UNIVERSIDADE FEDERAL DOS VALES DO JEQUITINHONHA E MUCURI

Programa de Pós-Graduação em Ciência Florestal

Julia Viotti Corrêa

FITOGEOGRAFIA DE ECÓTONES NO PLANALTO DIAMANTINO

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Dissertação apresentada ao programa de Pós-Graduação em Ciência Florestal da Universidade Federal dos Vales do Jequitinhonha e Mucuri, como requisito para obtenção do título de Mestre.

Orientadora: Prof.ª Dr.ª Anne Priscila Dias Gonzaga

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JULIA VIOTTI CORRÊA

Fitogeografia de ecótones no Planalto Diamantino

Dissertação apresentada ao MESTRADO EM CIÊNCIA FLORESTAL, nível de MESTRADO como parte dos requisitos para obtenção do título de MESTRA EM CIÊNCIA FLORESTAL

Orientador (a): Prof.ª Dr.ª Anne Priscila Dias Gonzaga

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DIAMANTINA

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RESUMO

Entender as configurações pretérita e presente dos ecossistemas é fundamental para a sua conservação ao longo dos próximos anos, em especial frente às mudanças climáticas em curso. Neste estudo, investigamos como sete fitofisionomias de Cerrado presentes no Planalto Diamantino, uma região ecotonal chave da Reserva da Biosfera da Serra do Espinhaço (RBSE), respondem a variações ambientais e históricas. Para tanto, utilizou-se um banco de dados de 546 espécies, levantado pela equipe do laboratório de Fitogeografia, Vegetação e Ecologia (PHYVE) em treze localidades distribuídas entre Capão de Mata (CAP), Floresta Estacional Semidecidual (FES), Cerrado *stricto sensu* (CSS), Cerrado Rupestre (CER), Campo Rupestre (CAR), Campo Úmido (CUM) e Vereda (VER). A partir de uma abordagem multidimensional da biodiversidade, a pesquisa revelou que a flora é muito distinta entre as fitofisionomias, resultado que evidencia sua singularidade, e que as diversidades filogenética e funcional apontam para filtragem ambiental e estratégias de adaptação específicas a diferentes habitats. O Capítulo 1 foca na diversidade β-filo-taxonômica entre fitofisionomias e sugere que a heterogeneidade do habitat é um de seus *drivers*. A partir de um Escalonamento Multidimensional Não-Métrico (NMDS), investigou-se como variáveis bioclimáticas, edáficas, de fogo e relevo atuantes na composição florística do Cerrado influenciam a distribuição das vegetações. O NMDS revelou dois grupos florísticos distintos, resultado que foi corroborado pelos baixos valores encontrados para o índice de similaridade de Jaccard (< 50%) entre todos os pares. Além disso, observou-se que a diversidade filogenética varia entre os tipos de vegetação, com agrupamento significativo observado em sítios de FES, CAR, CUM e VER e mais de 80% dos pares apresentando alto *turnover* (< 50%) para a métrica de similaridade filogenética de Sorensen (PhyloSor). O Capítulo 2, por sua vez, investiga a diversidade de traços funcionais nas mesmas localidades, concentrando-se na influência da filtragem ambiental e da história evolutiva. A abordagem filo-funcional revelou quatro clusters de traços distintos atrevés de uma Análise de Coordenadas Principais (PCoA), baseados primariamente nas combinações possíveis de atributos de tricomas foliares e tipo de fruto, provavelmente em resposta ao gradiente sul-norte de temperatura e umidade presente na Serra do Espinhaço e de outros fatores, como profundidade de solo e disponibilidade hídrica. Os tipos de vegetação exibem padrões únicos de traços, com CAR e CER apresentando maiores valores de riqueza (FRic) e dispersão funcional (FDis), e CUM e VER, de divergência (FDiv) e equitabilidade funcional (FEve). A filtragem ambiental é evidente em todos as fitofisionomias com base em FRic ou FDis. A decomposição da diversidade funcional ao longo dos nós da filogenia apresentou sinal filogenético significativo para hábito e forma de vida na metacomunidade. Nossas descobertas fornecem *insights* sobre os mecanismos que moldam as múltiplas dimensões da diversidade de espécies vegetais em *hotspots* de Cerrado na RBSE. A preservação dos ecótones viabiliza o funcionamento e a identidade de cada fitofisionomia, sendo, portanto, diretrizes de conservação voltadas à totalidade do ecossistema fundamentais para a manutenção de sua heterogeneidade ambiental e biodiversidade.

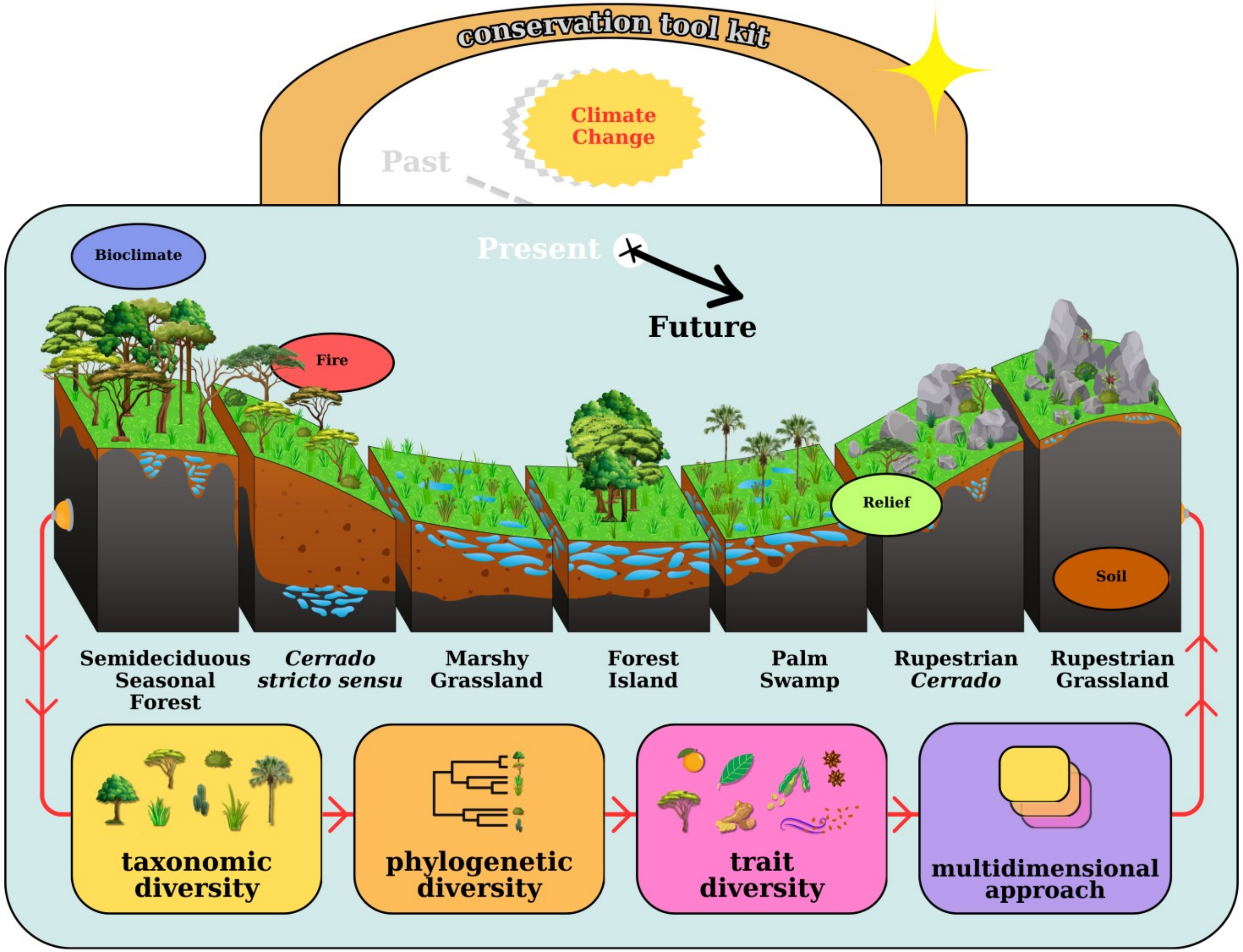
Palavras-chave: Cerrado. Diversidade multidimensional. Heterogeneidade ambiental. *Hotspot*. Reserva da Biosfera da Serra do Espinhaço.

ABSTRACT

Understanding the historical and present configurations of ecosystems is vital for their conservation in the face of ongoing climate changes. In this study, we investigated how seven *Cerrado* vegetation types in the Diamantino Plateau, a key ecotonal region of the Espinhaço Range Biosphere Reserve (ERBR), respond to environmental and historical variations. To this end, we utilized a database of 546 species collected by the team from the laboratory of Phytogeography, Vegetation, and Ecology (PHYVE) across thirteen locations distributed among Forest Island (FI), Semideciduous Seasonal Forest (SSF), *Cerrado stricto sensu* (CSS), Rupestrian *Cerrado* (RC), Rupestrian Grassland (RG), Marshy Grassland (MG), and Palm Swamp (PS). Through a multidimensional biodiversity approach, the research revealed that the flora is very distinct—therefore unique—among the vegetation types and that phylogenetic and functional diversities point to environmental filtering and specific adaptation strategies to different habitats. In Chapter 1, we explore the β-phylotaxonomic diversity within the vegetation types and propose that habitat heterogeneity plays a significant role in driving this diversity. Our study utilized Non-Metric Multidimensional Scaling (NMDS) to examine the *Cerrado* key bioclimatic, edaphic, fire, and relief variables on the distribution of vegetation types. The NMDS analysis identified two distinct floristic groups, supported by the low values of the Jaccard similarity index (< 50%) among all pairs. Additionally, we observed varying levels of phylogenetic diversity among the vegetation types, with significant clustering in sites of SSF, RG, MG, and PS, and more than 80% of the pairs showing high turnover (< 50%) for the Sorensen's phylogenetic similarity metric (PhyloSor). In Chapter 2, we delve into the same locations' trait diversity, with a specific focus on how environmental filtering and evolutionary history impact it. Our phylofunctional approach uncovered four distinct trait clusters through a Principal Coordinate Analysis (PCoA), primarily based on potential combinations of leaf trichome and fruit type attributes. These clusters appear to be a result of the south-north temperature and humidity gradient in the Espinhaço Range, as well as other factors such as soil depth and water availability. Each type of vegetation displays unique trait patterns. RG and RC demonstrate higher values of functional richness (FRic) and dispersion (FDis), while MG and PS exhibit higher functional divergence (FDiv) and evenness (FEve). Environmental filtering is apparent in all types based on either FRic or FDis. The decomposition of trait diversity among the nodes of the phylogeny resulted in a significant phylogenetic signal for habit and life form in the metacommunity. Our research offers valuable insights into the factors that impact the diverse range of plant species in the *Cerrado* hotspots within the ERBR. The preservation of ecotones is vital for the unique functioning and individual character of each vegetation type. As a result, conservation strategies that encompass the entire ecosystem are imperative for sustaining its environmental heterogeneity and biodiversity.

Keywords: *Cerrado*. Multidimensional diversity. Environmental heterogeneity. Hotspot. Espinhaço Range Biosphere Reserve.

GRAPHICAL ABSTRACT



SUMÁRIO

INTRODUÇÃO GERAL

A Fitogeografia é um ramo da ciência dedicado ao estudo da origem, da distribuição, das adaptações e das associações das plantas ao longo do tempo e do espaço, isto é, em relação a sua história evolutiva e a sua distribuição geográfica (Pinto et al. 2023). No contexto destas atribuições, as medidas de biodiversidade podem ser muito úteis, por descreverem as propriedades gerais das comunidades e permitirem comparar diferentes regiões, táxons e níveis tróficos (Leclerc & Megneville 2022).

A biodiversidade é um conceito multifacetado que tem pelo menos três dimensões: 1) Diversidade taxonômica: uma medida sensível a riqueza e abundância de espécies; 2) Diversidade filogenética: uma medida sensível à história evolutiva das espécies; e 3) Diversidade funcional: uma medida que considera as características biológicas das espécies (Chao et al. 2021). Além dessas dimensões, a diversidade é classificada em local (α), entre dois locais (β) e regional (γ), sendo esta seu somatório em todos os locais considerados (Whittaker 1972).

A título ilustrativo, as diversidades taxonômica, filogenética e funcional podem se combinar com as escalas α, β e γ. Este trabalho trata da diversidade α-funcional quando apresenta métricas funcionais por fitofisionomia; β-filogenética quando apresenta a porcentagem dos ramos da árvore filogenética compartilhada entre duas fitofisionomias; e γ-taxonômica quando apresenta o número total de espécies encontrado no conjunto das fitofisionomias consideradas no estudo. Dessa forma, a adoção de uma abordagem multidimensional da biodiversidade deve ser encorajada em estudos ecológicos (Altermatt et al. 2020).

Uma abordagem que considera múltiplas medidas para elucidar o funcionamento das comunidades e seus processos de montagem, em diferentes escalas, pode fornecer resultados holísticos e, portanto, mais assertivos para o entendimento e a conservação dos ecossistemas (Bhardwaj et al. 2023). Esta abordagem tem importância destacada quando a comunidade focal é vulnerável (Smith & Goetz 2021). O aumento das temperaturas terrestres, por exemplo, representa uma grande ameaça aos ecótones devido à sua sensibilidade climática (Costa et al. 2023).

Os ecótones, zonas de transição onde ecossistemas distintos se encontram e interagem, são uma parte importante da paisagem por abrigarem espécies únicas e oferecerem habitat adicional às espécies regionais de ampla distribuição, além de possuírem identidade própria e contribuírem para as áreas *core* (Souza et al. 2020).

A Serra do Espinhaço abriga uma região ecotonal resultante do encontro de três biomas: a Caatinga, o Cerrado e a Mata Atlântica, sendo os dois últimos *hotspots* de biodiversidade (Andrade et al. 2018). Esta faixa de relevo se divide em dois segmentos: o norte, denominado Chapada Diamantina, na Bahia, e o sul, em Minas Gerais, subdividido em Serra do Espinhaço Setentrional e Meridional (Machado & Gonzaga 2021). O segmento sul foi aprovado como Reserva da Biosfera da Serra do Espinhaço (RBSE) em 2005 devido a sua importância histórica, cultural, econômica e ambiental (UNESCO 2020).

O Cerrado é um ecossistema único e diversificado, composto por várias formações vegetais, como florestas, savanas e campos (Ribeiro & Walter 2008). Embora existam algumas espécies compartilhadas entre os tipos de vegetação, a flora deste bioma tem características distintas e difere dos biomas adjacentes (Ab'Saber 2003, Oliveira-Filho & Ratter 1995). O objeto de estudo deste trabalho são ecótones de Cerrado—embora as formações florestais em foco estejam também sob influência do Domínio Atlântico (Coelho et al. 2016)—na borda leste do Planalto Diamantino, porção central da RBSE ainda pouco estudada, caracterizados por sete fitofisionomias: Floresta Estacional Semidecidual, Capão de Mata, Cerrado *stricto sensu*, Cerrado Rupestre, Vereda, Campo Rupestre e Campo Úmido.

A considerável heterogeneidade florística e o complexo mosaico de tipos de vegetação no bioma Cerrado são altamente dependentes de fatores como o regime de fogo, a fertilidade e a disponibilidade hídrica do solo (Bueno et al. 2018). Ao longo deste complexo gradiente estrutural, apenas 11% do bioma é protegido em unidades de conservação e terras indígenas (Sano et al. 2019), o que põe em risco sua alta biodiversidade e provisão de serviços ecossistêmicos (Rodrigues et al. 2022).

No início deste século, o Painel Intergovernamental sobre Mudanças Climáticas já alertava para o fato de que, embora as mudanças ecológicas em resposta às alterações climáticas ocorram em todos os lugares, os sinais são detectados primeiro nos ecótones, o que os coloca em situação de ameaça (Leary et al. 2001). A perda de biodiversidade em escala global, em grande parte impulsionada por mudanças climáticas e de uso da terra, exige o desenvolvimento de diretrizes transparentes para estratégias de conservação eficazes (de Kort et al. 2020).

É neste cenário que se propõe esta dissertação, intitulada Fitogeografia de ecótones no Planalto Diamantino. Este é um dos produtos previstos no projeto APQ-01284-22—Padrões taxonômicos, funcionais e história evolutiva da vegetação em ecótones do Espinhaço Meridional e áreas adjacentes, aprovado e financiado pelo Edital Nº 001/2022 da FAPEMIG.

Nesta pesquisa, utilizamos múltiplas abordagens para compreender as diferenças florísticas, a funcionalidade e os processos evolutivos da flora dos ecótones na RBSE. Para tanto, abordamos as principais perguntas:

a. Como variáveis climáticas, edáficas, topográficas e de fogo afetam a circunscrição das fitofisionomias?

b. O *turnover* filogenético entre as fitofisionomias aumenta junto à dissimilaridade ambiental?

c. Há convergência ou divergência de traços funcionais nas fitofisionomias?

d. Os traços funcionais se associam majoritariamente a fatores históricos (filogenéticos) ou ecológicos?

Para responder a estas perguntas, a dissertação conta com dois capítulos em formato de artigo, na formatação padrão das revistas Elsevier. Seu texto original foi adaptado para evitar repetições. O primeiro artigo,—intitulado *Drivers of β-phylotaxonomic diversity in ecotones within the Espinhaço Range Biosphere Reserve*—, foi realizado a partir de análises filo-taxonômicas. O segundo artigo,—intitulado *Tracking the phylofunctional trajectories of ecotones in the Espinhaço Range Biosphere Reserve*—, tratou da diversidade funcional da vegetação e de sua decomposição ao longo da árvore filogenética.

As principais hipóteses dos capítulos são:

H_a. Variáveis edáficas desempenham um papel de destaque na composição de espécies, já que os sítios de estudo compartilham condições semelhantes de temperatura, precipitação e altitude;

H_b. Na vereda e no campo úmido, caracterizados por suas condições edáficas singulares, manifesta-se um *turnover* filogenético mais acentuado em virtude da composição distinta de espécies em comparação com outras fitofisionomias no Cerrado;

H_c. Traços semelhantes são agrupados, indicando convergência funcional;

H_d. Os traços funcionais se associam majoritariamente a fatores ecológicos, particularmente à filtragem ambiental.

Os resultados aqui apresentados são fruto dos esforços conjuntos ao longo dos anos de vários pesquisadores do laboratório de Fitogeografia, Vegetação e Ecologia (PHYVE) da Universidade Federal dos Vales do Jequitinhonha e Mucuri (UFVJM) e de outras Instituições de Ensino Superior. Pesquisas como esta têm sido realizadas por categorias ainda muito desvalorizada no Brasil, mas ansiosas por contribuir na conservação de um grande patrimônio: o Cerrado. Que sua leitura seja proveitosa!

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Chapter 1: Drivers of β-phylotaxonomic diversity in ecotones within the Espinhaço Range Biosphere Reserve

ABSTRACT

This study aimed to gain insight into the wide range of vegetation types in the *Cerrado* ecotones of the Diamantino Plateau, Brazil, emphasizing species diversity and phylogenetic structure. Our analysis of thirteen sites representing seven distinct vegetation types considered various environmental factors such as climate, soil composition, and other variables to evaluate the taxonomic and phylogenetic diversity of plant species. Our NMDS ordination revealed two distinct floristic groups, and the significant differences in floristic composition among vegetation types underscore the importance of habitat heterogeneity in promoting biodiversity. We observed that phylogenetic diversity varied across vegetation types, with significant clustering in some habitats indicating the influence of environmental filtering. Additionally, there was a high plant species turnover between vegetation types, suggesting unique phylogenetic structures. These findings highlight the need for targeted conservation efforts and additional research in this ecotonal landscape.

Keywords: Diamantino Plateau. Evolutionary history. Floral composition. Habitat heterogeneity. Transition zones.

1 INTRODUCTION

The ancient mountainous region known as the Espinhaço Range is a significant geological feature in southeastern Brazil. It is the largest and most continuous orogenic belt in the country, and it serves as a natural divider between the São Francisco River basin and the river basins that drain directly into the Atlantic Ocean (UNESCO 2020). In addition, it is the only UNESCO Brazilian biosphere reserve where three biomes meet: *Caatinga*, *Cerrado*, and the Atlantic Forest, being the last two hotspots of biodiversity (Andrade et al. 2018).

Research often suggests that species in biodiversity hotspots are particularly vulnerable to climate change due to their narrow ranges and persistence in regions of climatic stability over evolutionary time scales (Trew & Maclean 2021). The Espinhaço Range Biosphere Reserve (ERBR) is a region of speciation and persistence of different plant lineages, owing to its unique geological and climatic conditions (Vasconcelos et al. 2020). The area is characterized by lineages with limited reach, which have evolved in isolation through cyclical changes (Costa et al. 2023a).

Also, investigating the dynamics of ecotones can potentially offer valuable insights into the effects of climate change on both ecotones and adjacent ecosystems (Smith & Goetz 2021). These areas may be more than systems that originated from the surrounding core areas, as they may have undergone a series of evolutionary processes that have rendered them biologically distinctive systems (Souza et al. 2020). As a transitional landscape, the ERBR is especially sensitive to changing conditions (Costa et al. 2023a, b), making it a crucial site for the study of plant evolution and diversification.

Our study focused on a highly diverse *Cerrado* ecotonal area located in the Diamantino Plateau. However, it is worth noting that forest formations within the area are also under the influence of the Atlantic Domain (Coelho et al. 2016). To determine the α and β-diversity of this area, we employed taxonomic and phylogenetic approaches. The Plateau is found to be a floristic district within the Southern Espinhaço province, given its particular levels of species richness and endemism (Colli-Silva et al. 2019). Our study area is home to seven distinct vegetation types: Semideciduous Seasonal Forest, Forest Island (*Capão de Mata*), *Cerrado stricto sensu*, Rupestrian *Cerrado*, Palm Swamp (*Vereda*), Rupestrian Grassland, and Marshy Grassland.

The *Cerrado* biome is a unique and diverse ecosystem, consisting of various vegetation formations such as forests, savannas, and grasslands (Ribeiro & Walter

2008). Although there are some shared species among vegetation types, the flora of this biome has distinctive features and differs from adjacent biomes (Ab'Saber 2003, Oliveira-Filho & Ratter 1995). The considerable floristic heterogeneity and complex mosaic of vegetation types in the *Cerrado* biome are highly dependent on factors such as the fire regime, soil fertility, and soil water availability (Bueno et al. 2018).

In this context, our objective was to explore the vegetation types in the *Cerrado* ecotones of the Diamantino Plateau and answer a few key questions. Firstly, we aimed to determine how climatic, edaphic, and environmental factors impact these vegetation types. Based on our hypothesis, we expected edaphic factors to play a significant role in controlling the variation in species composition since the study sites share similar temperature, precipitation, and elevation conditions.

Secondly, we wanted to investigate whether phylogenetic diversity is influenced by vegetation types. We anticipated that forested areas would have higher phylogenetic diversity due to fewer limiting conditions than the other types. Thirdly, we explored how communities are structured phylogenetically. We hypothesized that communities would be predominantly clustered in the rupestrian grasslands, due to tough environmental conditions related to soil texture and water availability.

Finally, we examined whether phylogenetic turnover between vegetation types increases with environmental dissimilarity. We expected greater turnover in palm swamp and marshy grassland communities due to their distinct floristic composition from other *Cerrado* vegetation types based on permanent or seasonal flooding of the soil. A thorough understanding of the ecological dynamics of the region is crucial to effectively managing the ecotones on the Diamantino Plateau.

2 METHODOLOGY

2.1 Study area

The study area is in the northeastern portion of the Diamantino Plateau, Minas Gerais, Brazil (Fig. 1, Table 1).

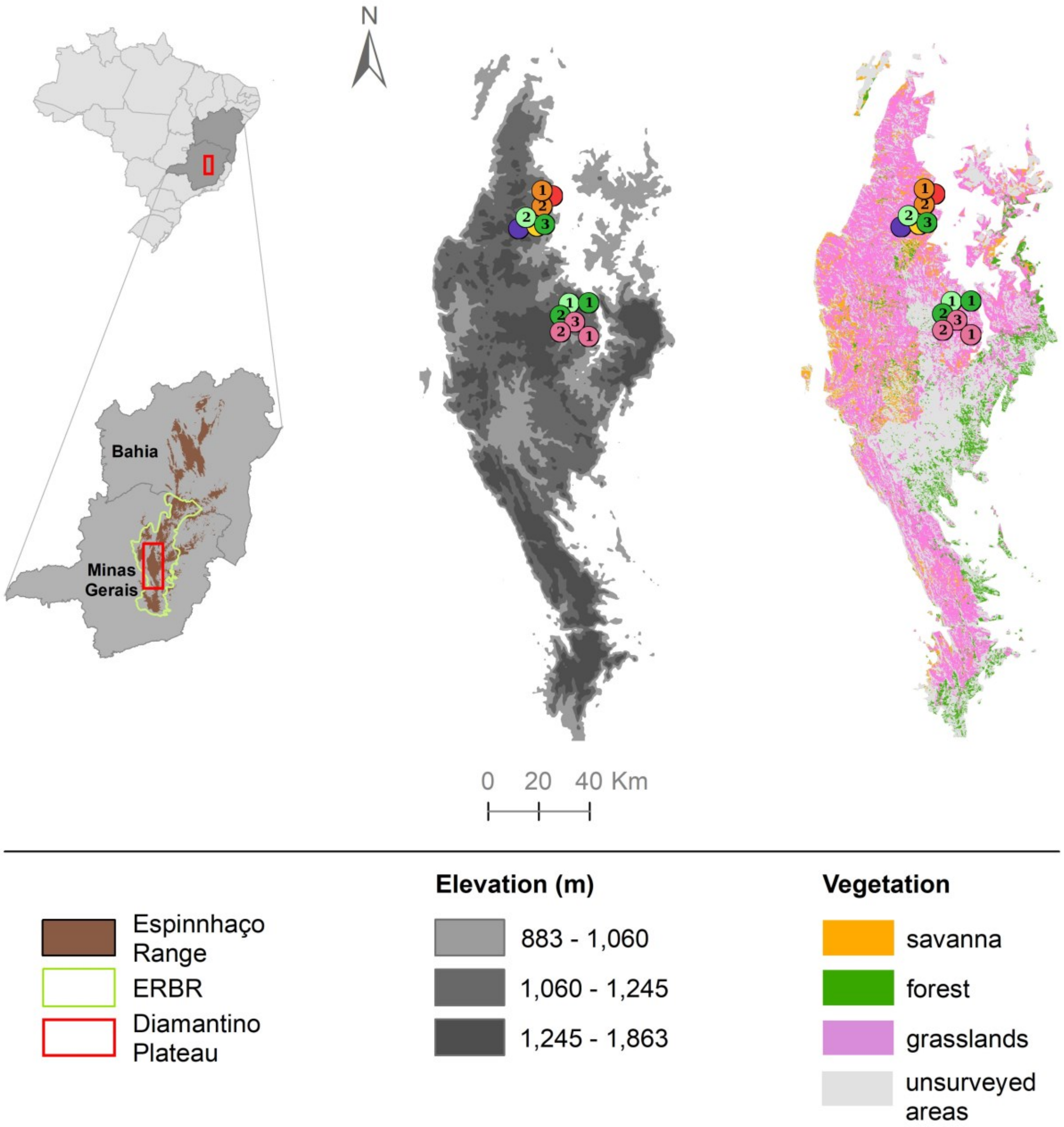

Figure 1. Map of study sites in the Espinhaço Range Biosphere Reserve (ERBR), Brazil. Vegetation types are indicated by colour of circle. Semideciduous seasonal forests (green), forest islands (light green), *cerrado stricto sensu* (yellow), rupestrian *cerrados* (orange), palm swamp (red), rupestrian grasslands (pink), and marshy grassland (purple). Study sites' numbers are listed in Table 1.

Our database consists of thirteen sites, distributed in seven vegetation types within the *Cerrado* biome: Semideciduous Seasonal Forest (SSF), Forest Island (FI), *Cerrado stricto sensu* (CSS), Rupestrian *Cerrado* (RC), Palm Swamp (PS), Rupestrian Grassland (RG), and Marshy Grassland (MG) (Fig. 1, Table 1).

Table 1 Geographic and environmental information of the study sites

Vegetation type	**Code**	**Study site**	**Coordinates** (decimal degrees)	**Total area sampled** (m^2)	**Annual mean temperature**[1] (°C)	**Annual mean precipitation**[1] (mm)	**Elevation**[1] (m)	**Soil Class**[2]	**Reference**
Forest Island	FI	①	-18.187674, -43.579352	1300	18.7	1491	1354	Acrisol	Moura et al. 2021
		②	-17.892621, -43.731637	3200	19.4	1362	1230	Gleysol	Costa et al. 2022
Semideciduous Seasonal Forest	SSF	①	-18.164832, -43.508920	10000	20.5	1338	942	Arenosol	Silva et al. 2020
		②	-18.194111, -43.590210	10000	18.2	1496	1380	Acrisol	Costa et al. 2020
		③	-17.878812, -43.670032	12000	19.9	1327	1158	Cambisol	Silva et al. 2020
Cerrado stricto sensu	CSS	●	-17.885007, -43.687855	10000	19.4	1357	1116	Arenosol	Costa et al. 2022
Rupestrian *Cerrado*	RC	①	-17.788838, -43.638930	10000	20.8	1172	679	Arenosol	unpublished
		②	-17.792346, -43.641464	40	20.9	1165	727	Arenosol	Mello 2012
Palm Swamp	PS	●	-17.794439, -43.620528	15	22.0	1159	696	Gleysol	Mello 2012
Rupestrian Grassland	RG	①	-18.282853, -43.518437	5000	19.3	1448	1088	Arenosol	Roberto 2023
		②	-18.256203, -43.594580	61820	19.5	1426	1174	Arenosol	Freire et al. 2021
		③	-18.197192, -43.590773	5000	18.4	1495	1407	Arenosol	Oliveira et al. 2014
Marshy Grassland	MG	●	-17.900236, -43.744962	15	19.4	1363	1265	Gleysol	Mello 2012

Source: Authors 2024, FAO 2022[2], Fick & Hijmans 2017[1].

The study area is classified as Cwb in terms of climate, denoting dry winters and warm summers (Köppen & Geiger 1936). Within Minas Gerais, we observe these climatic patterns in elevated areas, such as the Espinhaço Range (Antunes 1986). The study sites have an elevation ranging from 679 m to 1407 m. The average annual precipitation ranges from 1159 mm to 1496 mm, while the average annual temperature varies between 18.2 ºC and 22 ºC (Table 1).

The Diamantino Plateau has landscapes supported by a flat surface from the Tertiary period, interrupted by valleys that cut through pre-Cambrian quartzite and conglomerate layers (Lacerda & Saadi 2017). The area's geological makeup is primarily composed of quartzites and filites, which serve as the main components of the shallow, alibic and dystrophic soils (Mucida et al. 2019). The most prevalent soil types are Arenosol, Gleysol, Cambisol and Plinthosol. Additionally, Histosols can be found in wetlands and low-lying areas (Abreu Filho et al. 2021).

2.2 Dataset

We collected data on 546 species from the references in Table 1. The Phytogeography, Vegetation, and Ecology (PHYVE) laboratory team conducted these surveys, providing reliable sampling and species identification for community-level analysis. To ensure consistency among vegetation types, we used the sampled square meter as a plot for all sites (Hsieh et al. 2022). We based our analysis on incidence data (Chao et al. 2005, Chao et al. 2006, Hsieh et al. 2022, Rezende et al. 2020), updated all species names according to Flora e Funga do Brasil (2024), and removed any records that could not be identified at the species level.

To analyze how species compositional variation correlates with the *Cerrado* key ecological factors of soil fertility, water availability, and fire (Bueno et al. 2018), we obtained 20 variables (Fig. 2). We included elevation as an integrative environmental variable (Bueno et al. 2018) to test our first hypothesis. We collected all variables with a spatial resolution of 30 seconds.

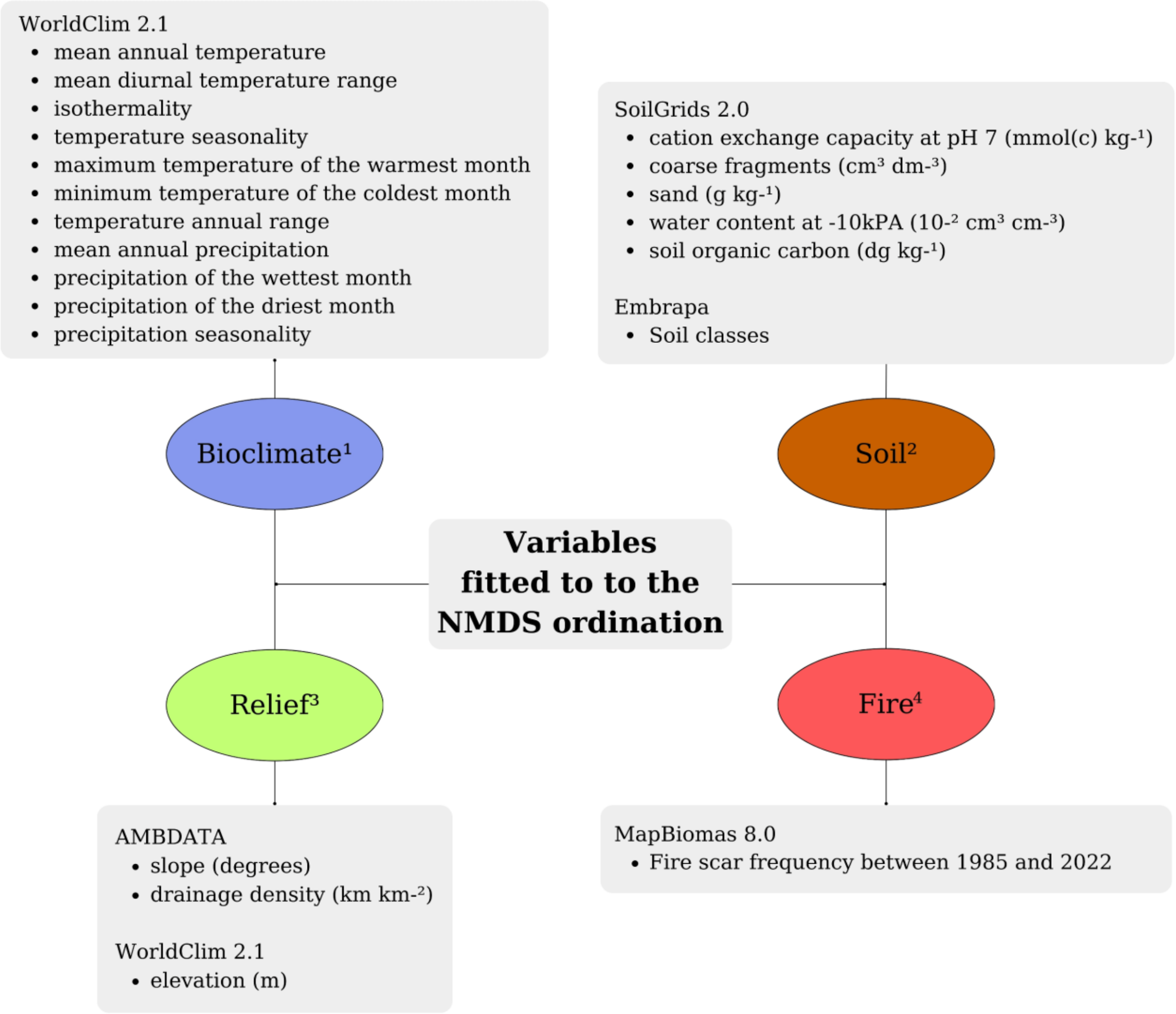

Figure 2. Variables fitted to the NMDS ordination.
Source: Amaral et al. 2013[3], Embrapa 1999[2], Fick & Hijmans 2017[1,3], MapBiomas Project 2023[4], Poggio et al. 2021[2].

We utilized the volume of coarse fragments and the percentage of slope as proxies for soil depth (Poesen & Lavee 1994), the volume of soil water content and drainage density as proxies for soil water availability (Berhanu & Hatiye 2020, Graf et al. 2014), the cation exchange capacity and the volume of soil organic carbon as proxies for soil fertility (Brady & Weil 2017, Lal 2016, Nel et al. 2023), and the fire scar frequency as a proxy for fire frequency (Kehrwald et. al 2016).

2.3 Taxonomic diversity

To analyze species richness across different vegetation types, we generated sampling curves of Hill numbers alongside 95% confidence intervals for species richness, based on incidence data from sampling units (Rodrigues & Fidelis 2022). We plotted the curves using the base ten logarithm of the total area sampled in square meters for each type of vegetation and omitted the confidence intervals from the graph to effectively visualize the progression trends in diversity.

Next, we performed a Non-Metric Multidimensional Scaling (NMDS) analysis to determine the floristic consistency between the vegetation types, using the species composition data from the study sites (McCune & Grace 2002). We adopted Simpson distance as the floristic dissimilarity metric to account for differences in species richness among sites (Kreft & Jetz 2007). To evaluate compositional differences within the NMDS framework, we used Multi-Response Permutation Procedures (MRPP) and Analysis of Similarities (ANOSIM) (Bueno et al. 2018). After the initial analysis, we fitted environmental variables to the NMDS ordination. In parallel, we calculated the Jaccard similarity index between vegetation types, using the methods outlined by Kent & Coker (1992) and Mueller-Dombois & Ellenberg (2002). Finally, we created a Venn diagram to display the total, exclusive, and shared number of species among vegetation types.

We conducted all analyses in the R 4.2.1 Statistical Environment (R Core Team 2019) using the packages: ‘iNEXT’ (Hsieh et al. 2022) and ‘vegan’ (Oksanen et al. 2016).

2.4 Phylogenetic diversity

We created a phylogenetic tree with 546 tips and 416 internal nodes, using the Angiosperm Phylogeny Group IV system (The Catalogue of Life Partnership 2017). We utilized a mega-tree approach under scenario 3, whereby tips of a new genus or species not included in the mega-tree are added to the midpoint between the family or genus branch and the basal node (Jin & Qian 2019). To explore how vegetation types can influence phylogenetic diversity, we computed species richness and phylogenetic diversity (PD) - the sum of branch lengths in a phylogeny, encompassing species in the community (Faith 1992). Additionally, we calculated ses.PD to normalize this measure for species richness. To do so, we drew the same number of species from the phylogeny as present in the community, with 999 iterations (Rezende et al. 2020).

We tested the third hypothesis using two indices - ses.MPD and ses.MNTD, as different processes may act at different evolutionary time scales (Mazel et al. 2016). The ses.MPD index analyzes the standardized effect size of the mean phylogenetic distance (MPD), which is the average phylogenetic distance between two taxa in the phylogeny. This reveals relationships that are deep in the phylogeny. Conversely, the ses.MNTD index examines the standardized effect size of the mean nearest taxon distance (MNTD), which is the average phylogenetic distance between a taxon and its nearest neighbor in the phylogeny. This reflects relationships closer to the tips (Webb et al. 2008).

For the fourth question, we used the phylogenetic Sorensen's similarity (PhyloSor) metric to calculate the phylobetadiversity. We aimed to investigate whether the phylogenetic turnover between vegetation types increases with environmental dissimilarity. The PhyloSor metric determines the proportion of shared species' branch length relative to the total branch length of all species in two communities (Bryant et al. 2008). We conducted all analyses in the R 4.2.1 Statistical Environment (R Core Team 2019) using the following packages: ‘picante’ (Kembel et al. 2010), ‘phytools’ (Revell 2012) and ‘V.PhyloMaker’ (Jin & Qian 2019).

3 RESULTS

Fabaceae (43), Myrtaceae (35), Asteraceae (34), Melastomataceae (27) and Poaceae (27), the most species-rich families in the study area, account for 30% (116) of the total species richness. The analyses of potential species richness, species composition and floristic similarity showed that the seven vegetation types converge in exhibiting very distinct flora (Figs. 3, 4). We found all differences between the types to be significant by the analysis of the confidence intervals (95%) of the curves.

Moreover, the curves indicated higher potential species richness for SSF, FI and RG, while PS, MG and CSS presented the lowest potential. Accordingly, the NMDS, the ANOSIM and the MRPP indicated that two groups (ANOSIM, $R = 0.68$, $p = 0.015$; MRPP, $A = 0.10$, $p = 0.014$) provide better categorization of sites, with the same level of discrimination, rather than seven groups (ANOSIM, $R = 0.48$, $p = 0.016$; MRPP, $A = 0.15$, $p = 0.014$) (Fig. 4).

The first group (left side of the compositional space) consisted of RG, RC, CSS, FI and SSF, which had a distinct floral composition compared to the second group (right side), MG and PS. A stress value of 0.058, a stress-based R^2 of 0.997 and a fit-based R^2 of 0.988 indicate that two dimensions are sufficient to represent the variation in the data and the overall match between the configuration and the data is excellent.

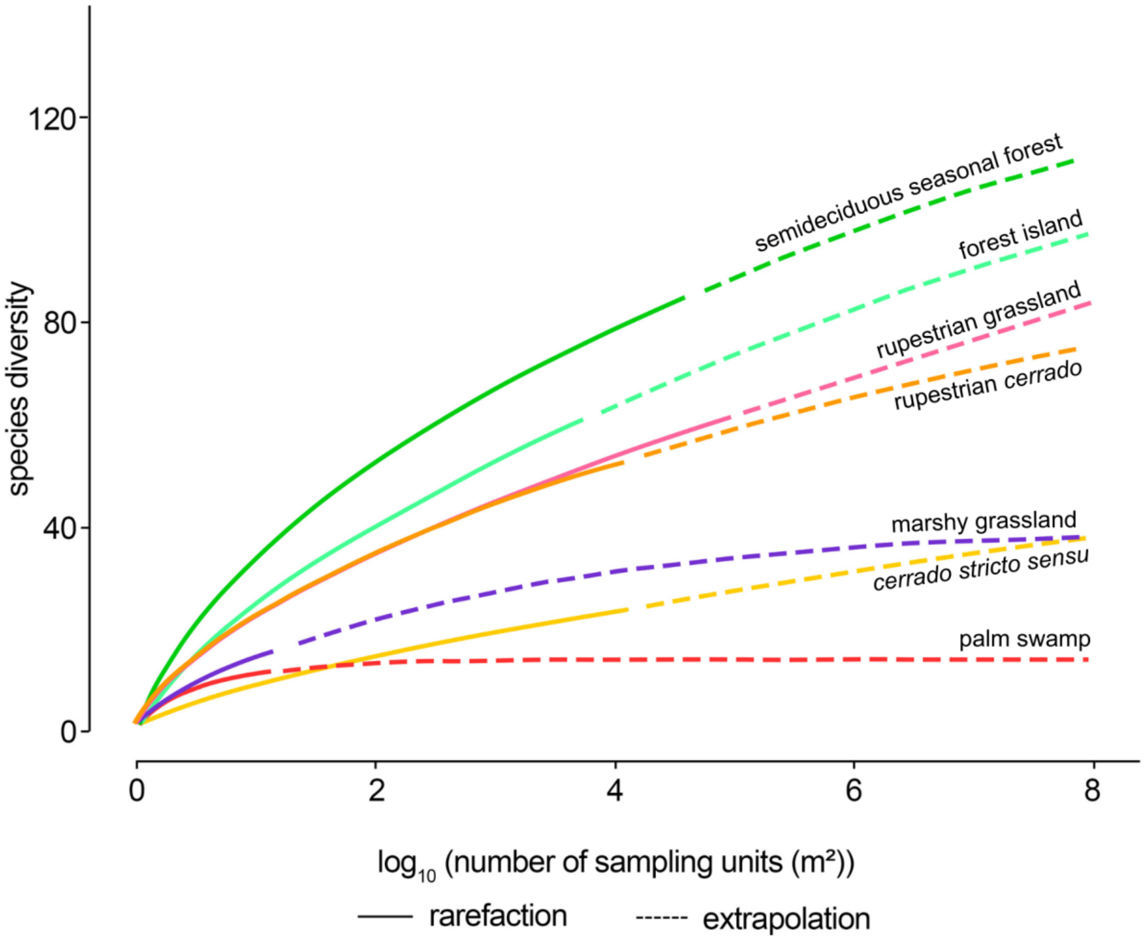

Figure 3. Sampling curves of Hill numbers for species richness, based on incidence data from sampling units in seven vegetation types in the Diamantino Plateau, Brazil. Vegetation types are indicated by colour of the curve. Semideciduous seasonal forests (green), forest islands (light green), *cerrado stricto sensu* (yellow), rupestrian *cerrados* (orange), palm swamp (red), rupestrian grasslands (pink) and marshy grassland (purple).

The Jaccard index values indicate that the vegetation types have a low similarity in terms of their species composition with values below the minimum threshold of 50% (Gauch 1982) (Fig. 4). The different types have few species in common and no species is present in all of them. The pairs with the highest floristic similarity were MG – PS (S_J = 29%) and SSF – FI (S_J = 17%), while PS – RG (S_J = 1.3%), and MG – RC (S_J = 2.9%) had the lowest floristic similarity.

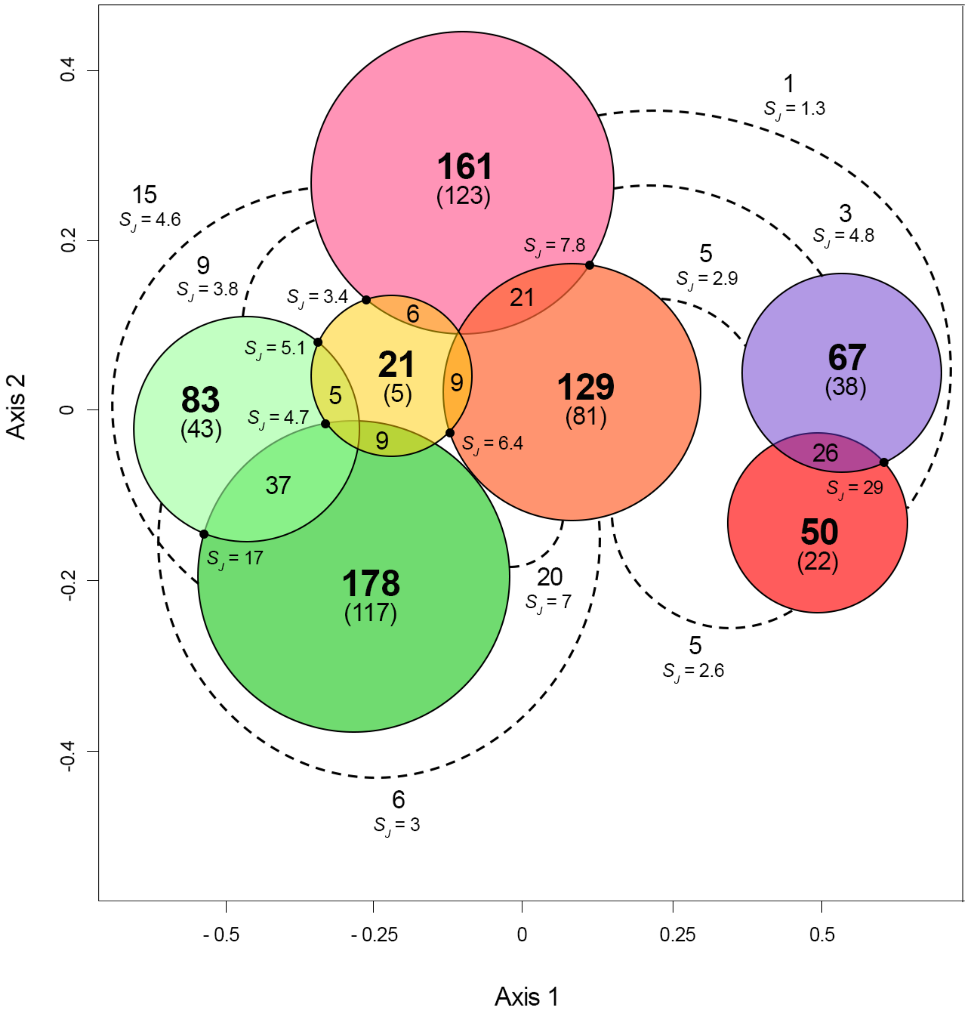

Figure 4. Species turnover among seven vegetation types. The circles represent the vegetation types. Semideciduous seasonal forests (green), forest islands (light green), *cerrado stricto sensu* (yellow), rupestrian *cerrados* (orange), palm swamp (red), rupestrian grasslands (pink) and marshy grassland (purple). Numbers in bold represent the total species in the vegetation type and the number in brackets gives the number of exclusive species; numbers on the dashed lines and in the congruence of circles represent the shared species. The Jaccard similarity index (S_J (%)) is shown on dashed lines and at the black dots in the congruence of circles.

None of the selected variables was key to explaining species composition within the two groups (Tables S1, S2). Conversely, we found a strong correlation between phylogenetic diversity (PD) and species richness (Figs. 5, S1). The SSF and RG (study site 1 for both) displayed the highest PD values, while RG (study site 3) had the lowest. The standardized metric of PD (ses.PD) showed the highest values for the rupestrian types (study site 2 for both) and a low value for PS (Fig. 5, Table S3). In terms of the standardized metric of MPD (ses.MPD), both forest types (study site 1 for both) showed high values while RG (study site 1) had a low one. In contrast, ses.MNTD had the highest value for MG and the lowest value for SSF (study sites 2 and 3) .

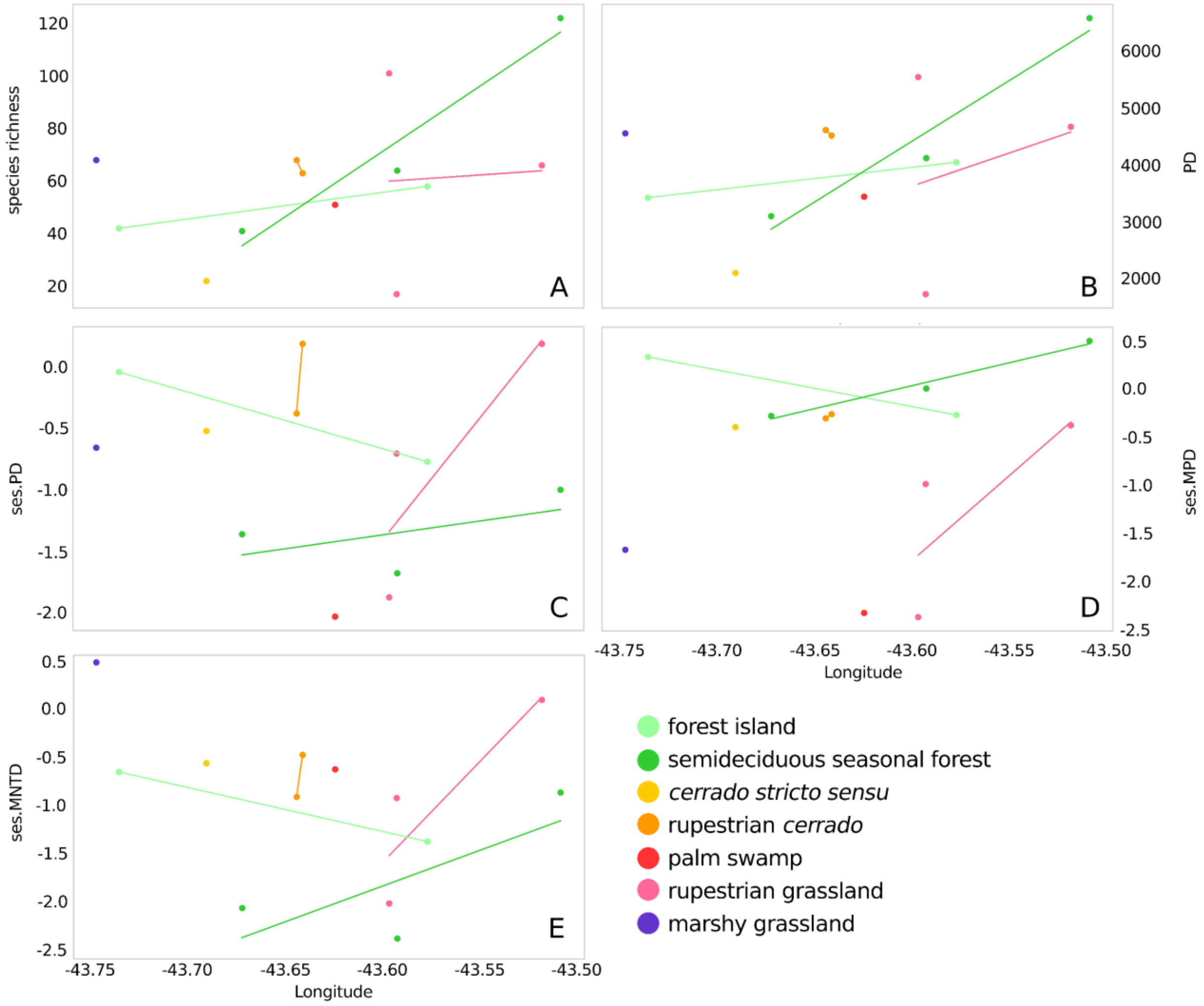

Figure 5. Phyloalpha diversity considering the longitude from different vegetation types in the Diamantino Plateau. A) species richness, B) phylogenetic diversity (PD), C) phylogenetic diversity standardized by the variation in species richness (ses.PD) and the standardized measures of D) mean pairwise distance (ses.MPD) and E) mean nearest taxon distance (ses.MNTD). Each circle represents the value for a single study site.

More than 90% of the study sites ses.MPD and ses.MNTD values fell between -1.96 and 1.96, indicating that phylogenetic diversity is not significantly different from what would be expected from a random distribution (Fig. 5, Table S3). However, we observed significant p-values ($p < 0.05$) for ses.MPD in RG (study sites 1 and 3), MG and PS, indicating phylogenetic clustering in these locations. Additionally, we found significant p-values ($p < 0.05$) for ses.MNTD in RG (study site 1) and SSF (study sites 2 and 3), suggesting phylogenetic clustering in these areas as well (Table S3).

Based on our analysis using PhyloSor, PS exhibited the highest levels of phylogenetic turnover (Fig. 6). We observed four instances of similarity that exceeded 50%: PS – MG (61%); SSF – FI (55%); SSF – RC (52%); RC – RG (51%). However, more than 80% of the pairs presented values lower than 50%, indicating high turnover and phylogenetic dissimilarity. SSF and PS exhibited the lowest similarity value (26%).

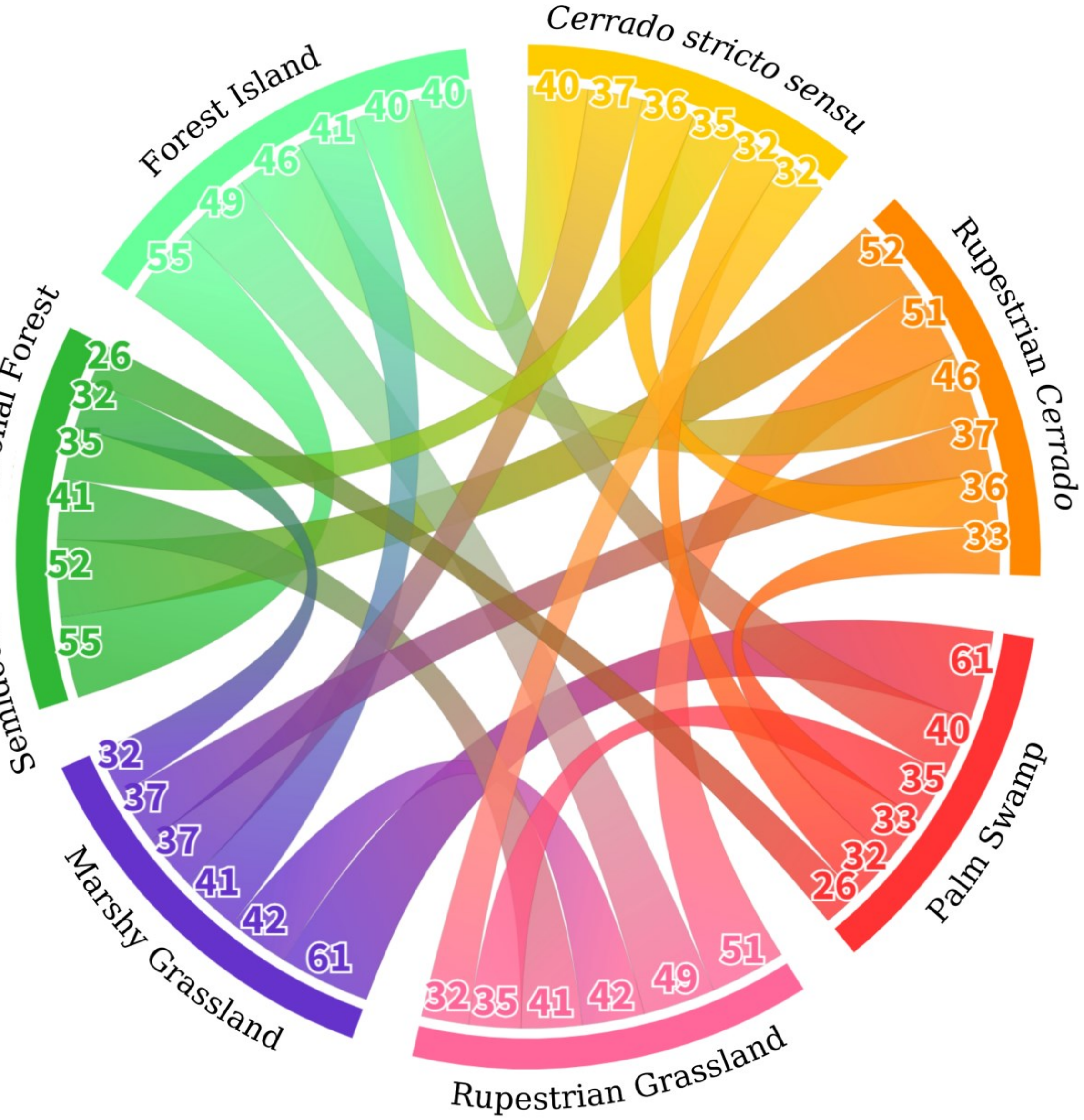

Figure 6. Phylogenetic turnover among the different vegetation types found in the Diamantino Plateau, Brazil. Numbers represent the Phylogenetic Sorensen’s Similarity (PhyloSor) percentage.

4 DISCUSSION

The observed potential species richness among vegetation types, with SSF, FI, and RG displaying higher potential species richness, supports the role of habitat heterogeneity in shaping species diversity (Connell 1978, Huston 1994, Whittaker 1975). Following the habitat heterogeneity hypothesis, a greater number of species may successfully coexist within heterogeneous environments (Stein et al. 2014) such as the Diamantino Plateau (Machado & Gonzaga 2021) (Fig. 7).

The *Cerrado* forests have high spatial heterogeneity on the landscape scale (Oliveira-Filho & Ratter 2002, Redford & Fonseca 1986), while the Rupestrian Grassland consists of a diverse range of habitats, distinguished by substrate configuration, vegetation continuity, exposed rock proportion, and the presence of rock blocks and sand sediments (Conceição 2000, Conceição & Pirani 2005, 2007).

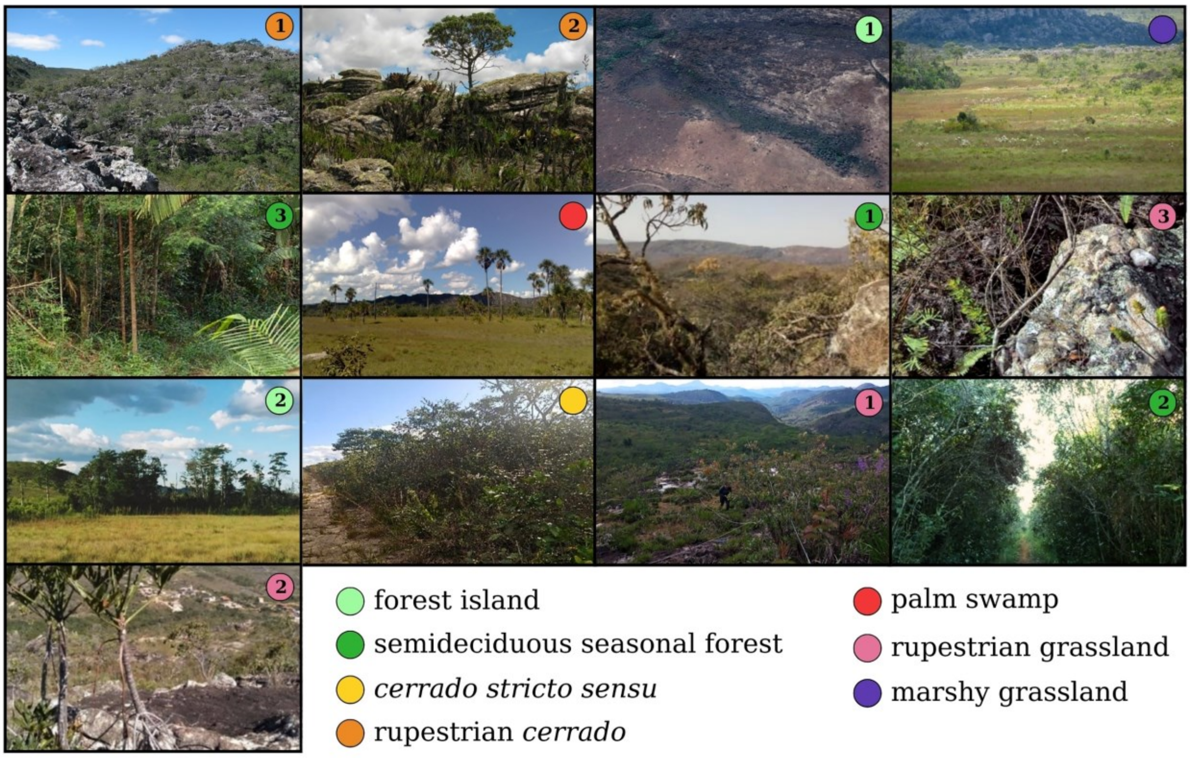

Figure 7. Heterogeneous landscape on the Diamantino Plateau, Brazil. Study sites' numbers are listed in Table 1.

Fabaceae exhibited the highest species richness amongst the sampled taxa. It is the most diverse and species-rich family in the Brazilian flora; approximately 50% of its species are native to the country (Soares et al. 2024). This result is in line with the family's extraordinary array of life forms and morphological structures, rendering it among the most diverse across a vast range of major global biomes (Flora e Funga do Brasil 2024). The most species-rich families of the area reflect the study sites' formations: Fabaceae and Myrtaceae trees in the forests, Asteraceae and Melastomataceae shrubs in the savannas, and Poaceae herbs in the grasslands (Almeida et al. 2023).

Furthermore, we found the seven focal vegetation types better divided into two distinct floristic groups based on their species composition. Given that our study area spans a narrow latitudinal range, likely, the variables we selected alone are not sufficiently sensitive to circumscribe the vegetation types distribution (Rapini et al. 2021). However, one might note that this flora is mainly composed of edaphic-specialist species (Fernandes et al. 2024, Lambers et al. 2018, Oliveira et al. 2015).

Tropical quartzite highlands are deeply fragmented at multiple levels due to recurrent fire disturbance, complex topography, and edaphic heterogeneity (Pacifico et al. 2021, Rapini et al. 2021). For this reason, we strongly believe that the edaphic conditions play a role in determining the species composition among the vegetation types (Costa et al. 2023b, Gomes et al. 2023, Gomes et al. 2021, Loiola et al. 2023), but to determine so, the use of a local-scale database is encouraged rather than a 30-second resolution dataset (Fernandes et al. 2024).

Secondly, we expected that phylogenetic diversity would be higher in forested areas due to fewer limiting conditions. While this hypothesis was partially supported, as some forested study sites indeed exhibited high values for PD and ses.PD, the rupestrian types had similar results for both metrics. Biotic interactions—such as competition among species with comparable filtered functional traits—, dispersion limitation and other environmental variables—such as soil—, might help explain the phylogenetic diversity distribution in the area (Abrahão et al. 2019, Le Bagousse-Pinguet et al. 2017, Silveira et al. 2019, Tameirão et al. 2021).

The geographic disjunction among Rupestrian Grassland sky islands serves as a significant driver of genetic disruptions, ultimately contributing to high species diversity (Silveira et al. 2016). In the context of analyzing morphological variation among species over their evolutionary trajectory inferred from genetic data, it becomes apparent that divergence histories are not only specific to each species but also that defining a species based on morphology alone may obscure unrecognized species diversity and instances of unexpected hybridization (Fiorini et al. 2023).

Heterogeneity of microhabitats also fosters frequent species turnover, contributing to high beta-diversity (Andrino et al. 2021, Araújo et al. 2022, Loiola et. al 2023, Nunes et al. 2020) as seen in our PhyloSor results. Additionally, as Old, Climatically Buffered, Infertile Landscapes (OCBILs), they have been accessible for independent colonizations for an extended period and provided prolonged climatic stability, enabling the diversification of species (Rapini et al. 2021). These landscapes have hosted lineages from both historical and recent radiations, resulting in the accumulation of species diversity over time (Cowling et al. 2014, Eiserhardt et al. 2017, Jansson & Dynesius 2002).

The highest values found for ses.PD and ses.MNTD suggest a greater lineage diversity in these communities, while the highest value of ses.MPD in the forest types are probably a result of ancient diversification in the lineages (Cupertino-Eisenlohr & Oliveira-Filho 2020, Qian et al. 2017, Rapini et al. 2021). These ancient lineages may have evolved from exaptations, allowing them to colonize the Rupestrian Grassland from adjacent biomes, likely selected by edaphic rather than climatic filters, as suggested for the Cape Floristic Region (Santen & Linder 2020).

Furthermore, disturbances, such as fires, or significant changes in climate, such as extreme temperature shifts, can reduce the pressure of natural selection in highly competitive communities, allowing populations that are well adapted to one substrate to outcompete others on a different one (Levin 2003, Rajakaruna 2018). Over time, these populations may adapt to the new conditions without that disturbance and become established in the new environment, leading to ecological divergence from their original habitat (Rapini et al. 2021).

Thirdly, the harsh conditions in the Diamantino Plateau would also be responsible for the clustered phylogenetic pattern found for species in the phylogeny within SSF, RG and the soaked communities for all the ses metrics. Soil texture and water availability in Rupestrian Grassland may reduce the number of species by selecting those best adapted (Negreiros et al. 2014). Moisture works similarly in PS and MG (Munhoz & Felfili 2008, Silva et al. 2022).

In the study sites of SSF where we observed phylogenetic clustering, it is pertinent to acknowledge that the presence of rocky outcrops in the soil might have affected certain plots. However, we cannot assume that this pattern is caused only by environmental filtering, since all the other vegetation types presented random phylogenetic values, suggesting that phylogenetic restrictions did not play a role in the species pool adapted to the environmental conditions present in the study area (Rezende et al. 2019).

Finally, we expected greater turnover in PS and MG due to distinct floristic compositions and soil soaking conditions. The substantial turnover observed in these habitats aligns with this hypothesis, suggesting the influence of edaphic factors and evolutionary history (Guimarães et al. 2002, Munhoz & Felfili 2008, Ramos et al. 2006, Resende et al. 2013). The high floristic and phylogenetic dissimilarity among our focal vegetation types highlights the unique ecological conditions fostered by these transitional zones, emphasizing their role as hotspots of biodiversity and their evolutionary trajectories (Souza et al. 2020).

Such ecological uniqueness is a priority for conservation due to the rich biological heritage of ecotonal regions (Costa et a. 2023a, Whittaker 1975). Conservation strategies tailored to these ecotonal areas must consider the dynamic nature of ecotones and the specific ecological niches they harbor, ensuring the maintenance of habitat heterogeneity essential for supporting diverse plant communities. By safeguarding these ecotonal landscapes, we can not only protect endemic and endangered species (Colli-Silva et al. 2019) but also maintain ecosystem resilience in the face of ongoing environmental changes.

5 CONCLUSION

Our findings show that the current flora in the focal vegetation types can be best categorized into two floristic groups with high β-phylotaxonomic diversity in an environment with harsh conditions. We believe that this phenomenon is influenced by environmental heterogeneity, including fire disturbance, complex topography, and edaphic conditions, as well as climatic stability, biotic interactions, and dispersion limitation.

In relation to our hypotheses:

1st. Not supported: The selected edaphic variables were not sensitive enough to distinguish the vegetation types, so we recommend the use of a local-scale database instead of a 30-second resolution dataset in similar studies;

2nd. Partially supported: Rupestrian grasslands and rupestrian *cerrados* displayed high phylogenetic diversity together with forests, likely due to biological interactions—such as competition among species with similar filtered functional traits—, allowing well-adapted populations to specialize on different microhabitats, and ultimately leading to ecological divergence;

3rd. Partially supported: The clustered phylogenetic pattern found in semideciduous seasonal forests, rupestrian grasslands, and soaked communities is likely related to soil texture and water availability;

4th. Supported: We observed greater turnover in palm swamp and marshy grassland- communities due to distinct floristic compositions, suggesting the influence of edaphic factors and evolutionary history on their floral composition.

We hope that our results help emphasize the potential impact of climate change on the unique and vulnerable ecosystem of this highly diverse region in the ERBR.

SUPPLEMENTARY MATERIAL

Table S1 Variables and their associations with NMDS axes for seven groups

Variable	NMDS1	NMDS2	R^2	Pr(>R)
coarse fragments (0-5)	0.13128	-0.9913	0.1896	**0.32**
coarse fragments (5-15)	0.09113	-0.9958	0.1608	0.386
coarse fragments (15-30)	0.09587	-0.9954	0.1237	0.496
coarse fragments (30-60)	0.03216	-0.9995	0.0295	0.853
coarse fragments (60-100)	0.23506	-0.972	0.0222	0.886
coarse fragments (100-200)	0.40723	0.91333	0.0572	0.738
drainage density	0.17792	-0.984	0.0877	0.628
elevation	-0.4787	0.87801	0.163	0.404
fire scar frequency	-0.7711	0.63668	0.0349	0.837
isothermality	0.99991	-0.0133	0.1272	0.494
maximum temperature of the warmest month	0.49291	-0.8701	0.1917	**0.367**
mean annual precipitation	-0.7111	0.7031	0.1639	0.425
mean annual temperature	0.56895	-0.8224	0.1757	0.399
mean diurnal temperature range	0.74578	-0.6662	0.1538	0.431
minimum temperature of the coldest month	0.52138	-0.8533	0.1568	0.433
precipitation of the driest month	-0.8694	0.4942	0.1983	**0.35**
precipitation of the wettest month	-0.6491	0.76067	0.1441	0.448
precipitation seasonality	0.80386	-0.5948	0.1738	0.387
sand (0-5)	-0.2631	0.96477	0.0145	0.931
sand (5-15)	-0.2422	0.97023	0.026	0.88
sand (15-30)	-0.317	0.94843	0.0259	0.884
sand (30-60)	-0.4632	0.88625	0.0288	0.87
sand (60-100)	-0.3182	0.94804	0.0338	0.852
sand (100-200)	-0.4021	0.91559	0.011	0.949
slope	0.17685	0.98424	0.1017	0.591
soil organic carbon (0-5)	-0.7157	0.69844	0.0252	0.885
soil organic carbon (5-15)	-0.9705	0.24132	0.0272	0.884
soil organic carbon (15-30)	-0.7237	0.69012	0.0399	0.829
soil organic carbon (30-60)	-0.8784	0.47789	0.0311	0.865
soil organic carbon (60-100)	-0.788	0.61563	0.0348	0.85
soil organic carbon (100-200)	-0.6996	0.71456	0.0348	0.845
soil texture	-0.9993	0.01154	0.0193	0.899
temperature annual range	0.46438	-0.8856	0.2174	**0.316**
temperature seasonality	0.23289	-0.9725	0.1501	0.457
water content (0-5)	-0.0167	0.99986	0.0993	0.606
water content (5-15)	0.02042	0.99979	0.0585	0.675
water content (15-30)	-0.0044	0.99999	0.0936	0.613
water content (30-60)	0.01403	0.9999	0.0828	0.627
water content (60-100)	0.03478	0.99939	0.0714	0.67
water content (100-200)	0.01639	0.99987	0.0859	0.631

Source: Authors 2024.

Table S2 Variables and their associations with NMDS axes for two groups

Variable	**NMDS1**	**NMDS2**	**R^2**	**Pr(>R)**
coarse fragments (0-5)	0.12995	-0.9915	0.1926	**0.339**
coarse fragments (5-15)	0.08989	-0.996	0.1657	0.394
coarse fragments (15-30)	0.09458	-0.9955	0.1275	0.485
coarse fragments (30-60)	0.03199	-0.9995	0.0305	0.873
coarse fragments (60-100)	0.22413	-0.9746	0.024	0.892
coarse fragments (100-200)	0.42025	0.90741	0.0561	0.775
drainage density	0.18376	-0.983	0.0816	0.655
elevation	-0.4954	0.86865	0.1585	0.402
fire scar frequency	-0.7623	0.64728	0.0349	0.854
isothermality	0.99904	0.04369	0.1268	0.501
maximum temperature of the warmest month	0.50741	-0.8617	0.1873	**0.356**
mean annual precipitation	-0.7291	0.6844	0.162	0.406
mean annual temperature	0.58643	-0.81	0.1722	0.383
mean diurnal temperature range	0.76611	-0.6427	0.1519	0.432
minimum temperature of the coldest month	0.54046	-0.8414	0.1528	0.417
precipitation of the driest month	-0.8836	0.46827	0.197	**0.328**
precipitation of the wettest month	-0.6672	0.74485	0.1419	0.464
precipitation seasonality	0.82533	-0.5647	0.1719	0.378
sand (0-5)	-0.2606	0.96544	0.0146	0.94
sand (5-15)	-0.2415	0.97041	0.026	0.887
sand (15-30)	-0.3171	0.9484	0.0259	0.888
sand (30-60)	-0.4696	0.88288	0.0285	0.867
sand (60-100)	-0.3217	0.94685	0.0333	0.853
sand (100-200)	-0.4054	0.91416	0.0109	0.952
slope	0.18442	0.98285	0.096	0.58
soil organic carbon (0-5)	-0.7689	0.63932	0.0243	0.877
soil organic carbon (5-15)	-0.9898	0.14216	0.0269	0.863
soil organic carbon (15-30)	-0.7521	0.65908	0.0391	0.817
soil organic carbon (30-60)	-0.9133	0.40733	0.0305	0.852
soil organic carbon (60-100)	-0.8209	0.57104	0.0341	0.84
soil organic carbon (100-200)	-0.733	0.68026	0.0339	0.842
soil texture	-0.9792	-0.2031	0.0191	0.889
temperature annual range	0.47463	-0.8802	0.2132	**0.313**
temperature seasonality	0.23825	-0.9712	0.144	0.453
water content (0-5)	-0.0167	0.99986	0.0979	0.625
water content (5-15)	0.02045	0.99979	0.0581	0.691
water content (15-30)	-0.0043	0.99999	0.0926	0.634
water content (30-60)	0.01412	0.9999	0.0821	0.645
water content (60-100)	0.03508	0.99938	0.0704	0.682
water content (100-200)	0.01671	0.99986	0.0844	0.647

Source: Authors 2024.

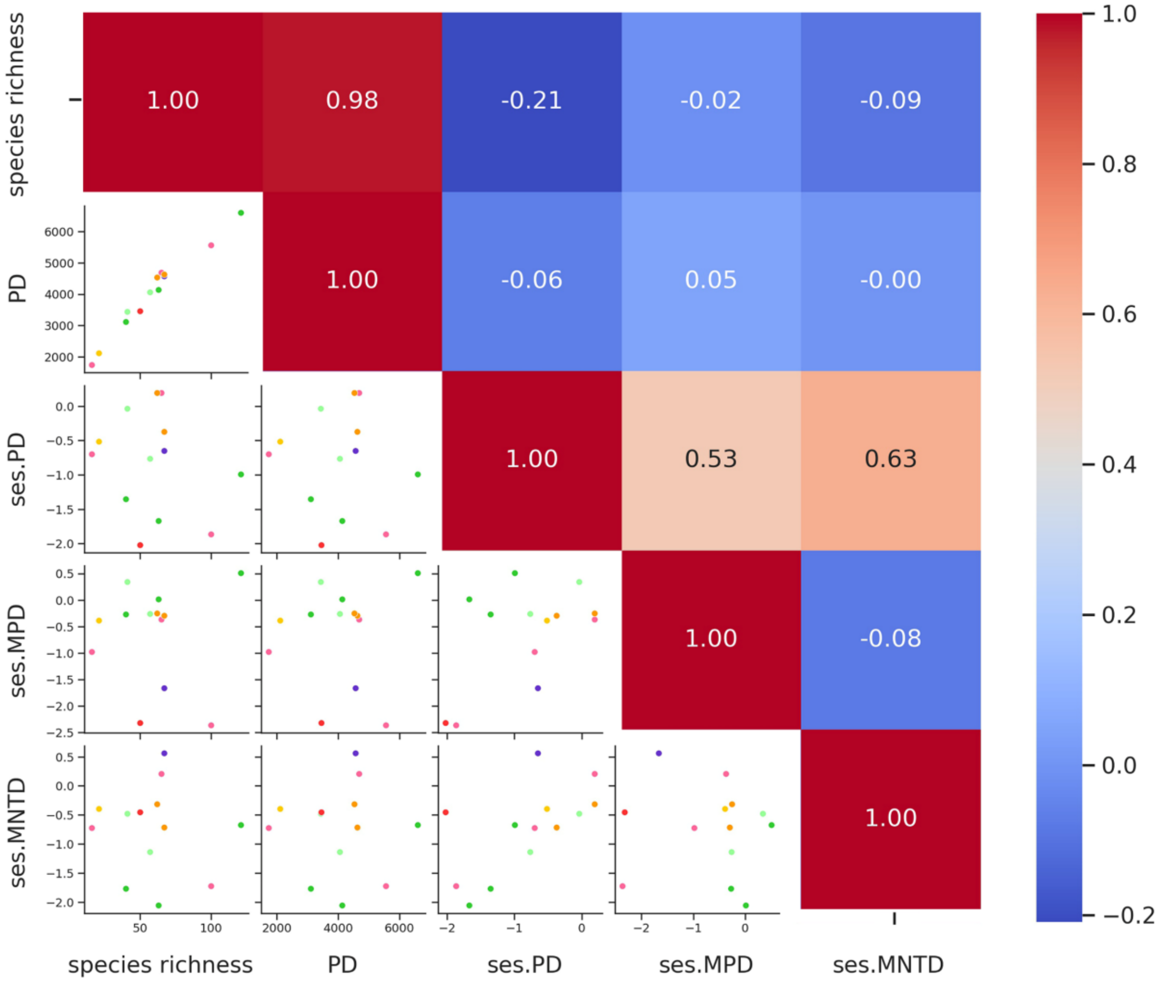

Figure S1. Pairplot and correlation heatmap between phyloalpha diversity standardized metrics. The circles represent the vegetation types. Semideciduous seasonal forests (green), forest islands (light green), *cerrado stricto sensu* (yellow), rupestrian *cerrados* (orange), palm swamp (red), rupestrian grasslands (pink) and marshy grassland (purple).

Table S3 Phyloalpha diversity metrics and standardized effect sizes across study sites

Vegetation type	Code	Study site	Longitude	Species richness	PD	ses.PD	p-value	ses.MPD	p-value	ses.MNTD	p-value
Forest Island	FI	1	-43.73333	41	3436.7	-0.037	0.505	0.34167788	0.873	-0.4797132	0.318
		2	-43.57483	57	4059.6	-0.765	0.211	-0.26257335	0.507	-1.1394213	0.132
Semideciduous Seasonal Forest	SSF	1	-43.50634	121	6598.8	-0.993	0.164	0.50838858	0.772	-0.6748061	0.268
		2	-43.59021	63	4135.8	-1.67	0.039	0.01311179	0.701	-2.0585049	0.019
		3	-43.67003	40	3112	-1.354	0.087	-0.27207432	0.409	-1.7700979	0.03
Cerrado stricto sensu	CSS	●	-43.68839	21	2113.4	-0.516	0.299	-0.38831432	0.269	-0.3966779	0.353
Rupestrian *Cerrado*	RC	1	-43.64202	67	4628.6	-0.373	0.369	-0.29657387	0.451	-0.7169214	0.242
		2	-43.63893	62	4532.9	0.1919	0.577	-0.2531538	0.504	-0.3162266	0.383
Palm Swamp	PS	●	-43.62223	50	3456.5	-2.022	0.014	-2.32377278	0.001	-0.4547725	0.331
Rupestrian Grassland	RG	1	-43.59444	100	5561.2	-1.865	0.029	-2.3671161	0.001	-1.7255699	0.029
		2	-43.51595	65	4686.9	0.1921	0.589	-0.36912688	0.388	0.2054067	0.599
		3	-43.59065	16	1739.3	-0.699	0.221	-0.98077812	0.044	-0.7255362	0.23
Marshy Grassland	MG	●	-43.74498	67	4571	-0.651	0.249	-1.66636824	0.002	0.5599498	0.72

Source: Authors 2024.

Scripts

#curvas de rarefação#

#Instalando e carregando pacotes
```
install.packages("iNEXT")
library(iNEXT)
install.packages("ggplot2")
library(ggplot2)
install.packages("ggthemes")
library(ggthemes)
```

#Definindo o diretório
```
setwd("C:/Users/Julia Viotti Corrêa/Desktop/curvas")
```

#Carregando os dados de comunidade
```
dados <- read.csv("C:/Users/Julia Viotti Corrêa/Desktop/curvas/nmds.csv")
```

#Exemplo "incidence_raw"
```
data <- as.data.frame(t(dados))

campestre <- data[1:565, 1:4]
campestre <- as.matrix((campestre > 0) + 0)

savanica <- data[1:565, 5:8]
savanica <- as.matrix((savanica > 0) + 0)

florestal <- data[1:565, 9:13]
florestal <- as.matrix((florestal > 0) + 0)
```

#Criando a lista
```
data.list <- list(campestre, savanica, florestal)
names(data.list) <- c("campestre", "savanica", "florestal")
```

#Plotando as curvas
```
out <- iNEXT(data.list, q = 0, datatype="incidence_raw", endpoint=50)

ggiNEXT(out, type=1, facet.var="Both", color.var="Assemblage")
```

#Exemplo "incidence_freq"

#Definindo os vetores com os dados fornecidos
```
CAR <- c(485,60,40,12,9,6,4,3,3,2,2,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1)
CAP <- c(365,23,18,4,4,3,3,2,2,2,2,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1)
CSS <- c(400,5,5,2,1,1,1,1,1,1,1,1,1)
FES <-
c(450,61,20,16,9,8,5,4,4,4,4,3,3,2,2,2,2,2,2,2,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1
,1,1)
CUM <- c(117,38,22,2,1,1,1,1,1)
VER <- c(117,22,22,2,2,1,1)
```

```r
CER <- c(400,50,31,8,6,5,3,3,2,2,2,2,1,1,1,1,1,1,1,1,1,1,1,1,1,1,1)

#Criando a lista
minha_lista <- list(
  CAR = CAR,
  CAP = CAP,
  CSS = CSS,
  FES = FES,
  CUM = CUM,
  VER = VER,
  CER = CER
)

names(minha_lista) <- c("CAR", "CAP", "CSS", "FES", "CUM", "VER", "CER")

#Plotando as curvas
out.inc <- iNEXT(minha_lista, datatype="incidence_freq", q = 0, endpoint = 2000)
ggiNEXT(out.inc, type=3, facet.var="Both", color.var="Assemblage")
```

#NMDS#

```r
#Instalando e carregando pacotes
install.packages("vegan")
library(vegan)
install.packages("ggplot2")
library(ggplot2)
install.packages("gridExtra")
library(gridExtra)

#Definindo o diretório
setwd("C:/Users/Julia Viotti Corrêa/Desktop/NMDS")

#Carregando a planilha dos dados da comunidade e variáveis ambientais
#Este script requer dados de comm.csv com a coluna de áreas
comm <- read.table("C:/Users/Julia Viotti Corrêa/Desktop/NMDS/nmds.csv", sep =
",", row.names = 1,
                   header = T)

variaveis <- read.table("C:/Users/Julia Viotti
Corrêa/Desktop/NMDS/resultados_raster.csv", sep = ",", row.names = 1,
               header = T)

#Função para calcular a distância de Simpson
simpson_distance <- function(comm) {
  #Calcula o número de espécies
  n_species <- ncol(comm)
  #Inicializa a matriz de distância
  dist_matrix <- matrix(0, nrow = nrow(comm), ncol = nrow(comm))
```

```
  #Loop para calcular a distância
  for (i in 1:(nrow(comm) - 1)) {
    for (j in (i + 1):nrow(comm)) {
      #Calcula a soma do mínimo das contagens para cada espécie
      min_sum <- sum(pmin(comm[i, ], comm[j, ]))
      #Calcula a distância de Simpson
      dist_matrix[i, j] <- 1 - (min_sum / pmin(sum(comm[i, ]), sum(comm[j, ])))
      dist_matrix[j, i] <- dist_matrix[i, j]
    }
  }

  return(as.dist(dist_matrix))
}


#Calcula a matriz de dissimilaridade usando a distância de Simpson
dissimilarity_matrix <- simpson_distance(comm)

#Realiza o NMDS
nmds_result <- metaMDS(dissimilarity_matrix, trymax=100, k=2)

#Ajusta as variáveis ambientais ao NMDS
envfit_result <- envfit(nmds_result, variaveis, perm=999)

#Cria o gráfico do NMDS
nmds_plot <- ordiplot(nmds_result, type = "n") # 'n' cria um plot sem pontos

#Cria um dataframe a partir dos escores do NMDS
nmds_scores <- as.data.frame(scores(nmds_result))

#Adiciona a coluna de área ao dataframe dos escores do NMDS
nmds_scores$area <- comm$area

#Adiciona pontos com cores específicas
#ATUALIZAR CORES DE ACORDO COM NÚMERO DE ÁREAS OU FISIONOMIAS (áreas com mesma fitofisionomia têm código de cor igual)
cores <- c("#ff6699", "#ff6699", "#ff6699", "#99ff99", "#99ff99", "#ffcc00",
          "#33cc33","#33cc33", "#33cc33", "#6633cc","#ff3333", "#ff9900", "#ff9900")

for (i in 1:nrow(nmds_scores)) {
  points(nmds_result, display = "sites", pch = 16, col = cores[i], select = i)
}

#Adiciona vetores de variáveis ambientais ao gráfico
plot(envfit_result, col = 'black', add = TRUE) #'add = TRUE' adiciona os vetores a um gráfico já existente

p.max=0.05 #Valores de p significativos
```

```
#Imprime os resultados da significância das variáveis ambientais
print(envfit_result)
print(nmds_result)

#Calcula o coeficiente de determinação baseado no stress
stress_based_R2 <- 1 - nmds_result$stress^2

#Gera o gráfico de stress
stressplot(nmds_result)
```

#MRPP e ANOSIM#

```
#Instalando e carregando o pacote
Install.packages("vegan")
library(vegan)

#Definindo o diretório
setwd("C:/Users/Julia Viotti Corrêa/Desktop/NMDS")

#Carregando dados de comunidade e de variáveis ambientais
comm <- read.csv("C:/Users/Julia Viotti Corrêa/Desktop/NMDS/nmds.csv")

variaveis <- read.csv("C:/Users/Julia Viotti Corrêa/Desktop/NMDS/resultados_raster.csv")

#Calculando a matriz de dissimilaridade usando Bray-Curtis
dissimilarity_matrix <- vegdist(comm, method = "bray")

#Realizando o NMDS
nmds_result <- metaMDS(dissimilarity_matrix, trymax=100)

#Plotando os resultados do NMDS
plot(nmds_result$points, type = "n") #Configura um plot vazio

points(nmds_result$points, col = as.factor(variaveis$fitofisionomia)) #Plota os pontos com cores baseadas na fisionomia

#Realizando o MRPP
mrpp_result <- mrpp(dissimilarity_matrix, variaveis$fitofisionomia)

#Realizando a ANOSIM
anosim_result <- anosim(dissimilarity_matrix, variaveis$fitofisionomia)

#Imprimindo os resultados
print(mrpp_result)
print(anosim_result)
```

#Jaccard#

#Instalando e carregando o pacote
```
Install.packages("vegan")
library(vegan)
```

#Definindo o diretório
```
setwd("C:/Users/Julia Viotti Corrêa/Desktop/NMDS")
```

#Carregando a planilha dos dados da comunidade
```
comm <- read.table("C:/Users/Julia Viotti Corrêa/Desktop/NMDS/nmds.csv", sep =
",", row.names = 1,
                   header = T)
```

#Calculando Jaccard
```
jaccard <- betadiver(comm, "j")
jaccard
```

#métricas filogenéticas e modelos nulos#

#Instalando e carregando pacotes
```
Install.packages(“picante”)
library(picante)
install.packages(“V.PhyloMaker”)
library(V.PhyloMaker)
install.packages(“phytools”)
library(phytools)
```

#Definindo o diretório
```
setwd("C:/Users/Julia Viotti Corrêa/Desktop/filo")
```

#Carregando planilha com os dados da filogenia
```
splist <- read.table("filo.txt", h=T, stringsAsFactors = T)
```

#Criando a árvore filogenética (esse comando demora um pouco a rodar)
```
phy <- phylo.maker(splist)
```

#Extraindo a parte necessária para desenhar a árvore
```
tree <- phy$scenario.3
```

#Plotando a árvore
```
phytools::plotTree(tree)
```

#Exportando a árvore para a pasta do diretório
```
write.tree(tree, "tree.tre")
```

#Carregando os dados de comunidade
```
comm <- read.csv("C:/Users/Julia Viotti Corrêa/Desktop/filo/nmds.csv", row.names =
1)
```

```
#Carregando a árvore no seu ambiente de trabalho (só para o caso de ela não
estar carregada ainda)
tree = read.tree("tree.tre")

#Mean Pairwise Distance (MPD)
#Análise com dados de incidência das espécies nas comunidades
resultados_MPD_PA <- mpd(comm, cophenetic(tree),
              abundance.weighted = FALSE)

#Mostra os valores de MPD para cada comunidade
resultados_MPD_PA

#Mean Nearest Taxon Distance (MNTD)
#Análise com dados de presença e ausência das espécies nas comunidades
resultados_MNTD_PA <- mntd(comm, cophenetic(tree),
               abundance.weighted = FALSE)

#Phylogenetic diversity (PD)
resultados_PD <- pd(comm,tree)

#Mostra o valor de PD e riqueza de espécies para cada comunidade
resultados_PD

#NRI ou SES_MPD
resultados_SES_MPD <- ses.mpd(comm, cophenetic(tree),
                null.model = "taxa.labels",
                abundance.weighted = FALSE,
                runs = 999)

#Mostra a riqueza de espécies, MPD observado, média e desvio padrão dos
valores de MPD das aleatorizações, SES e o valor de p
head(resultados_SES_MPD)
resultados_SES_MPD

#NTI ou SES_MNTD
resultados_SES_MNTD <- ses.mntd(comm, cophenetic(tree),
                 null.model = "taxa.labels",
                 abundance.weighted = FALSE,
                 runs = 999)

#Mostra a riqueza de espécies, MNTD observado, média e desvio padrão dos
valores de MNTD das aleatorizações, SES e o valor de p
head(resultados_SES_MNTD)
resultados_SES_MNTD

#SES_PD
#Mostra a riqueza de espécies, MNTD observado, média e desvio padrão dos
valores de PD das aleatorizações, SES e o valor de p
resultados_SES_PD <- ses.pd(comm, tree,
               null.model = "independentswap",
```

```
                    runs = 999)
resultados_SES_PD
#Phylosor
resultados_Phylosor <- phylosor(comm, tree)
resultados_Phylosor

#Standardized effect size do Phylosor

#Modelo nulo que rearranja o nome das espécies na filogenia
modelos_nulo <- phylosor.rnd(comm, tree,
                     null.model = "taxa.labels", runs = 9)

#Função para calcular o SES e o valor de P
ses.physo <- function(obs, nulo_phylosor){
  nulo_phylosor <- t(as.data.frame(lapply
                         (nulo_phylosor, as.vector)))
  physo.obs <- as.numeric(obs)
  physo.mean <- apply(nulo_phylosor, MARGIN = 2,
                 FUN = mean, na.rm = TRUE)
  physo.sd <- apply(nulo_phylosor, MARGIN = 2,
                FUN = sd, na.rm = TRUE)
  physo.ses <- (physo.obs - physo.mean)/physo.sd
  physo.obs.rank <- apply(X = rbind(physo.obs,
                          nulo_phylosor), MARGIN = 2,
                   FUN = rank)[1, ]
  physo.obs.rank <- ifelse(is.na(physo.mean), NA,
                    physo.obs.rank)
  data.frame(physo.obs, physo.mean, physo.sd,
          physo.obs.rank, physo.ses,
          physo.obs.p = physo.obs.rank/
            (dim(nulo_phylosor)[1] + 1))
}

#Resultado
resultados <- ses.physo (resultados_Phylosor, modelos_nulo)

resultados
```

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Chapter 2: Tracking the phylofunctional trajectories of ecotones in the Espinhaço Range Biosphere Reserve

ABSTRACT

This study investigates trait diversity in *Cerrado* ecotones on the Diamantino Plateau, Brazil, focusing on the influence of environmental filtering and evolutionary history. Using a phylofunctional approach, we analyzed 546 plant species across seven vegetation types. Results revealed four distinct trait clusters primarily based on leaf trichomes and type of fruit. Vegetation types exhibit unique trait patterns, with rupestrian vegetation showing the highest functional richness (FRic) and dispersion (FDis), and soaked vegetation the highest functional divergence (FDiv) and eveness (FEve). Environmental filtering is evident across all types based on either FRic or FDis. Phylogenetic analysis indicates a significant signal for habit and life form in the metacommunity. Our findings provide insights into the mechanisms shaping plant traits in diverse *Cerrado* ecosystems, enabling more assertive conservation strategies.

Keywords: Abiotic filtering. Environmental heterogeneity. Evolutionary history. Hotspot. Trait diversity.

1 INTRODUCTION

Plant functional traits refer to the physical, chemical, and biological characteristics of individual plants with significant effects on their fitness, including their morphology, chemical composition, physiology, and timing of phenological events (McElwain et al. 2024). Their patterns of variation provide clues to the evolution of fundamental plant form (Capdevila et al. 2023). Also, they determine not only how plants acquire, process, and store resources, but also how they respond to abiotic and biotic environmental disturbances (Díaz et al. 2022).

Environmental stress and disturbance gradients drive plant morphological variability (Fernandes et al. 2024). The stress-gradient hypothesis proposes that higher elevations in mountainous regions tend to have more stressful conditions for plants (Loiola et al. 2023). Physical stress at high elevations may be caused, for example, by high UV radiation, extremely thin soils, low nutrient availability, and water deficit (Azevedo et al. 2023).

Harsher environmental conditions lead to trait convergence through environmental filtering, which in turn plays a significant role in shaping the characteristics of organisms in those environments (Tameirão et al. 2021). Accordingly, trait divergence and limiting similarity are more significant in favorable and productive habitats. However, the effect of these trends might vary depending on the specific traits being studied (Bernard-Verdier et al. 2012, Spasojevic & Suding 2012) and the part of the stress gradient being examined (Bernard-Verdier et al. 2012).

For this reason, we employed a phylofunctional approach in this study to determine the α-diversity of a *Cerrado* ecotonal area on the Diamantino Plateau, the wider central portion of the Espinhaço Range in Brazil. It is worth noting that the forest formations within the area are also under the influence of the Atlantic Domain (Coelho et al. 2016). This area is home to seven distinct vegetation types: Semideciduous Seasonal Forest, Forest Island (*Capão de Mata*), *Cerrado stricto sensu*, Rupestrian *Cerrado*, Palm Swamp (*Vereda*), Rupestrian Grassland, and Marshy Grassland. It is an ideal location for this research due to its climate, diverse geography, and unique soil characteristics (Machado & Gonzaga 2021), allowing for the study of a long productivity gradient within a relatively small area (Kovács-Láng et al. 2008).

Despite being an ancient orogenic belt with a medium elevation of ca. 1000 m, the Espinhaço Range is characterized by highly restrictive environmental conditions (Loiola et al. 2023). Plants adapt to environmental stress through various physiological, biochemical, morphological, and phenological changes (Tameirão et al. 2021). On this basis, we aimed to answer the following questions: 1) What is the relationship between trait diversity and species/vegetation types? 2) Is there convergence or divergence? 3) Are functional traits and species distribution in the vegetation types mainly associated with historical (phylogenetic) or ecological factors?

We expected that environmental filtering would result in the convergence of the selected functional traits across all vegetation types in our study area due to plant adaptations to stress conditions. Investigating plant traits helps elucidate the dynamics and structure of ecological communities and their responses to natural and anthropogenic disturbances, enabling more effective conservation practices for the ecosystems (Tameirão et al. 2021).

2 METHODOLOGY

2.1 Study area

We collected data in thirteen study sites on the Diamantino Plateau, Minas Gerais, Brazil (Fig. 1, Table 1 in Chapter 1).

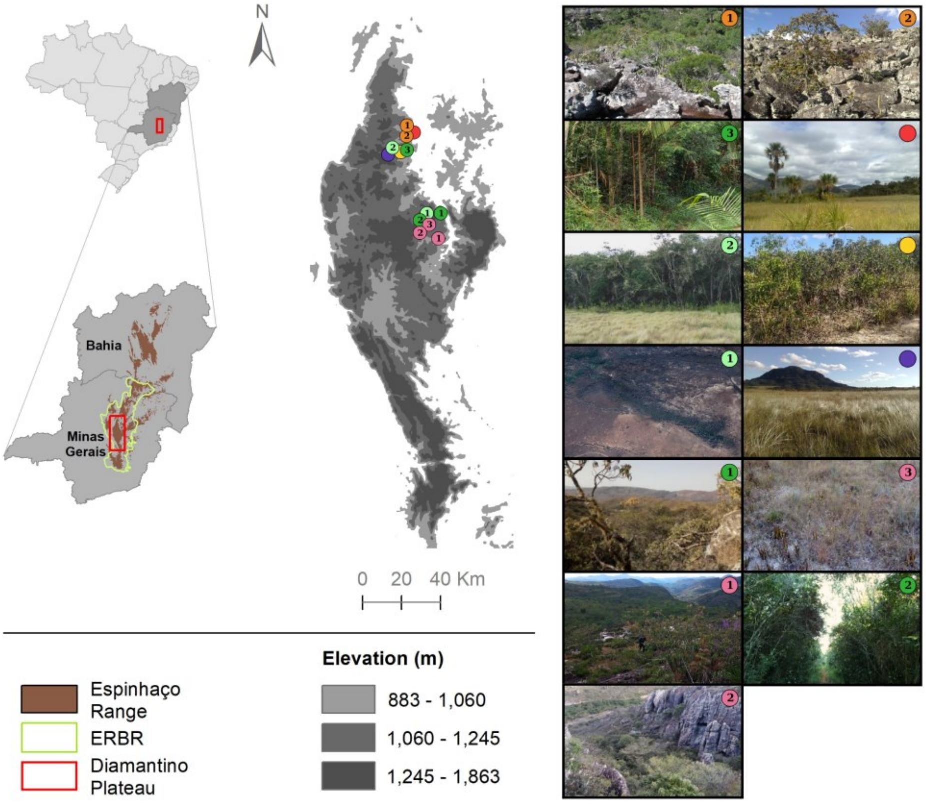

Figure 1. Map of study sites in the Espinhaço Range Biosphere Reserve (ERBR), Minas Gerais, Brazil. Vegetation types are indicated by colour of circle. Semideciduous seasonal forests (green), forest islands (light green), *cerrado stricto sensu* (yellow), rupestrian *cerrados* (orange), palm swamp (red), rupestrian grasslands (pink), and marshy grassland (purple).

Our study area is a distinct and diverse ecosystem that encompasses a variety of vegetation formations typical of the *Cerrado* biome, including forests, savannas, and grasslands. The complex mix of different vegetation types and significant differences in plant species within this biome are heavily influenced by factors such as soil fertility, soil water availability, and the fire regime (Bueno et al. 2018). The sites are distributed in seven vegetation types: Semideciduous Seasonal Forest (SSF), Forest Island (FI), *Cerrado stricto sensu* (CSS), Rupestrian *Cerrado* (RC), Palm Swamp (PS), Rupestrian Grassland (RG), and Marshy Grassland (MG) (Fig. 1, Table 1 in Chapter 1).

This region falls under the Cwb climate classification, indicating dry winters and warm summers (Köppen & Geiger 1936). Elevations of the study sites range from 679 m to 1407 m. The average annual precipitation ranges from 1159 mm to 1496 mm, while the average annual temperature varies between 18.2 ºC and 22 ºC. The prevalent soil types in the study area include Arenosol and Acrisol (Table 1 in Chapter 1).

The Diamantino Plateau has flat landscapes from the Tertiary period interrupted by valleys cutting through pre-Cambrian quartzite and conglomerate layers (Lacerda & Saadi 2017). It is mostly composed of quartzites and filites, which are the primary components of shallow, alibic, and dystrophic soils (Mucida et al. 2019). Common soil types include Neosols, Gleissols, Cambisols, and Plinthosols, with Organosols found in wetlands and low-lying areas (Abreu Filho et al. 2021).

2.2 Trait diversity

Our study involved collecting and analyzing data on six categorical functional traits considered to reflect plant strategies, including habit, life form, leaf texture, leaf trichomes, type of fruit, and dispersal syndrome (Table 2). We obtained species' updated names and trait information from Flora e Funga do Brasil (2024). We analyzed 546 species from the surveys conducted by the Phytogeography, Vegetation, and Ecology (PHYVE) laboratory team to assure reliable sampling and species identification for community-level analysis (Table 1 in Chapter 1). We based all the analyses on species incidence data (Chao et al. 2005, 2006, Hsieh et. al 2022, Rezende et al. 2020).

Firstly, to assess the relationship between trait diversity and species, we conducted a Principal Coordinate Analysis (PCoA) using the plant species' attribute table. PCoA is a multivariate technique used to explore and visualize patterns in complex datasets by reducing the dimensionality of the data while preserving the original distances or dissimilarities between observations (Gower & Legendre 1986).

Secondly, we applied a *k*-means clustering analysis on the PCoA functional space to identify groups of plant species based on their trait similarities. *K*-means clustering is an unsupervised machine learning algorithm used for partitioning datasets into a predetermined number of clusters, with each cluster representing observations that are more like each other than those in other clusters (Lloyd 1982).

Table 2 Functional trait attributes used to categorize the 546 species found in the study area, and their ecological definition

Trait	Attributes	Definition
Habit	Herb Subshrub Shrub Treelet Tree Palm tree Liana Climbing	The general outer appearance of a plant, associated with different strategies for resource uptake and niche occupation[1]
Life form	Therophyte Geophyte Hemicryptophyte Chaemaphyte Phanerophyte Helophyte	Location of the bud of a plant during seasons with adverse conditions[2]
Leaf texture	Membranous Herbaceous Papyraceous Chartaceous Coriaceous Rigid Succulent Leafless	The consistency of a leaf blade, related to the nature of its tissues, its water content, the environment, and its mechanical resistance[3]
Leaf trichomes	Present Absent	Epidermal protuberances on the leaves, protecting them from UV light, insect predation, and excess transpiration[4]
Type of fruit	Dry Fleshy	The form and function of a fruit, related to seed protection and dispersal strategies[5]
Dispersal syndrome	Anemochory Autochory Zoochory	Suites of fruit and seed characteristics that attract different dispersal agents. They relate to fertility, spatial distribution, genetic structure, population viability, and maintenance of dispersed fauna[6]

Source: Almeida & Almeida 2018[3], Costa 2017[6], Dardick & Callahan 2014[5], Norton 1915[1], Pattanaik et al. 2014[4,] Raunkiær 1934[2], van der Pilj 1982[6].

Next, we calculated the functional richness (FRic), divergence (FDiv), dispersion (FDis), and evenness (FEve) metrics using two matrices (Laliberté & Legendre 2010, Mason et al. 2005, Villéger et al. 2008). The initial matrix is a community table that displays the incidence of each species among vegetation types. The second matrix is an attribute table that underwent a functional dissimilarity transformation through the Gower distance method (Botta-Dukát 2005). We then converted this matrix to a numerical format by conducting the PCoA.

In the context of functional metrics, FRic quantifies the total range or volume of functional trait space occupied by species within a community, providing insights into the extent of niche differentiation; FDiv assesses the extent of dissimilarity or divergence among species in their functional traits, reflecting the degree of niche complementarity or overlap; FDis measures the average distance of individual species from the centroid of all species in the trait space, indicating the degree of functional diversity across multiple dimensions; and FEve evaluates the evenness of functional trait distribution within communities, indicating the equitable distribution of functional traits among species (Laliberté & Legendre 2010). Together, these metrics offer a comprehensive understanding of community assembly processes, ecosystem functioning, and responses to environmental changes (Laliberté & Legendre 2010, Mason et al. 2005, Villéger et al. 2008).

Finally, to assess if functional traits and species distribution in the vegetation types are associated with historical or ecological factors and if there is trait convergence/divergence, we explored the mechanisms governing community assembly by examining whether the observed values of FRic and FDis were higher or lower than what was expected by null models (Mouchet et al. 2010). These two indices reflect the processes that affect the arrangement and dispersion of species in response to the environment. When the values are lower than expected, it suggests functional convergence due to environmental filtering (Mason et al. 2013).

We conducted all analyses in the R 4.2.1 Statistical Environment (R Core Team 2019) using the packages: ‘ade4’ (Dray & Dufour 2007), ‘cluster’ (Maechler et al. 2023), ‘FD’ (Laliberté et al. 2014), ‘picante’ (Kembel et al. 2010), and ‘vegan’ (Oksanen et al. 2016).

2.3 Decomposing trait diversity among the nodes of the phylogenetic tree

To further determine whether functional traits and species distribution are associated with historical or ecological factors in vegetation types, we assessed the phylogenetic signal of the evaluated traits. We utilized the Angiosperm Phylogeny Group IV system (The Catalogue of Life Partnership 2017) to create a robust phylogenetic tree comprising 546 tips and 416 internal nodes. Employing the mega-tree technique under scenario 3, whereby newly incorporated genus or species tips were affixed to the midpoint between the family or genus branch and the tree's basal node (Jin & Qian 2019). Finally, we pruned the megaphylogeny to retain only 21 plant species.

This selection process involved the identification of three species for each vegetation type, in which two represent the most restricted species within a type and one represents the species with the most comprehensive distribution among the other types (Flora e Funga do Brasil 2024) (Table S1). The objective of this approach was to prioritize the particular identity of each vegetation type while still establishing a connection between them, given their ecotonal nature.

To determine if there is a phylogenetic signal, we employed the approach developed by Pavoine et al. (2010) and Pavoine (2020). We evaluated the attributes of the sampled species at both metacommunity and vegetation type levels, assuming that increasingly distantly related species are more likely to have increasingly different biological traits, as stated by the Brownian motion model (Pavoine et al. 2010). This approach allows us to assess the evolutionary patterns and relationships between traits and lineage divergence. Once we constructed a phylogenetic tree based on the sampled species, we proceeded with testing the distribution of traits across the tree.

Our tests aimed to determine if trait diversity was evenly distributed among nodes, if a single node expressed the full range of trait diversity, or if trait values were concentrated at either the root or the tips of the phylogeny. These tests included the single-node, few-nodes and root/tips skewness tests (Pavoine et al. 2009, Pavoine 2020). Detecting a skew towards the root of the phylogeny would indicate a phylogenetic signal.

Finally, to assess the relationship between trait diversity and vegetation types within our pruned phylogenetic tree, we checked the correlation between sampled species' attributes and vegetation types. We conducted all analyses in the R 4.2.1 Statistical Environment (R Core Team 2019) using the packages: ‘adiv’ (Pavoine 2020), ‘ape’ (Paradis et al. 2004), ‘corrplot’ (Wei & Simko 2017), ‘phytools’ (Revell 2012), and ‘V.PhyloMaker’ (Jin & Qian 2019).

3 RESULTS

According to the PCoA and the *k*-means clustering, we identified four main clusters of attributes in the functional space. By reducing the dimensionality of the data, these analyses indicated that the functional space can be essentially classified based on the presence or absence of leaf trichomes and the type of fruit (Fig. 2).

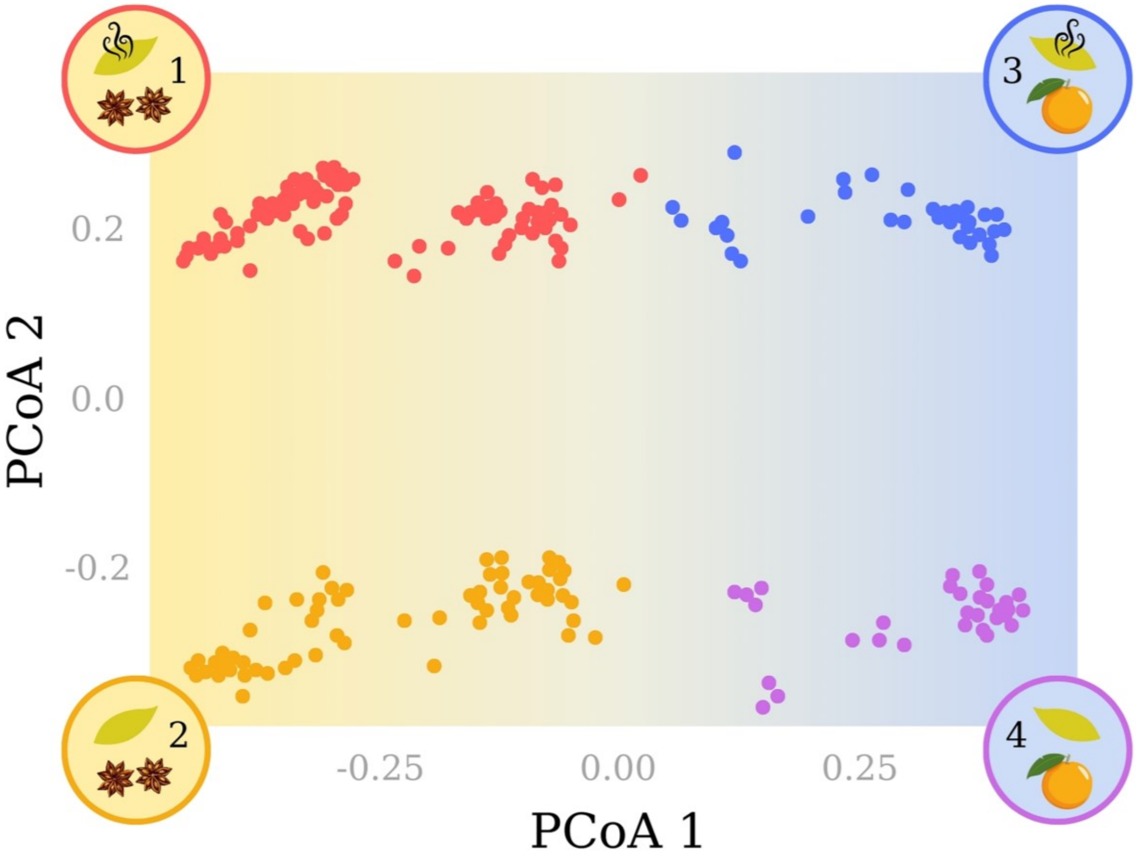

Figure 2. Principal Coordinate Analysis (PCoA) representing 546 species' attributes for the six focal traits and the k-mean clusters. Clusters are indicated by colour of circle. Present leaf trichomes and dry fruits (red), absent leaf trichomes and dry fruits (yellow), present leaf trichomes and fleshy fruits (blue), absent leaf trichomes and fleshy fruits (purple). Background gradient varies from yellow to blue, indicating a transition from a predominantly open environment to a forested one.

Cluster 1 primarily contains typical genera found in RC and RG, including *Kielmeyera*, *Lavoisiera*, *Microstachis*, and *Waltheria*. However, it also included *Comanthera*, *Drosera*, and *Paspalum* from MG. Cluster 2 is mainly composed of MG and PS indicator genera, such as *Cyperus*, *Rhynchospora*, *Syngonanthus* and *Xyris*, but also *Cattleya*, *Chamaecrista* and *Vellozia* from RC and RG. Therefore, clusters 1 and 2 represent species in less shaded environments and more exposed to UV radiation, such as savannas and grasslands.

Conversely, genera often found in FI and SSF were included in cluster 3 (e.g. *Myrcia*, *Campomanesia*) and cluster 4 (e.g. *Eugenia*, *Ocotea*, *Pouteria*, *Vitex*). Clusters 3 and 4 therefore represent species found in more shaded environments, such as forests. Moreover, the functional diversity metrics showed that RC, RG, PS and MG presented the highest values (Table 3).

Table 3 Functional α-diversity metrics across study sites

Vegetation type	Code		SRic	FRic	FDiv	FDis	FEve
Forest Island	FI	●	83	0.4954	0.1104	0.0569	0.3322
Semideciduous Seasonal Forest	SSF	●	178	0.6420	0.1101	0.0593	0.3318
Cerrado stricto sensu	CSS	●	21	0.5519	0.0815	0.0697	0.2856
Rupestrian *Cerrado*	RC	●	129	0.7345	0.0945	0.0883	0.3073
Palm Swamp	PS	●	50	0.5154	0.2826	0.0500	0.5316
Rupestrian Grassland	RG	●	161	0.7638	0.1113	0.0877	0.3337
Marshy Grassland	MG	●	67	0.6184	0.2801	0.0527	0.5293

SRic (Species Richness), Fric (Functional Richness), FDiv (Functional Divergence), FDis (Functional Dispersion), and FEve (Functional Eveness).
Source: Authors 2024.

The significance tests and the ses metrics using null models for FRic showed that all vegetation types exhibit clustering of similar traits indicating environmental filtering (p-value < 0.05, negative ses values), except CSS (p-value = 0.976, ses = 0.952). Regarding FDis, all communities indicated environmental filtering (p-value < 0.05, negative ses values).

With respect to the pruned phylogeny, we found no significant bias towards the single-node, few-nodes, and root/tips skewness tests in terms of the diversity of biological and morphological attributes in each plant species at the vegetation type level (Fig. 3). However, there is a significant phylogenetic signal in habit and life form at the metacommunity level (p-value < 0.05).

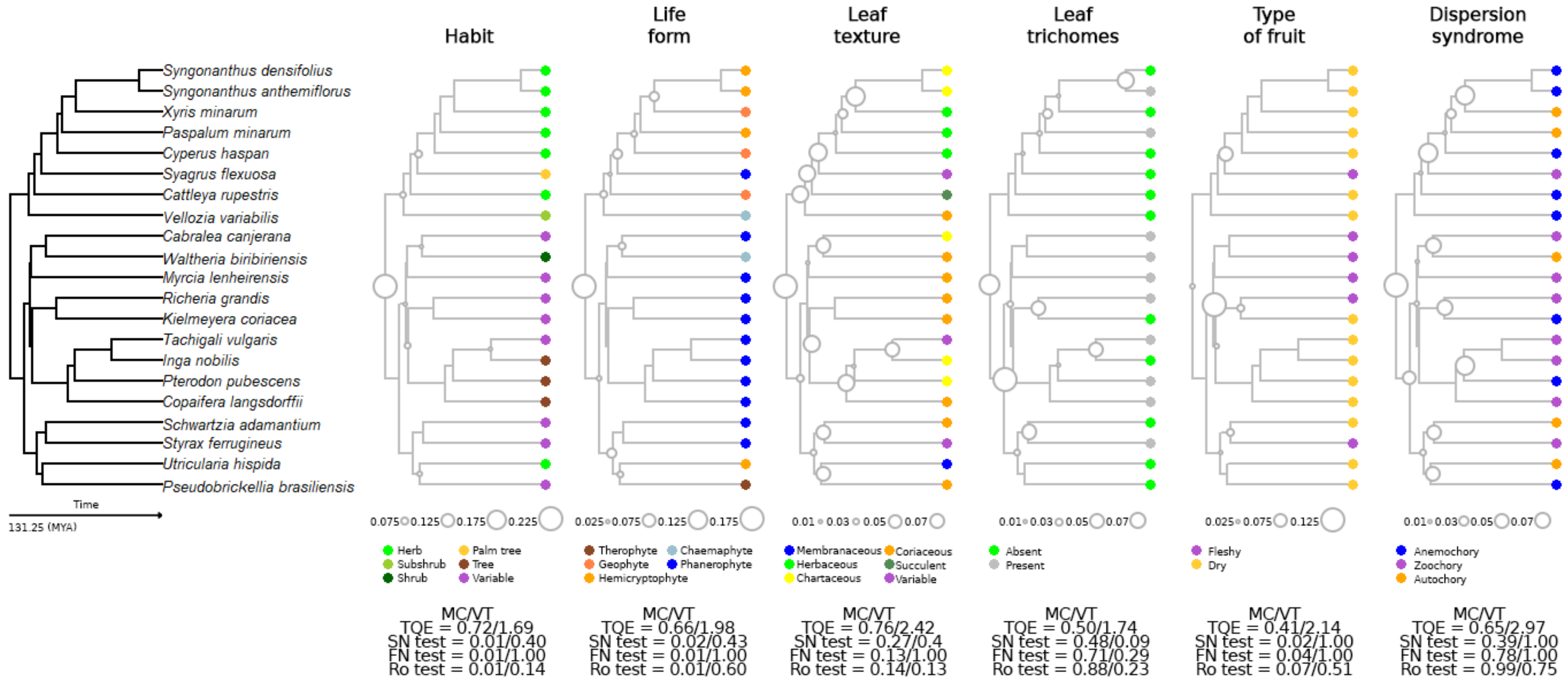

Figure 3. Decomposition of the attributes' diversity of habit, life form, leaf texture, leaf trichomes, type of fruit, and dispersal syndrome among the phylogenetic tree for the selected plant species. Circles at nodes provide the contribution of nodes to trait diversity, scales are given below each tree. The larger the circle, the larger the trait diversity in that node. Results of the permutation tests are given at the bottom of each tree: SN, single-node skewness test; FN, few-nodes skewness test; Ro, root/tips skewness test (two-sided). Total quadratic entropy (TQE) represents the overall value of trait diversity, the higher the TQE, the higher the diversity of trait attributes in each species. We used the phylogenies presented in the figure for the phylogenetic signal analysis within the metacommunity (MC). Results for the seven vegetation types (VT) separate analyses are given below phylogenies.

Despite the presence of strong correlations (> 0.7, < -0.7) between the selected species' attributes and the vegetation types, these correlations account for less than 8% of the total pairs (Fig. 4).

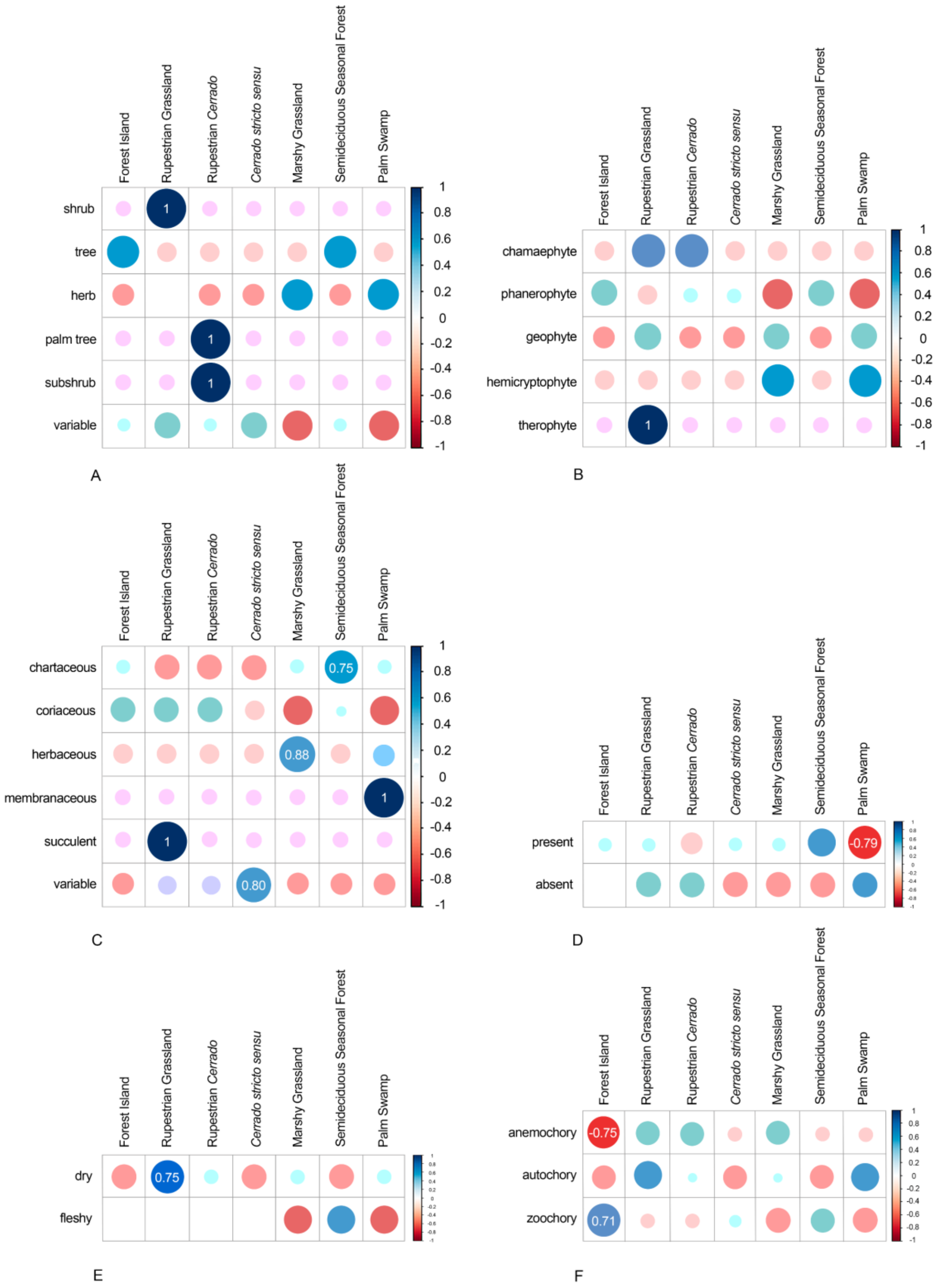

Figure 4. Correlation plots showing the association of the functional attributes in the pruned phylogeny and the vegetation types. Blue circles indicate a positive association, while red circles indicate a negative association. A) habit, B) life form, C) leaf texture, D) leaf trichomes, E) type of fruit, F) dispersion syndrome.

4 DISCUSSION

Our study results demonstrate that while our initial hypothesis was not entirely corroborated, there was strong evidence for trait convergence resulting from environmental filtering in all vegetation types, based on either FRic or FDis metrics and the weak correlations prevailing between the selected species' attributes and the vegetation types. Moreover, we observed a phylogenetic signal for habit and life form at the metacommunity level, i.e., the similarities in species attributes are not random for these specific traits, but rather influenced by their evolutionary relationship in the ecotone (Pavoine et al. 2010).

In connection to the relationship between trait diversity and species, we identified the leaf trichomes and the type of fruit as the most explanatory traits along the functional space, with attributes varying from predominantly open to forested areas. Different types of fruits are linked to different life-history strategies that determine the competitive ability of species in communities and their ability to adapt to the environment (Lotan & Izhaki 2013, Traveset et al. 2004). Conversely, leaf trichomes protect plants from UV light, herbivore attack and water loss (Bickford 2016).

The precipitation and temperature gradient from south to north in Espinhaço leads to higher humidity and milder temperatures in the southeast, while the northwest experiences drier and warmer conditions (Silveira et al. 2016). This gradient, combined with variables such as soil depth and water availability, plays a key role in determining whether open (e.g. grasslands, savannas) or forested formations thrive in a particular area (Machado & Gonzaga 2021). The PCoA indicated that, despite developing in open formations and being exposed to high levels of radiation, some of the MG and PS species (cluster 2 in Fig. 2) do not exhibit leaf trichomes.

In this context, trichomes could serve as useful mechanisms against radiation damage and water loss (Bickford et al. 2016, Wang et al. 2021). However, considering its soil water availability, these features may not be as essential as they would be in open vegetation on shallow, well-drained soils like RC and RG (cluster 1 in Fig. 2) (Waseem et al. 2021). The prevalent functional attributes for leaf trichomes in Table S2 further support this assumption. Additionally, the prevalent dispersal syndromes (anemochory, autochory) in these vegetations align with their open configuration and the type of fruit (dry) indicated in clusters 1 and 2.

In MG and PS, the varying saturation levels of soil,—where some areas are constantly inundated with water while others are only affected during the rainy season—, cause variations in plant species among different areas, even within the same vicinity (Munhoz & Felfili 2008). This pattern explains why genera from MG (*Comanthera*, *Drosera*, *Paspalum*) are in cluster 1 and genera from RC and RG (*Cattleya*, *Chamaecrista*, *Vellozia*) are in cluster 2, demonstrating MG has other soil conditions than waterlogging reflecting the marsh species' traits, and thus that typical rupestrian species may share similar traits with them.

Similarly, we would expect that the presence of trichomes is less critical in clusters 3 and 4, as they group species in shaded environments of SSF and FI. It's important to note that the present leaf trichomes in cluster 4 (also referred to in Table S2) don't necessarily mean that the species in these study sites have leaf trichomes, but rather that they may have them.

We assume this adaptation is likely to be observed in forest plots affected by shallow soils and rocky outcrops, where water availability may deviate from the typical conditions. Additionally, the type of fruit (fleshy) of these clusters aligns with the most predominant attributes of this trait (Table S2) and what is expected for tropical forests' predominant syndromes (Cabacinha et al. 2021).

In terms of FRic and FDis, the rupestrian vegetation had the greatest values among the types, implying more functions and a functionally spread community in the multivariate trait space, with higher functional diversity (Weigel et al. 2016). These areas host diverse organisms that rival forests in terms of species number and exceed them in the proportion of endangered flora (Fernandes et al. 2018, Lima et al. 2010, Munhoz & Proença 1998, Pinto et al. 2009, Simon & Proença 2000), fact that aligns with their being floristic transitions for the other types (Fig. 4 in Chapter 1). Also, these values indicate they are the most influenced by the environment among the different types (Laliberté & Legendre 2010), as suggested by phylogenetic clustering (Table S3 in Chapter 1).

The soaked vegetation presented the greatest FDiv and FEve values. PS is a complex ecosystem that develops in wet patches in the soil, determined by variations in topography and alternating soil layers with distinct levels of permeability (Bijos et al. 2017). Despite the complexity of the habitats, the species richness in these ecosystems is comparatively lower than that found in other *Cerrado* vegetation types, likely due to edaphic conditions and other biotic factors (Silva et al. 2022). In this way, it exhibited phylogenetic clustering (Table S3 in Chapter 1), along with functional divergence (FDiv).

In MG communities, plants encounter contrasting environmental scenarios due to environmental seasonality, which, along with soil saturation, can act as environmental filters and functional divergence drivers (Pataca et al. 2023). We believe that the higher values of FEve in these communities may be attributed to the smaller number of study sites compared to RG, for example. Nevertheless, the findings are consistent with the distribution of vegetation types in the Espinhaço Range, which is primarily covered by RG (Silva et al. 2019).

Concerning phylogeny, Souza et al. (2020) support the findings of trait diversity among the tree nodes. The results showed that the isolated vegetation types do not exhibit a phylogenetic signal for traits, while the metacommunity does. This indicates that the ecotone is not simply a combination of its core areas, but rather a biologically distinct system with unique evolutionary processes and importance for conservation (Smith & Goetz 2021).

In this environment, characterized by stable climatic conditions over time (Rapini et al. 2021), species have maintained consistent outer appearance and bud location, demonstrating stability in resource uptake strategies and niche occupation in a challenging environment (Norton 1915, Raunkiær 1934). While variable habit may be a strategy for expanding distribution across different habitats in the Espinhaço, it has been stable throughout the evolution of these species. Other traits, such as leaf trichomes and dispersal syndrome (with less significant p-values), may have been more useful in colonizing and persisting in new microhabitats due to the likely lower costs (trade-offs) associated with their variation (Maire et al. 2013).

Finally, we draw attention to the fact that the significance of ecotones lies not only in their uniqueness but also in their ability to provide additional habitat for widespread regional species, thereby supporting the functioning and identity of each vegetation type (Smith & Goetz 2021, Souza et al. 2020).

5 CONCLUSION

Our research demonstrates that the presence of trichomes and the type of fruit play a significant role in explaining the relationship between functional diversity and the species/vegetation types found in the ERBR. These traits' attribute combinations are likely the response to differences in precipitation and temperature from south to north Espinhaço, as well as variations in soil depth and water availability determining the presence of more open or shaded vegetation. The rupestrian vegetation, representing the floristic transition in the area, serves multiple functions, emphasizing the importance of its conservation in functional terms.

Our findings showed that the focal vegetation types present trait convergence caused by environmental filtering for the set of functional traits. Traits such as leaf trichomes may have been more useful in colonizing and persisting in new microhabitats, while habit and life form showed a phylogenetic signal at the metacommunity level, indicating that studying ecotones as biologically distinct systems may provide information that would otherwise be inaccessible.

The preservation of all vegetation types is essential for maintaining ecotones; conversely, the preservation of ecotones supports the functioning and identity of each vegetation type. Conservation guidelines should be targeted at the entire ecosystem to maintain its environmental heterogeneity and trait diversity.

SUPPLEMENTARY MATERIAL

Table S1 Selected species by vegetation type based on their distribution

Vegetation type	Distribution[1]	Species
Forest Island	R	*Myrcia lenheirensis* Kiaersk.
	R	*Richeria grandis* Vahl
	C	*Inga nobilis* Willd.
Semideciduous Seasonal Forest	R	*Cabralea canjerana* (Vell.) Mart.
	R	*Pterodon pubescens* (Benth.) Benth.
	C	*Copaifera langsdorffii* Desf.
Cerrado stricto sensu	R	*Kielmeyera coriacea* Mart. & Zucc.
	R	*Styrax ferrugineus* Nees & Mart.
	C	*Tachigali vulgaris* L.G.Silva & H.C.Lima
Rupestrian *Cerrado*	R	*Schwartzia adamantium* (Cambess.) Bedell ex Gir.-Cañas
	R	*Vellozia variabilis Mart. ex Schult. & Schult.f.*
	C	*Syagrus flexuosa* (Mart.) Becc.
Palm Swamp	R	*Syngonanthus densifolius* Silveira
	R	*Xyris minarum* Seub.
	C	*Utricularia hispida* Lam.
Rupestrian Grassland	R	*Cattleya rupestris* (Lindl.) Van den Berg
	R	*Waltheria biribiriensis* J.G. Saunders ex T.S. Coutinho & Colli-Silva
	C	*Pseudobrickellia brasiliensis* (Spreng.) R. M. King & H. Rob.
Marshy Grassland	R	*Syngonanthus anthemiflorus* (Bong.) Ruhland
	R	*Paspalum minarum* Hack.
	C	*Cyperus haspan* L.

Distribution among types: C) comprehensive, R) restricted.
Source: Authors, Flora e Funga do Brasil[1] 2024.

Table S2 Predominant trait attributes among vegetation types. Commas separate different attributes that a species can assume, slashes separate different attributes with equal predominance within a type.

			Trait					
Vegetation type	**Code**		**Habit**	**Life form**	**Leaf texture**	**Leaf trichomes**	**Type of fruit**	**Dispersal syndrome**
Forest Island	FI	●	shrub, tree	phanerophyte	coriaceous	present/absent	fleshy	zoochory
Semideciduous Seasonal Forest	SSF	●	tree	phanerophyte	chartaceous/coriaceous	present	fleshy	zoochory
Cerrado stricto sensu	CSS	●	shrub, tree	phanerophyte	coriaceous	present/absent	dry	anemochory/zoochory
Rupestrian *Cerrado*	RC	●	shrub, tree/herb	phanerophyte	coriaceous	present	dry	anemochory
Palm Swamp	PS	●	herb	hemicryptophyte	herbaceous	absent	dry	autochory
Rupestrian Grassland	RG	●	shrub	phanerophyte	coriaceous	present	dry	anemochory
Marshy Grassland	MG	●	herb	hemicryptophyte	herbaceous	present/absent	dry	anemochory/autochory

Source: Authors 2024.

Scripts

#PCoA e *k*-means clustering#

```
#Instalar e carregar os pacotes necessários
install.packages("cluster")
library(cluster)
install.packages("ggplot2")
library(ggplot2)

#Definir o diretório
setwd("C:/Users/Julia Viotti Corrêa/Desktop/fun")

#Carregar a planilha dos traços funcionais
attributes_data <- read.table("C:/Users/Julia Viotti Corrêa/Desktop/fun/att.csv", sep = ",", row.names = 1,
                       header = T)

#Converter todas as colunas para fatores
attributes_data[] <- lapply(attributes_data, factor)

#Calcular a matriz de distância de Gower
gower_dist <- daisy(attributes_data, metric = "gower")

#Realizar a PCoA
pcoa_results <- cmdscale(gower_dist, k = 2)

#Converter os resultados para um data frame
pcoa_df <- as.data.frame(pcoa_results)
names(pcoa_df) <- c("PCO1", "PCO2")

#Realizar a análise de cluster k-means com um número determinado de clusters
num_clusters <- 4  #Definir o número de clusters com base na sua análise
kmeans_result <- kmeans(pcoa_df, centers = num_clusters)

#Adicionar a informação do cluster ao data frame
pcoa_df$Cluster <- as.factor(kmeans_result$cluster)

#Criar um gráfico dos resultados da PCoA com clusters, sem rótulos de espécies
ggplot(pcoa_df, aes(x = PCO1, y = PCO2, color = Cluster)) +
  geom_point() +
  theme_minimal() +
  labs(x = "PCO 1",
       y = "PCO 2")

#Salvar o arquivo com o resultado dos cluster em .csv na pasta do diretório
write.csv(kmeans_result[["cluster"]], "klust4.csv", row.names = TRUE)
```

#Métricas funcionais e modelos nulos#

```
#----------------I PARTE----------------
#Instalando e carregando pacotes
install.packages("FD")
library(FD)
install.packages("ade4")
library(ade4)
install.packages("picante")
library(picante)
install.packages("vegan")
library(vegan)
install.packages("betapart")
library(betapart)
install.packages("ggplot2")
library(ggplot2)
install.packages("gridExtra")
library(gridExtra)
install.packages("ggrepel")
library(ggrepel)
install.packages("GGally")
library(GGally)

#Definindo o diretório
setwd("C:/Users/Julia Viotti Corrêa/Desktop/fun")

#Carregando a planilha dos dados da comunidade e dos traços funcionais
att <- read.table("C:/Users/Julia Viotti Corrêa/Desktop/fun/att.csv", sep = ",",
row.names = 1,
              header = T)
comm <- read.table("C:/Users/Julia Viotti Corrêa/Desktop/fun/comm.csv", sep = ",",
row.names = 1,
               header = T)

#Dando match nas colunas de comm com as linhas de att
colnames(comm) <- rownames (att)

#Criando um vetor de distâncias via método de Gower (variáveis categóricas)
att.dis <- gowdis(att)

#Transformando o vetor de distância não-euclidiana em euclidiana por meio do
método de Cailliez
att.cai <- cailliez(att.dis, TRUE)

#----------------II PARTE----------------
##PCoA dos atributos categóricos
#PCoA da matriz de distância funcional (Gower)
pcoa_traits_cat <- pcoa(att.dis, correction = "cailliez")
```

```
#Criando um objeto de dados (escores) para o ggplot
eixos_cat <- as.data.frame(pcoa_traits_cat$vectors[,1:2]) # Selecionar os dois primeiros eixos

#Plotando o gráfico de ordenação
plot_trait_cat <- ggplot(eixos_cat, aes(x = Axis.1, y = Axis.2)) +
  geom_point(pch = 21, size = 4, alpha = 0.7, color = "black", fill = "cyan4") +
  geom_text_repel(aes(Axis.1, Axis.2, label = rownames(eixos_cat))) +
  geom_hline(yintercept = 0, linetype = 2) +
  geom_vline(xintercept = 0, linetype = 2) +
  labs(x = "PCO 1", y = "PCO 2", title = "Dados categóricos")

plot_trait_cat

#----------------III PARTE----------------
##Calculando as métricas funcionais
#Riqueza de espécies
richness <- dbFD(att.cai, comm)$nbsp

head(richness)

#Grupos Funcionais (CWM)
functcomp(x = att, a = as.matrix(comm), CWM.type = c("dom"))

#Riqueza funcional ou "Functional Richness (FRic)"
fric <- dbFD(att.cai, comm)$FRic

head(fric)

#Divergência funcional ou "Functional Divergence (FDiv)"
fdiv <- dbFD(att.cai, comm)$FDiv

head(fdiv)

#Dispersão funcional ou "Functional Dispersion (FDis)"
fdis <- dbFD(att.cai, comm)$FDis

head(fdis)

#Regularidade funcional ou "Functional evenness (FEve)"
feve <- dbFD(att.cai, comm)$FEve

head(feve)

#Criando uma tabela com os resultados de todas as métricas
metricas <- data.frame(richness = richness,
                        fric = fric,
                        fdiv = fdiv,
                        fdis = fdis,
                        feve = feve)
```

```
head(metricas)

#Salvando a tabela no formato .csv na pasta do diretório
write.table(metricas, "metricas.csv", row.names=T, sep=",", dec=".")

#Construindo um gráfico para comparar o comportamento das métricas
metricas=read.csv("metricas.csv", sep=",")

ggpairs(metricas)

#----------------IV PARTE----------------

##Índices de diversidade de modelos nulos
#Script com base nas métricas reais

#Calcule a probabilidade P
P<-((length(which(((feve)<0.4)==TRUE)))+((length(which(((feve)==0.4)==TRUE)))/2))/1001

#Calcule o efeito padronizado (SES)
SES<-2*(P-0.5)

#Imprima os resultados
print(P)

print(SES)

#Script com base nas métricas fabricadas
#Criando e dimensionando a matriz de comunidade
npar <- dim(comm)[1]
nsp <- dim(comm)[2]

#Criando a matriz de presença/ausência
#Comando para caso os atributos sejam contínuos, mas vamos rodá-lo mesmo assim!
mp <- replace(comm, comm > 0, 1)

#Criando vetor de riqueza de espécies em cada parcela
vr <- apply(mp, 1, sum)

#Criando vetor de incidência das espécies
vi <- apply(mp, 2, sum)

#Determinando o número de iterações
iterations <- 1000  #Reduzir para testar

#Criando a tabela com os resultados dos modelos nulos
results <- matrix(nrow = iterations, ncol = (5 * npar), 0)
```

```
#Gerando os modelos nulos
for (h in 1:iterations) {
  nm <- matrix(nrow = npar, ncol = nsp, 0)
  pp <- 1:nsp
  inc <- vi
  for (i in 1:npar) {
    if(length(pp) < vr[i]) {
      pp2 <- 1:nsp
      pp3 <- pp2[-pp]
      nn <- min(vr[i] - length(pp), length(pp3))
      if (nn > 0) {
        pp4 <- sample(pp3, nn)
        psp <- sort(c(pp, pp4))
      } else {
        psp <- pp
      }
    } else {
      psp <- sort(sample(pp, vr[i]))
    }
    nm[i, psp] <- 1
    inc[psp] <- inc[psp] - 1
    pp <- setdiff(1:nsp, which(inc == 0))
  }

  #Canculando os índices de diversidade
  colnames(nm) <- rownames(att)
  div.func <- dbFD(x = att.cai, a = nm, w.abun = T, stand.x = T, stand.FRic = T, m = 5)
  indices <- c(div.func[[3]], div.func[[5]], div.func[[6]], div.func[[7]], div.func[[8]])
  results[h,] <- indices
  cat("Iteração", h, "completa\n")  #Adicionado para monitoramento
}

#Atribuindo nomes às colunas da nossa tabela de resultados
parc <- rownames(comm)
colnames(results) <- c(paste("FRic", parc, sep = "_"), paste("FEve", parc, sep = "_"),
                       paste("FDiv", parc, sep = "_"), paste("FDis", parc, sep = "_"))

#Conferindo e exportando os resultados
view(results)

write.csv(results, file = "C:/Users/Julia Viotti
Corrêa/Desktop/fun/indices_modelos_nulos_novo.csv", row.names = FALSE)

#Carregando 'results'
results <- read.table("C:/Users/Julia Viotti
Corrêa/Desktop/fun/indices_modelos_nulos_novo.csv", sep = ",",
                  header = T)

#Modelos nulos
#Exemplo para a métrica FEve em campo rupestre
```

```
#Suponha que 'feve_real_CAR' seja o valor de FEve observado para campo rupestre (CAR)
feve_real_CAR <- 0.4954 #Substitua pelo valor de seu dado observado

#Extraia FEve dos modelos nulos (supondo que FEve esteja em uma coluna específica)
null_fric <- results[, "FEve_CAR"]

#Calcule a probabilidade P
P <- (length(which(null_fric < 0.4)) + (length(which(null_fric == 0.4)) / 2)) / nrow(results)

#Calcule o SES
SES <- 2 * (P - 0.5)

#Imprima os resultados
print(P)
print(SES)

P<-((length(which(((null_fric) <0.4)==TRUE)))+((length(which(((null_fric)==0.4)==TRUE)))/2))/1001
P
SES<-2*(P-0.5)
SES
```

```
#sinal filogenético#
```

```
#Instalando e carregando pacotes
install.packages("devtools")
devtools::install_github("ropensci/phylopicr")
devtools::install_github("jinyizju/V.PhyloMaker")
devtools::install_github("liamrevell/phytools")
install.packages("ape")
install.packages("phangorn")
install.packages("phytools")
install.packages("geiger")

library(V.PhyloMaker)
library(phytools)
library(ape)
library(adiv)
library(FD)
library(phangorn)
library(geiger)
library(devtools)
library(adiv)

#Definindo o diretório
setwd("C:/Users/Julia Viotti Corrêa/Desktop/filofun")
```

```
#Carregando a planilha da filogenia
splist <- read.table("filo.txt", h=T, stringsAsFactors = T)

#Criando a árvore filogenética (esse comando demora um pouco a rodar!)
phy <- phylo.maker(splist)

#Extraindo a parte necessária para desenhar a árvore
tree <- phy$scenario.3

#Plotando a árvore
phytools::plotTree(tree)

#Exportando a árvore para a pasta de diretório
write.tree(tree, "tree.tre") #Note the .tre file extension here

#Carregando a árvore no seu ambiente de trabalho (só para o caso de ela não estar carregada ainda)
tree <- read.tree("C:/Users/Julia Viotti Corrêa/Desktop/filofun/tree.tre")

#Carregando as matrizes de comunidade a atributos
comm <- read.table("C:/Users/Julia Viotti Corrêa/Desktop/filofun/comm.csv", sep = ",", row.names = 1, header = T)

att <- read.table("C:/Users/Julia Viotti Corrêa/Desktop/filofun/att.csv", sep = ",", row.names = 1, header = T)

habit <- read.table("C:/Users/Julia Viotti Corrêa/Desktop/filofun/habit.dis.csv", sep = ",", row.names = 1, header = T)

form <- read.table("C:/Users/Julia Viotti Corrêa/Desktop/filofun/form.dis.csv", sep = ",", row.names = 1, header = T)

texture <- read.table("C:/Users/Julia Viotti Corrêa/Desktop/filofun/consistence.dis.csv", sep = ",", row.names = 1, header = T)

trichome <- read.table("C:/Users/Julia Viotti Corrêa/Desktop/filofun/trichome.dis.csv", sep = ",", row.names = 1, header = T)

fruit <- read.table("C:/Users/Julia Viotti Corrêa/Desktop/filofun/fruit.dis.csv", sep = ",", row.names = 1, header = T)

dispersion <- read.table("C:/Users/Julia Viotti Corrêa/Desktop/filofun/dispersion.dis.csv", sep = ",", row.names = 1, header = T)

#Criando a matriz de distância para atributos categóricos (Gower)
att.dis <- gowdis(att)
habit.dis <- gowdis(habit)
form.dis <- gowdis(form)
consistence.dis <- gowdis(texture)
trichome.dis <- gowdis(trichome)
```

```
fruit.dis <- gowdis(fruit)
dispersion.dis <- gowdis(dispersion)

#Definindo a paleta de cores para os atributos de cada traço
habit_colors <- c("variavel" = "mediumorchid3", "arvore" = "sienna4", "erva" =
"green", "arbusto" = "darkgreen", "subarbusto" = "yellowgreen", "palmeira" =
"#FFCC33")
form_colors <- c("camefita" = "lightblue3", "hemicriptofita" = "orange", "geofita" =
"sienna1", "fanerofita" = "blue", "terofita" = "sienna4")
text_colors <- c("cartacea" = "yellow", "coriacea" = "orange", "herbacea" = "green",
"membranacea" = "blue","suculenta" = "palegreen4", "variavel" = "mediumorchid3")
tri_colors <- c("presente" = "gray", "ausente" = "green")
fru_colors <- c("carnoso" = "mediumorchid3", "seco" = "#FFCC33")
dis_colors <- c("zoocorica" = "mediumorchid3", "anemocorica" = "blue", "autocorica"
= "orange")

#Atribuindo as cores dos atributos para cada ponta na árvore
#Você só é capaz de executar um dos comandos a seguir por vez neste script
#Rode um e passe para as próximas etapas
#Quando terminar tudo, retorne a este ponto e faça tudo de novo para o
próximo traço
tip_colors <- habit_colors[att[tree$tip.label, "habit"]]
tip_colors <- form_colors[att[tree$tip.label, "form"]]
tip_colors <- text_colors[att[tree$tip.label, "texture"]]
tip_colors <- tri_colors[att[tree$tip.label, "trichome"]]
tip_colors <- fru_colors[att[tree$tip.label, "fruit"]]
tip_colors <- dis_colors[att[tree$tip.label, "dispersion"]]

#R test (p values < 0.05 rejeitam padrão aleatório)
#Atenção ao argumento dis, defina o campo de acordo com seu interesse
rtestdecdiv(tree, comm, dis = habit.dis, tol = 1e-08,
          option = 1:5, formula = c("QE", "EDI"),
          vranking = c("complexity", "droot"),
          ties.method = c("average", "first", "last", "random",
                      "max", "min"), statistic = 1:3, optiontest = NULL, nrep = 99)

#Decomposição da diversidade funcional
#Você pode rodar opções 1:5 e as fórmulas “QE” ou “EDI”
#ncom é o número da linha da comunidade de interesse em comm.csv
comm.habit <- decdiv(tree, comm, dis = habit.dis,
                option=1, formula = "QE")
plot.decdiv(comm.habit, ncom = 1, show.tip.label = TRUE, type = "phylogram", cex =
0.8, no.margin = TRUE,
          edge.width = 2, edge.color = "gray", label.offset = 0.005)
tiplabels(pch = 16, col = tip_colors, bg = NA, cex = 1.2, adj = c(0.5, 0.5))

#Cálculo de QE
QE(comm, dis = habit.dis, formula = c("QE"))
discomQE(comm, dis = habit.dis, formula = c("QE")
```

#gráfico de correlação#

```
#Instalando e carregando o pacote
install.packages("corrplot")
library(corrplot)

#Definindo o diretório
setwd("C:/Users/Julia Viotti Corrêa/Desktop/filofun")

#Carregando os dados do arquivo .csv
dados <- read.csv('C:/Users/Julia Viotti Corrêa/Desktop/filofun/dispersion.csv', sep = ",", header = TRUE)

#Convertendo a primeira coluna para um fator
dados$Comunidade <- as.factor(dados$Comunidade)

#Convertendo comunidades para variáveis dummy
comunidades_dummies <- model.matrix(~ Comunidade - 1, data = dados)

#Juntando os dados das comunidades (agora como variáveis dummy) com os atributos
dados_correlacao <- cbind(comunidades_dummies, dados[, -1])

#Calculando a matriz de correlação
matriz_correlacao <- cor(dados_correlacao, use = "pairwise.complete.obs")

#Extraindo apenas o quadrante de interesse da matriz de correlação
num_comunidades <- length(unique(dados$Comunidade))

#Quantidade de atributos (colunas menos a coluna de comunidade)
num_atributos <- ncol(dados) - 1

#Extraindo o quadrante de interesse
quadrante_interesse <- matriz_correlacao[(num_comunidades + 1):(num_comunidades + num_atributos), 1:num_comunidades]

#Criando o gráfico de correlação para o quadrante de interesse usando 'corrplot'
corrplot(quadrante_interesse, method = "circle",
        title = "Correlação entre Comunidades e Atributos",
        tl.pos = "lt", tl.cex = 0.7, cl.cex = 0.7,
        addCoef.col = "black", number.cex = 0.5,
        col = colorRampPalette(c("#BB4444", "#EE9988", "#FFFFFF", "#77AADD", "#4477AA"))(200))

#Salva o gráfico em um arquivo, se necessário
png('C:/Users/Julia Viotti Corrêa/Desktop/filofun/corrplot.png')
corrplot(quadrante_interesse, method = "circle")
#dev.off()
```

#Para maiores informações sobre a organização das planilhas e dados em cada análise, consulte os manuais de cada pacote.

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CONSIDERAÇÕES FINAIS

A investigação detalhada das fitofisionomias do Planalto Diamantino, através desta dissertação, revelou a complexidade e a singularidade dos ecótones da Reserva da Biosfera da Serra do Espinhaço (RBSE). Os resultados obtidos, fundamentados na análise multidimensional da biodiversidade, enfatizam a necessidade urgente de preservar estas áreas de transição não apenas em face das mudanças climáticas em curso, mas também como medida para salvaguardar sua herança evolutiva e biodiversidade excepcional.

Conforme demonstrado no Capítulo 1, a diversidade β-filo-taxonômica entre as fitofisionomias estudadas sugere que a heterogeneidade de habitat é um vetor significativo na configuração da composição florística destas áreas. A identificação de dois grupos florísticos distintos reforça a percepção de que a composição de espécies de Cerrado no Planalto Diamantino se comporta de maneira semelhante entre as vegetações rupestres, as florestas e o Cerrado *stricto sensu*, mas divergente em relação aos Campos Úmidos e Veredas.

Por sua vez, o Capítulo 2 aprofunda-se na diversidade de traços funcionais sob a influência da filtragem ambiental e da história evolutiva nas fitofisionomias. Os padrões únicos de traços identificados entre os tipos de vegetação corroboram a ideia de que estratégias de adaptação específicas a diferentes habitats são fundamentais para a sobrevivência das espécies vegetais nestas áreas ecotonais. Este capítulo evidencia, ainda, a presença de convergência funcional entre as fitofisionomias, e ressalta a importância não só dos fatores ecológicos na formação dos ecossistemas do Planalto Diamantino, mas também da sua complexa história evolutiva.

A combinação dos resultados destes dois capítulos destaca a relevância dos padrões pretéritos e presentes para a conservação futura das fitofisionomias do Cerrado na RBSE. O reconhecimento de sua singularidade, através de sua identidade taxonômica, funcional e filogenética, oferece um caminho para a elaboração de estratégias de conservação mais eficazes e direcionadas. É necessário que tais estratégias considerem a totalidade do ecossistema, visando a manutenção de sua heterogeneidade ambiental e, portanto, de sua biodiversidade.

Além disso, o extrativismo sem manejo, a mineração e as mudanças no uso da terra apresentam desafios adicionais para a preservação destas áreas. As turfeiras, por exemplo, destacam-se como áreas de importância ecológica que necessitam de proteção. Estas práticas ameaçam não apenas a integridade física destes ecossistemas, mas também sua capacidade de se adaptar e responder às mudanças climáticas futuras.

Neste contexto, a presente dissertação contribui significativamente para o entendimento da fitogeografia de ecótones no Planalto Diamantino, fornecendo *insights* valiosos sobre os mecanismos que moldam a biodiversidade nestas áreas. Espera-se que os achados aqui relatados possam auxiliar na formulação de políticas públicas e iniciativas de conservação que reconheçam a complexidade e a importância destes ecossistemas, garantindo sua preservação para as gerações futuras.

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