	-	-	-	0.4495	-	0.5770	-	-	-	-	-	-	-	-	-	-	-	-
<i>Calea hymenolepis</i> Baker	-	-	-	-	-	0.0296	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Calea robinsoniana</i> Pruski	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1295	-
<i>Calea teucrifolia</i> (Gardner) Baker	-	-	-	-	-	-	-	-	-	0.1344	-	-	-	-	-	-	-	-	-	-	-
<i>Campuloclinium megacephalum</i> (Mart. ex Baker) R.M.King & H.Rob.	-	-	0.0325	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chresta souzae</i> H.Rob.	-	-	-	-	-	-	-	0.0160	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chromolaena cf. squalida</i> (DC.) R.M.King & H.Rob.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0229	-
<i>Chromolaena laevigata</i> (Lam.) R.M.King & H.Rob.	-	-	0.3129	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chromolaena vindex</i> (DC.) R.M.King & H.Rob.	-	0.8194	1.4062	0.8334	-	-	-	-	1.8512	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chrysolaena desertorum</i> (Mart. ex DC.) Dematt.	-	-	-	-	-	-	-	-	-	-	0.0233	-	0.2153	-	-	-	-	-	-	-	-
<i>Clibadium armanii</i> (Balb.) Sch.Bip. ex O.E.Schulz.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0320
<i>Echinocoryne holosericea</i> (Mart. ex DC.) H.Rob.	-	-	-	-	-	-	-	0.9460	-	-	-	-	-	-	-	-	-	-	-	-	-

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Elephantopus biflorus</i> (Less.) Sch.Bip.	-	-	-	-	-	-	-	-	-	-	-	-	0.0693	-	-	-	-	-	-	-	-
<i>Erechtites hieracifolius</i> (L.) Raf. ex DC.	-	-	-	0.0559	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Grazielia intermedia</i> (DC.) R.M.King & H.Rob.	-	-	-	-	-	-	0.0829	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ichthyothere latifolia</i> Baker	-	-	0.0041	0.0326	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ichthyothere terminalis</i> (Spreng.) S.F.Blake	-	-	-	-	-	0.2541	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lepidaploa aurea</i> (Mart. ex DC.) H.Rob.	0.1261	-	-	-	-	-	-	-	-	-	-	-	0.2554	-	-	-	-	-	-	-	-
<i>Lepidaploa remotiflora</i> (Rich.) H.Rob.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1714	-
<i>Lepidaploa rufogrisea</i> (A.St.-Hil.) H.Rob.	-	-	-	-	-	-	-	-	0.1328	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lessingianthus</i> <i>argyrophyllus</i> (Less.) H.Rob.	-	0.0042	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lessingianthus</i> <i>crystalinae</i> (H.Rob.) H.Rob.	-	-	-	-	-	-	-	-	0.0457	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lessingianthus</i> <i>psilophyllus</i> (DC.) H.Rob.	-	-	0.0975	-	-	-	-	-	-	0.3465	-	-	-	-	-	-	-	-	-	-	-
<i>Lessingianthus souzae</i> (H.Rob.) H.Rob.	-	-	-	-	-	-	-	0.1359	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Mikania microcephala</i> DC.	-	-	0.5121	-	-	-	-	-	-	-	0.3147	-	-	-	-	-	-	-	-	-	-
<i>Mikania officinalis</i> Mart.	0.0084	0.2450	1.1542	0.0186	-	0.0127	-	0.0107	0.1868	-	-	-	-	-	-	-	0.0080	-	-	0.2247	-
<i>Raulinoreitzia</i> <i>leptophlebia</i> (B.L.Rob.) R.M.King & H.Rob.	0.1807	0.1309	0.2926	0.5168	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Raulinoreitzia tremula</i> (Hook. & Arn.) R.M.King & H.Rob.	-	-	-	-	-	-	-	-	-	-	0.0894	-	-	-	-	-	-	-	0.1605	-	-

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Riencourtia oblongifolia</i> Gardner	0.0084	-	0.5812	1.0569	-	-	0.2968	-	0.8426	-	-	-	-	-	-	-	-	-	-	-	-
<i>Riencourtia tenuifolia</i> Gardner	-	-	-	-	-	-	-	-	-	-	0.0194	-	-	-	-	-	-	-	-	-	-
<i>Senecio adamantinus</i> Bong.	-	-	-	0.2095	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Stevia heptachaeta</i> DC. <i>Symphiopappus</i> <i>compressus</i> (Gardner) B.L.Rob.	-	0.0591	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Trichogonia salviifolia</i> Gardner	-	-	-	-	-	-	-	-	-	-	-	-	0.3394	-	-	-	-	-	-	-	-
<i>Vernonanthura</i> <i>membranacea</i> (Gardner) H.Rob.	-	-	-	-	-	-	-	-	-	0.0318	-	-	-	-	-	-	-	-	-	-	-
<i>Vernonanthura</i> <i>polyanthes</i> (Sprengel) Vega & Dematteis	-	-	0.0975	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Vernonanthura</i> <i>rubriramea</i> (Mart. ex DC.) Loeuille & P.N.Soares	0.0630	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Vernonanthura</i> <i>westiniana</i> (Less.) H.Rob.	-	-	-	-	-	-	-	0.5596	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Wedelia bishopii</i> H.Rob.	-	-	0.0691	-	-	0.1779	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Wedelia souzae</i> H.Rob.	-	-	-	-	-	-	-	0.5143	-	-	-	-	-	-	-	-	-	-	-	-	-
Blechnaceae <i>Telmatoblechnum</i> <i>serrulatum</i> (Rich.) Perrie, D.J. Ohlsen & Brownsey	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0724	-
Boraginaceae <i>Cordia insignis</i> Cham.	-	-	-	-	-	-	-	0.2505	-	-	-	-	-	-	-	-	-	-	-	-	-
Burmanniaceae <i>Burmannia bicolor</i> Mart.	-	-	-	-	-	-	-	1.2552	-	-	-	-	-	-	-	-	-	-	-	-	-

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Burmannia capitata</i> (Walter ex J.F.Gmel.) Mart.	-	-	-	-	-	-	-	0.0107	-	0.0248	0.1282	-	-	-	-	-	-	-	0.0076	-	-
<i>Burmannia flava</i> Mart.	-	-	-	-	-	-	-	0.7355	-	0.0141	-	-	-	-	-	-	-	-	-	-	-
Calophyllaceae																					
<i>Kielmeyera speciosa</i> A.St.-Hil.	-	-	-	-	-	-	-	-	-	-	0.2953	-	-	-	-	-	-	-	-	-	-
Campanulaceae																					
<i>Lobelia brasiliensis</i> A.O.S.Vieira & G.J.Sheph.	-	-	0.1666	0.6192	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Siphocampylus</i> <i>lauroanus</i> Handro & M.Kuhlman.	-	-	-	-	-	-	-	-	0.0042	-	-	-	-	-	-	-	-	-	-	-	-
Celastraceae																					
<i>Peritassa campestris</i> (Cambess.) A.C. Sm.	-	-	0.2235	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Convolvulaceae																					
<i>Aniseia martinicensis</i> (Jacq.) Choisy	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1604	-	-	-	-
<i>Evolvulus lagopodioides</i> Meisn.	-	-	-	-	-	-	0.0044	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Evolvulus</i> <i>pterygophyllus</i> Mart.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1643	-	-
<i>Evolvulus sericeus</i> Sw.	-	-	-	-	-	-	-	-	-	-	-	-	0.0438	-	-	-	-	-	-	-	-
<i>Ipomoea geophiliifolia</i> K. Afzel.	0.0925	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ipomoea procurrens</i> Meisn.	-	0.0042	-	-	-	-	-	-	0.7596	-	-	-	-	-	-	-	-	-	-	-	-
Costaceae																					
<i>Costus spiralis</i> (Jacq.) Roscoe	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2032	0.6337	1.0413	-	-	-
Cucurbitaceae																					
<i>Cayaponia espelina</i> (Silva Manso) Cogn.	0.0210	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cyperaceae																					

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Bisboeckelera</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3417	-	-	-	-	-
<i>Bulbostylis conifera</i> (Kunth) C.B.Clarke	-	-	-	-	-	-	-	-	-	-	-	-	0.01824	-	0.0483	-	0.4612	-	-	-	-
<i>Bulbostylis consanguinea</i> (Kunth) C.B.Clarke	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0743	-	-	-	-	-
<i>Bulbostylis edwalliana</i> (Boeckeler) Prata	-	-	-	-	-	-	-	-	-	-	-	0.2341	-	-	-	-	-	-	-	-	-
<i>Bulbostylis emmerichiae</i> T.Koyama	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3201	-	0.0363	-	-	-
<i>Bulbostylis fasciculata</i> Uittien	-	-	-	-	-	0.0169	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bulbostylis hirtella</i> (Schr.) Urb.	-	0.2957	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bulbostylis jacobinae</i> (Steud.) Lindm.	-	-	-	-	-	-	-	0.7542	1.3822	0.5304	-	-	0.4999	-	-	-	-	-	-	1.7941	-
<i>Bulbostylis junciformis</i> (Kunth) C.B.Clarke	-	-	0.0081	-	-	-	-	-	0.0042	-	-	-	-	-	-	1.0035	-	-	-	-	-
<i>Bulbostylis paradoxa</i> (Spreng.) Lindm.	-	-	-	-	-	-	0.0655	-	0.7928	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bulbostylis scabra</i> (J.Presl & C.Presl) C.B.Clarke	-	-	-	-	-	-	-	0.2958	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bulbostylis sellowiana</i> (Kunth) Palla	0.2059	0.0422	0.0610	1.6249	-	-	-	1.9027	0.3819	-	-	-	-	-	0.7806	0.2062	0.1604	-	-	-	0.0160
<i>Bulbostylis vestita</i> (Kunth) C.B.Clarke	-	-	-	-	-	-	-	-	-	-	-	0.0768	-	-	-	-	-	-	-	-	-
<i>Calyptracarya glomerulata</i> (Brongn.) Urb.	-	-	-	0.2840	-	-	-	-	0.8551	-	1.1151	-	-	-	0.0991	-	-	-	0.2140	-	-
<i>Cyperus brasiliensis</i> (Kunth) Batters	-	-	-	0.0047	-	-	-	-	-	-	0.1010	-	-	-	0.0266	-	1.2032	0.1373	-	-	-
<i>Cyperus haspan</i> L.	-	-	-	-	-	-	-	0.7195	-	-	-	-	0.1496	-	0.2948	-	-	-	-	-	-
<i>Cyperus intricatus</i> Schr. ex Schult.	-	-	-	-	-	-	-	0.4131	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cyperus rigens</i> C.Presl	-	-	-	-	-	-	-	-	2.5112	-	-	-	-	-	-	-	-	-	-	-	-

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Cyperus</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0190	-
<i>Eleocharis filiculmis</i> Kunth	-	-	-	-	0.0183	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eleocharis geniculata</i> (L.) Roem. & Schult.	-	-	-	-	-	-	-	0.0266	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eleocharis minima</i> Kunth	-	-	-	-	-	-	-	0.0373	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Exochogyne amazonica</i> C.B.Clarke	-	-	-	-	-	-	-	-	0.5977	0.3182	0.1865	0.2816	0.01824	0.0907	-	0.6064	0.0401	-	0.0153	-	-
<i>Lagenocarpus rigidus</i> Nees	17.189	0.5702	-	8.6274	-	-	7.8773	-	0.2366	0.0778	1.5036	2.0263	0.0365	5.0950	9.8170	6.8152	3.0281	10.680	-	-	-
<i>Lagenocarpus verticillatus</i> (Spreng.) T.Koyama & Maguire	-	-	-	-	-	-	-	-	-	-	-	0.5633	-	-	0.2296	0.9266	-	-	-	-	-
<i>Rhynchospora albiceps</i> Kunth	-	0.0465	-	-	0.0776	-	-	-	0.8509	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rhynchospora asperula</i> (Nees) Steud.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0175	0.6434	-	-	-	-	-
<i>Rhynchospora barbata</i> (Vahl) Kunth	-	-	-	-	-	-	1.1303	-	0.0166	-	-	-	0.1642	-	-	-	2.2380	-	-	-	-
<i>Rhynchospora brasiliensis</i> Boeckeler	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0985	-	-	-	-	-
<i>Rhynchospora brevirostris</i> Griseb.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1088	-	-	-	-	-	-
<i>Rhynchospora castanea</i> T.Koyama.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1981	0.6726
<i>Rhynchospora confinis</i> (Nees) C.B. Clarke.	-	-	0.0284	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.2766	0.3352	7.9393
<i>Rhynchospora consanguinea</i> (Kunth) Boeckeler	0.2732	1.3685	0.1097	3.2964	-	-	4.6740	-	0.0540	0.0071	0.3924	-	0.1788	0.0536	1.3341	1.4375	0.8904	1.2149	-	-	-
<i>Rhynchospora elatior</i> Kunth	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.9696	-	-	-	-	-
<i>Rhynchospora emaciata</i> (Nees) Boeckeler	-	5.5288	0.0569	-	-	-	6.4327	-	-	0.3642	1.3909	1.1741	1.2406	-	10.837	0.5941	-	2.0256	-	-	-
<i>Rhynchospora exaltata</i> Kunth	-	-	-	-	-	-	-	-	-	-	0.4662	-	-	-	-	-	-	-	-	-	-

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Rhynchospora eximia</i> (Nees) Boeckeler	-	-	-	-	-	-	-	-	-	-	0.2759	-	-	-	-	-	-	-	-	-	-
<i>Rhynchospora globosa</i> (Kunth) Roem. & Schult.	2.5763	1.8753	0.8819	3.5013	7.4873	11.795	2.5530	1.9134	4.2006	0.2581	4.0096	31.253	-	1.9910	12.355	21.237	18.666	19.547	24.790	14.403	38.760
<i>Rhynchospora hirta</i> (Nees) Boeckeler	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2.6077	0.1662	1.1350	0.1813	-	-	-
<i>Rhynchospora</i> <i>holoschoenoides</i> (Rich.) Herter	-	0.6378	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rhynchospora</i> <i>marisculus</i> Lindl. & Nees	-	1.6557	-	3.4594	-	-	0.0567	-	0.5147	-	-	-	-	2.3414	-	-	0.1003	0.1321	-	-	-
<i>Rhynchospora nervosa</i> (Vahl) Boeckeler	-	-	-	-	0.2464	-	0.0044	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rhynchospora robusta</i> (Kunth) Boeckeler	-	-	-	-	0.0183	-	-	0.0160	0.8052	-	-	0.7205	-	-	-	-	-	-	-	-	-
<i>Rhynchospora rugosa</i> (Vahl) Gale	0.0210	0.6124	2.3612	2.1929	-	-	-	0.8901	-	-	-	0.0914	-	-	0.1788	0.1724	1.4599	0.4041	-	-	0.1081
<i>Rhynchospora</i> sp1	-	-	-	-	-	-	-	1.1779	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rhynchospora</i> sp2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.1685	-
<i>Rhynchospora</i> sp3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2057	0.5245
<i>Rhynchospora speciosa</i> (Kunth) Boeckeler	-	-	-	-	-	-	-	-	-	-	-	0.2963	-	-	-	-	-	-	-	-	-
<i>Rhynchospora</i> <i>spruceana</i> C.B.Clarke	-	-	0.4105	-	10.540	21.692	-	4.3598	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Rhynchospora tenella</i> (Ness) Boeckeler	-	-	-	-	-	-	-	-	-	-	-	0.3658	-	-	-	-	-	-	-	-	-
<i>Rhynchospora tenuis</i> Link	3.6900	1.6599	1.4387	20.961	0.1506	-	0.6241	1.1539	3.2085	0.4314	10.401	5.6289	-	3.0999	-	-	-	-	15.032	6.7119	3.6874
<i>Rhynchospora velutina</i> (Kunth) Boeck.	-	-	-	-	-	-	-	-	-	0.0035	-	0.0219	-	-	-	-	-	-	0.5618	0.2552	0.0400
<i>Scleria distans</i> Poir.	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3792	-	-	-	-	-	-	-
<i>Scleria hirtella</i> Sw.	-	-	-	-	0.0183	0.5252	0.0611	0.1332	0.4234	-	-	-	-	-	-	-	0.2206	0.0052	-	-	-
<i>Scleria leptostachya</i> Kunth	0.4833	0.4477	0.7356	2.9519	-	0.1059	2.0904	1.5883	2.0131	0.0990	-	-	-	-	-	-	-	-	0.0229	0.0419	0.0200

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Scleria ramosa</i> C.B.Clarke	-	-	-	-	0.0137	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Scleria reticularis</i> Michx. ex Willd.	-	-	-	-	-	-	-	-	-	-	0.0427	-	0.1058	-	-	-	-	-	-	-	-
<i>Scleria retroserrata</i> Kük.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0838	-
Dioscoreaceae																					
<i>Dioscorea</i> <i>amaranthoides</i> C.Presl	-	-	-	-	-	-	-	-	1.9799	-	-	-	-	-	-	-	-	-	-	-	-
<i>Dioscorea anomala</i> Griseb.	-	-	-	-	-	-	0.0218	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Dioscorea debilis</i> Uline ex R.Knuth	-	-	-	-	0.0593	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Droseraceae																					
<i>Drosera communis</i> A.St.-Hil.	-	-	-	-	-	-	-	-	-	0.0283	0.0777	0.0768	-	-	-	1.2498	-	-	0.0420	0.0229	0.0240
<i>Drosera intermedia</i> Hayne	-	-	-	-	-	-	-	-	-	-	0.0622	-	-	-	-	-	-	-	-	-	-
<i>Drosera montana</i> A.St.- Hil.	-	0.0676	-	0.0093	-	-	0.0611	0.4530	0.6890	0.0035	-	-	-	-	-	-	-	-	-	-	-
<i>Drosera</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2790	-	0.1081
Ericaceae																					
<i>Gaylussacia brasiliensis</i> (Spreng.) Meisn.	-	0.0676	0.0853	0.6891	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Eriocaulaceae																					
<i>Comanthera</i> <i>xeranthemoides</i> (Bong.) L.R.Parra & Giul.	-	-	-	0.2561	-	-	-	-	0.1909	-	-	4.4841	0.8466	-	4.0820	0.7757	0.2166	2.0049	-	-	-
<i>Eriocaulon aquatile</i> Köm.	-	-	-	-	-	-	-	-	-	-	-	-	0.5291	-	-	-	-	-	-	-	-
<i>Eriocaulon humboldtii</i> Kunth	-	-	-	-	-	-	-	-	-	-	2.3662	-	-	-	-	0.5633	-	-	-	-	-
<i>Eriocaulon modestum</i> Kunth	-	-	-	-	-	-	-	0.0879	-	-	-	-	-	6.5378	-	-	-	-	-	-	-
<i>Eriocaulon sellowianum</i> Kunth	-	-	-	-	-	0.0678	0.0742	-	1.7765	-	-	-	-	-	-	-	-	-	-	-	-

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Eriocaulon steyermarkii</i> Moldenke	-	-	-	-	-	-	-	-	-	-	0.0078	-	-	-	-	-	-	-	-	-	-
<i>Leiothrix crassifolia</i> (Bong.) Ruhland	-	-	-	-	-	-	-	-	-	-	-	5.7057	-	-	-	-	-	-	-	-	-
<i>Leiothrix flavescens</i> (Bong.) Ruhland	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.1851	0.0882	-	-	-	-
<i>Paepalanthus</i> <i>chiquitensis</i> Herzog	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1508	-	-	0.2293	0.3809	0.2322
<i>Paepalanthus</i> <i>distichophyllus</i> Mart.	-	-	-	-	-	-	-	-	-	-	-	1.0241	-	-	-	-	-	-	-	-	-
<i>Paepalanthus</i> <i>echinoides</i> Trovó	-	-	-	-	-	-	-	-	-	-	-	-	0.0292	-	-	-	-	-	-	-	-
<i>Paepalanthus</i> <i>elongatulus</i> Ruhland	-	-	0.8494	-	-	-	-	-	-	-	-	-	-	-	1.4912	-	-	-	-	-	-
<i>Paepalanthus elongatus</i> (Bong.) Körn.	-	-	-	-	-	0.5125	-	2.2865	0.9422	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paepalanthus</i> <i>ericaulooides</i> Ruhland	-	-	-	-	-	-	-	-	0.6932	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paepalanthus flaccidus</i> (Bong.) Kunth	-	0.0253	0.7397	0.8101	-	-	-	0.0826	1.3822	-	2.4050	-	-	-	-	-	-	-	-	-	-
<i>Paepalanthus lundii</i> Körn.	-	0.1605	-	0.2561	-	-	-	-	0.3943	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paepalanthus</i> <i>polytrichoides</i> Kunth	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.8503	-	-	-	-
<i>Paepalanthus</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0571	-
<i>Paepalanthus</i> sp2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0200
<i>Syngonanthus</i> <i>anthemiflorus</i> (Bong.) Ruhland	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1233	-	-	-	-	-	-
<i>Syngonanthus</i> <i>bisumbellatus</i> (Steud.) Ruhland	-	-	-	-	-	-	-	-	-	-	0.2292	-	-	-	-	-	-	-	-	-	-
<i>Syngonanthus</i> <i>caulescens</i> (Poir.) Ruhland	-	-	-	-	-	0.0296	-	0.1999	-	-	-	-	-	-	-	-	-	-	0.1032	-	-
<i>Syngonanthus davidsei</i> Huft	-	-	-	-	-	-	-	0.5383	-	-	-	-	-	-	-	-	-	-	0.0803	-	0.0080

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Syngonanthus densiflorus</i> (Körn.) Ruhland	-	-	0.0813	0.4377	-	-	-	-	1.4984	-	1.5114	0.3621	-	-	0.0653	-	-	-	0.6153	0.0190	-
<i>Syngonanthus densifolius</i> var. <i>brachyphyllus</i> Moldenke	-	-	-	-	-	-	-	-	-	-	0.0777	-	-	-	-	-	-	-	-	-	-
<i>Syngonanthus densus</i> (Körn.) Ruhland	-	-	-	-	-	-	-	-	0.1868	-	-	-	-	-	-	-	-	-	-	-	-
<i>Syngonanthus fischerianus</i> (Bong.) Ruhland	-	3.7633	-	-	-	-	-	-	-	-	0.0971	-	-	0.0907	2.5884	-	0.0562	-	-	-	-
<i>Syngonanthus gracilis</i> (Bong.) Ruhland	0.0168	-	0.2154	-	-	-	0.8379	-	0.7098	-	-	-	0.1824	-	-	0.1170	0.2808	-	-	-	-
<i>Syngonanthus helminthorrhizus</i> (Mart. ex Körn.) Ruhland	-	-	-	-	-	-	-	-	-	-	0.0855	-	-	0.1608	-	-	-	-	-	-	-
<i>Syngonanthus humboldtii</i> (Kunth) Ruhland	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2513	-	-	-
<i>Syngonanthus nitens</i> Ruhland	0.1219	0.0084	-	0.0838	-	0.0847	0.0655	-	0.5936	0.3253	0.7693	0.0585	0.1350	0.1154	1.8730	4.7282	0.9666	0.4093	0.4281	-	1.2692
<i>Syngonanthus verticillatus</i> (Bong.) Ruhland	-	-	-	-	-	-	-	-	-	-	-	0.1573	-	-	-	0.3848	-	-	-	-	-
<i>Syngonanthus xeranthemoides</i> (Bong.) Ruhland	-	-	-	-	-	-	0.0131	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Erythroxylaceae																					
<i>Erythroxylum campestre</i> A.St.-Hil.	-	-	-	-	-	-	0.5630	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euphorbiaceae																					
<i>Croton agoensis</i> Baill.	-	-	-	-	-	-	-	-	-	-	0.1010	-	-	-	-	-	-	-	-	-	-
<i>Croton antisiphiliticus</i> Mart.	-	-	0.4308	-	-	0.0212	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Croton glandulosus</i> L.	-	-	-	-	-	-	-	-	-	0.0354	-	-	-	-	-	-	-	-	-	-	-
<i>Croton junceus</i> Baill.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1642

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Croton pedicellatus</i> Kunth.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1601
<i>Dalechampia linearis</i> Baill.	-	-	-	-	0.0091	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Euphorbia cordeiroae</i> P. Carillo & V.W. Steinm.	-	-	-	-	-	-	-	0.1146	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Euphorbia elodes</i> Boiss. <i>Euphorbia hypericifolia</i> L.	-	-	-	-	-	-	0.0480	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Euphorbia</i> <i>potentilloides</i> Boiss.	-	0.0338	-	0.0931	-	-	-	-	-	-	0.0350	-	0.5984	-	-	-	-	-	-	-	-
<i>Microstachys bidentata</i> (Mart.& Zucc.) Esser	0.0462	-	-	-	-	0.0042	-	0.0853	-	-	0.2797	-	0.5692	-	-	-	0.5856	-	-	-	-
<i>Sebastiania</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0535	0.1333	0.1521
Fabaceae																					
<i>Aeschynomene</i> <i>genistoides</i> (Taub.) Rudd	-	-	-	-	-	0.0720	1.0779	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Aeschynomene</i> <i>paniculata</i> Willd. ex Vogel	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2493	0.1644	-	-	-	-
<i>Bauhinia curvula</i> Benth. <i>Calliandra dysantha</i> Benth.	-	-	-	-	-	0.7157	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Calopogonium</i> <i>mucunoides</i> Desv.	-	0.1478	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chamaecrista</i> <i>brachyrachis</i> (Harms) H.S.Irwin & Barneby	-	-	0.0569	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chamaecrista conferta</i> (Benth.) H.S.Irwin & Barneby	-	-	-	-	0.0046	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chamaecrista</i> <i>cotinifolia</i> (G.Don) H.S.Irwin & Barneby	-	-	-	-	-	0.0466	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chamaecrista desvauxii</i> (Collad.) Killip	-	-	-	-	-	-	-	1.7295	0.0166	-	0.0427	0.0073	1.3976	0.0907	0.0556	-	0.4572	0.3419	-	-	0.0641

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Chamaecrista desvauxii</i> var. <i>mollissima</i> (Benth.) H.S.Irwin & Barneby	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1790	-
<i>Chamaecrista diphylla</i> (L.) Greene	-	-	-	-	-	-	0.0480	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chamaecrista nictitans</i> (L.) Moench	-	-	-	-	-	-	-	-	0.9049	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chamaecrista ramosa</i> (Vogel) H.S.Irwin & Barneby	-	-	-	-	-	-	-	-	-	-	-	-	1.3355	-	-	-	-	-	-	-	-
<i>Chamaecrista repens</i> var. <i>multijuga</i> (Benth.) H.S.Irwin & Barneby	-	-	-	-	-	-	-	-	-	-	-	-	0.8976	-	-	-	-	-	-	-	-
<i>Collaea aschersoniana</i> (Taub.) Burkart	-	-	-	-	1.1452	0.0085	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Crotalaria vespertilio</i> Benth.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1401
<i>Desmodium</i> <i>platycarpum</i> Benth.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0190	-
<i>Eriosema congestum</i> Benth.	-	-	-	-	0.0365	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eriosema crinitum</i> (Kunth) G.Don	-	-	0.0163	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2599	0.2247	-
<i>Eriosema longifolium</i> Benth.	-	-	-	-	-	-	-	-	0.6558	-	-	-	-	-	-	-	-	-	-	-	-
<i>Galactia stereophylla</i> Harms	-	-	0.0203	-	-	-	-	0.0107	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Mimosa clausenii</i> Benth.	-	-	-	-	-	0.6437	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Mimosa pumilio</i> Barneby	-	-	-	-	-	1.6305	0.0611	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Mimosa pyrenea</i> Taub.	-	-	-	-	-	-	-	-	-	0.0248	-	-	-	-	-	-	-	-	-	-	-
<i>Mimosa sensitiva</i> L.	-	-	-	-	-	-	-	2.5610	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Mimosa</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	0.0876	-	-	-	-	-	-	-	-
<i>Stylosanthes capitata</i> Vogel	-	-	-	-	-	-	-	-	-	-	-	-	0.2883	-	-	-	-	-	-	-	-

Family/ Species	Relative cover (%) of the sites																					
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3	
<i>Stylosanthes scabra</i> Vogel	-	-	-	-	-	-	-	-	0.4773	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Stylosanthes</i> sp1	-	-	-	-	-	-	-	-	-	0.0283	-	-	-	-	-	-	-	-	-	-	-	
Gentianaceae																						
<i>Chelonanthus alatus</i> (Aubl.) Pulle	-	-	-	-	0.0046	-	-	-	0.0291	0.0283	-	-	-	-	-	-	-	-	-	-	-	
<i>Chelonanthus</i> <i>matogrossensis</i> (J.G.M.Pers. & Maas) Struwe & V.A.Albert.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3631	-	
<i>Curtia tenuifolia</i> (Aubl.) Knobl.	-	-	0.0691	-	-	-	-	1.1033	0.3902	0.0460	0.0233	0.0146	-	-	0.0048	0.0154	-	-	0.0268	-	0.0400	
<i>Deianira nervosa</i> Cham. & Schlttdl.	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0165	-	-	-	-	-	-	-	
<i>Schultesia gracilis</i> Mart.	-	-	-	-	-	-	-	0.2585	-	0.0035	-	-	-	-	-	-	-	-	-	-	-	
<i>Schultesia guianensis</i> (Aubl.) Malme	-	-	-	-	-	-	-	-	0.9132	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Schultesia heterophylla</i> Miq.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1112	-	-	-	-	-	-	
<i>Schultesia pohliana</i> Progel	-	-	-	-	-	-	-	-	0.5022	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Schultesia</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0688	-	
<i>Schultesia subcrenata</i> Klotzsch & Griseb.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0440	
<i>Tetrapollinia</i> <i>caerulescens</i> (Aubl.) Maguire & B.M.Boom	-	-	-	-	-	-	-	0.0373	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Sinningia allagophylla</i> (Mart.) Wiehler	-	-	-	0.0233	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Sinningia elatior</i> (Kunth) Chautems	-	-	0.4308	-	-	-	-	-	1.3448	-	-	-	-	-	-	-	-	-	-	0.0803	0.1867	0.0160
Gleicheniaceae																						
<i>Dicranopteris flexuosa</i> (Schrad.) Underw.	-	-	-	-	-	-	-	-	-	-	0.1632	-	-	-	-	-	-	-	-	-	-	
Hypericaceae																						
<i>Vismia</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2255	0.1105	-

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
Iridaceae																					
<i>Deluciris violacea</i> (Klatt) A.Gil & Lovo	-	-	-	-	-	-	-	-	-	-	-	-	-	2.3084	-	-	-	-	-	-	-
<i>Pseudotrimezia</i> <i>cathartica</i> (Klatt) Ravenna	-	-	-	-	-	-	0.0524	-	0.0249	0.3395	-	-	-	-	-	-	-	-	-	-	-
<i>Pseudotrimezia</i> <i>juncifolia</i> (Klatt) Lovo & A.Gil	-	-	-	-	-	-	0.5019	-	2.5278	0.1945	-	0.6803	-	-	-	0.0739	0.1083	0.0777	-	-	-
<i>Sisyrrinchium restioides</i> Spreng.	-	0.0169	0.0853	-	-	-	-	-	0.1038	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sisyrrinchium vaginatum</i> Spreng.	0.0420	0.1478	0.0894	0.2049	-	0.2033	0.0044	-	0.0042	0.1273	0.0311	0.0183	0.1861	-	-	0.0062	0.0241	-	-	0.0076	-
Juncaceae																					
<i>Juncus effusus</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8.3766	-	-	-	-	-	-
Lamiaceae																					
<i>Cantinoa subrotunda</i> (Pohl ex Benth.) Harley & J.F.B.Pastore	-	-	-	0.7636	-	-	-	-	1.4445	-	-	-	-	-	-	-	-	-	-	1.6342	-
<i>Hyptis campestris</i> Harley & J.F.B. Pastore	-	-	-	-	0.0228	0.0847	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hyptis conferta</i> Pohl ex Benth.	-	-	-	-	0.8852	0.2795	-	-	-	0.0672	-	-	-	-	-	-	-	-	-	-	-
<i>Hyptis crenata</i> Pohl ex Benth.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.2417	-
<i>Hyptis hamatidens</i> Epling & C.D.Jativa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1529	-	-
<i>Hyptis lantanifolia</i> Poit.	-	-	-	-	-	-	-	0.5809	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hyptis lanuginosa</i> Glaz. ex Epling	-	-	-	-	-	-	0.0262	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hyptis linarioides</i> Pohl ex Benth.	0.0336	0.3717	0.0935	0.0838	0.2783	0.0508	0.2968	-	0.0872	0.4066	-	-	-	-	-	-	1.9853	-	-	-	-
<i>Hyptis lutescens</i> Pohl ex Benth.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1401
<i>Hyptis nudicaulis</i> Benth.	-	-	-	-	-	-	0.0480	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Hyptis rotundifolia</i> Benth.	-	-	-	-	-	-	0.3404	-	0.1868	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hyptis</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	0.2335	-	-	-	-	-	-	-	-
<i>Hyptis</i> sp2	-	-	-	-	-	-	-	-	-	-	-	-	0.0693	-	-	-	-	-	-	-	-
<i>Hyptis velutina</i> Pohl ex Benth.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2714	0.8647	0.7687
<i>Marsypianthes</i> <i>burchellii</i> Epling	-	-	-	-	-	-	-	0.5383	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cassyntha filiformis</i> L.	-	0.2957	0.2438	0.1071	-	-	-	0.0320	-	-	-	-	0.3284	-	0.5220	0.5048	0.0321	0.1451	-	-	-
Lentibulariaceae																					
Lentibulariaceae sp1	-	-	-	-	-	-	-	-	-	0.0106	-	-	-	-	-	-	-	-	-	-	-
<i>Utricularia amethystina</i> Salzm. ex A.St.-Hil. & Girard	-	-	-	-	-	-	0.3448	-	0.0125	-	-	-	-	-	-	-	-	-	-	-	-
<i>Utricularia hispida</i> Lam.	-	-	-	0.0093	-	-	-	-	-	-	0.1438	0.0037	0.0292	-	-	-	-	-	-	-	-
<i>Utricularia neottiioides</i> A.St.-Hil. & Girard	-	0.0253	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Utricularia</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0038	-	-
<i>Utricularia</i> sp2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0076	-	-
<i>Utricularia</i> sp3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0497	-	-
<i>Utricularia subulata</i> L.	-	-	-	-	-	-	-	0.1306	-	-	-	0.0037	-	-	-	-	-	-	-	-	-
Loganiaceae																					
<i>Spigelia riedeliana</i> (Progel) E.F.Guim. & Fontella	-	-	-	-	-	-	-	-	-	-	-	0.0805	-	-	-	-	-	-	-	-	-
Lycopodiaceae																					
<i>Lycopodiella</i> <i>alopeuroides</i> (L.) Cranfill	-	-	-	-	-	-	-	0.0160	-	0.0990	-	-	-	-	-	-	-	-	-	-	-
<i>Palhinhaea cernua</i> (L.) Franco & Vasc.	-	-	-	-	-	-	-	-	-	-	0.5867	-	0.7444	0.1113	-	-	-	-	-	-	-
Lythraceae																					
<i>Cuphea antisiphilitica</i> Kunth	-	-	-	-	-	0.0042	-	-	-	-	-	-	0.4233	-	7.9924	1.4006	1.4920	5.2325	-	-	-

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Cuphea ferruginea</i> Pohl ex Koehne	-	-	-	-	-	-	-	-	-	0.0071	-	-	-	-	-	-	-	-	-	-	-
<i>Cuphea linarioides</i> Cham. & Schldl.	-	0.0084	-	-	-	-	-	-	-	-	0.7887	-	-	-	-	-	-	-	-	-	-
<i>Cuphea pohlii</i> Lourteig	-	-	-	0.1397	-	-	-	-	0.3902	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cuphea spermacoce</i> A.St.-Hil.	-	0.0042	0.0488	-	-	-	-	0.0187	-	-	-	-	-	0.0247	-	-	-	-	-	-	-
<i>Cuphea spermacoce</i> A.St.-Hil. var. spermacoce	-	-	-	-	-	-	0.0044	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cuphea spermacoce</i> var. <i>erectifolia</i> (Koehne) T.B.Cavalc. & S.A.Graham	-	-	-	-	-	-	-	-	1.8180	-	-	-	-	-	-	-	-	-	-	-	-
<i>Diplusodon argenteus</i> Lourteig	-	-	-	-	-	-	0.0262	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Diplusodon</i> <i>ramosissimus</i> Pohl	-	-	-	-	0.0913	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Diplusodon sessiliflorus</i> Koehne	-	-	-	-	-	-	-	0.1892	-	-	-	-	-	-	-	-	-	-	-	-	-
Malpighiaceae																					
<i>Byrsonima subterranea</i> Brade & Markgr.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.4533	-	-	-
<i>Byrsonima umbellata</i> Mart. ex A.Juss.	-	-	-	-	-	-	-	-	-	-	0.4274	-	0.4123	-	-	-	-	-	0.2905	-	-
<i>Heteropterys pannosa</i> Griseb.	-	-	-	-	-	0.1821	-	-	0.6932	-	-	-	-	-	-	-	-	-	-	-	-
Malpighiaceae sp1	-	-	-	-	-	-	-	-	-	0.0106	-	-	-	-	-	-	-	-	-	-	-
<i>Tetrapteryx ambigua</i> (A.Juss.) Nied.	-	-	0.0244	-	-	-	0.0916	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Malvaceae																					
<i>Byttneria</i> <i>melastomaefolia</i> A.St.- Hil.	-	-	-	-	-	0.0339	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Byttneria palustris</i> Cristóbal	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0153	0.0609	0.2442

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Melochia villosa</i> (Mill.) Fawc. & Rendle.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.4723	0.1441
<i>Pavonia rosa- campestris</i> A.St.-Hil.	-	-	-	-	-	0.0042	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Peltaea lasiantha</i> Krapov. & Cristóbal	-	-	0.0122	-	-	-	-	0.0666	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Waltheria indica</i> L.	-	-	-	-	-	0.0339	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Melastomataceae																					
<i>Acisanthera uniflora</i> (Vahl) Gleason	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2981	0.0533	0.5805
<i>Cambessedesia espora</i> (A.St.-Hil. ex Bonpl.) DC.	-	0.0042	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cambessedesia hilariana</i> (Kunth) DC.	-	-	-	-	-	-	-	1.1166	0.5687	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chaetogastra gracilis</i> (Bonpl.) DC.	0.2606	0.6082	-	0.1955	-	-	-	0.4637	0.1577	-	-	-	-	-	-	-	-	-	-	-	-
<i>Chaetostoma armatum</i> (Spreng.) Cogn.	-	-	-	-	-	-	-	-	-	0.2157	-	-	-	-	-	-	-	-	-	-	-
<i>Desmoscelis villosa</i> (Aubl.) Naudin	0.0925	0.0634	0.0081	0.0652	-	-	-	-	0.0166	-	-	0.0073	0.0292	0.2886	-	-	0.0762	0.3005	-	0.0267	-
<i>Fritzschia lanceiflora</i> (Mart. & Schrank ex DC.) M.J.R.Rocha & P.J.F.Guim.	-	0.2196	-	-	-	-	-	-	0.0166	-	-	-	-	-	-	-	-	-	-	-	-
<i>Lavoisiera imbricata</i> (Thunb.) DC.	-	0.1732	1.7475	0.1164	-	-	-	0.0133	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Leandra aurea</i> (Cham.) Cogn.	-	-	0.0366	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Leandra polystachya</i> (Naudin) Cogn.	-	-	0.1341	0.0372	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Macairea radula</i> (Bonpl.) DC.	-	-	0.4389	-	-	-	-	-	-	0.0071	1.3055	-	0.7298	1.5664	-	-	-	-	-	0.6095	-
<i>Miconia albicans</i> (Sw.) Triana	-	-	-	-	-	-	-	-	-	-	-	-	0.6386	-	-	-	-	-	-	-	-

Family/ Species	Relative cover (%) of the sites																					
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3	
<i>Miconia chamissois</i> Naudin	-	-	0.4633	0.1630	0.2281	-	-	0.0133	0.4856	-	-	-	-	-	0.0411	-	-	0.2746	0.8256	0.2857	0.1201	
<i>Microlicia confertiflora</i> Naudin	-	-	-	-	-	-	-	-	0.4109	-	-	1.1667	-	-	-	-	-	-	-	-	-	
<i>Microlicia euphorbioides</i> Mart.	-	0.0042	0.0732	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Microlicia fasciculata</i> Mart. ex Naudin	-	-	0.0284	-	0.1916	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Microlicia insignis</i> Schltdl.	-	-	-	-	-	-	0.0131	-	-	-	-	-	-	-	-	-	-	-	-	1.9694	0.0561	
<i>Microlicia polystemma</i> Naudin	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2362	0.1041	
<i>Microlicia psammophila</i> Wurdack	-	-	-	-	-	-	0.8336	0.2425	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Microlicia ramosa</i> Pilg.	-	0.1605	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Microlicia serpyllifolia</i> D.Don	0.5001	0.5153	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2293	0.0876	1.3412
<i>Microlicia</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	0.0730	-	-	-	-	-	-	-	-	
<i>Microlicia</i> sp2	-	-	-	-	-	-	-	-	-	-	-	-	0.0365	-	-	-	-	-	-	-	-	
<i>Microlicia</i> sp3	-	-	-	-	-	-	-	1.7055	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Microlicia viminalis</i> (DC.) Triana	-	-	-	-	-	-	-	-	-	-	-	-	0.2153	-	-	0.4156	-	0.6139	-	-	-	
<i>Noterophila genliseoides</i> (Hoehne) Kriebel & M.J.R.Rocha	-	-	-	-	-	-	-	-	0.6683	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Noterophila limnobios</i> (DC.) Mart.	-	0.0507	-	-	-	-	-	-	0.0083	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Ossaea congestiflora</i> (Naudin) Cogn.	-	-	0.3617	0.0885	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Pterolepis repanda</i> (DC.) Triana	-	-	-	-	-	0.0424	-	-	-	-	-	-	-	-	-	-	0.0080	-	-	-	-	
<i>Pterolepis riedeliana</i> Cogn.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3440	0.1257	0.0440
<i>Rhynchanthera cordata</i> DC.	-	-	-	-	-	-	-	0.2958	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Rhynchanthera grandiflora</i> (Aubl.) DC.	-	0.5237	-	-	-	-	-	-	-	-	-	-	0.5838	-	-	-	-	-	-	-	-	

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Rhynchanthera ursina</i> Naudin	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0268	1.1390	-
<i>Siphanthera cordata</i> Pohl ex DC.	-	-	-	-	-	-	-	-	0.0540	-	0.0505	-	-	-	-	-	-	-	-	-	-
<i>Siphanthera subtilis</i> Pohl ex DC.	-	-	-	-	-	-	-	-	0.7554	-	-	-	-	-	-	-	-	-	0.0497	0.2438	0.4044
<i>Tibouchina aegopogon</i> (Naudin) Cogn.	-	-	-	-	-	-	-	-	0.2490	-	-	-	-	-	-	-	-	-	-	-	-
<i>Tococa nitens</i> (Benth.) Triana	-	-	-	-	-	-	-	-	-	-	0.7887	-	-	-	-	0.2986	0.3209	0.1088	-	-	-
<i>Trembleya parviflora</i> (D.Don) Cogn.	4.5390	0.0549	1.8532	0.6379	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Trembleya phlogiformis</i> Mart. & Schrank ex DC.	0.4539	-	0.0122	-	-	-	-	-	0.0042	0.0106	-	-	-	0.0577	-	-	-	-	-	-	-
Menispermaceae																					
<i>Cissampelos ovalifolia</i> DC.	-	-	0.0081	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Myrtaceae																					
<i>Campomanesia</i> <i>pubescens</i> (Mart. ex DC.) O.Berg	-	-	-	-	-	-	-	1.6229	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Eugenia involucrata</i> DC.	-	-	0.0163	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Myrcia depauperata</i> Glaz. ex P.O.Rosa & Proença	-	-	-	-	-	-	-	-	-	0.4950	-	-	-	-	-	-	-	-	-	-	-
<i>Myrcia guianensis</i> (Aubl.) DC.	-	-	0.0569	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Myrcia linearifolia</i> Cambess.	-	-	-	-	-	0.0169	0.2706	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Myrcia variabilis</i> DC.	-	-	0.0366	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Psidium firmum</i> O.Berg	-	-	0.0163	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ochnaceae																					
<i>Ouratea lanceolata</i> (Pohl) Engl.	-	-	-	-	-	0.0169	-	-	-	0.0495	-	-	-	-	-	-	-	-	-	-	-
<i>Sauvagesia linearifolia</i> A.St.-Hil.	-	-	0.0122	-	-	-	-	2.4091	0.2241	0.0849	-	0.0037	-	-	-	-	0.1364	-	0.0268	0.3428	-

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Sauvagesia racemosa</i> A.St.-Hil.	0.0504	-	0.0244	0.0140	-	-	-	-	-	-	0.2836	0.0293	-	-	-	-	-	-	-	-	-
<i>Sauvagesia tenella</i> Lam.	-	-	-	-	-	-	-	-	-	0.0106	-	-	-	-	-	-	-	-	-	-	-
Onagraceae																					
<i>Ludwigia nervosa</i> (Poir.) H.Hara	0.0210	0.0296	-	0.0093	-	0.3896	-	0.4717	0.2989	-	-	0.0183	-	-	0.6163	-	0.2767	-	0.3898	0.5904	0.3163
Orchidaceae																					
<i>Cleistes</i> sp1	-	-	-	0.0093	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cleistes</i> sp2	-	-	-	-	-	-	-	-	-	0.0071	-	-	-	-	-	-	-	-	-	-	-
<i>Cyrtopodium fowliei</i> L.C.Menezes	-	-	-	-	-	-	-	0.0187	-	-	-	-	-	-	-	0.0554	-	-	-	-	-
<i>Eltroplectris</i> sp1	-	-	-	-	-	-	0.1571	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Epistephium laxiflorum</i> Barb.Rodr.	-	-	-	-	-	-	-	-	-	0.0636	-	-	-	-	-	-	-	-	-	-	-
<i>Habenaria magniscutata</i> Catling	-	-	-	-	-	-	0.0131	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Habenaria schwackei</i> Barb.Rodr.	-	-	-	-	-	-	0.0044	-	-	-	-	-	-	-	-	-	-	0.0777	-	-	-
<i>Habenaria secundiflora</i> Barb.Rodr.	-	-	-	-	-	-	-	-	-	0.0071	-	-	-	-	-	-	-	-	-	-	-
Orchidaceae sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1796	-	0.1001
Orchidaceae sp2	-	-	-	-	-	-	-	-	-	0.0035	-	-	-	-	-	-	-	-	-	-	-
Orobanchaceae																					
<i>Buchnera juncea</i> Cham. & Schltdl.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0382	-	-
<i>Buchnera lavandulacea</i> Cham. & Schltdl.	-	-	-	-	-	-	-	0.4850	-	-	0.0466	-	-	-	-	-	-	-	-	-	-
<i>Buchnera palustris</i> (Aubl.) Spreng.	-	-	-	-	-	-	-	-	-	0.0636	-	-	-	-	-	-	-	-	-	-	-
<i>Esterhazyia macrodonta</i> (Cham.) Benth.	-	-	-	-	-	-	-	-	-	-	0.1438	-	-	-	-	-	-	-	-	-	-
<i>Melasma stricta</i> (Benth.) Hassl.	-	-	0.0041	-	-	-	-	-	-	0.0318	-	-	-	-	-	-	-	-	-	-	-
Oxalidaceae																					

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Oxalis densifolia</i> Mart. & Zucc. ex Zucc.	-	-	0.0244	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Passifloraceae																					
<i>Passiflora villosa</i> Vell.	-	-	-	-	-	-	-	0.0826	-	-	-	-	-	-	-	-	-	-	-	-	-
Phyllanthaceae																					
<i>Phyllanthus niruri</i> L.	-	-	-	-	-	-	-	-	-	0.2263	-	-	-	-	0.2320	-	0.1083	0.2513	-	-	-
<i>Phyllanthus</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3466	0.1802
Piperaceae																					
<i>Piper fuliginum</i> Kunth	-	-	-	-	0.0411	-	-	-	-	-	-	-	-	-	-	-	0.0802	-	0.0764	-	0.0400
Poaceae																					
<i>Agenium leptocladum</i> (Hack.) Clayton	-	-	0.3942	-	-	-	-	-	1.1083	-	-	-	-	-	-	-	-	-	-	-	-
<i>Agenium villosum</i> (Nees) Pilg.	-	-	-	-	-	2.0286	-	-	-	-	-	-	-	-	-	0.5602	14.126	0.9999	-	-	-
<i>Andropogon bicornis</i> L.	-	-	4.9988	-	4.3254	3.8159	0.0218	-	-	0.0990	-	-	-	-	0.3625	-	-	-	-	-	-
<i>Andropogon carinatus</i> Nees	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5124	-	-	0.0855	-	-	-
<i>Andropogon fastigiatus</i> Sw.	-	-	-	-	-	-	-	-	-	0.6541	-	-	-	-	-	-	-	-	-	-	-
<i>Andropogon gayanus</i> Kunth	-	-	-	-	-	-	-	-	-	-	1.0840	-	-	-	-	-	-	-	-	-	-
<i>Andropogon hypogynus</i> Hack.	-	-	-	-	-	-	-	-	-	-	-	-	2.7951	-	-	-	-	-	-	-	-
<i>Andropogon lateralis</i> Nees	1.2608	2.2132	2.0523	0.0838	-	-	-	-	-	-	-	-	-	-	0.1595	-	4.1912	-	3.2258	6.8795	4.8645
<i>Andropogon leucostachyus</i> Kunth	1.2608	0.7941	6.6691	2.6958	-	-	0.4277	0.6902	1.4154	-	2.0204	0.0073	0.1423	-	-	-	-	0.6838	1.7734	7.7023	7.5149
<i>Andropogon macrothrix</i> Trin.	-	-	-	-	-	-	-	-	0.3445	-	0.0233	-	-	-	-	-	-	-	-	-	0.3483
<i>Andropogon selloanus</i> (Hack.) Hack.	-	-	-	-	-	-	-	-	-	1.0608	-	-	-	0.6595	0.2779	-	-	-	-	-	-
<i>Andropogon</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10.461	6.6319	4.6563
<i>Andropogon virgatus</i> Desv.	2.7486	11.594	7.4169	4.3160	14.441	1.2197	11.692	6.6622	6.0144	-	0.2292	0.6584	2.4448	0.1031	5.9163	-	-	0.6372	-	-	-

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Aristida capillacea</i> Lam.	-	-	-	-	-	-	6.4851	0.1306	3.1172	4.5402	-	-	-	-	-	-	-	-	-	-	-
<i>Aristida riparia</i> Trin.	-	-	-	-	-	0.1186	0.5630	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Aristida setifolia</i> Kunth	-	-	-	-	-	-	-	-	-	0.0460	-	-	-	-	-	-	-	-	-	-	-
<i>Aristida torta</i> (Nees) Kunth	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.1971
<i>Arthropogon villosus</i> Nees	-	-	-	-	7.9162	3.1679	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Arundinella hispidula</i> (Humb. & Bonpl. ex Willd.) Kuntze	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.0472	1.4285	0.4644
<i>Axonopus aureus</i> P. Beauv.	0.3278	1.2713	0.0163	-	0.1369	0.1016	-	0.5756	0.0249	0.1414	-	1.4374	-	-	-	-	-	-	-	-	-
<i>Axonopus brasiliensis</i> (Spreng.) Kuhlmann	0.5211	4.7136	-	2.5095	0.1004	0.1567	0.4844	0.0933	0.0249	6.2586	1.5852	-	0.4087	-	-	-	-	0.0881	0.0917	0.0419	0.3283
<i>Axonopus cf. polydactylus</i> (Steud.) Dedecca	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.4780	-
<i>Axonopus comans</i> (Trin. ex Döll) Kuhlmann	11.448	-	-	-	-	-	0.1004	-	-	-	-	7.4650	-	-	0.6018	0.0585	-	1.0517	-	-	-
<i>Axonopus fastigiatus</i> (Nees ex Trin.) Kuhlmann	-	-	-	-	-	2.1430	-	-	0.4151	-	-	-	-	-	-	0.4525	-	-	-	-	-
<i>Axonopus pellitus</i> (Nees ex Trin.) Hitchc. & Chase	-	-	5.9742	-	-	-	-	1.2232	-	-	-	-	-	-	-	-	3.1805	-	-	-	-
<i>Axonopus siccus</i> (Nees) Kuhlmann	-	-	-	-	-	-	-	-	-	-	-	-	0.9706	-	-	-	-	-	-	-	-
<i>Cenchrus ciliaris</i> L.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2400	-
<i>Cenchrus polystachios</i> (L.) Morrone	-	-	-	-	-	-	-	-	-	-	0.3458	-	-	-	-	-	-	-	-	-	-
<i>Coleataenia caricoides</i> (Nees ex Trin.) Soreng	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.2852
<i>Coleataenia stenodes</i> (Griseb.) Soreng	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5085
<i>Echinolaena inflexa</i> (Poir.) Chase	-	2.7581	1.8695	0.4796	-	-	0.3186	0.6023	1.2328	11.842	-	-	-	-	0.5341	0.1478	0.0401	0.0544	-	-	-

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Elionurus muticus</i> (Spreng.) Kuntze	-	-	-	-	-	-	-	-	-	-	0.0272	-	-	-	-	-	-	-	-	-	-
<i>Eriochrysis cayemensis</i> P. Beauv.	-	0.0211	-	-	-	-	-	-	-	-	0.1943	-	-	-	-	-	-	-	-	-	-
<i>Eriochrysis filiformis</i> (Hack.) Filg.	-	-	-	-	-	-	-	-	-	-	0.0233	-	-	-	-	-	-	-	-	-	-
<i>Gymnopogon fastigiatus</i> Nees	-	-	-	Nees	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0229	-	-
<i>Gymnopogon foliosus</i> (Willd.) Nees	-	-	-	-	-	-	-	-	-	0.1025	-	-	-	-	-	-	-	3.8363	0.2943	0.6361	-
<i>Hildaea pallens</i> var. <i>major</i> (Nees) C.Silva & R.P.Oliveira	-	-	-	-	-	-	-	1.6309	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Hyparrhenia bracteata</i> (Humb. & Bonpl. ex Willd.) Stapf	-	-	0.8250	0.8660	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Ichnanthus</i> sp1	-	-	-	-	-	-	-	-	-	0.0248	-	-	-	-	-	-	-	-	-	-	-
<i>Lasiacis ligulata</i> Hitchc. & Chase	-	-	-	-	-	-	-	0.0213	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Melinis minutiflora</i> P.Beauv.	-	-	-	-	-	-	-	0.5037	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Mesosetum</i> <i>elytrochaetum</i> (Hack.) Swallen	-	-	-	-	-	-	-	-	0.1660	-	-	-	-	-	-	-	-	-	-	-	-
<i>Mesosetum loliiforme</i> (Hochst.) Chase	-	-	-	-	-	-	1.8548	-	1.6437	0.1980	-	0.2048	-	-	-	-	-	-	-	-	-
<i>Mesosetum penicillatum</i> Mez	-	-	-	-	-	-	-	1.4870	-	-	-	-	-	-	1.5274	-	-	-	-	-	-
<i>Mesosetum</i> sp1	-	-	-	-	-	-	-	1.8468	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Oedochloa camporum</i> (Swallen) C.Silva & R.P.Oliveira	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	3.1264	4.5406	9.9612
<i>Oedochloa procurrens</i> (Nees ex Trin.) C.Silva & R.P.Oliveira	-	1.7866	0.1422	-	0.1871	4.8026	1.7544	2.0200	1.0418	-	-	-	-	-	-	0.0185	-	0.0803	-	-	-
<i>Otachyrium seminudum</i> Hack. ex Send. & Soderstr.	-	0.4139	-	0.3678	-	-	-	13.698	-	-	-	-	-	-	-	-	-	-	-	-	-

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Otachyrium versicolor</i> (Döll) Henrard	-	-	-	-	0.0091	-	-	-	-	-	-	-	-	38.303	-	-	-	-	-	-	-
<i>Panicum campestre</i> Nees ex Trin.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	5.8240	-	0.0259	-	-	-
<i>Panicum cervicatum</i> Chase	-	-	-	-	1.4555	-	-	-	0.7098	-	-	-	-	-	-	-	-	-	-	-	-
<i>Panicum olyroides</i> Kunth	-	-	0.0732	-	-	-	-	0.1119	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Panicum rudgei</i> Roem. & Schult.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.6192	-	-
<i>Paspalum</i> <i>approximatum</i> Döll	-	-	-	-	-	-	-	-	-	-	0.8198	-	-	-	-	-	0.0160	-	-	-	-
<i>Paspalum decumbens</i> Sw.	-	-	-	-	1.1133	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paspalum dedecae</i> Quarín	-	5.3725	10.380	-	0.0183	2.0710	-	0.9647	-	-	-	1.7556	-	-	4.3454	22.816	12.209	10.209	-	-	-
<i>Paspalum ellipticum</i> Döll	-	-	-	1.8577	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paspalum foliiforme</i> S.Denham	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5925
<i>Paspalum</i> <i>gardnerianum</i> Nees	-	-	-	-	-	-	-	-	2.7312	-	-	-	-	-	-	-	-	-	0.3822	2.0075	1.8737
<i>Paspalum geminiflorum</i> Steud.	18.870	-	0.3617	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paspalum glaucescens</i> Hack.	2.1266	-	3.2716	-	0.4563	-	-	-	3.3206	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paspalum hyalinum</i> Nees ex Trin.	-	0.3717	0.7112	-	-	-	0.0742	-	2.1667	-	-	0.1865	0.6678	-	-	-	3.9626	-	-	-	-
<i>Paspalum imbricatum</i> Filg.	-	-	-	0.8567	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paspalum lanciflorum</i> Nees ex Steud.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1203	-	-	-	-
<i>Paspalum lineare</i> Trin.	26.137	29.891	21.674	20.891	41.247	25.902	20.804	11.083	8.6211	41.378	1.8805	15.830	7.2213	14.621	0.2586	2.5211	10.949	7.7399	16.767	16.372	1.2091
<i>Paspalum maculosum</i> Trin.	-	1.4910	-	1.0057	-	-	1.1347	-	1.2992	13.879	-	-	19.7665	-	-	-	0.6618	0.1787	-	-	-
<i>Paspalum multicaule</i> Poir.	-	-	-	-	-	-	-	-	0.7845	-	1.0529	-	0.9232	-	-	-	-	-	-	-	0.1601
<i>Paspalum plicatulum</i> Michx.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.3773

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Paspalum polyphyllum</i> Nees	-	-	-	0.1071	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2487	-	-	-
<i>Paspalum</i> sp1	-	-	-	-	-	-	-	0.0240	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paspalum trichostomum</i> Hack.	-	-	-	-	-	3.2738	-	-	-	-	7.3471	-	5.0757	-	-	-	-	-	-	-	-
Poaceae sp1	-	-	-	-	-	-	-	-	-	-	0.5206	-	-	-	-	-	-	-	-	-	-
Poaceae sp2	-	-	-	-	-	-	-	-	-	7.2628	-	-	-	-	-	-	-	-	-	-	-
Poaceae sp3	-	-	-	-	-	-	-	-	-	1.0466	-	-	-	-	-	-	-	-	-	-	-
Poaceae sp4	-	-	-	-	-	-	-	-	-	0.3395	-	-	-	-	-	-	-	-	-	-	-
Poaceae sp5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4.9304	0.7390	0.6566
Poaceae sp6	-	-	-	-	-	-	-	-	-	0.0035	-	-	-	-	-	-	-	-	-	-	-
<i>Rugoloa pilosa</i> (Sw.) Zuloaga	-	-	-	-	0.1871	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Saccharum</i> <i>angustifolium</i> (Nees) Trin.	-	-	-	-	-	-	0.7506	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Saccharum asperum</i> (Nees) Steud.	-	-	-	-	-	-	-	-	0.2864	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sacciolepis myuros</i> (Lam.) Chase	-	-	-	-	-	-	-	-	0.4109	-	-	-	-	-	-	-	-	-	0.3555	0.1257	-
<i>Schizachyrium</i> <i>brevifolium</i> (Sw.) Nees ex Buse	-	-	-	-	-	-	-	0.3971	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Schizachyrium</i> <i>condensatum</i> (Kunth) Nees	-	-	-	2.6213	-	-	-	-	0.1951	-	-	-	-	-	-	-	-	-	-	-	-
<i>Schizachyrium</i> <i>microstachyum</i> (Desv. ex Ham.) Roseng., B.R.Arrill. & Izag.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.9096	-	-
<i>Schizachyrium</i> <i>sanguineum</i> (Retz.) Alston	0.0504	2.7834	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Schizachyrium tenerum</i> Nees	-	-	0.1626	-	-	-	0.2488	-	0.2241	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sporobolus pyramidatus</i> (Lam.) Hitchc.	-	-	-	-	6.6387	4.4215	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Trachypogon macroglossus</i> Trin.	-	-	-	-	-	-	-	-	0.0083	-	-	-	-	-	-	-	-	-	-	-	-
<i>Trachypogon spicatus</i> (L.f.) Kuntze	-	0.1816	-	-	-	0.2541	16.361	-	1.1124	3.5819	44.075	-	40.0146	15.582	11.209	12.291	7.2915	20.414	0.5886	8.8831	2.5503
<i>Trichantheium caaguazuense</i> (Henrard) Zuloaga & Morrone	-	-	-	-	-	-	-	0.0666	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Trichantheium cyanescens</i> (Nees ex Trin.) Zuloaga & Morrone	-	-	-	-	-	-	-	-	-	0.1238	-	0.1244	0.2080	-	0.9957	0.0616	0.3128	-	0.4128	0.1409	-
<i>Trichantheium parvifolium</i> (Lam.) Zuloaga & Morrone	0.3572	0.1901	0.2438	0.0186	-	0.3939	-	-	1.0792	0.0106	-	-	1.4596	-	-	-	-	-	0.0573	-	-
<i>Trichantheium schwackeanum</i> (Mez) Zuloaga & Morrone	-	-	-	-	-	-	-	-	-	-	-	-	0.3685	-	-	-	-	-	-	-	-
<i>Trichantheium wettsteinii</i> (Hack.) Zuloaga & Morrone	-	1.8289	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Tristachya leiostachya</i> Nees	-	0.4097	6.8723	-	-	-	-	-	1.3324	-	-	-	-	-	-	-	-	-	-	-	-
Polygalaceae																					
<i>Asemeia hebeclada</i> (DC.) J.F.B.Pastore & J.R.Abbott	-	-	0.0041	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Monnina stenophylla</i> A.St.-Hil. & Moq.	-	-	-	-	-	-	-	-	0.4732	-	-	-	-	-	-	-	-	-	-	-	-
<i>Polygala abreu</i> Marques & J.F.B.Pastore	-	-	-	-	-	-	-	-	0.0083	-	-	-	-	-	-	-	-	-	-	-	-
<i>Polygala adenophora</i> DC.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0031	0.1845	-	-	-	-
<i>Polygala carphoides</i> Chodat	-	-	-	0.0093	-	-	-	-	0.0955	-	-	-	-	-	-	-	-	-	-	-	-
<i>Polygala celosioides</i> Mart. ex A.W.Benn.	-	-	-	-	-	-	-	1.6789	0.2781	-	-	-	-	-	-	0.0431	0.4452	0.0104	-	-	-
<i>Polygala chapadensis</i> Chod. ex Grondona	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0153	-	0.0641

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Polygala fendleri</i> Chodat	-	-	-	0.0512	-	-	-	-	-	0.0035	-	-	-	-	-	-	-	-	-	-	-
<i>Polygala gracilis</i> Kunth	-	-	-	-	-	-	-	0.3704	-	-	-	-	-	-	-	0.0246	0.0562	-	-	-	-
<i>Polygala juncea</i> A.St.- Hil. & Moq.	-	-	-	-	-	-	-	0.0087	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Polygala longicaulis</i> Kunth	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0154	0.1043	-	-	-	-
<i>Polygala poaya</i> Mart.	-	-	-	-	-	-	-	-	0.2034	-	-	-	-	-	-	-	-	-	-	-	-
<i>Polygala sedoides</i> A.W.Benn.	-	-	-	-	-	-	-	-	0.0540	0.0106	-	-	-	-	-	-	-	-	0.0153	-	0.0040
<i>Polygala</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0040
<i>Polygala tenuis</i> DC.	-	0.1140	-	-	-	-	-	-	0.5894	0.0495	0.0155	-	0.1168	-	-	-	-	-	0.0076	-	0.0040
<i>Polygala timoutou</i> Aubl.	-	-	-	-	-	-	-	0.2558	-	0.0283	-	0.0037	-	-	-	-	-	-	-	-	-
Pontederiaceae																					
Pontederiaceae sp1	-	-	-	-	-	-	-	-	-	0.0035	-	-	-	-	-	-	-	-	-	-	-
Proteaceae																					
<i>Roupala montana</i> Aubl.	-	-	-	-	-	-	-	0.4290	-	-	-	-	-	-	-	-	-	-	-	-	-
Rapateaceae																					
<i>Cephalostemon</i> <i>angustatus</i> Malme	-	-	-	-	-	-	-	-	-	-	2.4283	-	-	2.1023	-	-	-	-	0.8829	1.2532	0.0280
<i>Cephalostemon</i> <i>riedelianus</i> Körn.	-	-	-	-	-	-	-	-	-	-	-	13.551	-	-	-	-	-	-	-	-	-
Rhamnaceae																					
Rhamnaceae sp1	-	-	-	-	-	-	-	-	-	-	-	-	0.0292	-	-	-	-	-	-	-	-
Rosaceae																					
<i>Rubus urticifolius</i> Poir.	-	-	0.1869	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rubiaceae																					
<i>Borreria alata</i> (Aubl.) DC.	-	-	-	-	-	-	-	-	0.0332	-	-	-	-	-	-	-	-	-	-	-	-
<i>Borreria capitata</i> (Ruiz & Pav.) DC.	-	0.1098	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.1676	-
<i>Borreria latifolia</i> (Aubl.) K.Schum.	0.0294	-	-	0.0792	-	-	-	-	-	-	-	0.0256	-	-	-	-	-	-	0.1720	1.1923	0.0881

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Borreria</i>																					
<i>marticrovettiana</i>																					
E.L.Cabral	-	-	-	-	-	-	-	-	0.1992	-	-	-	-	-	-	-	-	-	-	-	-
<i>Borreria poaya</i> (A.St.-Hil.) DC.	-	-	-	-	-	-	-	-	-	-	0.0738	-	0.00730	0.0371	-	-	-	-	-	-	-
<i>Borreria suaveolens</i> G. Mey.	-	-	0.0325	-	-	-	-	0.0053	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Borreria tenella</i> (Kunth) Cham. & Schldl.	-	-	-	-	-	-	-	-	0.1287	0.2864	-	-	-	-	-	-	-	-	0.1796	-	-
<i>Borreria wunschmannii</i> K.Schum.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0648	0.2442
<i>Coccocypselum lanceolatum</i> (Ruiz & Pav.) Pers.	-	-	-	-	-	-	-	-	-	-	-	-	0.0839	-	-	-	-	-	-	-	-
<i>Coccocypselum lymanmithii</i> Standl.	-	0.1647	-	0.0140	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Declieuxia fruticosa</i> (Willd. ex Roem. & Schult.) Kuntze	0.0126	0.0634	-	-	-	-	-	-	-	-	-	-	0.0255	-	-	-	-	-	-	-	-
<i>Palicourea marcgravii</i> A.St.-Hil.	-	-	-	-	-	-	-	0.8208	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Palicourea officinalis</i> Mart.	-	-	-	-	-	-	-	0.1306	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Perama dichotoma</i> Poepp. & Endl.	-	-	-	-	-	-	-	-	-	-	0.0039	-	-	-	-	-	-	-	-	-	-
<i>Perama hirsuta</i> Aubl.	-	-	-	-	-	-	-	-	-	-	-	0.0110	-	-	-	-	0.0602	0.0078	-	-	-
Sapindaceae																					
<i>Serjania obtusidentata</i> Radlk.	-	-	-	-	-	-	-	-	0.1785	-	-	-	-	-	-	-	-	-	-	-	-
Selaginellaceae																					
<i>Selaginella</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2140	-	-
Siparunaceae																					
<i>Siparuna brasiliensis</i> (Spreng.) A.DC.	-	-	-	-	-	-	-	0.0720	0.8883	-	-	-	-	-	-	-	-	-	-	-	-
Solanaceae																					

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Brunfelsia obovata</i> Benth.	-	-	0.0813	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Cestrum tubulosum</i> Sendtn.	-	-	-	-	-	-	-	-	0.2947	-	-	-	-	-	-	-	-	-	-	-	-
<i>Solanum subumbellatum</i> Vell.	0.1135	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Symplocaceae																					
<i>Symplocos platyphylla</i> (Pohl) Benth.	-	-	-	-	-	-	-	-	-	-	0.0194	-	-	-	-	-	-	-	-	-	-
Turneraceae																					
<i>Piriqueta</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0956	-	-
<i>Turnera melochioides</i> var. <i>arenaria</i> Urb.	-	-	-	-	-	0.0296	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Turnera oblongifolia</i> Cambess.	0.0168	0.0169	0.0163	0.0559	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Velloziaceae																					
<i>Vellozia pumila</i> Goethart & Henrard	-	-	-	-	-	4.6205	1.1827	-	0.1826	-	-	-	-	-	-	-	-	-	-	-	-
Verbenaceae																					
<i>Lippia lacunosa</i> Mart. & Schauer	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2362	-
<i>Lippia rotundifolia</i> Cham.	-	-	0.0894	1.1873	-	-	-	-	1.5192	-	0.0583	-	0.4306	0.1195	-	-	-	-	-	0.2133	0.5765
Vitaceae																					
<i>Cissus spinosa</i> Cambess.	-	-	-	-	-	-	-	2.4250	-	-	-	-	-	-	-	-	-	-	-	-	-
Vochysiaceae																					
<i>Vochysia</i> sp1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2666	-
Xyridaceae																					
<i>Abolboda poarchon</i> Seub.	-	-	-	-	-	-	-	-	-	-	0.3497	-	-	-	0.2078	0.9604	-	-	0.1491	-	0.1401
<i>Abolboda pulchella</i> Humb.	-	-	-	-	-	-	0.1353	0.0133	-	-	-	0.0293	-	0.0453	-	0.2463	-	-	0.6727	-	-
<i>Xyris asperula</i> Mart.	-	0.1140	-	-	-	0.0042	-	-	-	0.0389	-	-	0.3248	0.1731	-	-	-	-	-	-	-

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Xyris blanchetiana</i> Malme	-	-	-	-	-	-	-	2.1506	1.4113	-	-	-	-	-	-	0.0277	-	-	-	-	-
<i>Xyris caroliniana</i> Walter	-	0.3421	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Xyris ciliata</i> Thunb.	-	-	-	-	-	-	-	-	-	-	-	0.1463	-	-	-	-	-	-	-	-	-
<i>Xyris cylindrostachya</i> Kral & Wand.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.2002
<i>Xyris dawsonii</i> L.B.Sm. & Downs	-	-	-	-	-	-	0.6415	-	-	-	-	-	-	-	0.1788	-	-	-	-	-	-
<i>Xyris diaphanobracteata</i> Kral & Wand.	0.1471	-	-	-	-	-	-	-	0.2158	-	-	-	-	0.0948	-	-	-	-	-	-	-
<i>Xyris fallax</i> Malme	-	-	-	-	-	-	-	1.8015	0.1204	-	-	-	0.1131	-	-	0.3017	-	-	-	-	-
<i>Xyris goyazensis</i> Malme	-	-	-	-	-	-	-	-	0.0332	-	-	-	-	-	-	-	-	-	-	-	-
<i>Xyris guaranitica</i> Malme	-	2.0189	0.1991	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Xyris hymenachne</i> Mart.	-	0.4942	0.8616	0.1071	-	-	-	0.5250	0.1411	0.3218	-	-	-	-	1.5758	0.4494	0.2527	6.9266	-	-	-
<i>Xyris jupicai</i> Rich.	0.4581	-	-	-	0.0228	0.0042	-	-	0.0332	-	0.2176	-	0.0109	0.1113	-	-	-	-	-	-	-
<i>Xyris lacerata</i> Pohl ex Seub.	-	-	-	-	-	-	0.0349	-	-	0.0141	-	-	-	-	-	-	-	-	0.1567	0.1486	0.0280
<i>Xyris lanuginosa</i> Seub.	-	-	-	-	-	-	-	-	-	-	-	-	0.5729	-	-	-	-	-	-	-	-
<i>Xyris longifolia</i> Mart.	-	-	-	-	-	-	-	-	-	-	-	-	-	2.1394	-	-	-	-	-	-	-
<i>Xyris macrocephala</i> Vahl	-	2.7412	-	0.4842	-	0.4108	-	-	-	-	-	-	-	-	0.5655	0.0554	-	-	-	0.0609	-
<i>Xyris minarum</i> Seub.	-	-	-	-	-	-	-	-	-	-	-	0.1097	-	-	-	-	-	-	-	-	-
<i>Xyris paradisiaca</i> Wand.	-	-	-	-	-	-	-	0.0480	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Xyris paraensis</i> Poepp. ex Kunth	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.0154	1.2955	-	-	-	-
<i>Xyris pterygoblephara</i> Steud.	-	-	-	-	-	-	-	0.2505	-	-	-	-	-	-	-	-	-	0.4196	-	-	-
<i>Xyris roraimae</i> Malme	-	-	-	-	-	-	-	-	-	-	-	0.0037	-	-	-	-	-	-	-	-	-
<i>Xyris savanensis</i> Miq.	0.1975	0.0803	-	-	-	-	0.0611	1.6416	0.3113	-	0.0505	0.1170	-	-	-	1.9547	-	-	0.0306	0.0076	0.0761
<i>Xyris sceptrifera</i> Kral & Wand.	-	-	-	-	-	-	-	-	-	-	1.1617	-	-	-	-	-	-	-	-	-	-

Family/ Species	Relative cover (%) of the sites																				
	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	BA1	TO1	TO2	TO3	TO4	MT1	MT2	MT3
<i>Xyris schizachne</i> Mart.	-	1.7190	-	0.5122	-	-	0.0087	-	0.3155	-	-	0.1280	-	-	-	-	-	-	-	-	-
<i>Xyris seubertii</i> L.A.Nilsson	0.5716	-	-	-	-	-	-	0.4797	-	-	-	-	-	-	1.7353	0.9173	-	-	-	-	-
<i>Xyris</i> sp1	-	-	-	-	-	-	-	-	-	-	0.1476	-	-	-	-	-	-	-	-	-	-
<i>Xyris</i> sp2	-	-	-	-	-	-	-	-	-	-	0.5595	-	-	-	-	-	-	-	-	-	-
<i>Xyris</i> sp3	-	-	-	-	-	-	-	-	-	0.1202	-	-	-	-	-	-	-	-	-	-	-
<i>Xyris</i> sp4	-	-	-	-	-	-	-	-	-	0.1061	-	-	-	-	-	-	-	-	-	-	-
<i>Xyris</i> sp5	-	-	-	-	-	-	-	-	-	0.0141	-	-	-	-	-	-	-	-	-	-	-
<i>Xyris</i> sp6	-	-	-	-	-	-	-	-	-	0.0424	-	-	-	-	-	-	-	-	-	-	-
<i>Xyris</i> sp7	-	-	-	-	-	-	-	-	-	0.1768	-	-	-	-	-	-	-	-	-	-	-
<i>Xyris tenella</i> Kunth	-	-	-	-	-	-	-	-	0.1785	0.2546	-	0.0622	0.0401	-	-	-	-	-	-	-	-
<i>Xyris tortula</i> Mart.	-	-	-	1.0103	-	-	1.7631	0.5383	0.2117	-	-	0.2963	0.1277	1.4881	0.9136	1.2436	0.3449	0.3549	0.1720	-	0.1161
<i>Xyris trachyphylla</i> Mart.	-	-	-	-	-	-	-	-	-	-	-	1.2106	-	-	-	-	-	-	-	-	-
<i>Xyris veruina</i> Malme	1.7315	-	-	-	-	-	0.5368	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Xyris vestita</i> Malme	-	-	-	-	-	-	-	-	-	0.0919	-	-	-	-	-	-	-	-	-	-	-
Zingiberaceae																					
<i>Renealmia</i> <i>dermatopetala</i> K.Schum.	-	-	-	-	0.0456	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table S5. Physical and chemical soil properties (Ca = calcium (cmolc dm⁻³), Mg = magnesium (cmolc dm⁻³), Al = aluminum concentration (cmolc dm⁻³), K = potassium (cmolc dm⁻³), P = phosphorus (mg gm⁻³), OM = organic matter (%), CEC = cation exchange capacity (mg gm⁻³), V = cation saturation (%), Prec. = Precipitation, T. = Temperature, Min = Minimum, Max = Maximum, SD = standard deviation). The site codes are described in Fig. 1. N = 15

Site	Measures	Ca	Mg	Al	K	P	OM	CEC	V	pH (CaCl)	Clay (%)	Silt (%)	Sand (%)	Altitude (m)	Annual Prec. (mm)	Mean T. Min/Max (°C)
DF1	Minimum	0.10	0.10	0.50	0.06	1.20	5.70	7.00	2.55	4.10	13.00	1.00	59.00	1127	1650	15/26
	Maximum	0.20	0.10	1.20	0.09	5.60	20.00	11.70	4.26	4.40	32.00	10.00	82.00			
	Mean	0.11	0.10	0.67	0.08	3.51	14.95	9.06	3.44	4.27	25.33	6.80	67.87			
	SD	0.04	0.00	0.20	0.01	1.37	4.57	1.49	0.51	0.10	4.92	2.04	5.82			
DF2	Minimum	0.10	0.00	0.20	0.05	0.50	0.71	5.39	1.96	3.90	19.00	5.00	21.00	1114	1567	15/26
	Maximum	0.70	0.10	1.40	0.15	4.70	6.90	16.60	12.36	4.50	65.00	14.00	76.00			
	Mean	0.32	0.09	0.47	0.09	1.97	1.90	9.15	6.02	4.17	44.07	10.13	45.80			
	SD	0.21	0.04	0.29	0.04	1.45	1.61	2.47	2.76	0.15	14.88	2.47	17.29			
DF3	Minimum	0.10	0.10	0.20	0.09	0.50	6.90	4.57	3.48	3.80	11.00	5.00	54.00	1193	1691	15/26
	Maximum	0.20	0.10	3.20	0.21	13.20	22.00	11.50	8.08	4.80	37.00	10.00	84.00			
	Mean	0.11	0.10	1.20	0.15	4.85	14.70	8.79	4.58	4.20	25.40	7.13	67.47			
	SD	0.04	0.00	0.98	0.03	4.21	5.26	2.11	1.15	0.27	7.64	1.85	9.40			
DF4	Minimum	0.10	0.10	1.00	0.08	3.70	10.80	10.90	2.12	4.00	11.00	5.00	64.00	1164	1540	15/26
	Maximum	1.40	0.50	2.30	0.19	9.60	20.00	20.90	10.05	4.60	28.00	8.00	84.00			
	Mean	0.33	0.16	1.54	0.12	5.54	16.32	14.94	3.95	4.33	18.60	5.60	75.80			
	SD	0.32	0.12	0.43	0.03	1.64	2.61	3.23	1.93	0.19	4.97	1.06	5.94			
GO1	Minimum	0.10	0.10	0.90	0.06	1.50	2.20	4.41	2.25	3.60	16.00	5.00	62.00	822	1743	18/29
	Maximum	0.20	0.10	11.50	0.31	4.30	5.70	17.90	9.21	4.00	30.00	8.00	79.00			
	Mean	0.19	0.10	4.51	0.11	2.89	3.43	9.47	4.94	3.85	21.87	6.07	72.07			
	SD	0.03	0.00	4.00	0.06	0.87	1.06	3.40	1.92	0.11	4.66	1.22	5.81			
GO2	Minimum	0.20	0.10	1.40	0.08	1.50	3.00	8.19	2.41	3.70	9.00	4.00	82.00	822	1743	18/29
	Maximum	0.30	0.20	3.10	0.16	3.00	6.30	16.70	6.27	4.00	13.00	5.00	87.00			
	Mean	0.21	0.11	2.18	0.10	2.38	4.65	11.81	3.80	3.88	10.20	4.40	85.40			
	SD	0.03	0.03	0.50	0.02	0.46	1.01	2.32	1.01	0.08	1.42	0.51	1.88			

Site	Measures	Ca	Mg	Al	K	P	OM	CEC	V	pH (CaCl)	Clay (%)	Silt (%)	Sand (%)	Altitude (m)	Annual Prec. (mm)	Mean T. Min/Max (°C)
GO3	Minimum	0.10	0.00	0.70	0.06	0.80	0.70	3.09	1.31	3.50	13.00	5.00	66.00	1244	1830	16/26
	Maximum	1.10	0.20	4.00	0.19	4.00	27.00	27.05	7.59	4.00	27.00	7.00	82.00			
	Mean	0.29	0.08	1.85	0.12	2.90	9.54	13.01	4.39	3.76	16.73	5.27	78.00			
	SD	0.31	0.07	0.99	0.04	1.00	8.13	8.31	1.90	0.17	4.18	0.70	4.77			
GO4	Minimum	0.20	0.10	0.10	0.02	2.10	1.60	6.20	2.47	3.90	9.00	4.00	66.00	1078	1830	16/26
	Maximum	0.30	0.20	3.00	0.17	8.80	28.50	15.49	9.66	5.00	27.00	7.00	87.00			
	Mean	0.22	0.11	1.45	0.07	3.80	9.93	10.53	4.44	4.27	14.80	5.20	80.00			
	SD	0.04	0.03	0.89	0.05	2.01	6.70	2.73	2.06	0.25	5.82	1.01	6.73			
GO5	Minimum	0.20	0.10	0.60	0.03	3.70	1.70	4.44	3.18	3.50	7.00	3.00	84.00	1073	1373	14/27
	Maximum	3.10	0.80	2.30	0.22	20.00	17.00	20.69	19.79	4.30	11.00	5.00	90.00			
	Mean	0.57	0.20	1.29	0.09	7.65	8.49	10.88	7.36	3.91	9.00	4.00	87.00			
	SD	0.80	0.19	0.50	0.05	4.31	5.27	5.16	4.69	0.25	1.00	0.38	1.31			
GO6	Minimum	0.20	0.10	1.10	0.04	3.00	2.40	5.17	2.13	3.40	9.00	4.00	82.00	993	1146	16/28
	Maximum	0.30	0.20	3.20	0.11	10.80	26.00	22.07	11.02	4.20	13.00	5.00	87.00			
	Mean	0.21	0.11	2.00	0.06	5.53	8.31	12.65	4.02	3.89	10.40	4.40	85.20			
	SD	0.04	0.04	0.69	0.02	2.10	7.74	5.34	2.27	0.26	1.12	0.51	1.57			
GO7	Minimum	0.20	0.10	1.00	0.03	2.10	1.90	1.45	2.72	3.00	7.00	3.00	79.00	798	1314	20/30
	Maximum	0.50	0.30	30.00	0.37	17.50	26.50	22.20	31.26	4.20	16.00	5.00	90.00			
	Mean	0.29	0.15	4.15	0.15	5.88	19.49	11.97	8.12	3.50	10.54	4.15	85.31			
	SD	0.12	0.07	7.79	0.10	4.06	8.17	6.32	7.69	0.43	2.88	0.69	3.52			
MG1	Minimum	0.10	0.05	1.30	0.04	1.50	6.50	10.00	0.71	3.20	9.00	4.00	76.00	686	1157	15/28
	Maximum	0.50	0.20	4.60	0.21	6.40	29.00	36.16	5.13	4.00	19.00	5.00	87.00			
	Mean	0.15	0.09	2.36	0.08	2.85	16.08	19.11	2.06	3.57	12.13	4.73	83.13			
	SD	0.12	0.05	0.93	0.04	1.32	6.32	6.66	1.07	0.21	2.92	0.46	3.23			
MG2	Minimum	0.20	0.10	0.40	0.02	1.80	1.40	2.26	1.23	3.40	7.00	3.00	79.00	725	1029	18/31
	Maximum	0.40	0.20	3.00	0.08	6.00	16.50	30.98	16.99	4.10	16.00	5.00	90.00			
	Mean	0.23	0.12	1.63	0.04	3.15	6.71	12.71	5.70	3.81	11.33	4.40	84.27			
	SD	0.06	0.04	0.91	0.02	1.50	5.34	8.88	4.90	0.20	3.27	0.74	3.94			

Site	Measures	Ca	Mg	Al	K	P	OM	CEC	V	pH (CaCl)	Clay (%)	Silt (%)	Sand (%)	Altitude (m)	Annual Prec. (mm)	Mean T. Min/Max (°C)
BA1	Minimum	0.20	0.10	1.30	0.03	1.20	9.00	17.53	1.23	3.20	7.00	3.00	79.00	781	1204	18/31
	Maximum	0.30	0.20	2.90	0.05	4.70	24.00	28.45	2.44	3.80	16.00	5.00	90.00			
	Mean	0.22	0.12	2.09	0.03	2.14	15.67	22.50	1.69	3.44	10.87	4.33	84.60			
	SD	0.04	0.04	0.45	0.01	0.79	4.22	3.53	0.38	0.16	2.75	0.62	3.29			
MT1	Minimum	0.20	0.10	0.40	0.02	1.20	1.60	2.34	4.36	3.90	10.00	4.00	70.60	417	1495	22/31
	Maximum	0.30	0.20	5.00	0.14	10.40	30.00	12.50	14.45	4.60	19.00	5.00	86.00			
	Mean	0.25	0.15	1.36	0.04	4.23	9.20	5.92	9.30	4.29	13.43	4.85	80.33			
	SD	0.05	0.05	1.51	0.03	2.45	9.57	3.05	3.39	0.20	2.91	0.33	4.31			
MT2	Minimum	0.20	0.10	0.40	0.02	1.80	1.10	2.75	4.37	4.20	9.00	4.00	79.00	432	1495	22/31
	Maximum	0.40	0.20	1.40	0.05	5.00	13.00	9.40	13.31	4.60	16.00	6.00	87.00			
	Mean	0.25	0.14	0.71	0.03	3.01	3.43	5.16	9.15	4.33	11.80	4.87	83.33			
	SD	0.07	0.05	0.24	0.01	0.92	3.09	1.90	2.79	0.14	2.01	0.64	2.53			
MT3	Minimum	0.20	0.10	0.40	0.02	1.50	1.20	2.14	3.67	3.50	9.00	4.00	79.00	403	1495	22/31
	Maximum	0.40	0.30	1.80	0.22	26.20	28.00	27.41	21.93	4.60	16.00	6.00	87.00			
	Mean	0.27	0.16	0.64	0.03	4.33	3.95	5.66	11.85	4.28	12.50	4.86	82.64			
	SD	0.07	0.06	0.36	0.05	6.19	6.82	6.32	5.23	0.25	2.26	0.52	2.61			
TO1	Minimum	0.20	0.10	0.30	0.02	1.80	1.10	2.15	3.44	3.40	6.00	3.00	88.00	490	1700	23/30
	Maximum	0.30	0.20	3.00	0.12	9.20	19.00	14.19	25.80	4.20	8.00	4.00	90.00			
	Mean	0.26	0.13	1.67	0.05	4.20	10.35	8.61	8.31	3.79	6.93	3.60	89.47			
	SD	0.05	0.05	0.82	0.03	2.33	6.74	4.05	6.77	0.23	0.70	0.51	0.83			
TO2	Minimum	0.20	0.10	0.40	0.03	0.80	1.60	2.38	2.99	3.60	7.00	3.00	79.00	502	1700	23/30
	Maximum	0.50	0.30	2.90	0.10	6.70	18.00	15.73	15.87	4.30	16.00	5.00	90.00			
	Mean	0.25	0.12	1.73	0.06	2.26	8.53	8.50	7.22	3.91	9.27	3.93	86.80			
	SD	0.08	0.06	0.80	0.03	1.83	5.45	3.73	3.81	0.20	3.06	0.80	3.75			
TO3	Minimum	0.20	0.10	1.20	0.04	1.20	3.30	5.99	3.38	3.60	7.00	3.00	76.00	519	1700	23/30
	Maximum	0.60	0.20	3.20	0.10	5.00	18.00	15.99	8.70	4.10	19.00	6.00	90.00			
	Mean	0.33	0.14	2.18	0.07	2.43	10.00	11.36	5.40	3.91	10.47	4.40	85.13			
	SD	0.17	0.05	0.67	0.02	1.08	4.42	2.78	1.58	0.18	4.02	1.12	4.91			

Site	Measures	Ca	Mg	Al	K	P	OM	CEC	V	pH (CaCl)	Clay (%)	Silt (%)	Sand (%)	Altitude (m)	Annual Prec. (mm)	Mean T. Min/Max (°C)
TO4	Minimum	0.20	0.10	0.60	0.02	0.30	2.00	3.66	1.80	3.30	5.00	3.00	87.00	495	1700	23/30
	Maximum	0.80	0.20	4.80	0.14	8.50	19.00	29.53	15.31	4.10	9.00	5.00	92.00			
	Mean	0.31	0.15	2.69	0.07	2.51	10.65	14.48	5.48	3.71	6.93	3.67	89.40			
	SD	0.16	0.05	1.28	0.04	2.22	6.66	7.99	3.72	0.29	1.03	0.62	1.30			

Table S6. Significance among *veredas* or hierarchical cluster analysis groups with regards to the soil variables (Ca = calcium, Mg = magnesium, Al = aluminum concentration, K = potassium, P = phosphorus, OM = organic matter, CEC = cation exchange capacity, V = cation saturation). Group 1 = DF1, DF2, DF3, DF4, GO1, GO2, GO3, GO4, GO5, GO6; Group 2 = MG1, MT1, MT2, MT3, TO1, TO2, TO3, TO4; Group 3 = BA1, GO7, MG2. The site codes are described in Fig. 1. Values in bold are significant at $p < 0.05$

Soil variable	<i>Veredas</i>			hierarchical cluster analysis groups					
	Kruskal-Wallis chi-squared	df	<i>p</i> -value	Kruskal-Wallis chi-squared	df	<i>p</i> -value	<i>p</i> -value Group 1 x Group 3	<i>p</i> -value Group 1 x Group 2	<i>p</i> -value Group 2 x Group 3
Ca	113.38	20	4.72E-15	21.073	2	2.66E-05	0.00710	6.30E-05	0.32380
Al	146.74	20	2.20E-16	10.69	2	0.004772	0.00190	0.53470	0.02110
Mg	69.42	20	2.26E-07	18.319	2	0.000105	0.01550	0.00010	0.39140
K	183.83	20	2.20E-16	78.403	2	2.20E-16	2.50E-06	2.00E-16	0.31000
V	147.32	20	2.20E-16	36.108	2	1.44E-08	0.00400	7.10E-07	4.00E-05
CEC	133.46	20	2.20E-16	26.294	2	1.95E-06	0.00027	0.00259	3.10E-05
P	111.26	20	1.16E-14	13.619	2	0.001103	0.00400	7.10E-07	4.00E-05
OM	150.92	20	2.20E-16	15.507	2	0.000429	0.00075	0.38692	0.00055
pH	208.91	20	2.20E-16	53.721	2	2.16E-12	3.30E-13	0.08600	2.00E-08
Sand	221.43	20	2.20E-16	70.966	2	3.89E-16	7.60E-08	1.90E-14	0.31000
Silt	177.08	20	2.20E-16	59.718	2	1.08E-13	1.30E-07	1.10E-11	0.88000
Clay	221.29	20	2.20E-16	83.561	2	2.20E-16	4.40E-08	2.00E-16	0.11000

Table S7. Bioclimatic variables corresponding to the location of the 21 *vereda* sites in Central Brazil. The site codes are described in Fig. 1

Code	Bioclimatic variables	Sites																				
		BA1	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	MT1	MT2	MT3	TO1	TO2	TO3	TO4
BIO1	annual mean temperature (°C)	22.6	20.3	20.7	20.5	20.3	22.9	22.9	20.7	21.5	20.6	21.9	23.6	21.6	23.0	24.1	24.0	24.2	24.6	24.5	24.5	24.6
BIO4	temperature seasonality (°C) (standard deviation ×100)	128.9	121.1	112.2	124.1	110.3	91.3	92.1	89.2	93.6	148.6	106.2	91.8	190.1	136.5	146.9	149.0	148.2	86.7	88.8	88.3	88.9
BIO5	max temperature of warmest month (°C)	30.6	27.7	28.1	27.9	27.6	30.1	30.1	27.9	28.7	27.7	28.8	31.0	29.0	31.3	32.9	32.8	33.0	33.7	34.0	33.9	34.0
BIO8	mean temperature of wettest quarter (°C)	23.2	20.9	21.2	21.1	20.7	23.1	23.1	20.9	21.7	21.4	22.2	23.8	23.0	23.7	24.8	24.7	25.0	24.5	24.5	24.5	24.5
BIO9	mean temperature of driest quarter (°C)	20.8	18.6	19.2	18.8	18.8	21.7	21.7	19.6	20.3	18.5	20.5	22.6	18.8	21.1	22.0	21.9	22.1	23.7	23.5	23.5	23.6
BIO10	mean temperature of warmest quarter (°C)	23.7	21.3	21.6	21.4	21.2	23.8	23.8	21.6	22.4	21.7	22.9	24.6	23.5	24.2	25.4	25.2	25.5	25.7	25.6	25.6	25.7
BIO11	mean temperature of coldest quarter (°C)	20.8	18.5	19.0	18.7	18.6	21.6	21.6	19.5	20.2	18.4	20.3	22.5	18.8	21.1	22.0	21.8	22.1	23.6	23.5	23.4	23.5
BIO12	annual precipitation (mm)	1704	1513	1509	1514	1533	1634	1634	1664	1652	1546	1630	1413	1110	1646	1584	1592	1576	1398	1302	1301	1258
BIO14	precipitation of driest month (mm)	2	8	8	8	9	4	4	6	5	7	9	4	9	2	4	4	3	2	1	1	1
BIO15	precipitation seasonality (%) (Coefficient of Variation)	94.2	78.8	76.7	79.6	76.2	85.3	85.3	82.8	83.1	85.6	78.9	86.5	86.6	95.6	81.8	81.8	82.0	84.2	84.6	84.6	84.8

Code	Bioclimatic variables	Sites																				
		BA1	DF1	DF2	DF3	DF4	GO1	GO2	GO3	GO4	GO5	GO6	GO7	MG1	MG2	MT1	MT2	MT3	TO1	TO2	TO3	TO4
BIO16	precipitation of wettest quarter (mm)	965	730	713	734	721	815	815	816	810	807	792	723	618	951	771	775	768	694	651	650	630
BIO17	precipitation of driest quarter (mm)	13	29	31	29	33	14	14	21	19	28	29	20	33	14	23	22	22	11	9	9	8
BIO18	precipitation of warmest quarter (mm)	458	424	433	421	442	465	465	478	476	401	463	361	458	441	432	434	428	350	323	324	311
BIO19	precipitation of coldest quarter (mm)	13	49	53	47	56	32	32	40	38	42	55	30	33	14	41	42	40	38	33	33	30

Table S8. Pearson correlation analysis among bioclimatic variables ($|r| \geq 0.7$). BIO1 = Annual mean temperature, BIO4 = Temperature seasonality, BIO5 = Max temperature of warmest month, BIO8 = Mean temperature of wettest quarter, BIO9 = Mean temperature of driest quarter, BIO10 = Mean temperature of warmest quarter, BIO11 = Mean temperature of coldest quarter, BIO12 = Annual precipitation, BIO14 = Precipitation of driest month, BIO15 = Precipitation seasonality, BIO16 = Precipitation of wettest quarter, BIO17 = Precipitation of driest quarter, BIO18 = Precipitation of warmest quarter, BIO19 = Precipitation of coldest quarter

	BIO1	BIO4	BIO5	BIO8	BIO9	BIO10	BIO11	BIO12	BIO14	BIO15	BIO16	BIO17	BIO18
BIO4	-0.17949												
BIO5	0.978389	-0.14925											
BIO8	0.973378	0.047742	0.953397										
BIO9	0.961961	-0.44057	0.934118	0.874248									
BIO10	0.992367	-0.07239	0.973354	0.990066	0.926058								
BIO11	0.966095	-0.42653	0.940131	0.881899	0.999635	0.931987							
BIO12	-0.28539	-0.07486	-0.34343	-0.29723	-0.25179	-0.33993	-0.25641						
BIO14	-0.8578	0.340925	-0.86444	-0.79333	-0.87225	-0.825	-0.88102	0.088862					
BIO15	0.366171	0.121921	0.319505	0.4111	0.296639	0.393996	0.312262	0.036921	-0.58933				
BIO16	-0.17926	0.103756	-0.24126	-0.14535	-0.20377	-0.20041	-0.19954	0.865861	-0.08956	0.500265			
BIO17	-0.75743	0.545712	-0.74537	-0.64539	-0.83898	-0.71017	-0.84388	0.075979	0.942523	-0.57427	-0.08502		
BIO18	-0.5808	0.340297	-0.65447	-0.49385	-0.63379	-0.56111	-0.63244	0.671412	0.545033	-0.05176	0.609676	0.49982	
BIO19	-0.48411	-0.00636	-0.44296	-0.50722	-0.43354	-0.49986	-0.4503	0.025749	0.713792	-0.96211	-0.40009	0.697491	0.136676

Table S9. Moran's I spatial autocorrelation test for the residuals of each OLS model ($\alpha = 0.05$)

Response	Observed	Expected	Standard deviation	<i>p</i> -value
sesPD	-0.222	-0.05	0.172	0.318
sesMPD	-0.078	-0.05	0.172	0.869
sesMNTD	-0.178	-0.05	0.173	0.459

Table S10. Parameter estimates of environmental predictors extracted from a linear model on standardized phylogenetic diversity (sesPD) of the studied *veredas* ($\alpha = 0.05$). OM = organic matter, BIO11 = mean temperature of coldest quarter, BIO12 = annual precipitation, BIO18 = precipitation of warmest quarter

sesPD	Estimate	Standard error	t value	<i>p</i>
Intercept	-1.306	0.166	-7.862	6.94E-07
OM	0.731	0.193	3.781	0.001
BIO12	0.41	0.245	1.671	0.114
BIO11	0.723	0.245	2.948	0.009
BIO18	0.474	0.304	1.559	0.138
Residual standard error	0.761			
Degrees of freedom	16			
Adjusted R ²	0.451			
F-statistic	5.107			
<i>p</i> -value	0.007			

Table S11. Parameter estimates of environmental predictors extracted from a linear model on standardized phylogenetic structure (sesMPD) of the studied *veredas* ($\alpha = 0.05$). OM = organic matter, BIO12 = annual precipitation

sesMPD	Estimate	Standard error	t value	<i>p</i>
Intercept	-1.252	0.196	-6.361	5.42E-06
BIO12	0.835	0.214	3.902	0.001
OM	0.460	0.214	2.149	0.045
Residual standard error	0.902			
Degrees of freedom	18			
Adjusted R ²	0.411			
F-statistic	8.003			
<i>p</i> -value	0.003			

Table S12. Parameter estimates of environmental predictors extracted from a linear model on standardized phylogenetic structure (sesMNTD) of the studied *veredas* ($\alpha = 0.05$). OM = organic matter, BIO11 = mean temperature of coldest quarter, BIO12 = annual precipitation

sesMNTD	Estimate	Standard error	t value	<i>p</i>
Intercept	-0.902	0.139	-6.451	5.98E-06
OM	0.759	0.16	4.729	0.0001
BIO11	0.604	0.156	3.865	0.001
BIO12	0.527	0.162	3.246	0.004
Residual standard error	0.64			
Degrees of freedom	17			
Adjusted R ²	0.567			
F-statistic	9.749			
<i>p</i> -value	0.0005			

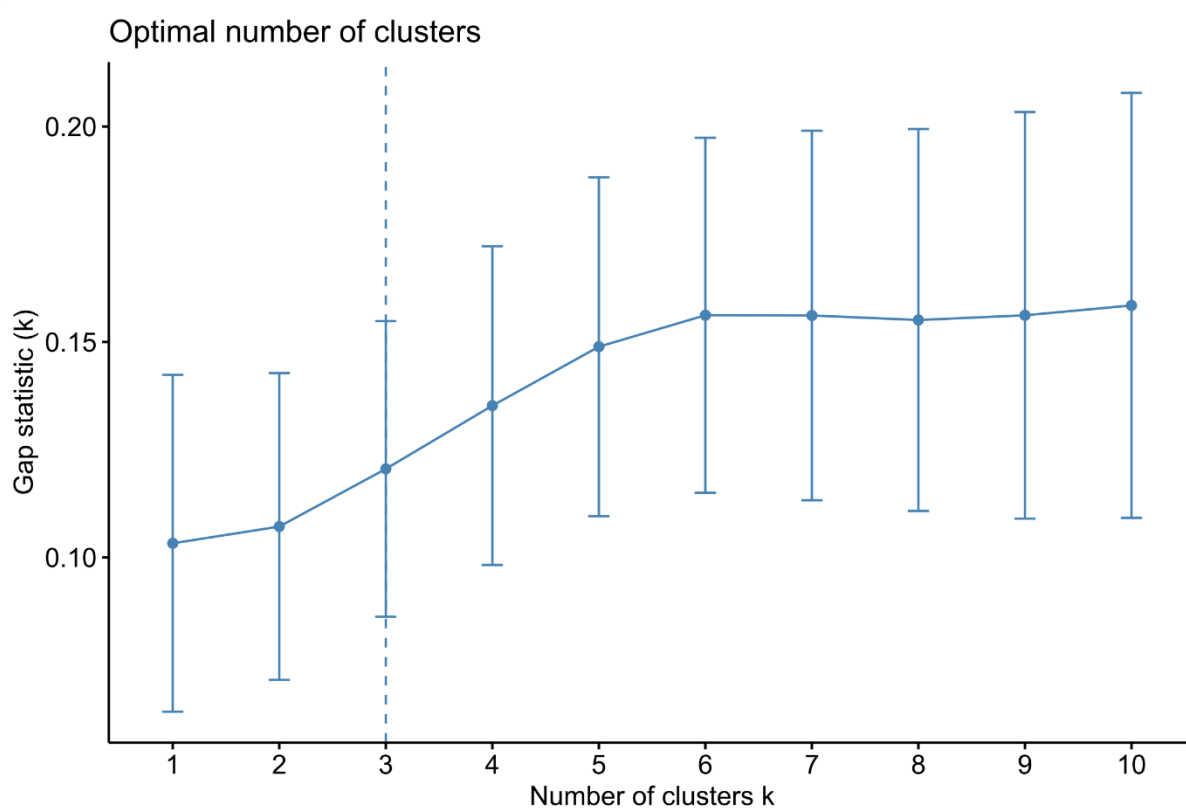


Figure S1 Number of optimal cluster-k findings using the gap statistic method

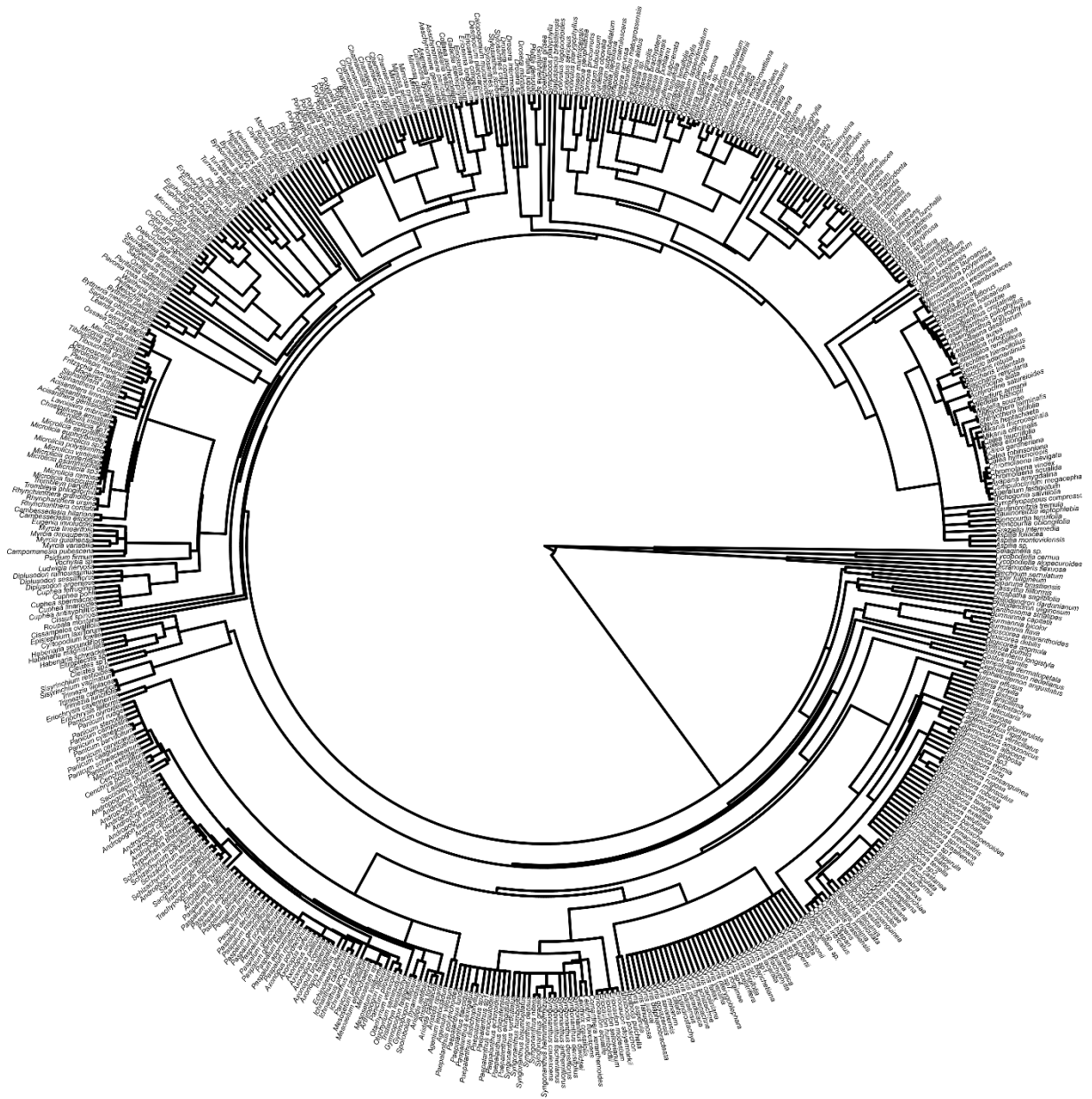


Figure S2 Phylogenetic tree of the 21 herbaceous-shrub species of *veredas*

