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RESEARCH

Heterogeneity in Arbuscular Mycorrhizal Fungi and Plant Communities of the Brazilian Cerrado, Transitional Areas toward the Caatinga, and the Atlantic Forest

Juliana Souza de Pontes[1] · Fritz Oehl[2,3] · Cicero Donizete Pereira[4] · Cynthia Torres de Toledo Machado[4] · Danny Coyne[5] · Danielle Karla Alves da Silva[2] · Leonor Costa Maia[2]

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Abstract

The Cerrado is the most diverse tropical savanna worldwide and the second-largest biome in South America. The objective of this study was to understand the heterogeneity and dynamics of arbuscular mycorrhizal fungi (AMF) in different types of natural Cerrado vegetation and areas that are transitioning to dryer savannas or tropical rainforests and to elucidate the driving factors responsible for the differences between these ecosystems. Twenty-one natural sites were investigated, including typical Cerrado forest, typical Caatinga, Atlantic Rainforest, transitions between Cerrado and Caatinga, Cerrado areas near Caatinga or rainforest, and Carrasco sites. Spores were extracted from the soils, counted, and morphologically analyzed. In total, 82 AMF species were detected. AMF species richness varied between 36 and 51, with the highest richness found in the area transitioning between Cerrado and Caatinga, followed by areas of Cerrado close to Caatinga and typical Cerrado forest. The types of Cerrado vegetation and the areas transitioning to the Caatinga shared the highest numbers of AMF species (32–38). Vegetation, along with chemical and physical soil parameters, affected the AMF communities, which may also result from seasonal rainfall patterns. The Cerrado has a great AMF diversity and is, consequently, a natural refuge for AMF. The plant and microbial communities as well as the diversity of habitats require urgent protection within the Cerrado, as it represents a key AMF hotspot.

Keywords AMF · Biodiversity · Glomeromycota · Hotspot · Refuge · Tropical vegetation

Introduction

The Brazilian Cerrado is the world's most diverse tropical savanna and the second-largest biome in South America. It is situated to the south of the Amazon rainforest and spans over 2 million km^2. The Cerrado is adjacent to two arid biomes: the Chaco in Argentina and Bolivia to the southeast and the Caatinga in northeastern Brazil. This positioning creates a corridor connecting these biomes and serves as a geographical barrier separating the Amazon rainforest from the Atlantic rainforest [1]. The Cerrado ecosystem exhibits close interactions with neighboring biomes, such as the Amazon, the Caatinga, and the Atlantic Forest, giving rise to transitional areas [2]. These transitional zones host unique plant species and act as refuges of biodiversity [3]. The soil heterogeneity and pronounced climatic seasonality within the Cerrado account for the high biodiversity of this biome and its various phytophysionomies, including croplands, natural savannas, and unique floristic characteristics [4–6].

✉ Danielle Karla Alves da Silva
daniellekarlas@yahoo.com.br

1 Programa de Pós-Graduação em Ciências Biológicas, Centro de Biociências, Universidade Federal de Pernambuco, Av. da Engenharia s/n, Recife, PE 50740-600, Brazil

2 Departamento de Micologia, Centro de Biociências, Universidade Federal de Pernambuco, Av. da Engenharia s/n, Recife, PE 50740-600, Brazil

3 Agroscope, Competence Division of Plants and Plant Products, Plant Protection Products—Impact and Assessment, Müller-Thurgau-Strasse 29, CH-8820 Wädenswil, Switzerland

4 Embrapa Cerrados, BR 020-km 18, Brasilia, DF 73310-970, Brazil

5 International Institute of Tropical Agriculture (IITA), Oyo Road, Ibadan, Nigeria

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The combination of high biodiversity, a significant degree of endemism, and notable levels of degradation plays a pivotal role in the Cerrado. This biome ranks as one of the 25 most important biodiversity hotspots in the world [7].

Currently, approximately 50% of the original vegetation in the Cerrado remains intact, while the other 50% is utilized for the cultivation of annual or perennial crops and pastures [8]. However, only 6.5% of the natural vegetation is protected [9], and there is a need for further studies to gain a better understanding of biodiversity in the Cerrado and to identify the most crucial areas for biological conservation. In recent decades, research in the Cerrado has primarily concentrated on floral diversity [10], with limited attention given to studies aimed at comprehending the multifunctionality of ecosystems in relation to invertebrates and microorganisms [11].

Arbuscular mycorrhizal fungi (AMF) are soil microorganisms that establish symbiotic associations with approximately 80% of terrestrial plants [12]. They enhance the living conditions of their hosts and improve soil structure and fertility. AMF contribute to increased nutrient absorption by plants and, consequently, enhance plant nutrition through their extraradical hyphal network. In return, they receive organic compounds produced by the plant during photosynthesis, which are essential for their development [12]. These soil fungi are directly influenced by various factors, including vegetation type, plant composition, soil type, and climatic conditions [13]. These factors affect species composition, richness, diversity, and the spatial and seasonal distribution of AMF [13, 14].

AMF communities can be studied using classical microscopic/morphological identification of spores extracted from soils [15] and modern molecular analyses of soils or root systems [16, 17]. Both methods have their respective advantages and limitations [18, 19]. Whenever possible, it is advisable to combine both methods, although due to limitations in time, knowledge, and experience, this rarely occurs [20].

It is well established that plant growth and diversity are strongly affected by the diversity of AMF [21]. Environmental factors related to the structure of AMF communities associated with a vegetation gradient in the Cerrado have revealed the importance of plant composition and its conservation in structuring these communities in this biome [6]. Climate, soil texture, plant cover, soil management, land use systems, and seasonality all impact the composition and diversity of AMF species in the Cerrado [22, 23]. In addition to soil properties, plant composition can influence the structure of AMF communities in various Cerrado physiognomies [24]. However, studies on AMF diversity in natural savanna systems remain limited [6, 25, 26], particularly those exploring the connection between plant diversity and belowground microbial diversity. Research in this area is valuable for providing insights into the concurrent diversity changes in the Cerrado and for highlighting the heterogeneity of plant and AMF communities across different ecosystems. So far, only a handful of studies have addressed AMF diversity in the natural Cerrado [27] because the primary focus has typically been on examining the influence of land use and cropping systems on plant diversity within the Cerrado [23, 28].

Given that the Cerrado savanna shares its borders with several other biomes in the heart of South America, which can vary in terms of aridity and humidity, it provides an excellent opportunity to examine the diversity of AMF in these transitional areas and compare them with the adjacent savanna and forest types. The primary aim of this study was to gain insights into the heterogeneity and dynamics of AMF communities within different types of natural Cerrado vegetation and adjacent areas transitioning to tropical rainforests, specifically the Atlantic rainforest, as well as the drier savanna forests known as Caatinga in Brazil. The study also sought to identify the key factors or drivers responsible for the primary differences observed between these ecosystems.

Our study hypothesized that (i) the AMF diversity of the typical Cerrado differs from the others environments studied; (ii) a clear gradient of shifts in AMF diversity will be detected from the most humid to the driest vegetation types; and (iii) the AMF diversity and community composition of the typical Cerrado sites are comparable, despite their significant geographical distances. According to Silva et al. [29], lower AMF diversity may be expected in stable habitats than in unstable habitats. In our context, this may imply that typical Cerrado, Caatinga, and Atlantic rainforests have lower AMF spore diversity than transition areas or the Carrasco outcrops. The information gathered in our study will contribute to the knowledge of biodiversity protection and conservation "in situ" [30, 31]. In particular, this should prove especially useful for the successful conservation of the increasingly threatened Cerrado [10].

Materials and Methods

Study Areas and Sites

The study sites were located in proximity to two Natural State Parks, namely, "Parque Estadual Caminho dos Gerais" and "Parque Estadual da Mata Seca", situated in the northeastern region of Minas Gerais. Additionally, three typical Cerrado areas were selected in the Distrito Federal, at approximately 1000 km distance in the heart of the Cerrado biome, at the same latitude as the "Natural State Park" of Minas Gerais.

Twenty-one natural sites were investigated (Fig. 1), spanning five municipalities: Planaltina-DF (located in the

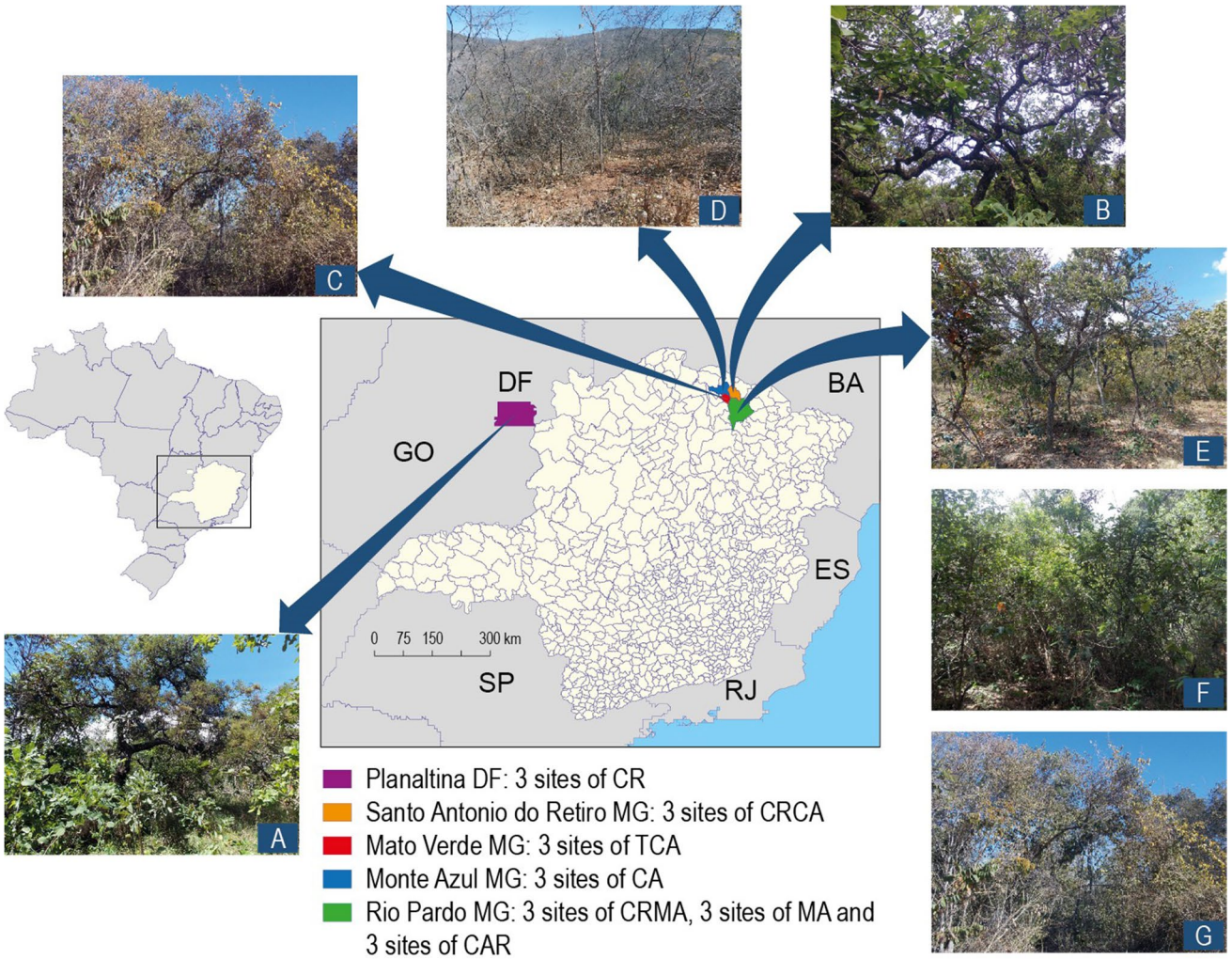

Fig. 1 Selected study areas and vegetation types in four municipalities in the north of Minas Gerais and adjacent District Federal (Planaltina, Brasilia): **A**—Cerrado *stricto sensu* (CR), **B**—Cerrado close to Caatinga (CRCA), **C**—Transition between Cerrado and Caatinga (TCA), **D**—Caatinga (CA), **F**—Cerrado close to Atlantic rainforest (CRMA), **F**—Atlantic rainforest (MA), **G**—Carrasco (CAR). DF Districto Federal/Federal District, MG Minas Gerais State)

Federal District, Central-West Brazil, entirely within the Cerrado biome), and Monte Azul, Mato Verde, Santo Antonio do Retiro, and Rio Pardo de Minas (border municipalities in the northern part of Minas Gerais State, bordering Bahia). In the latter three municipalities, the predominant climate is classified as tropical with a dry summer, according to the Köppen climate classification system [32]. The elevation in these areas ranges from 600 to 800 m, with an average annual temperature ranging from 22 to 24 °C and average annual precipitation ranging from 700 to 1000 mm. The region experiences two well-defined seasons [32]: a wet season from October to March and a dry season from April to September. This region is characterized as a shrub-dominated ecotone zone between the Cerrado (tropical savanna) and Caatinga (semiarid) biomes. The primary soil types are Ferralsols and Leptosols [33]. In the Planaltina study area, the typical climate is a tropical zone with a dry winter [32]. The elevation in this area ranges from 800 to 1200 m, with an average annual precipitation of 1300 to 1600 mm, strong climatic seasonality (a 6-month dry season and a 6-month wet season), and an average annual temperature of 20 to 22 °C [32]. The most representative vegetation type is Cerrado shrubland, and the dominant soil type is Ferralsol [34].

In Planaltina, three study sites within the Cerrado *stricto sensu* (savanna forests) were investigated (CR) (15° 36′ 35″ S; 47° 39′39″ W; 1200 m a.s.l). In Monte Azul, three study sites were selected within the Caatinga *stricto sensu* (dry savanna) vegetation (CA), which had undergone slight degradation due to human activities (15° 09′ 18″ S; 42° 52′ 29″ W; 800 m a.s.l.). In Santo Antonio do Retiro (15° 20′ 22″ S; 42° 37′ 26″ W; 1000 m a.s.l.), three sites within Cerrado areas close to Caatinga were studied (CRCA). In Mato Verde

(15° 23′ 50″ S; 42° 51′ 59″ W; 541 m a.s.l.), three transition areas between the Cerrado and Caatinga were investigated (TCA). In Rio Pardo de Minas, nine sites were selected (15° 36′ 3″ S; 42° 32′ 40″ W; 750–800 m a.s.l.), and three vegetation types were studied: Atlantic Rainforest (MA), Cerrado areas close to the Atlantic Rainforest (CRMA), and Cerrado areas close to Carrasco (CAR). Carrasco is characterized by a landscape with small, branched, and aggregated bushes, featuring open or dense vegetation.

Soil Sampling and Analyses

Soil sampling was conducted during two distinct seasons: the first sampling took place in November/December 2013, during the wet summer season, and the second sampling occurred in August 2014, during the dry winter season. At each of the 21 study sites, four plots were established, each measuring 5 × 20 m and spaced 20 m apart. Within each plot, ten subsamples were randomly collected and thoroughly mixed, resulting in approximately 4 kg of soil sampled per plot. In total, 168 samples were generated (21 study sites × 4 replicates per site × 2 sampling dates). The physical and chemical soil analyses were conducted at the Soil Laboratory of Embrapa Cerrados, following standard methods [35].

AMF Bait Culturing

A portion of each composite soil sample was utilized to establish trap cultures. For each field plot replicate at every site and treatment, one pot of trap culture was established for each collection date to ensure an adequate supply of healthy glomerospores for morphological analysis. The collected soil was mixed at a 1:1 (v/v) ratio with oven-sterilized sand (105 °C/24 h) and placed in 2 kg plastic pots. These pots were then sown with ten seeds of sorghum (*Sorghum bicolor* (L.) Moench) and millet (*Pennisetum glaucum* L.) to serve as host plants. The trap cultures were maintained in a greenhouse for two multiplication cycles, each lasting 4 months. The greenhouse conditions included day temperatures ranging from 26 to 33 °C, night temperatures between 23 and 27 °C, and a relative air humidity of approximately 80%. Pots were watered regularly every second day. At the conclusion of each cycle, soil samples were collected for spore extraction and the morphological identification of AMF species.

Extraction of AMF Spores

Glomerospores collected from field samples and trap cultures were extracted through a process involving wet sieving, followed by water and sucrose centrifugation [36, 37]. To identify AMF species, glomerospores extracted from either field samples or trap cultures were prepared on slides with PVLG (polyvinyl alcohol lactoglycerol) and PVLG + Melzer's reagent (1:1 v/v) and observed under a light microscope. Species were identified according to Schenck and Pérez [38], Błaszkowski [39], and all available original and amended species descriptions. The classification adhered to Oehl et al. [40] and the most recent updates [41]. It should be noted that several morphotypes could not be identified to the species level with certainty and some of them represent new records for science.

Ecological Indices

To assess the AMF communities and their composition, various parameters were determined for each sample, including spore density, species richness, absolute and relative spore abundances for each species, evenness, and diversity. Species richness was defined as the number of species recorded in each study area. The ecological indices were evaluated as follows: Shannon index $H' = - \Sigma (Pi \ln [Pi])$, where $Pi = ni/N$, ni = number of individuals of species i, and N = total number of individuals of all species; Pielou's evenness index (J) = H′/Log (S), where H′ is the value obtained by the Shannon index and S = total number of species [42]. Margalef's index was calculated based on the equation $d = S - 1/\text{Log}N$, where S = number of species and N = total number of spores in the sample. Richness was represented by the number of AMF species registered in each study area. The frequency of occurrence (FO) of a species (i) was estimated by the equation FO = Ji/k, where JI = number of samples where the species I occurred and k = total number of soil samples [43]. Based on Zhang et al. [44], the frequency of occurrence was classified as dominant (FO> 50%), very common (30% <FO ≤50%), common (10% <FO ≤30%), and rare (FO ≤10%). The relative abundance (RA) of AMF species was calculated by the ratio between the total number of species and the total number of species in the area [45]. The ecological indices were calculated using the PRIMER 6.0 program [46].

Data Analyses

The data related to soil attributes, species richness, and diversity parameters were subjected to analysis of variance (ANOVA), and means were compared using the Tukey test ($P < 0.05$) with the assistance of Assistat 7.6 beta [47]. The spore density data were also subjected to analysis of variance (ANOVA), and means were compared using the Tukey test ($p < 0.05$), using the package ExpDes.pt and the function *fat2.dic* [48]. The graph was made using the ggplot2 package [49].

The relative abundance data of the AMF species were used to assess changes in the AMF community through multivariate analysis. To test for significant differences in the composition of AMF communities among the studied

areas, permutational multivariate analysis of variance (PERMANOVA) was conducted based on the Bray–Curtis distance [50] using the *adonis* function in the vegan package with 1000 permutations [51]. Nonmetric multidimensional scaling (NMDS) based on the Bray–Curtis distance [52] was used to calculate dissimilarities in the AMF community composition among areas, and the *envfit* function was used to determine relationships between soil properties and the AMF community using the vegan package [51].

Indicator species analysis was employed [53] to verify which species were more associated with each area. This analysis uses the abundance and frequency of occurrence to calculate the indication value (IndVal). The *multipatt* function from the indicspecies package [54] was used to calculate the IndVal, and its significance was tested using a Monte Carlo test with 1000 permutations. Species were considered indicators when $p<0.05$ and IndVal $\geq 25\%$. Venn diagrams were generated using the "Calculate and draw custom Venn diagrams" tool available online (http://bioinformatics.psb.ugent.be/webtools/Venn/), and Venn diagram graphs were created using the Canva app (http:/canva.com).

Results

Chemical and Physical Soil Parameters

The Caatinga dry savannas exhibited the highest soil pH levels and contained the greatest levels of potassium (K), magnesium (Mg), and calcium (Ca). These areas also had the highest percentage of silt. Conversely, Carrasco areas displayed the lowest pH values, while Cerrado *stricto sensu* had the lowest levels of K and Ca and the highest clay contents (Table 1).

Spore Abundance

The average spore densities ranged from 6.6 g^{-1} soil in the Cerrado savannas to 29.8 g^{-1} soil in the Caatinga. Only in the Atlantic Rainforest and in the transition between the Cerrado and Caatinga were spore abundance lower in the dry season than in the wet season, while no differences were observed between the two seasons in the other ecosystems. In general, the Caatinga, the transition between the Cerrado and Caatinga, and the Cerrado close to the Atlantic Rainforest exhibited the highest spore abundances (Fig. 2).

AMF Species Richness

AMF species richness varied between 36 and 51 (Table 2), with the highest richness found in the Cerrado/Caatinga transition (51), followed by the Cerrado close to the Caatinga (48), the typical Cerrado in Planaltina (45), and the Cerrado close to the Atlantic Rainforest (43). The different Cerrado vegetation types shared the highest numbers of AMF species (24 species; Fig. 3C), as well as the Cerrado/Caatinga transition and the Cerrado in transition to Caatinga (21).

AMF Species Diversity

In total, 82 AMF species were detected (Table 2), belonging to 24 genera and 12 families (Acaulosporaceae, Ambisporaceae, Archaeosporaceae, Dentiscutataceae, Diversisporaceae, Entrophosporaceae, Gigasporaceae, Glomeraceae, Intraornatosporaceae, Paraglomeraceae, Racocetraceae, and Scutellosporaceae). The genera with the highest species richness were *Acaulospora* (22 species) and *Glomus* (18 species), followed by *Entrophospora*, *Rhizoglomus*, and *Paraglomus* (4), *Cetraspora*, *Fuscutata*, *Gigaspora*, and *Sclerocystis* (3), *Ambispora*, *Dentiscutata*, *Funneliformis*, and *Racocetra* (2), *Albahypha*, *Archaeospora*, *Bulbospora*, *Diversispora*, *Dominikia*, *Intraornatospora*, *Kuklospora*, *Orbispora*, *Paradentiscutata*, and *Scutellospora* (1; Table 2).

Table 1 Physical and chemical soil attributes in the seven vegetation types (Cerrado and transition areas towards Caatinga dry savanna and Atlantic rainforest)

Areas	OM g/kg	pH (H_2O)	P mg/kg	K mg/kg	Mg mg/kg	Ca mg/kg	Al mg/kg	Clay (%)	Silt (%)	Sand (%)
CR	3.6 a	4.6 bc	7.0 a	58.6 d	0.2 b	0.2 c	1.0 bc	53.2 a	7.6 b	39.2 c
CRCA	1.5 b	4.7 b	4.6 a	87.1 bcd	0.5 b	0,7 b	0.7 c	24.5 bc	5.2 cd	70.3 ab
TCA	3.1 a	4.6 b	5.5 a	102.6 b	0.5 b	0.6 bc	1.3 b	10.1 c	8.2 bc	81.6 a
CA	3.9 a	5.6 a	3.9 a	187.3 a	3.0 a	4.0 a	0.1 d	28.4 b	16.7 a	54.8 bc
CRMA	2.0 b	4.6 bc	4.6 a	91.9 bc	0.5 b	0.3 bc	1.2 bc	25.5 bc	7.5 bc	67.0 ab
MA	1.5 b	4.6 bc	5.3 a	67.2 cd	0.4 b	0.3 bc	0.9 bc	23.7 bc	8.4 bc	67.8 ab
CAR	3.2 a	4.3 c	5.2 a	112.4 b	0.5 b	0.3 bc	1.8 a	28.0 b	3.2 d	68.7 ab

CR Cerrado s*tricto sensu*, *CRCA* Cerrado close to the Caatinga, *TCA* Transition between Cerrado and Caatinga, *CA* typical Caatinga, *CRMA* Cerrado close to the Atlantic rainforest, MA Atlantic Rainforest, *CAR* Carrasco—bush vegetation

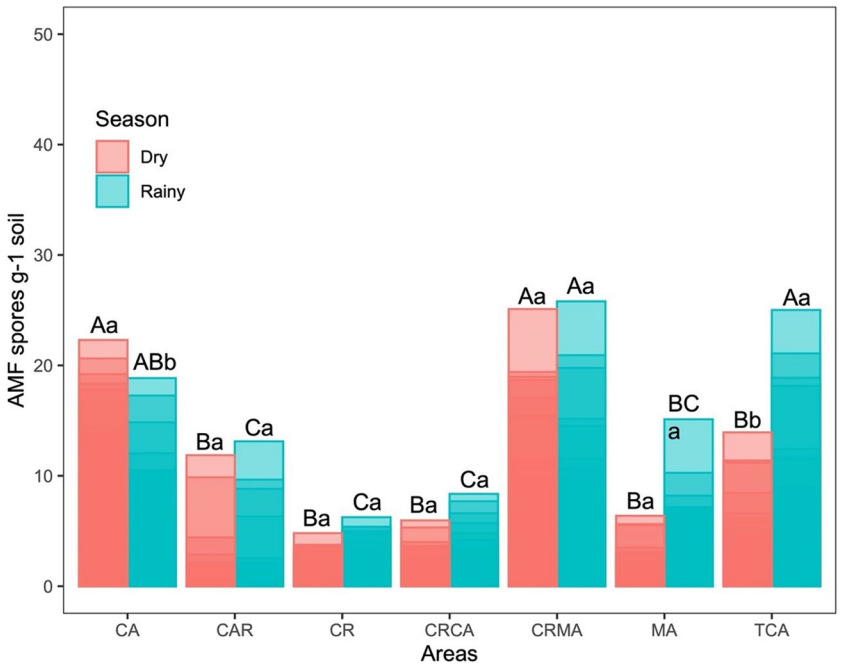

Fig. 2 Arbuscular mycorrhizal fungi (AMF) spores abundance in the different ecosystems and seasons: Areas in natural phytophysiognomies. Capital letters compare areas within each season, and small letters compare the periods within the areas. Columns with the same capital or small letter do not differ by the Tukey test at 5%. CR Cerrado *stricto sensu*, CRCA Cerrado close to the Caatinga, TCA Transition between Cerrado and Caatinga, CA typical Caatinga, CRMA Cerrado close to the Atlantic Rainforest, MA Atlantic Rainforest, CAR Carrasco—bush vegetation

Fifteen AMF species were found in all investigated ecosystems. The most abundantly sporulating species were *Glomus macrocarpum*, *Gl. brohultii*, *Glomus* sp. 2 (aff. *macrocarpum*), *Gl. glomerulatum*, and *Acaulospora mellea*, showing a high abundance in all ecosystems. The following AMF species were classified as dominantly sporulating and frequently found in the soil samples: *Glomus macrocarpum* (in 100% of the samples), *Gl. glomerulatum* (83%), *Gl. brohultii* (82%), and *Acaulospora mellea* (77%).

In total, 37 species are considered rare. Some were recovered from just one ecosystem: *Acaulospora* sp.9, *A. sieverdingii*, *Entrophospora* sp., *Glomus* sp.3, *Glomus* sp.11, and *Rhizoglomus* sp.2 in the Caatinga, *Acaulospora tuberculata*, *Diversispora eburnea*, *Fuscutata aurea*, *Glomus* sp.1, *Kuklospora colombiana*, *Paraglomus pernambucanum*, and *Rhizoglomus* sp.1 in the transition Cerrado to Caatinga, *Glomus* sp. 9 in the Cerrado close to the Caatinga, *Acaulospora* sp.5 in the Atlantic Rainforest, and *Archaeospora trappei* and *Albahypha* sp. in the Carrasco. The other ecosystems did not have exclusive species.

AMF Diversity Indices

According to the Margalef index (Table 3), the highest diversity values were obtained in the Cerrado close to the Caatinga (2.77), in the Cerrado/Caatinga transition (2.64), and in the typical Cerrado (2.40), while the lowest value was observed for the Caatinga (1.45). In terms of species evenness, as indicated by the Pielou index (Table 3), the Caatinga had the lowest value (0.41), and the highest evenness was observed in Carrasco (0.59), with no differences in the remaining ecosystems. Comparable results were obtained for the Shannon diversity index, with the Caatinga exhibiting the lowest value (1.47) and the highest diversity observed in Carrasco (2.15), followed by the Cerrado-Caatinga transition (2.05) and the Cerrado close to the Caatinga (2.03).

AMF Indicator Species

The analysis of indicator species selected 34, with nine of these species being associated with just one area: *Acaulospora* sp. 9, *Acaulospora* sp. 7, *Entrophospora* sp. 2, and *Funneliformis halonatus* as indicators of the Caatinga area; *Scutellospora calospora* as an indicator of the transition between Cerrado and Caatinga; *Fuscutata heterogama* and *Fuscutata rubra* as indicators of the Cerrado area close to the Caatinga; *Acaulospora* sp. 4 as an indicator of the Atlantic Rainforest area; and *Glomus* sp. 4 as an indicator of the Carrasco area (Table 4). The areas of Cerrado *stricto sensu* and the Cerrado close to the Atlantic Forest did not have associated indicator species. Eight species were indicators of two areas simultaneously, and we highlighted *Bulbospora minima*, which was an indicator of both areas of the transition between Cerrado and Caatinga and the Cerrado *stricto sensu* (Table 4). Seventeen species were indicators of three to six areas, with a special mention for the species *Glomus* sp. 7, *Gigaspora margarita*, *Acaulospora mellea*, and *Glomus glomerulatum*, which were indicators of more than 5 areas simultaneously (Table 4).

Table 2 Relative abundance and frequency of arbuscular mycorrhizal fungi (AMF) species in the seven different vegetation areas

AMF species	CR	CRCA	TCA	CA	CRMA	MA	CAR	FO	Zhang
Glomus macrocarpum	63.03	50.99	29.97	61.56	60.20	52.44	24.96	100	D
Glomus glomerulatum	1.75	2.49	19.52	2.56	10.04	4.38	7.68	83	D
Glomus brohultii	2.70	18.74	13.45	11.14	4.49	24.20	25.77	82	D
Acaulospora mellea	9.29	5.26	1.98	0.01	6.53	7.12	1.38	77	D
Glomus sp. 7	0.21	4.46	1.10	4.11	3.35	0.19	2.68	70	D
Gigaspora margarita	0.44	0.68	0.18	0.01	0.02	0.27	0.99	61	D
Dentiscutata cerradensis	0.25	0.10	0.25	-	0.04	0.27	0.09	57	D
Glomus sp. 2 (aff. *macrocarpum*)	0.03	7.49	21.15	13.00	2.14	3.89	3.49	57	D
Funneliformis halonatus	0.16	0.19	0.08	0.49	0.02	0.08	0.24	56	D
Glomus sp. 10	6.08	3.24	0.27	0.52	6.20	0.53	0.46	56	D
Paradentiscutata bahiana	1.08	0.91	0.43	0.01	-	0.02	0.77	48	M
Acaulospora sp.3	0.24	0.27	2.44	0.01	0.15	1.01	0.19	45	M
Dominikia sp.1 (aff. *aurea*)	-	0.40	1.53	0.44	0.24	0.27	12.53	42	M
Glomus microcarpum	9.12	0.12	2.50	0.20	2.88	-	12.51	42	M
Ambispora appendicula	-	0.16	0.23	0.01	0.03	0.04	0.04	40	M
Acaulospora foveata	0.03	0.15	0.09	0.01	0.08	0.03	0.06	37	M
Acaulospora herrerae	0.03	0.15	0.09	0.01	0.08	0.03	0.06	37	M
Acaulospora scrobiculata	0.57	0.19	0.03	0.02	-	0.15	-	33	M
Orbispora pernambucana	0.29	0.08	0.17	-	-	0.10	0.52	33	M
Gigaspora gigantea	0.16	0.23	0.13	-	0.01	0.05	0.14	30	C
Acaulospora spinosa	0.16	0.04	0.08	-	0.06	0.05	-	25	C
Entrophospora etunicata	0.03	0.08	0.24	0.19	0.02	0.09	0.70	25	C
Acaulospora sp.2 (aff. *lacunosa*)	-	0.02	1.73	-	0.02	0.10	0.16	20	C
Racocetra tropicana	0.08	0.04	0.01	0.01	0.01	0.06	0.04	20	C
Acaulospora longula	0.10	0.85	0.14	0.02	0.73	0.02	0.03	19	C
Cetraspora gilmorei	0.06	0.05	0.12	-	-	0.09	-	18	C
Fuscutata heterogama	-	0.42	0.05	-	0.01	0.02	-	17	C
Paraglomus occultum	0.33	0.12	0.05	0.01	0.09	-	0.03	17	C
Acaulospora sp.4 (aff. *paulineae*)	0.08	-	-	-	0.02	0.80	-	15	C
Glomus sp.8	0.03	-	0.15	0.29	0.17	0.24	0.03	15	C
Acaulospora spinosissima	0.43	0.02	0.01	-	-	0.40	-	14	C
Bulbospora minima	0.87	-	0.12	-	0.02	-	-	14	C
Sclerocystis taiwanensis	-	0.16	-	0.03	0.03	-	0.03	14	C
Entrophospora sp.1	-	-	0.02	-	0.56	2.81	0.03	13	C
Intraornatospora intraornata	0.03	0.10	0.01	-	0.01	0.02	0.03	13	C
Acaulospora sp.7	-	-	-	0.35	-	-	0.05	12	C
Gigaspora decipiens	0.03	0.08	0.01	-	0.01	0.02	0.03	12	C
Ambispora sp.1	0.03	0.36	0.07	0.01	0.01	-	-	11	C
Cetraspora pellucida	0.06	-	0.01	-	0.01	0.05	-	11	C
Rhizoglomus clarum	0.13	0.02	0.05	-	0.26	0.02	-	11	C
Scutellospora calospora	-	0.02	0.44	-	-	0.02	-	11	C
Glomus sp.6	0.13	-	-	-	0.05	-	3.96	10	C
Funneliformis mosseae	0.05	0.02	-	0.02	-	0.02	-	8	R
Fuscutata rubra	0.03	0.10	-	-	-	0.02	-	8	R
Acaulospora sp. 9	-	-	-	0.13	-	-	-	7	R
Acaulospora sp.10	-	-	-	*	-	-	-	-	-
Cetraspora sp.1	-	*	-	-	-	-	-	-	-
Glomus ambisporum	-	0.35	0.03	-	0.01	-	-	7	R
Glomus sp. 5 (aff. *nanolumem*)	-	-	0.01	-	-	-	0.13	7	R
Glomus sp. 4	0.48	0.23	-	-	0.03	-	-	7	R
Racocetra fulgida	0.03	0.02	0.02	-	-	-	-	7	R

Table 2 (continued)

AMF species	CR	CRCA	TCA	CA	CRMA	MA	CAR	FO	Zhang
Acaulospora rehmii	0.03	-	-	-	0.01	0.02	0.03	6	R
Acaulospora sp.6 (aff. *spinosa*)	0.06	0.02	-	-	-	0.02	-	6	R
Entrophospora claroidea	-	0.07	0.21	-	0.18	0.05	-	6	R
Entrophospora sp. 2	-	-	-	1.24	-	-	-	6	R
Rhizoglomus intraradices	-	-	0.01	0.02	0.94	-	0.03	6	R
Glomus hyderabadensis	0.03	-	-	0.03	-	-	-	5	R
Glomus trufemii	0.95	-	-	0.29	0.01	-	-	5	R
Glomus sp.1 (aff. *australe*)	-	-	0.62	0.02	-	-	-	5	R
Paraglomus brasilianum	-	-	*	-	-	-	-	-	-
Sclerocystis clavispora	-	0.02	-	0.02	-	-	-	5	R
Sclerocystis sinuosa	-	0.05	-	0.01	-	-	0.04	5	R
Acaulospora morrowiae	-	-	0.01	-	0.19	-	-	4	R
Acaulospora reducta	-	0.12	0.01	-	-	-	-	4	R
Acaulospora sp. 1 (aff. *delicata*)	0.21	-	-	-	0.04	-	-	4	R
Acaulospora sp. 8	-	0.02	-	-	-	-	0.03	4	R
Archaeospora trappei	-	-	-	-	-	-	0.05	2	R
Dentiscutata scutata	0.03	-	-	-	0.01	-	-	2	R
Diversispora eburnea	-	-	0.04	-	-	-	-	2	R
Glomus sp. 3 (aff. *magnicaule*)	-	-	-	0.86	-	-	-	2	R
Kuklospora colombiana	-	-	0.08	-	-	-	-	2	R
Paraglomus sp.1	0.03	0.08	-	-	-	-	-	2	R
Acaulospora sieverdingii	-	-	-	0.01	-	-	-	1	R
Acaulospora tuberculata	-	-	0.01	-	-	-	-	1	R
Acaulospora sp.5 (aff. *scrobiculata*)	-	-	-	-	-	0.03	-	1	R
Albahypha sp.	-	-	-	-	-	-	0.06	1	R
Fuscutata aurea	-	-	0.02	-	-	-	-	1	R
Glomus sp.9	-	0.18	-	-	-	-	-	1	R
Glomus sp.11	-	-	-	1.95	-	-	-	1	R
Paraglomus pernambucanum	-	-	0.02	-	-	-	-	1	R
Rhizoglomus sp.1	-	-	0.03	-	-	-	-	1	R
Rhizoglomus sp. 2	-	-	-	0.42	-	-	-	1	R

*AMF species sporulating in trap cultures, but not detected in field samples FO: Frequency of occurrence, and classification according to Zhang et al. (2004): dominant (>50%: D), very frequent (30.1–50.0%: MC), frequent (10.1–30%: C), and rare (≤10%: R)

AMF Community Composition

The PERMANOVA revealed that the Carrasco area exhibited the most distinct AMF community, differing from all other areas (Table 5). Additionally, it was observed that the Caatinga *stricto sensu* area differed from the transition between the Cerrado and Caatinga and Cerrado *stricto sensu* areas (Table 5). The transition between the Cerrado and Caatinga areas also differed from the Cerrado close to the Caatinga and the Cerrado *stricto sensu* area (Table 5). The NMDS based on the AMF community showed that the AMF community composition exhibited significant differences between the various ecosystems, and the Envfit analysis showed the soil attributes that correlated with the AMF communities (Fig. 4), including Al (R^2=0.152; p=0.001), Ca (R^2=0.130; p=0.001), K (R^2=0.096; p=0.002), MO (R^2=0.037; p=0.04), Mg (R^2=0.070; p=0.004), and pH (R^2=0.133; p=0.001).

Discussion

The highest levels of organic matter were observed in the areas of Caatinga, typical Cerrado, Carrasco, and transition Cerrado to Caatinga, with lower levels recorded in the other areas. In terms of K, Mg, and Ca, the highest levels were found in Caatinga soils. These results can be correlated with current precipitation and, primarily, soil geochemistry. A similar pattern was observed for AMF spore abundance, with values decreasing from the driest to the wetter areas. Similar results were reported by Silva et al. [29] in a vegetation gradient, where Caatinga soils

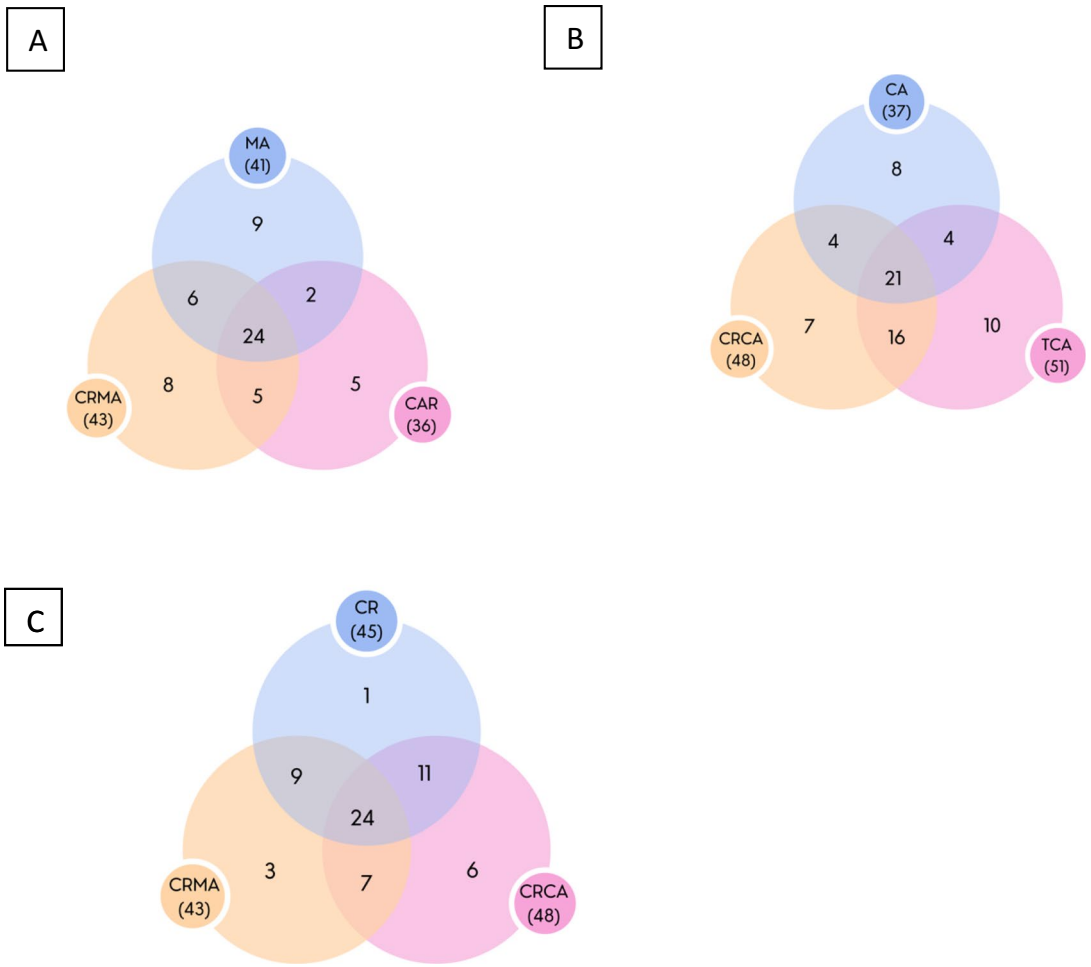

Fig. 3 Venn diagrams for AMF species richness for the different vegetation types and their neighborhood. CR Cerrado *stricto sensu*, CRCA Cerrado close to the Caatinga, TCA Transition between Cerrado and Caatinga, CA typical Caatinga, CRMA Cerrado close to the Atlantic Rainforest, MA Atlantic Rainforest, CAR Carrasco—bush vegetation

Table 3 Diversity indices for AMF in the study areas: Margalef (d), Simpson dominance (λ), Pielou eveness (J′), and Shannon diversity (H′)

Areas	Margalef (d)	Simpson (λ)	Pielou (J′)	Shannon (H′)
CR	2.37 ab	0.43 ab	0.48 ab	1.91 ab
CRCA	2.77 a	0.40 ab	0.48 ab	2.03 a
TCA	2.64 a	0.36 ab	0.48 ab	2.05 a
CA	1.45 c	0.51 a	0,.1 b	1.48 b
CRMA	1.88 bc	0.42 ab	0.48 ab	1.86 ab
MA	1.99 bc	0.43 ab	0.47 ab	1.79 ab
CAR	1.96 bc	0.32 b	0.59 a	2.15 a

CR Cerrado *stricto sensu*, *CRCA* Cerrado close to the Caatinga, *TCA* Transition between Cerrado and Caatinga, *CA* typical Caatinga, *CRMA* Cerrado close to the Atlantic rainforest, *MA* Atlantic Rainforest, *CAR* Carrasco—bush vegetation.

exhibited higher AMF spore abundances than the Atlantic Rainforest, and spore abundance was also higher in the dry season than in the wet season. In the typical Cerrado, no differences in AMF spore abundance were found between the wet and dry seasons, although other studies report higher abundances during the wet season [6, 55, 56].

The highest AMF species richness (45–52 species) was found in the transitional area between the Cerrado and Caatinga, the Cerrado adjacent to the Caatinga, and in the typical Cerrado far from the transition zones. According to Silva et al. [29], in stable habitats such as the Atlantic Rainforest, lower AMF species richness can be attributed to lower sporulation rates in those areas. These observations align with the findings of the current study, where *Acaulospora* and *Glomus* were the most frequently occurring AMF genera. Other studies indicate that *Acaulospora* species are more frequent in drier areas than in moister areas [29, 57], which is consistent with our study.

Table 4 Arbuscular mycorrhizal fungi (AMF) indicator species for the investigated ecosystems

CRCA	Indicator value (%)	*p*
Fuscutata heterogama	55.1	0.001****
Fuscutata rubra	40.8	0.006***
TCA		
Scutellospora calospora	49.1	0.001****
CA		
Acaulospora sp. 9	50.0	0.001****
Acaulospora sp. 7	45.6	0.002***
Entrophospora sp. 2	45.6	0.001****
Funneliformis halonatus	75.8	0.001****
MA		
Acaulospora sp. 4	63.8	0.001****
CAR		
Glomus sp.4	45.6	0.001****
CR + MA		
Acaulospora spinosissima	42.4	0.007***
Cetraspora pellucida	34.5	0.03**
CRCA + CRMA		
Acaulospora longula	42.7	0.03**
TCA + CR		
Bulbospora minima	48.5	0.001****
TCA + MA		
Cetraspora gilmorei	50.2	0.001****
Acaulospora sp. 2	46.3	0.01***
TCA + CAR		
Dominikia sp.	71.2	0.001****
CRMA + MA		
Entrophospora sp. 1	51.8	0.002***
CR + CRCA + CRMA		
Glomus sp. 10	61.3	0.003***
CR + CRCA + MA		
Acaulospora scrobiculata	58.2	0.001****
CR + TCA + CRMA		
Acaulospora spinosa	47.3	0.007***
CR + TCA + MA		
Dentiscutata cerradensis	66.4	0.001****
CR + TCA + CAR		
Orbispora pernambucana	60.0	0.001****
CRCA + TCA + CRMA		
Ambispora appendicula	68.6	0.001****
Acaulospora foveata	54.2	0.001****
CRCA +CA + CRMA		
Sclerocystis taiwanensis	40.0	0.03**
TCA + CA + CAR		
Entrophospora etunicata	46.4	0.01***
TCA + CRCA + CAR + CR		
Paradentiscutata bahiana	74.7	0.001****
TCA + MA + CRMA + CR		
Acaulospora sp. 3	57.8	0.05**
TCA + CAR + CRMA + CR		
Glomus microcarpum	58.9	0.001****
CA + TCA + MA + CRMA		
Glomus sp. 2	70.6	0.001****
CR + CRCA + TCA + MA + CAR		
Gigaspora margarita	74.1	0.001****
CR + CRCA + TCA + CRMA +MA		
Acaulospora mellea	93.2	0.001****
CA + TCA + CRCA + CAR + CRMA		
Glomus sp. 7	82.2	0.001****
CRCA + TCA + CA + CRMA + MA + CAR		
Glomus glomerulatum	76.3	0.005***

CR Cerrado *stricto sensu*, *CRCA* Cerrado close to the Caatinga, *TCA* Transition between Cerrado and Caatinga, *CA* typical Caatinga, *CRMA* Cerrado close to the Atlantic rainforest, *CAR* Carrasco—bush vegetation.

Significance level: * = $p<0.1$, ** $p<0.05$, *** $p<0.01$, **** $p<0.001$

The influence of vegetation was observed, as Cerrado areas, even when geographically distant, shared more than 30 species. Additionally, transitional areas also shared a high number of AMF species with the Cerrado. Similar to our findings, Silva et al. [29] also recorded higher diversity in transitional areas and lower diversity in humid forest areas, indicating the influence of the environment on AMF communities. Transitional areas between floristic domains, such as Carrasco, tend to exhibit higher diversity values due to the mixture of plant species [58]. This influence can also be observed for AMF communities, highlighting the importance of plant heterogeneity in maintaining AMF diversity.

Tchabi et al. [25] also reported higher AMF diversity in dryer savannas, specifically the so-called Sudan savanna, compared to moister savannas of the Guinea type in tropical Western Africa. In both our studies and theirs, the soil types can be considered comparable, as they represent very old tropical land surfaces that have developed over millions of years and are mainly classified as Ferralsols according to the World reference base [59] and Zech et al. [60]. We expect that the AMF community structure may be even more diverse than that detected here when using solely morphological identification tools. This is because in evergreen forests, a higher percentage of what was formerly known as 'nonsporulating' AMF may occur. They are capable of producing spores in single species cultures relatively fast [61–63]. However, such spores are often small, hyaline, thin-walled, and decompose quickly in moist soils. As a result,

Table 5 Permutation multivariate analysis of variance (PERMANOVA) based on the arbuscular mycorrhizal fungal community in areas with natural phytophysiognomies related to Cerrado

Pairs	*F*	*p* (adjusted Bonferroni)
CR vs CRCA	4.218172	0.084
CR vs TCA	8.651014	0.021**
CR vs CA	7.596536	0.021**
CR vs CRMA	3.234286	0.147
CR vs CAR	15.990849	0.021**
CRCA vs TCA	5.326490	0.042**
CRCA vs CA	4.507083	0.063
CRCA vs CRMA	2.240633	0.882
CRCA vs MA	2.579941	1.000
CRCA vs CAR	8.754790	0.021**
TCA vs CA	5.275170	0.021**
TCA vs CRMA	3.773374	0.147
TCA vs MA	4.246490	0.231
TCA vs CAR	5.123683	0.021**
CA vs CRMA	4.061449	0.084
CA vs MA	6.110320	0.084
CA vs CAR	10.838590	0.021**
CRMA vs CAR	10.034277	0.021**
MA vs CAR	8.338103	0.021**

The Bonferroni correction was applied to the *p* values to mitigate the error associated with multiple comparisons

CR Cerrado *stricto sensu*, *CRCA* Cerrado close to the Caatinga, Transition between Cerrado and Caatinga, *CA* typical Caatinga, *CRMA* Cerrado close to the Atlantic rainforest, *CAR* Carrasco—bush vegetation

these AMF species may sometimes go undetected when using our morphological approach on field soil samples.

Glomus macrocarpum emerged as the predominant species, demonstrating a generalist nature by its presence in all soil samples. Extensively documented in previous studies within Caatinga and Atlantic rainforests [64–66], this species exhibits a global distribution spanning all six continents (https://www.gbif.org/pt/species/2560123). Other norteworthy species in our investigation comprised *Glomus brohultii* and *Gl. glomerulatum*. The latter is commonly found in the Brazilian Cerrado [67], while *Gl. brohultii* has been recovered from the Amazon, Caatinga, and Atlantic Rainforest [65, 67, 68].

In the Cerrado and related areas, *Acaulospora mellea*, *Gi. margarita*, *D. cerradensis*, and *F. halonatus* dominated. Initially described in a typical Cerrado environment [69], *Dentiscutata cerradensis* has been observed in both natural and disturbed ecosystems within the Atlantic Rainforest, the Amazonian Rainforest, and the Caatinga [65]. *Acaulospora mellea* and *Gi. margarita* were prevalent in the Cerrado [67]. *Acaulospora mellea* exhibits a broad distribution in Brazil, spanning various biomes, including the Cerrado, Atlantic Rainforest, Amazon Rainforest, Caatinga, and Pantanal [48]. Its presence is also documented in warm climates countries such as Colombia, Mexico, and Taiwan (https://www.gbif.org/pt/species/2560123). *Gigaspora margarita*, widely distributed across all six Brazilian biomes [65], is also documented in North America, Europe, Asia, and Oceania (https://www.gbif.org/pt/species/2560123).

Of the 82 AMF species reported in the current study, 37 species are considered rare (species that occurred in less than 10% of the samples). Assis et al. [70] noted a higher

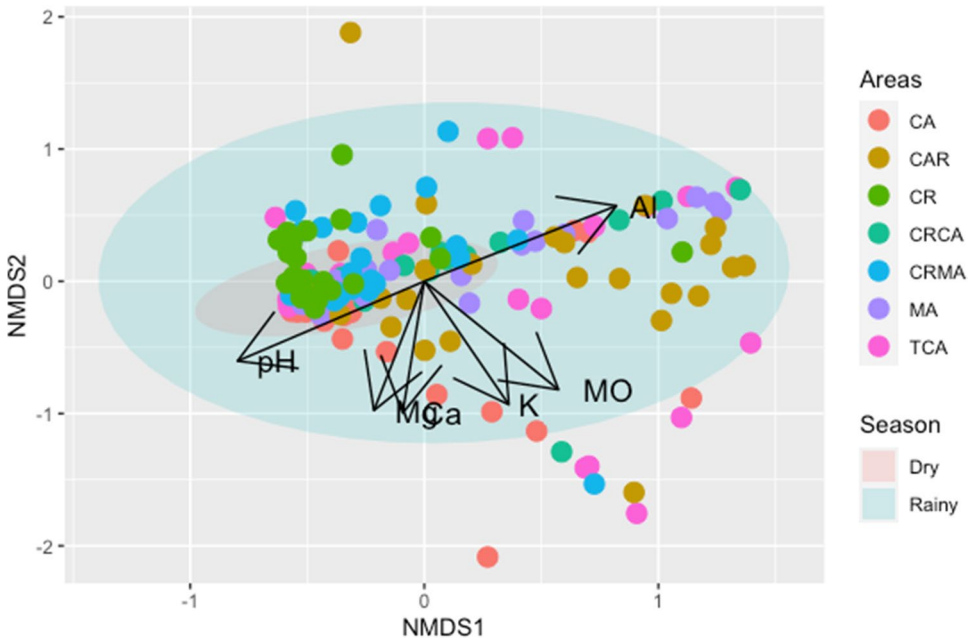

Fig. 4 Non-metric multidimensional analysis (NMDS) based on abundance data from AMF communities in areas with natural phytophysiognomies related to Cerrado and correlated with physical and chemical soil properties by Envfit analysis (stress 0.16). CR Cerrado *stricto sensu*, CRCA Cerrado close to the Caatinga, TCA Transition between Cerrado and Caatinga, CA typical Caatinga, CRMA Cerrado close to the Atlantic Rainforest, MA Atlantic Rainforest, CAR Carrasco—bush vegetation

number of rare species in natural ecosystems compared to agricultural ones and observed that in cultivated soils, some species may have disappeared, underscoring the importance of preserving natural habitats as refuges for vulnerable species. Among the rare species observed in our study, *Glomus hyderabadensis* represents the first record for Brazil. Three species were also not initially detected in field soil samples but were recovered from bait cultures in the greenhouse: *Acaulospora* sp.10 from the Caatinga, *Cetraspora* sp. from the Cerrado near the Caatinga, and *Paraglomus brasilianum* in the transition area between the Cerrado and Caatinga. The latter species was originally described in the Cerrado and is also known to occur in the Caatinga and the Amazonian Forest [65]. This species has also been identified from a range of ecosystems in Australia, Portugal, and the UK (https://www.gbif.org/pt/species/2560239).

The indicator species analysis assesses the likelihood of association with a specific group of interest, in this case, designated areas. The occurrence of a species is intricately linked to the optimum conditions conducive to its growth, thereby unveiling and delineating its habitat preferences [71, 72]. *Bulbospora minima* was identified as an indicator species of the transition between Cerrado and Caatinga and Cerrado *stricto sensu* areas, a result that reveals the preferred habitats for this species. This is noteworthy considering that it was originally described in Caatinga areas [73], and its occurrence has been predominantly reported in undisturbed areas of the Cerrado, Caatinga, and Atlantic Rainforest [23, 74, 75]. Another interesting result was the selection of the species *Glomus* sp. 7, *Gigaspora margarita*, *Acaulospora mellea*, and *Glomus glomerulatum* as indicators of five or more areas, confirming their generalist occurrence across Brazilian biomes, as reported by Maia et al. [65].

In the multivariate analysis, the AMF communities differed among the studied areas. The Carrasco area was closer to the Cerrado sites than to the Caatinga sites, which had also been observed by Araújo et al. [76] in plant vegetation analyses. Within the Cerrado, Carrasco is characterized by its specific and diverse vegetation, even though many of these plant species also occur in other Cerrado types. This may help to explain not only the relationship for the plant communities but also for the composition of AMF communities [77]. It is well established that soil characteristics can significantly impact microbial diversity and distribution. However, it is important to note that the microbial community, including AMF, can also influence soil chemical, physical, and biological properties [78]. The influence of high Al content and low pH on AMF communities in the Atlantic Rainforest was also noted by Rodrigues et al. [2021] in areas of the Atlantic Rainforest in the Brazilian Northeast. Carrasco areas presented an AMF community distinct from the other areas, and the AMF communities in Carrasco were related to higher OM and Al contents and lower values of pH and Mg. Some of these chemical attributes were found to influence AMF communities in other Cerrado areas [74].

Conclusions

Areas in the Cerrado that are in close proximity to the dry savanna of the Caatinga or the Atlantic Rainforest exhibit high AMF species richness. These areas are vital for preserving both AMF and the surrounding vegetation, given their remarkable heterogeneity. Both vegetation and soil quality parameters, influenced by historical, long-term and recent climatic changes, have a more significant impact on AMF communities than geographical distance. The Cerrado serves as a natural refuge for AMF, but much of it has already been lost to agricultural activities. It is imperative to urgently protect the remaining plant and microbial diversity as well as the variety of habitats within the Cerrado.

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Author Contribution All authors contributed to the study conception and design. Material preparation and data collection were performed by JSP, CDP, CTTM. The statistical analysis and graphs were performed by JSP, DKAS and FO. The first draft of the manuscript was written by JSP, LCM, DC, FO and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability The datasets generated during and/or analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Competing Interests The authors declare no competing interests.

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