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Soil texture and chemical attributes influence the community composition of arbuscular mycorrhizal fungi in the *Caatinga Biome*

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Abstract

Arbuscular mycorrhizal fungi (AMF) are obligate symbiotic microorganisms that form associations with a variety of plant species and are found in several biomes, such as the Brazilian Caatinga. This study aimed to determine the diversity, richness and distribution of AMF communities in four areas with different soil textural classes and vegetation type in the Caatinga. Nine soil and root samples were collected during the dry season in each area, totalling 36 sampling units. In total, 45 AMF species were recorded, with a predominance of the genera *Acaulospora* and *Glomus*. The highest species richness was observed in Open shrubby Caatinga, with a loamy sand textural class, which had higher density of glomerospores. A higher rate of mycorrhizal colonization was observed in 'Brejo de altitude', i.e. a mountain top rainforest, with sandy clay loamy soil. Soil texture was the main determining soil factor in structuring the AMF communities in the areas in addition to other factors—fine sand, coarse sand, phosphorus, hydrogen, aluminium, aluminium saturation and base saturation— were also important in determining the composition of the AMF communities in the areas studied.

Keywords – Ecology – Glomeromycota – glomerospores – mycorrhizae – semi-arid

Introduction

The Caatinga is one of the largest and most biodiverse areas of tropical dry forest in the world and is predominantly located in the semi-arid region of northeastern Brazil, covering an area of 912,529 km^2. The region encompasses a variety of environments and landscapes, including enclaves of humid tropical forests, wetlands, transitional vegetation from open fields to forests and rupestrian grasslands (Silva et al. 2017).

The vegetation of the Caatinga shows remarkable variation and heterogeneity, being shaped by environmental conditions and local, geomorphological characteristics (Silva et al. 2017). In this context, the importance of soil as a determining factor in the distribution and structuring of vegetation in different biomes is widely recognized (Arruda et al. 2020), including in the Caatinga, which has a wide range of soil types, from sandy and deep to relatively rich, shallow and clayey soils (Silva et al. 2017).

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The availability of nutrients, water, and the depth reached by the roots are some of the factors that favour the predominance of certain plant species in different types of soil (Silva et al. 2023). Similarly, soil texture plays a crucial role in carbon storage, directly influencing the retention and availability of nutrients, which impacts the structure of plant and microbial communities (Hamarashid et al. 2010). For example, coarse-textured soils, such as sandy soils, have a lower capacity to retain water and nutrients, but can lose less water through evaporation (Lane et al. 1998). On the other hand, fine-textured soils, such as clayey soils, retain more water and nutrients, but are more susceptible to evaporation (Lane et al. 1998). In the Caatinga, these soil characteristics vary according to the geological setting: sandy soils are typically found in sedimentary areas (sandy caatinga or carrasco), where deep, well-drained and low-fertility profiles support sparse shrubby vegetation, whereas clay-rich, shallow and stony soils with higher natural fertility occur in crystalline areas, sustaining a denser herbaceous layer dominated by "non-woody plants, predominantly annual herbaceous therophytes species" (Silva et al. 2017). However, in the Caatinga, both at a local and regional level, the presence and survival of plant species is not limited only to morphoanatomical adaptations to withstand stressful conditions, but also depends on broader ecological associations, such as those formed between the soil microbiota and plants, an example being symbiotic interactions with arbuscular mycorrhizal fungi (Maia et al. 2020).

Arbuscular mycorrhizal fungi (AMF) are obligate biotrophic microorganisms that live symbiotically in the roots of host plants (Smith & Read 2008). This symbiotic relationship dates back approximately 450 million years, from the first stages of plant colonization in the aquatic environment to the terrestrial environment (Tedersoo et al. 2020). AMF are cosmopolitan, present in all terrestrial ecosystems, in association with 78% of known plant species (Tedersoo et al. 2020).

Through their extensive mycelium, AMF facilitate and provide the host with a greater supply of water with more access to the mineral resources available in the soil, from micronutrients (e.g. iron, manganese) to macronutrients (e.g. nitrogen and potassium), especially phosphorus (P), and in return the plant provides the fungus with photosynthates (Smith & Read 2008).

Several factors, such as vegetation type, climate and soil characteristics, play a crucial role in the abundance and distribution of AMF at different spatial scales (local, regional and global) (Davison et al. 2015, Chaudhary et al. 2018). In general, three main groups of soil textural classes are recognized: sandy, loamy and clayey soils; within each group, there are specific textural classes, totaling 13 distinct categories (Centeno et al. 2017). In sandy and sandy loamy soils, the properties of sand predominate, accounting for an average of 70% of their composition; in contrast, the characteristics of the clay fraction are predominant in clayey, sandy-clayey and clayey-silty soils (Centeno et al. 2017).

The structure of Caatinga, characterized as a heterogeneous environment with a variety of vegetation types, each with specific soil characteristics and associated species has been detailed by Prado (2003) who identified at least 11 physiognomic categories. Among these types, the present study focused on four representative areas of this biome, which differed in vegetation structure: a Brejo de Altitude, consisting of humid forest enclaves with montane forest vegetation; Open Shrubby Caatinga, characterized by low, widely spaced shrubs and small trees with non-touching canopies; Dense Shrubby Caatinga, composed of taller shrubs and trees whose crowns touch or intertwine, forming a more continuous canopy; and a Riparian Forest, characterized by taller trees and a rich assemblage of woody and climbing species.

The aim of this study was to determine the diversity, richness, and distribution of AMF communities and to assess how different vegetation types, which are related to soils, influence these communities. The following four hypotheses were tested in this work: (1) the Brejo de altitude area with a sandy clay loam texture has greater AMF richness and diversity, considering that this type of soil contains a balanced mixture of sand, silt and clay, resulting in a good capacity for retaining moisture, nutrients and aeration (Centeno et al. 2017), conditions which can provide a favourable environment for the growth of and colonization by AMF; (2) a higher rate of mycorrhizal colonization should occur in plants living in these soils of the Brejo de altitude compared to colonization in plants growing in sandy soils as occurs in the Riparian Forest; (3) in areas with sandy soils, representatives of Gigasporales predominate, considering that they have been commonly referred to in this textural soil class; (4) the main factors determining the occurrence and distribution of AMF are mainly related to the soil type and soil texture in the four areas considered.

Materials & Methods

Study sites

The study sites encompass four areas in the Caatinga with different soil textural classes and vegetation: (1) Brejo de altitude (BA) (8°08’57.6”S 35°45’13.8”W and 8°09’01.6”S 35°45’15.6”W, altitude ranging from 805.48 to 836.05 masl) with sandy clay loam soil and montane forest vegetation in the municipality of Bezerros, Pernambuco; (2) Open shrubby Caatinga (OSC) (6°12’51.0”S 37°02’25.3”W and 6°12’57.2”S 37°02’25.5”W, altitude ranging from 142.50 to 152. 45 masl) with loamy sand soil characterized by low, widely spaced shrubs and small trees with non-touching canopies; (3) Dense shrubby Caatinga (DSC) (6°13’05.3”S 37°02’40.4”W and 6°13’00.2”S 37°02’43.4”W, altitude ranging from 142.81 to 147.16 masl) with sandy loam soil, consisting of taller shrubs and trees whose crowns touch or intertwine, forming a more continuous canopy, both in the municipality of Jucurutu, Rio Grande do Norte; (4) Riparian Forest (RF) (9°48’30.1”S 38°29’35.8”W and 9°48’36.8”S 38°29’35.7”W, altitude ranging from 697.17 to 699.19 masl) with sandy soil, characterized by taller trees and a closed understorey with a rich assemblage of woody and climbing species, in the municipality of Jeremoabo, state of Bahia (Table 1 and Fig. 1).

Table 1 Geographic coordinates, principal climatic characteristics and soil types of the study areas

Characteristics	Brejo de altitude (BA)	Open shrubby Caatinga (OSC)	Dense shrubby Caatinga (DSC)	Riparian Forest (RF)
Coordinates	8°08'57.6"S 35°45'13.8"W and 8°09'01.6"S 35°45'15.6"W	6°12'51.0"S 37°02'25.3"W and 6°12'57.2"S 37°02'25.5"W	6°13'05.3"S 37°02'40.4"W and 6°13'00.2"S 37°02'43.4"W	9°48'30.1"S 38°29'35.8"W and 9°48'36.8"S 38°29'35.7"W
Temperature*annual average	22.6°C	28.1°C	28.1°C	24°C
Precipitation*	545.7 mm	500 to 800 mm	500 to 800 mm	300 to 500 mm
Climate	tropical wet	semiarid hot and dry	semiarid hot and dry	semiarid hot
Soil type	Argisols	Luvisols and Neosols	Luvisols and Neosols	Planosols and Regosols
Textural classes	Sandy clay loam	Loamy sand	Sandy loam	Sandy

Brejo de altitude (BA) – Serra Negra Ecological Park

The Brejo de altitude (characterized as a mountain top rainforest) is in the Serra Negra Ecological Park, in the municipality of Bezerros, in the Agreste region of Pernambuco, and covers an area of around 3.24 hectares. The region's climate is rainy tropical, with a dry summer and an average annual temperature of 22.6°C and average annual rainfall of around 545.7mm (CPRM 2005a, Diaz et al. 2017).

The relief of the region is represented by the Borborema Plateau and plutonic igneous rocks of the deformed granitoid complex are predominantly found in the park, with predominant soils of the Yellow Red Argisols type at altitudes of up to 850 masl (CPRM 2005a, Diaz et al. 2017). The vegetation is classified as montane forest, typical of Brejo de Altitude within the Caatinga biome, and is characterized by a well-develop stratification with distinct herbaceous, shrubby, and arboreal layers, as well as by the predominance of humid-forest (Atlantic Forest) species intermingled with elements from the surrounding dry Caatinga vegetation (Silva et al. 2017, Gois et al. 2019).

Among the species commonly found are representatives of bryophytes from the families Metzgeriaceae, Calymperaceae, Fabroniaceae and Meteoriaceae (Pôrto et al. 2004), representatives of Pteridophytes, such as the families Polypodiaceae, Aspleniaceae, Dennstaedtiaceae, Hymenophyllaceae, Pteridaceae and Thelypteridaceae and representatives of angiosperms from the families Apocynaceae, Araceae, Asteraceae, Fabaceae, Myrtaceae and Orchidaceae (Sales et al. 1998).

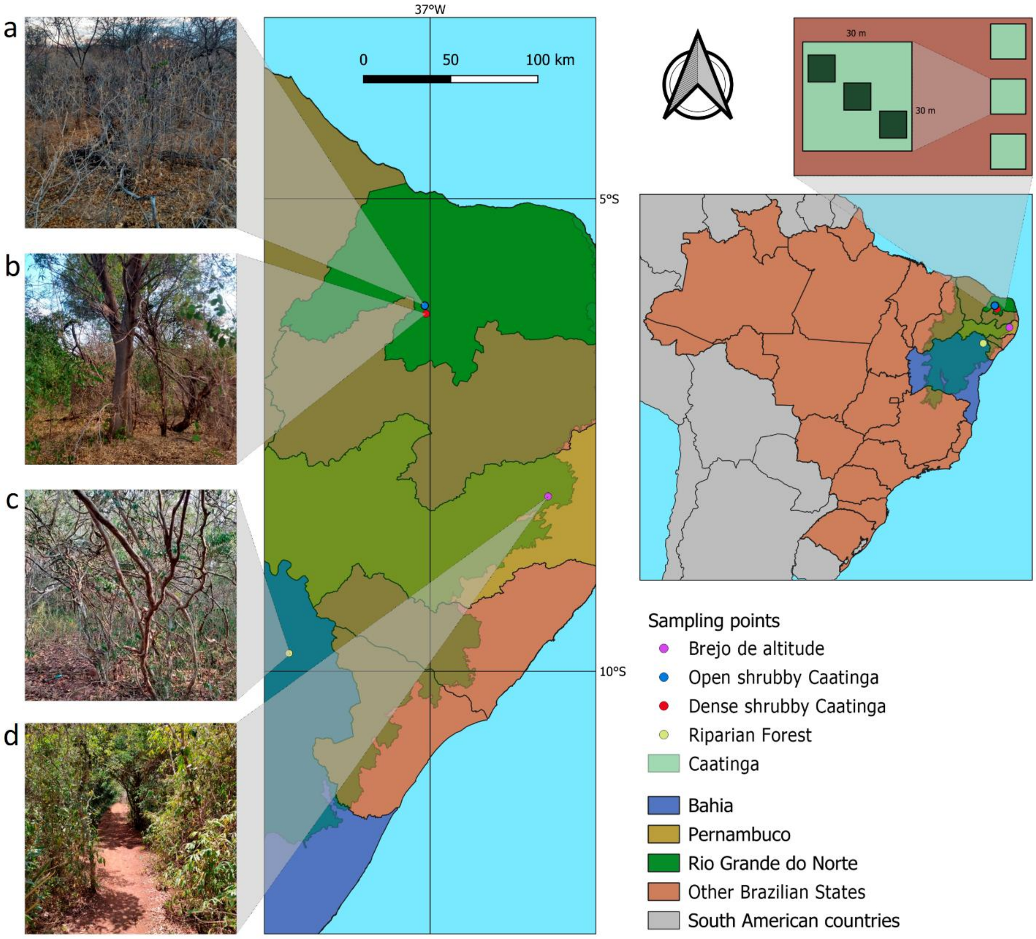

Fig. 1 – Map of sampling areas: (a) Open shrubby Caatinga. (b) Dense shrubby Caatinga. (c) Riparian Forest. (d) Brejo de altitude.

Open shrubby Caatinga (OSC) and Dense shrubby Caatinga (DSC) - Reserva Particular do Patrimônio Natural Stoessel de Brito

The Stoessel de Brito RPPN is in the municipality of Jucuturu, in the Central Mesoregion of Rio Grande do Norte and is spread over an area of around 818.50 hectares (de Oliveira et al. 2022). The RPPN is divided into two polygons, one of Open shrubby Caatinga and the other of Dense shrubby Caatinga, separated by the RN-118 state highway, which increases the area of the reserve to around 978 hectares (de Oliveira et al. 2022).

According to the Köppen classification, the RPPN's climate is hot and dry semi-arid (BSwh) with an average annual temperature of between 28°C and average annual rainfall of around 500 to 800 mm (CPRM 2005b, Diniz & Pereira 2015). The area is located on crystalline bedrock, with a predominance of Luvisol (brown, non-calcic) and Neosol (eutrophic litholic) soils on rugged terrain with altitudes varying between 145 and 600 masl (CPRM 2005b, Diniz & Pereira 2015), the vegetation in the RPPN is typically shrubby to arboreal Caatinga.

The Open Shrubby Caatinga (OSC) differs from the Dense Shrubby Caatinga (DSC) in vegetation structure, being characterized by low, widely spaced shrubs and small trees with non-touching canopies, forming a more open and discontinuous vegetation cover (de Oliveira et al. 2022). In contrast, Dense Shrubby Caatinga (DSC) is characterized by taller shrubs and trees whose crowns touch or intertwine, with an association of the genera *Mimosa*, *Caesalpinia* and *Croton* predominating (de Oliveira et al. 2022).

Riparian Forest (RF) – Ecological Station (ESEC) Raso da Catarina

The Raso da Catarina Ecological Station is in the state of Bahia, covering an area of 104 844.40 hectares and part of the municipalities of Paulo Afonso, Rodelas and Jeremoabo, bordered to the south by the Vaza-Barris river basin and to the north by the São Francisco sub-middle basin (Paes & Dias 2008).

According to the Köppen classification, the dominant climate in the Raso da Catarina ESEC is hot semi-arid (BSh), with an average annual temperature of 26°C and average annual rainfall ranging from 400 to 600 mm. The Raso da Catarina ESEC is located in the Tucano Sedimentary Basin, which is made up of a sedimentary complex of the Marizal Formation, on a low plateau with altitudes ranging from 400 to 600 masl and soils of the following types: Planosol, Regosol and non-calcic browns in general, quartz sand soils, deep, excessively drained and poor in alterable minerals, containing kaolinitic clay (Paes & Dias 2008).

The Riparian Forest within the Raso da Catarina ESEC is called the Pororoca Forest, a formation named after the abundance of individuals of *Clusia nemorosa*, popularly known as pororoca; this forest occurs on 29 hectares within the ESEC, in the municipality of Jeremoabo, Bahia, occupying 0.029% (width varying between 200 and 400 m) of the total area, and is characterized as an ecotone area between Caatinga/Cerrado/Seasonal Forest (Paes & Dias 2008).

In the Riparian Forest, trees reach up to 15 m in height, with a closed understorey of dry shrubs, on more fertile soils than the surrounding Caatinga areas. The forest is home to species of the Cactaceae family, epiphytes belonging to the Bromeliaceae and Orchidaceae families, and many lianas (Paes & Dias 2008). These distinct characteristics give the Riparian Forest a unique physiognomic and floristic composition compared to other Caatinga areas within the Raso da Catarina ESEC.

Sampling and analysis of the soil physicochemical attributes

Samples were taken only once in each study area during the dry season (between September and December 2021). Three plots (30×30 m) were delimited in each area, where three simple samples (2 kg) of soil and roots (0-20 cm deep) were collected, totaling nine samples per area and 36 sampling units.

Part of the soil samples (500 g from each sampling unit) was sent to the Agronomic Research Institute of Pernambuco (IPA), where chemical and physical analyses were carried out, following the methodologies established by EMBRAPA (1997). According to this methodology, the pH was determined in a soil: water solution (1:2.5), the contents of P, K^+ and Na^+ were extracted with Mehlich I solution, with P being quantified by spectrophotometry and Na^+ and K^+ by flame photometry. The Ca, Mg and Al contents were extracted with 1M potassium chloride (KCl) and quantified by titration. Particle size analyses (silt, clay, coarse and fine sand) were carried out using the pipette method (EMBRAPA 1997).

Extraction of glomerospores and sporocarps, quantification and identification of AMF species

Glomerospores and sporocarps from field samples were extracted from 100 g samples of soil by wet sieving (Gerdemann & Nicolson 1963) and centrifugation in water and 50% sucrose (Jenkins 1964 - modified). The glomerospores and sporocarps were quantified on a channeled plate using a steromicroscope (40×), separated by morphotype and mounted on slides with polyvinyl alcohol in lactoglycerol (PVLG) and PVLG + Melzer's reagent (1:1 v/v). The identification of

AMF species was based on the classification proposed by Oehl et al. (2011, updated 2026) and the work of Schenck and Pérez (1990), Błaszkowski (2012) and other, more recent studies.

Analyses of AMF colonization

The finest roots collected from the field in each soil sample (n=36) were washed in running water, diaphanized with KOH (10%) and stained with Trypan blue (0.05%) (Phillips & Hayman 1970). The percentage of colonization was estimated using the slide method (Giovannetti & Mosse 1980), which consists of mounting 100 1 cm root fragments per sample and considered colonized when they showed AMF structures: arbuscules, vesicles, hyphae and/or glomerospores.

Analysis of the most probable number (MPN) of infective propagules of AMF

The most probable number (MPN) of infective propagules of AMF in the soil was estimated according to Feldmann & Idczak (1992). For each area, a composite soil sample obtained from each plot was used (three samples/plot), diluted with sterilized sand (dilutions of 0; 1:10; 1:100 and 1:1000); five replicates were used for each dilution, with a total of 20 pots per plot and 60 pots per area. Maize (*Zea mays*) was used as the host plant, and after 30 days, the roots were harvested, washed, diaphanized and stained with 0.05% Trypan blue (Phillips & Hayman 1970). To determine the MPN of infective propagules, the roots were observed under a light microscope and evaluated for the presence or absence of characteristic AMF structures, and the percentage was estimated according to the data in Cochran's Table (Cochran 1950).

Statistical and ecological analyses

For the analysis of the AMF communities, the following were determined: glomerospore abundance, AMF species richness (S), Shannon-Wiener (H') and Simpson's (D1) diversity indices, dominance (D2) and Simpson's equitability (E). The formulas for calculating these indices are available in Morris et al. (2014).

The numbers of glomerospores were subjected to the Shapiro-Wilk test for normality and Bartlett's test for homogeneity of variances and transformed into log (x+1); the colonization data were arcsine transformed before analysis of variance (ANOVA). To determine whether the richness and diversity of AMF species varied among the areas, analysis of variance (ANOVA) was used and when significant differences were detected, the Tukey's test was applied ($P < 0.05$).

The relative abundance of species was calculated as the ratio between the number of glomerospores of a species and the total number of glomerospores in the areas. The frequency of occurrence (FO) of each species in each area was calculated using the following formula: $FO = Ji/k$, where FO represents the frequency of occurrence of the species, Ji is the number of samples from the area (9) in which the species was found, and k is the total number of soil samples by each area. The relative frequency of occurrence is expressed as a percentage and the AMF species were classified as dominant (FO > 50%), very common (FO between 31% and 50%), common (FO between 10% and 30%) and rare (FO < 10%) (Zhang et al. 2004).

Species richness was defined as the number of AMF species found in each area and to calculate the estimated number of species among the areas, the first-order Jackknife index (Jackknife 1) was applied, using the "specpool" function of the "vegan" package. To test for significant differences in the composition of the AMF communities and the chemical and physical attributes of the soil among the areas studied, multivariate permutation analyses of variance (PERMANOVA) were carried out, based on the Bray-Curtis distance, using the "adonis" function of the vegan package (Oksanen et al. 2022). To visualize dissimilarities in the composition of AMF communities, non-metric multidimensional scaling (NMDS) and Bray-Curtis distance was used, employing the "envfit" function with 999 permutations to determine which soil physico-chemical variables showed a significant correlation with the AMF communities using the vegan package.

To check whether a particular taxon was associated with a specific area, indicator species analyses were carried out (Dufrêne & Legendre 1997) using the "multipatt" function of the "indicspecies" package (Cáceres & Legendre 2009). Taxa were considered indicators if they had a significant P-value ($P < 0.05$) and an indication value (IndVal) $\geqslant$ 25%. For the univariate analysis of the soil physico-chemical attributes, the Kruskal-Wallis and Dunn non-parametric tests were used for multiple comparisons with P-values adjusted by Bonferroni. These analyses were carried out with the aid of the R program using the “stats” and “FSA” packages (R Core Team 2024).

Venn diagrams were created to show the number of exclusive and shared species between the areas, using the “Calculate and draw custom Venn diagrams” tool available at http://bioinformatics.psb.ugent.be/webtools/Venn/.

The significance of all statistical tests was based on $P < 0.05$, except in the case of multiple comparisons, where the P-value was corrected by the Bonferroni test. All statistical analyses were carried out using the R program (R Core Team 2024).

Results

Soil physico-chemical properties

In the four study areas the soil pH was acidic, ranging from 4.5 to 5.6 (H_2O) and the phosphorus content varied from 4.2 to 75.7 (mg/dm^3) with the highest values in the Open shrubby Caatinga (OSC) which also had higher values for calcium (Ca), sum of bases (SB) and base saturation (V). The highest values for potassium (K), sodium (Na), aluminium (Al) and magnesium (Mg) and cation exchange capacity (CEC) were found in the Brejo de altitude (BA) area (Table 2).

Table 2 Chemical properties of soil samples in the areas: Brejo de altitude (BA), Open shrubby Caatinga (OSC), Dense shrubby Caatinga (DSC), and Riparian Forest (RF).

Areas	P	pH	K	Na	Al	Ca	Mg	H	SB	CEC	m	V
	(mg/dm^3)	(H_2O)	($cmol/dm^3$)								(%)	
BA	5.4b	5.0b	0.4a	0.12a	0.8a	2.4ab	1.6a	11.6a	4.6ab	17.1a	17.2b	28.9b
OSC	4.3b	5.4ab	0.2b	0.05b	0.1b	1.8b	0.9b	3.1bc	3.0b	6.3b	4.9bc	49.2a
DSC	75.7a	5.6a	0.2b	0.06b	0.07b	3.8a	1.2ab	2.8b	5.2a	8.2b	1.8c	63.1a
RF	4.2b	4.5c	0.1c	0.02b	0.7a	0.35c	0.5c	4.9b	0.9c	6.5b	43.3a	14.8c

Means followed by the same letter in a column do not differ statistically by the Kruskal-Wallis test at 5%. SB: sum of bases; CEC: cation exchange capacity; m: aluminium saturation; V: base saturation.

With regard to the soil physical properties, the values for silt, clay and natural clay were also higher in this area, as was the percentage of residual moisture and water in the soil (Table 3). PERMANOVA based on soil components showed differences in chemical and physical composition among the four areas ($F = 22.487$, $df = 1$, $R^2 = 0.584$, $P = 0.006$).

Table 3 Physical properties of soil samples in the areas; Brejo de altitude (BA), Open shrubby Caatinga (OSC), Dense shrubby Caatinga (DSC), and Riparian Forest (RF).

Areas	Coarse sand	Fine sand	Silt	Clay	Flocculation	Residual moisture	water	Textural classes
	(%)							
BA	39.2b	15.2c	23.2a	22.4a	84.2b	2.9a	10.9a	Sandy clay loam
OSC	11.7c	68.0a	11.8b	8.5b	100a	1.5b	3.9b	Loamy sand
DSC	6.6d	73.4a	11.2b	8.8b	100a	1.6b	4.3b	Sandy loam
RF	70.0a	20.9b	1.4c	7.7b	100a	1.65b	2.96b	Sandy

Means followed by the same letter in a column do not differ statistically by the Kruskal-Wallis test at 5%.

Number of glomerospores

In general, the number of glomerospores recovered in the four areas (7,884 glomerospores) ranged from 55 to 631 glomerospores in 100 g^{-1} of soil/sample. There was a significant difference in the number of glomerospores among the areas (F = 5.613, df = 3, P = 0.003), with greater abundance in the Open shrubby Caatinga (OSC), with loamy sand soil (average of 296 glomerospores 100 g^{-1} soil), which differed from the Dense shrubby Caatinga (DSC) with sandy loam soil (average of 124 glomerospores 100 g^{-1} soil) where there was less abundance (Fig. 2).

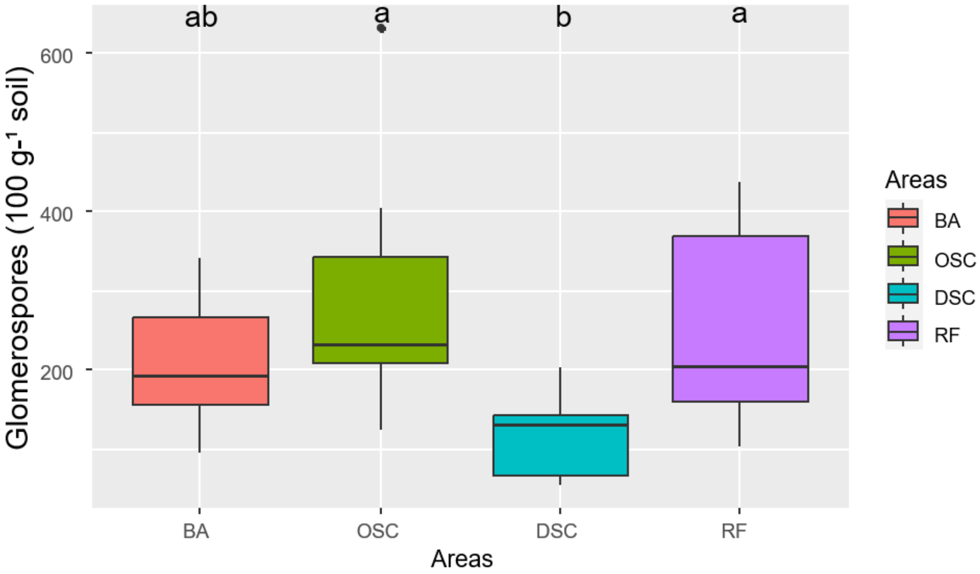

Fig. 2 – Number of glomerospores of soil samples in the areas; Brejo de altitude (BA), Open shrubby caatinga (OSC), Dense shrubby caatinga (DSC), and Riparian Forest (RF).

Mycorrhizal colonization

Total mycorrhizal colonization differed among the study areas (F = 12.3, df = 3, P = 0.00001), with the highest rate (61.9%) recorded in roots collected in the Brejo de altitude (BA) sandy clay loam soil, differing from the other areas (Fig. 3).

Most probable number (MPN) of infective AMF propagules

There was significant variation in the most probable number (MPN) of infective AMF propagules among the four studied areas, with values ranging from 13.33 to 70.33 MPN cm^{-3} of soil. The highest MPN of infective propagules was recorded in the Brejo de Altitude, while the lowest occurred in the Open Shrubby Caatinga. The Dense Shrubby Caatinga and Riparian Forest areas exhibited intermediate values (Table 4).

Species occurrence of AMF

In total, 45 AMF species were recorded in this study, with 12 identified only to genus level. Representatives of two classes (Archaeosporomycetes and Glomeromycetes) and five orders (Archaeosporales, Acaulosporales, Diversisporales, Gigasporales and Glomerales) of Glomeromycota were found, distributed in eleven families (Acaulosporaceae, Ambisporaceae, Dentiscutataceae, Diversisporaceae, Funneliformaceae, Gigasporaceae, Glomeraceae, Intraornatosporaceae, Racocetraceae, Sclerocystaceae and Scutellosporaceae) and 14 genera (Table 5).

Acaulospora and *Glomus* were the most representative genera with 12 and 10 species, respectively, corresponding to 48.9% of the total number of AMF species recorded in this study. *Racocetra* was represented by five taxa, *Gigaspora* by three taxa; *Cetraspora*, *Funneliformis*, *Fuscutata*, *Paradentiscutata* and *Scutellospora* were represented by two taxa, while the other genera (*Ambispora*, *Dentiscutata*, *Intraornatospora*, *Sclerocystis* and *Tricispora*) were represented by only one taxon.

Gigaspora gigantea, *Gi. margarita*, *Glomus brohultii*, *Gl. macrocarpum*, *Gl. microcarpum* and *Glomus* sp. 1 were present in all four areas (Table 5). Most species were classified as common. In the Brejo de altitude (BA), 14 common and five dominant and one very common species were recorded and in the Open shrubby Caatinga (OSC) 15 species were common, five very common and five dominants. In the Dense shrubby Caatinga (DSC), 10 species were common, four very common and three dominants, while in the Riparian Forest (RF), 18 common and three very common species were identified, two were dominant.

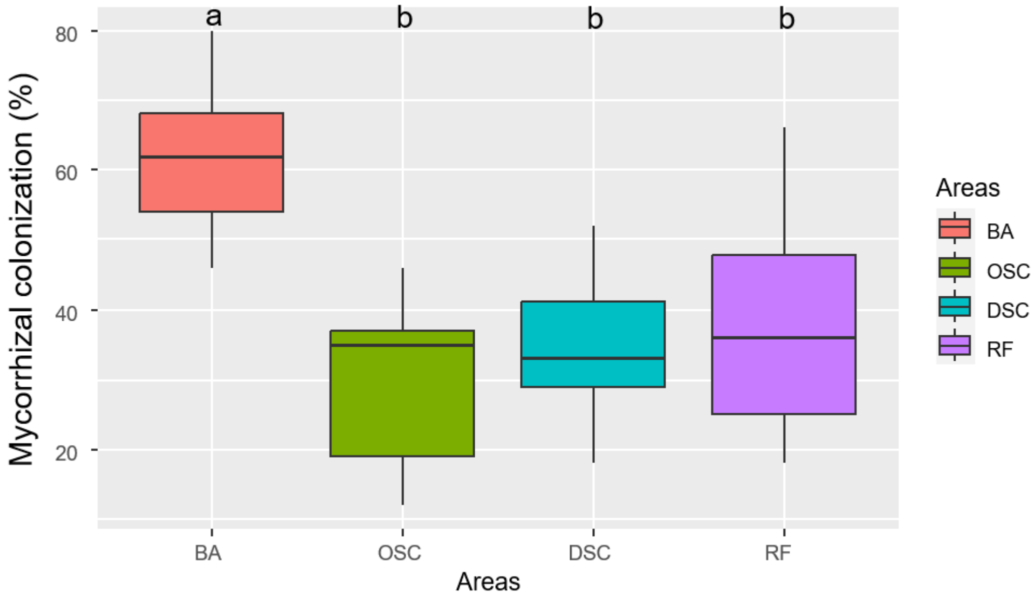

Fig. 3 – Total mycorrhizal colonization of root samples in the areas: Brejo de altitude (BA), Open shrubby caatinga (OSC), Dense shrubby caatinga (DSC), and Riparian Forest (RF).

Table 4 Most probable number (MPN) of infective AMF propagules in the areas: Brejo de altitude (BA), Open shrubby Caatinga (OSC), Dense shrubby Caatinga (DSC), and Riparian Forest (RF).

Areas	**MPN (cm^3 soil)**
Brejo de altitude	70.33
Open shrubby Caatinga	13.33
Dense shrubby Caatinga	46.33
Riparian Forest	26.66

Table 5 Relative abundance (RA) and frequency of occurrence (FO)* of AMF taxa recovered from soil samples in the areas: Brejo de altitude (BA), Open shrubby Caatinga (OSC), Dense shrubby Caatinga (DSC), and Riparian Forest (RF)

AMF Taxa	**Areas**							
	BA		**OSC**		**DSC**		**RF**	
	RA	**FO**	**RA**	**FO**	**RA**	**FO**	**RA**	**FO**
Archaeosporales								
Ambisporaceae								
Ambispora appendicula (Spain, Sieverd. & N.C. Schenck) C. Walker	–	–	2.72	D	0.81	VC	–	–
Acaulosporales								

Table 5 Continued

AMF Taxa	**Areas**							
	BA		**OSC**		**DSC**		**RF**	
	RA	**FO**	**RA**	**FO**	**RA**	**FO**	**RA**	**FO**
Acaulosporaceae								
Acaulospora aff. *scrobiculta*	–	–	0.20	C	–	–	–	–
Acaulospora aff. *tuberculata*	–	–	–	–	–	–	0.14	C
Acaulospora foveata Trappe & Janos	0.19	C	–	–	–	–	2.24	C
Acaulospora lacunosa J.B. Morton	0.29	C	–	–	–	–	–	–
Acaulospora mellea Spain & N.C. Schenck	–	–	0.60	C	–	–	–	–
Acaulospora punctata Oehl, Palenz., Sánchez-Castro, G.A.Silva, C.Castillo & Sieverd.	–	–	–	–	–	–	0.28	C
Acaulospora reducta Oehl, B.T. Goto & C.M.R. Pereira	–	–	0.05	C	–	–	–	–
Acaulospora scrobiculata Trappe	0.09	C	1.51	VC	4.24	VC	–	–
Acaulospora sp. 1	–	–	–	–	–	–	0.84	C
Acaulospora sp. 2	–	–	–	–	0.65	C	–	–
Acaulospora spinosa C. Walker & Trappe	0.38	C	–	–	–	–	–	–
Acaulospora tuberculata Janos & Trappe	–	–	0.10	C	–	–	0.14	C
Diversisporales								
Diversisporaceae								
Tricispora sp.	–	–	0.10	C	–	–	–	–
Gigasporales								
Dentiscutataceae								
*Dentiscutata cerradensis (*Spain & J. Miranda) Sieverd., F.A. Souza & Oehl	0.38	C	0.05	C	–	–	–	–
Fuscutata aurea Oehl, C.M. Mello & G.A. Silva	–	–	2.02	VC	1.96	C	–	–
Fuscutata heterogama Oehl, F.A. Souza, L.C. Maia & Sieverd.	–	–	2.67	VC	0.16	C	–	–
Gigasporaceae								
Gigaspora gigantea (T.H. Nicolson & Gerd.) Gerd. & Trappe	0.29	C	0.10	C	0.16	C	0.56	C
Gigaspora margarita W.N. Becker & I.R. Hall	0.19	C	0.55	VC	13.1	D	0.14	C
Gigaspora sp.	–	–	1.01	C	1.14	C	–	–
Intraornatosporaceae								
Intraornatospora intraornata (B.T. Goto & Oehl) B.T. Goto, Oehl & G.A. Silva	–	–	0.70	C	2.77	C	3.37	VC
Paradentiscutata aff. *bahiana*	0.09	C	–	–	–	–	–	–
Paradentiscutata bahiana Oehl, Magna, B.T. Goto & G.A. Silva	–	–	0.35	C	–	–	3.79	C
Racocetraceae								
Cetraspora gilmorei (Trappe & Gerd.) Oehl, F.A. Souza & Sieverd.	–	–	–	–	–	–	0.14	C

Table 5 Continued

AMF Taxa	**Areas**							
	BA		**OSC**		**DSC**		**RF**	
	RA	**FO**	**RA**	**FO**	**RA**	**FO**	**RA**	**FO**
Cetraspora sp.	0.77	C	–	–	–	–	–	–
Racocetra fulgida (Koske & C. Walker) Oehl, F.A. Souza & Sieverd.	–	–	0.05	C	–	–	–	–
Racocetra gregaria (N.C. Schenck & T.H. Nicolson) Oehl, F.A. Souza & Sieverd.	–	–	–	–	3.10	VC	–	–
Racocetra minuta (Ferrer & R.A. Herrera) Oehl, F.A. Souza & Sieverd.	–	–	–	–	–	–	0.14	C
Racocetra persica (Koske & C. Walker) Oehl, F.A. Souza & Sieverd.	0.09	C	–	–	–	–	–	–
Racocetra sp.	–	–	0.05	C	–	–	–	–
Scutellosporaceae								
Scutellospora alterata Oehl, J.S. Pontes, Palenz., I.C. Sánchez & G.A. Silva	–	–	–	–	–	–	0.56	C
Scutellospora calospora (T.H. Nicolson & Gerd.) C. Walker & F.E. Sanders	–	–	0.65	VC	4.41	VC	0.14	C
Glomerales								
Funneliformaceae								
Funneliformis halonatus (S.L. Rose & Trappe) Oehl, G.A. Silva & Sieverd.	0.97	D	–	–	–	–	0.14	C
Funneliformis sp.	–	–	–	–	–	–	3.08	VC
Glomeraceae								
GlomeraceaeGlomus brohultii R.A. Herrera, Ferrer & Sieverd.	43.4	D	38.5	D	23.5	D	48.3	D
Glomus glomerulatum Sieverd.	14.7	D	23.6	D	–	–	14.5	VC
Glomus macrocarpum Tul. & C. Tul.	22.3	D	15.1	D	40.0	D	17.5	D
Glomus microcarpum Tul. & C. Tul.	7.69	D	6.21	D	2.28	C	0.70	C
Glomus sp. 1	1.46	C	2.12	C	1.14	C	1.12	C
Glomus sp. 2	–	–	–	–	0.32	C	0.42	C
Glomus sp. 3	5.45	VC	0.60	C	–	–	0.84	C
Glomus sp. 4	0.29	C	–	–	–	–	0.84	C
Glomus sp. 5	0.38	C	–	–	–	–	–	–
Glomus sp. 6	0.38	C	–	–	–	–	–	–
Sclerocystaceae								
Sclerocystis sinuosa Gerd. & B.K. Bakshi	–	–	0.10	C	0.16	C	–	–
AMF taxa richness	**20**		**25**		**17**		**23**	

*Frequency of occurrence (FO): classification according to Zhang et al. (2004): dominant (>50%: D), very common (30 – 50.0%: VC), common (10 – 30%: C), and rare (≤10%: R).

Glomus brohultii and *Gl. macrocarpum* were the only species classified as dominant in all four areas and were also the species with the highest relative abundance, followed by *Glomus glomerulatum* (Table 5).

Species richness, diversity and dominance of AMF

Among the 45 AMF species, six were shared among the four collection areas (*Gi. gigantea*, *Gi. margarita*, *Glomus brohultii*, *Gl. macrocarpum*, *Gl. microcarpum* and *Glomus* sp. 1); seven were exclusive to the Brejo de altitude (BA) (*Acaulospora lacunosa*, *A. spinosa*, *Cetraspora* sp., *Glomus* sp. 5, *Glomus* sp. 6, *Paradentiscutata* aff. *bahiana* and *Racocetra persica*); six exclusives to the Open shrubby Caatinga (OSC) (*Acaulospora* aff. *scrobiculata*, *Acaulospora mellea*, *A. reducta*, *Racocetra fulgida*, *Racocetra* sp., and *Tricispora* sp); two exclusives to the Dense shrubby Caatinga (DSC) (*Acaulospora* sp. 2 and *Racocetra* gregaria); and seven exclusives to the Riparian Forest (RF) (*Acaulospora* aff. *tuberculata*, *A. punctata*, *Acaulospora* sp. 1, *Cetraspora gilmorei*, *Funneliformis* sp., *Racocetra minuta* and *Scutellospora alterata*) (Fig. 4).

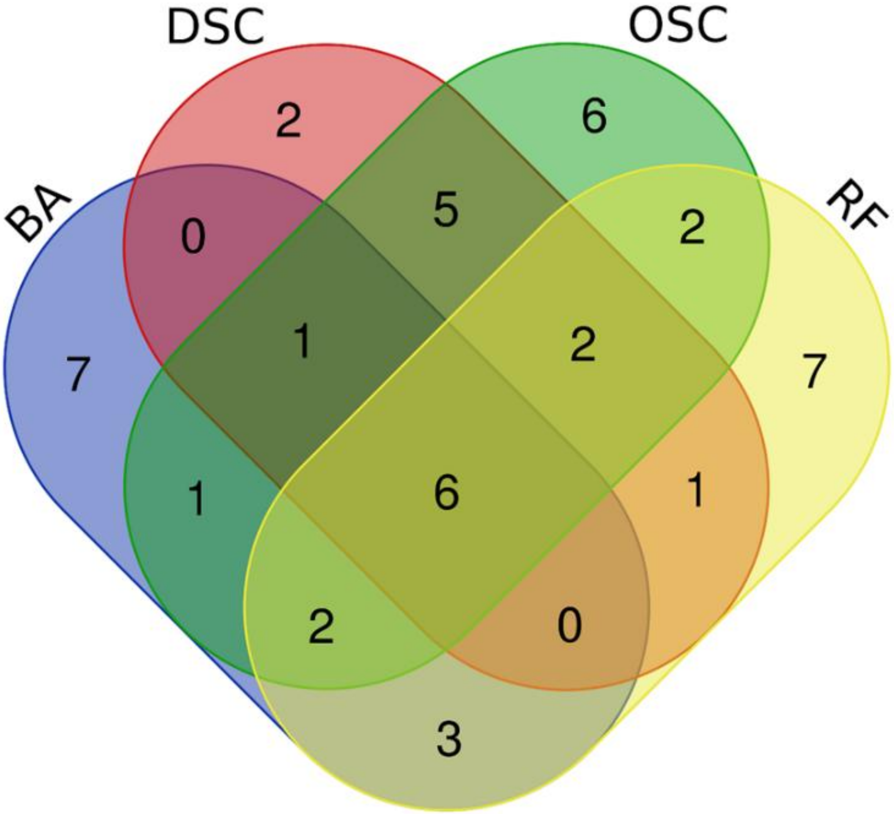

Fig. 4 – Representation of exclusive and shared AMF taxa richness in the areas; Brejo de altitude (BA), Open shrubby caatinga (OSC), Dense shrubby caatinga (DSC), and Riparian Forest (RF).

There was a significant difference in the richness of AMF taxa among the collection areas (F = 8.83, df = 3, P = 0.031), with the greatest richness in the Open shrubby Caatinga (OSC), which differed from the values found for the Dense shrubby Caatinga (DSC) and Riparian Forest (RF) areas (Fig. 5).

In the samples from the Brejo de altitude (BA), 20 species of AMF were recorded, with richness ranging from three to eight species per sample, while in the samples from the Open shrubby Caatinga (OSC), 25 species were recorded, with richness ranging from three to 11 taxa per sample. In the Dense shrubby Caatinga (DSC) samples, 17 species were recorded, with richness ranging from three to eight species per sample, while in the Riparian Forest (RF) 23 species were recorded, with richness ranging from four to six species per sample. There were no significant differences among the four areas in terms of Shannon (F = 0.676, df= 3, P = 0.573) and Simpson diversity (F = 0.077, df = 3, P = 0.972) indices. Similarly, there were no significant differences in Simpson's dominance (F = 0.462, df = 3, P = 0.711) and evenness (F = 1.553, df = 3, P = 0.22) indices among the areas studied.

Species accumulation curve

The analysis of the AMF species accumulation curve, based on the Jackknife 1 richness estimator, allowed us to access 65% of the expected richness for the Brejo de altitude (BA) and 68% for the Open shrubby Caatinga (OSC). In the Dense shrubby Caatinga (DSC), 70% of the expected richness was obtained, while in the Riparian Forest (RF) the value was lower: 62% (Fig. 6).

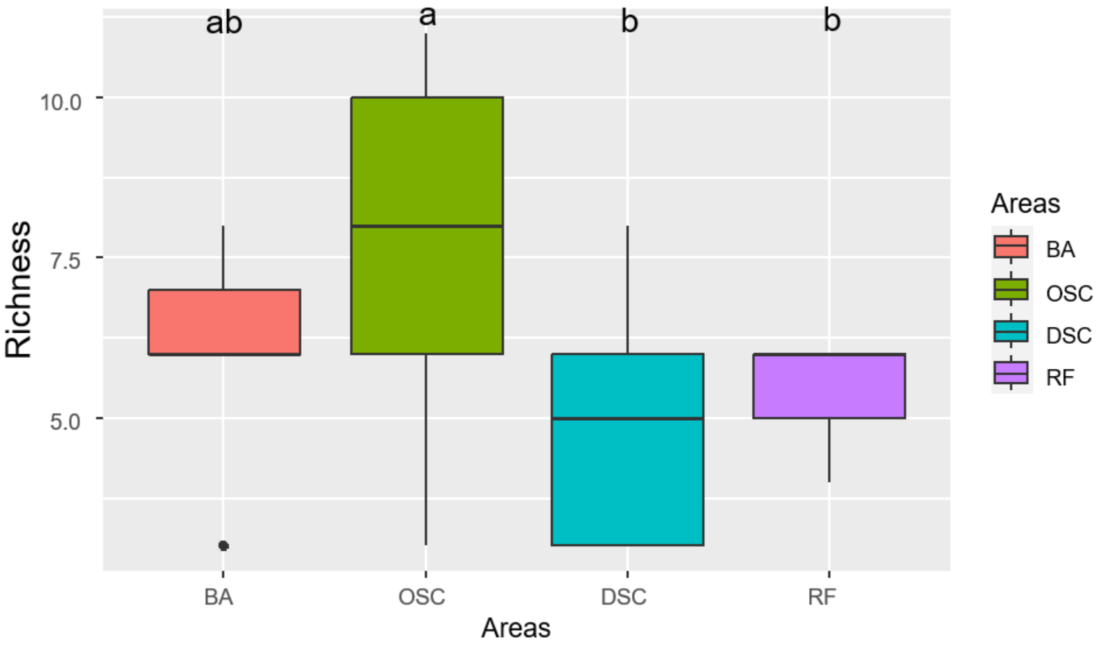

Fig. 5 – AMF taxa Richness of soil samples in the areas: Brejo de altitude (BA), Open shrubby caatinga (OSC), Dense shrubby caatinga (DSC), and Riparian Forest (RF).

Indicator species in the sample areas

The analysis of the indicator species selected *Funneliformis halonatus* as an indicator of the Brejo de altitude (BA) area, *Ambispora appendicula* and *Fuscutata aurea* as indicators of the Open shrubby Caatinga (OSC), *Gigaspora margarita* as an indicator of the Dense shrubby Caatinga (DSC) and *Funneliformis* sp. as an indicator of the Riparian Forest (RF). *Glomus brohultii* was indicative of the Brejo de altitude, Open shrubby Caatinga and Riparian Forest areas and *Acaulospora scrobiculata* proved to be indicative of the Open shrubby and Dense shrubby Caatinga areas (Table 6).

Community composition of AMF

Based on the PERMANOVA analysis, the composition of the AMF communities differs among the four study areas. The Dense shrubby Caatinga (sandy loam soil) differs from the other areas (Table 7).

The Non-Metric Multidimensional Scaling (NMDS) analysis showed the groups formed based on the composition of the AMF communities and the Envfit analysis selected the following soil attributes as structurers of the AMF communities: fine sand (R^2 = 0.3160, P = 0.001), coarse sand (R^2 = 0.1857, P = 0. 033), aluminum (Al) (R^2 = 0.1859, P = 0.043), phosphorus (P) (R^2 = 0.3624, P = 0.002), hydrogen (H) (R^2 = 0.1868, P = 0.042), aluminum saturation (m) (R^2 = 0. 1792, P = 0.037) and base saturation (V) (R^2 = 0.2648, P = 0.026) (Fig. 7). The contents of fine sand, phosphorus and base saturation are more correlated with the AMF communities in the Dense shrubby Caatinga (sandy loam), while the other attributes are correlated with the communities in the other three areas.

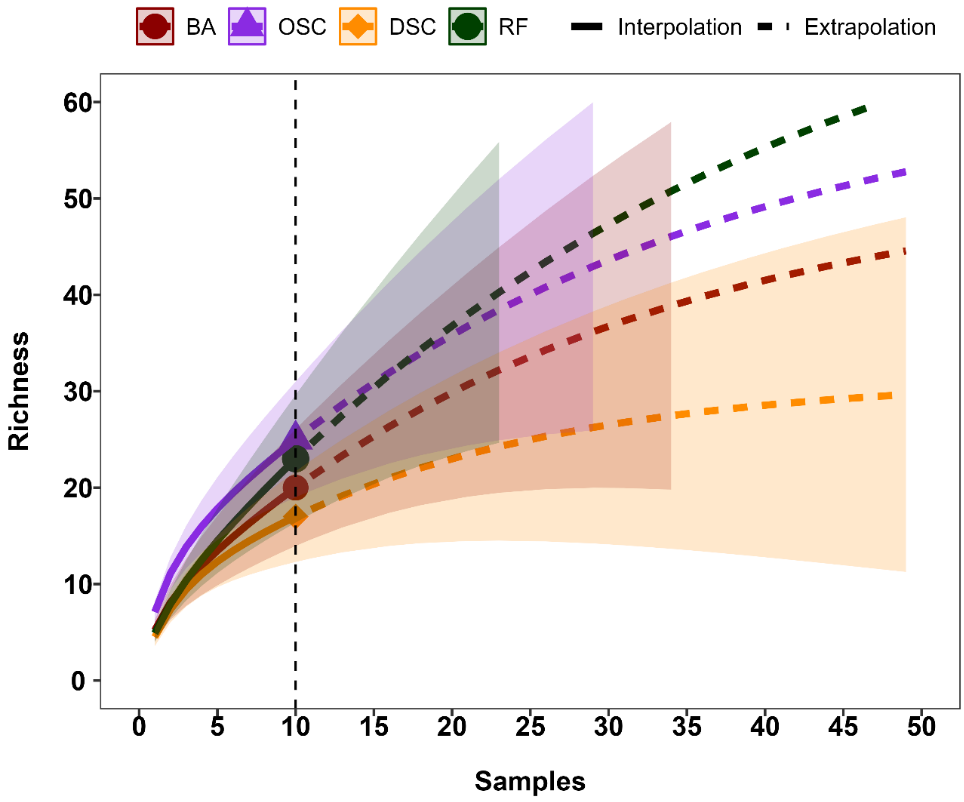

Fig. 6 – Accumulation curve of AMF species in the areas: Brejo de altitude (BA), Open shrubby caatinga (OSC), Dense shrubby caatinga (DSC), and Riparian Forest (RF).

Table 6 Indicator AMF species of soil samples in the areas: Brejo de altitude (BA), Open shrubby Caatinga (OSC), Dense shrubby Caatinga (DSC), and Riparian Forest (RF)

Areas and AMF species	IndVal (%) *	P
Brejo de altitude (BA)		
Funneliformis halonatus	71.1	0.003
Open shrubby Caatinga (OSC)		
Ambispora appendicula	84.4	0.001
Fuscutata aurea	58.5	0.025
Dense shrubby Caatinga (DSC)		
Gigaspora margarita	57.1	0.027
Riparian Forest (RF)		
Funneliformis sp.	66.7	0.008
BA + OSC		
Glomus glomerulatum	81.7	0.002
Glomus microcarpum	74.7	0.004
OSC + DSC		
Acaulospora scrobiculata	66.1	0.008
BA+ OSC + RF		
Glomus brohultii	93.9	0.001

*IndVal= Indicator value (>25%); P = Significance level (≤ 0.05).

Table 7 Permutation multivariate analysis of variance (PERMANOVA) based on AMF communities in the areas: Brejo de altitude (BA), Open shrubby Caatinga (OSC), Dense shrubby Caatinga (DSC), and Riparian Forest (RF)

Pairs	*F*	P
BA vs OSC	1.283603	1.000
BA vs DSC	6.502475	0.006 *
BA vs RF	1.070370	1.000
OSC vs DSC	5.225495	0.012 *
OSC vs RF	1.393057	0.948
DSC vs RF	5.592434	0.012 *

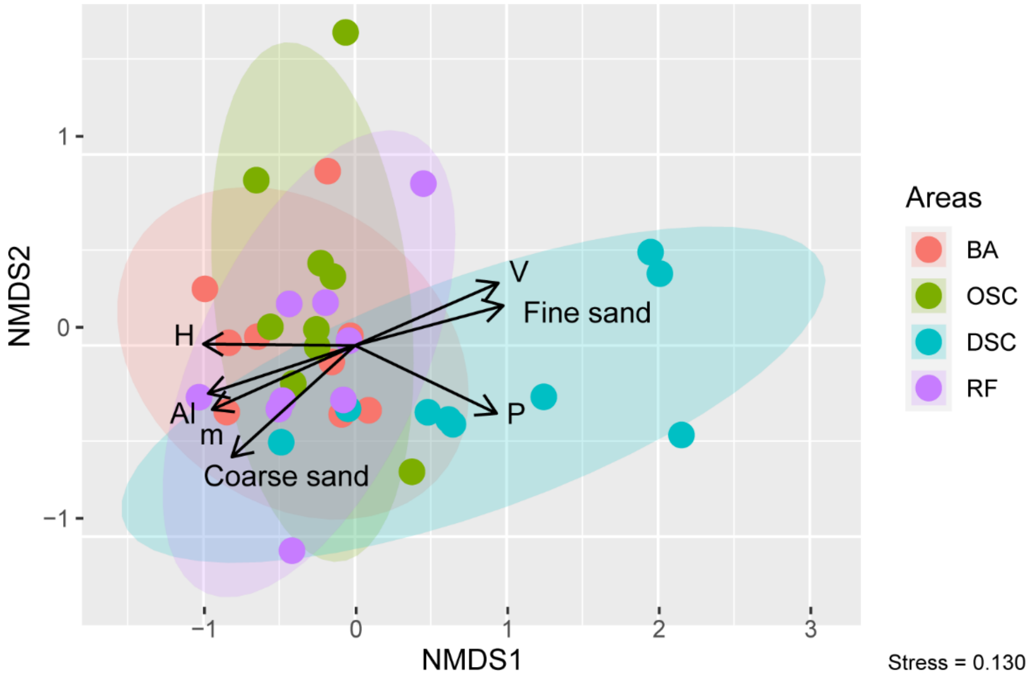

Fig. 7 – Non-metric multidimensional analysis (NMDS) based on abundance data from AMF communities, correlated with physical and chemical soil properties by Envfit analysis in the areas; Brejo de altitude (BA), Open shrubby Caatinga (OSC), Dense shrubby Caatinga (DSC), and Riparian Forest (RF).

Discussion

In this study, we investigated the structure of AMF communities in four areas of the Caatinga with soils of different textural classes and vegetation of diverse physiognomies; sandy clay loam (Brejo de altitude), loamy sand (Open shrubby Caatinga), sandy loam (Dense shrubby Caatinga) and sandy (Riparian Forest), identifying the species based on morphological analysis, and using ecological data on the richness, diversity and species composition of the AMF.

Soil texture, along with some chemical attributes and vegetation types, acted as the main determining factor in structuring AMF communities in this work. Geological and climatic processes, together with the action of organisms, have been fundamental in shaping the soils of the Caatinga (de Andrade et al. 2017); these complex interactions have resulted in a great diversity of soil types, that influences vegetation type and compose a true mosaic, where soil classes change significantly over short spatial intervals (de Andrade et al. 2017). It is widely reported that in this dry forest the floristic groups differ mainly according to the soil characteristics (de Andrade et al. 2017, Silva et al. 2023); these plant species, in turn, influence the associated microbial communities, in agreement with the results of other studies (Martínez-García et al. 2015, Teixeira-Rios et al. 2018, dos Passos et al. 2021).

In general, the values of the soil's physical and chemical properties were significantly higher in the Brejo de altitude area. The textural class of the soil in this area, characterized as sandy clay loam, reflects a balanced combination of sand, silt and clay particles (Centeno et al. 2017). The presence of clay gives the soil greater cohesion and contributes to a higher CEC (cation exchange capacity), while the sandy fraction improves drainage. These results were to be expected, given that the Brejo de altitude is in a higher altitude region and receives higher annual rainfall, resulting in denser vegetation and more developed soils with a rather atypical (moist) climatic condition compared to the rest of the Caatinga areas (Gois et al. 2019).

The higher P content found in the soil (sandy loam) in the area of Dense shrubby Caatinga may be associated with the type of bedrock (crystalline) from which this soil originates. Higher levels of nutrients such as P are commonly found in this environment, compared to the soils derived from previously weathered, sedimentary rocks (Salcedo 2006), as recorded in the Riparian Forest (sandy), with 4.2 mg P/dm^3. This heterogeneity of environments is home to various rocks/substrates with different P binding and retention capacities, which depend on characteristics such as local climatic and edaphic conditions (Salcedo 2006). In previous studies on the diversity of AMF, high levels of P in the soil have also been reported in other areas of the Caatinga (de Mello et al. 2012, Pontes et al. 2017, dos Passos et al. 2021).

The 29 AMF taxa identified in this study to species level correspond to 20,6% of the AMF richness (141 species) for the Brazilian semi-arid region (Lima et al. 2022) and 8.05% of the richness of all the species described (360 species) for the phylum Glomeromycota (Goto et al. 2024). The richness of AMF recorded in the Caatinga is quite variable and is related to sampling effort, soil type, vegetation and type of area (natural, anthropized), among others. Some studies have reported higher (Marinho et al. 2019, dos Passos et al. 2021), lower (Souza et al. 2016), and even similar richness of AMF (Pagano et al. 2013).

Representing 48.9% of the total number of AMF species recorded in this study, *Acaulospora* (12 species) and *Glomus* (10 species) were the most representative genera. These are the genera with the highest number of described species in Glomeromycota and are commonly found in arid as well as semi-arid regions, due to their ability to develop under adverse conditions (Vieira et al. 2020, Lima et al. 2022). Representatives of *Acaulospora* and *Glomus* invest their energy mainly in the rapid and high production of spores and rapid colonization of plants, with delicate and branched hyphae (Hart & Reader 2002, Chagnon et al. 2013).

The predominance of *Acaulospora* is possibly associated with higher acidity of soils (pH ranging from 4.5 to 5.6), corroborating previous findings (Vieira et al. 2020, dos Passos et al. 2021). This predominance is due to the intrinsic characteristic of the species of this genus, classified as stress tolerant and able to support a wide range of types of soils (Oehl et al. 2010, Chagnon et al. 2013).

The species found in all four areas (*Gigaspora gigantea*, *Gi. margarita*, *Glomus brohultii*, *Gl. macrocarpum*, *Gl. microcarpum* and *Glomus* sp. 1) have a wide occurrence in semi-arid regions of Brazil, as observed in several studies (Pontes et al. 2017, Marinho et al. 2019, dos Passos et al. 2021). Representatives of *Gigaspora* are commonly found in Caatinga areas; for example, *Gigaspora margarita* was found in abundance in the rhizosphere of umburana (*Commiphora leptophloeos*) (Teixeira-Rios et al. 2018). In areas of rocky outcrops (inselbergs) and adjacent areas of Caatinga, Sousa et al. (2018) recorded *Glomus brohultii* and *Gl. macrocarpum* with the highest abundance and frequency of occurrence, consistent with our results where *Glomus brohultii* and *Gl. macrocarpum* were the only species classified as dominant and with the highest relative abundance in the four areas.

It was possible to recover between 65% and 70% of the AMF species in the areas studied, according to the Jaccknife 1 index. This can be attributed to the greater complexity of the AMF communities in these areas and the number of samples analyzed (9/area, total n = 36). In addition, it is important to highlight that the sampling reflects only the specific conditions at the time of collection. Some AMF species may rarely or never sporulate in the field or persist in other types of propagules (Smith & Read 2008).

The difference in the richness of AMF taxa among the collection areas could be related to differences in soil characteristics and environmental variations, as pointed by Davison et al. (2015), as well as the composition of plant communities (Tedersoo et al. 2020, dos Passos et al. 2021) and intrinsic characteristics of AMF life strategies (Chagnon et al. 2013). The higher species richness (25) found in the Open shrubby Caatinga (loamy sand) can be attributed to the low phosphorus value, and the low residual moisture and water contents, factors that possibly stimulated sporulation of certain AMF species, as a resistance or as an adaptation strategy to survive, as reported in Caatinga areas (Pagano et al. 2013, da Silva et al. 2014, Teixeira-Rios et al. 2018). Also, it had already been reported in Caatinga areas that there was a greater dependence of vegetation on AMF for their survival and development, under adverse environmental conditions (Pagano et al. 2013). However, in the Dense shrubby Caatinga, AMF richness was lower despite the denser vegetation, probably due to the high soil phosphorus content (75.7 mg/dm^3), which may have diminished plant dependence on mycorrhizal associations, consequently limiting the establishment of diverse AMF taxa. Furthermore, the sparse canopy and discontinuous vegetation of the Open Shrubby Caatinga promote conditions where stress-tolerant and ruderal species, such as representatives of *Acaulospora* and *Glomus*, maintain higher sporulation rates as a persistence strategy, characteristic that may facilitate a greater occurrence of taxa of these genera (Chagnon et al. 2013).

Despite Shannon’s and Simpson's diversity indices, and Simpson's dominance and equitability, not being sensitive to shown differences in the AMF communities among the areas, their usage is essential for the comprehension of the assessment. Each index captures different aspects of community structure, such as species richness, dominance, and evenness, which together provide a more complete picture of the ecological patterns.

As no greater richness or significant difference in terms of AMF diversity was observed in the Brejo de altitude area (sandy clay loam soil), our first hypothesis was refuted. De Assis et al. (2018), when comparing a Brejo de Altitude area with an area of Arboreal Caatinga, also found no significant differences in the diversity or richness of AMF. Similarly, da Silva et al. (2014) found that richness did not vary across the vegetation gradient within the Brejo de Altitude in transition with a Caatinga forest.

Although vegetation influences the composition of AMF communities, this does not necessarily guarantee greater richness or diversity in more humid environments or in areas with denser vegetation, such as the Brejo de Altitude. Instead, local edaphic factors, such as soil texture and chemical attributes, play a more determining role than the phyto-physiognomy itself in structuring these communities (Lekberg et al. 2007, Oehl et al. 2010, Sousa et al. 2018).

On the other hand, the number of glomerospores differed statistically among the areas studied. In Caatinga areas, the sporulation rate is highly variable, with records ranging from 0 to 1000 glomerospores in 100 g^{-1} of soil (Maia et al. 2010). Sporulation patterns in these areas are influenced by local factors, such as water availability, variations in plant communities, the chemical and physical composition of the soil, as well as the phenology of the host (Teixeira-Rios et al. 2018).

The reason for the higher density of glomerospores recorded in the Open shrubby Caatinga and Riparian Forests areas may be related to the low phosphorus content found in these areas compared to the rest. The availability of phosphorus in the soil is one of the main elements that can affect the ability of AMF to produce propagules (Smith & Smith 2011). The lowest density of glomerospores was found in the Dense shrubby Caatinga, the area with the highest P content in the soil, reinforcing the above affirmative. As reported in other studies in Caatinga areas, higher concentrations of P is liable to decrease sporulation (de Mello et al. 2012, 2018).

In the Open shrubby Caatinga area, the sparse vegetation cover and more adverse environmental conditions also may lead AMF species to produce more glomerospores as a survival strategy. Similarly, the plant species present in this area may show a greater dependence on symbiosis with AMF to obtain nutrients, especially in soils with low phosphorus availability, as observed in this area and in the Riparian Forest (4.2 mg P/dm^3).

In the Riparian Forest, despite the denser and more diverse vegetation, the sandy soils are poor in phosphorus (4.2 mg P/dm^3), the low phosphorus content and the nutritional demand of plants may also justify the greater spore density recorded in this area.

Plant dependence on mycorrhizal associations tends to increase as soil phosphorus availability decreases, since AMF enhance the efficiency of phosphorus uptake and the overall acquisition of other nutrients (Smith & Read 2008, Smith & Smith 2011). Furthermore, several studies have demonstrated that vegetation composition can shape AMF community dynamics by selecting fungal taxa with different sporulation strategies and nutrient acquisition efficiencies (Hart & Reader 2002, Torrecillas et al. 2012, Tedersoo et al. 2020).

Mycorrhizal colonization differed statistically among the study areas. According to a review study, the rate of mycorrhizal colonization in plants from Caatinga areas is usually less than 50% (Maia et al. 2010), as has been confirmed in other studies; it rested between 6.3% and 36.5% in Caatinga areas in Paraíba (Souza et al. 2016). The higher colonization rate in roots from Brejo de altitude (61.9%), with sandy clay loam soil, confirms our second hypothesis, that there would be higher colonization rates in plants from this area. This type of soil, with a balanced combination of particle sizes, has the advantages of both the sandy fraction, which provides greater porosity that stimulates root growth, and the clay fraction, which contributes to water and nutrient retention (Carrenho et al. 2007, Pauwels et al. 2023). In addition, the local conditions, such as higher altitude and humidity, dense vegetation, atypical of other Caatinga areas (Gois et al. 2019), may have favored mycorrhizal colonization, by improving soil nutrient availability and creating conditions that support fungal growth and plant-fungus exchanges, which may explain the higher colonization rates observed in plants from this area.

The variation in the most probable number (MPN) of AMF infective propagules among the areas studied, reflects the influence of soil and vegetation characteristics, as demonstrated in previous studies (Mergulhão et al. 2007, Carneiro et al. 2012, de Mello et al. 2018). The highest MPN was recorded in the Brejo de altitude (70.33 per cm^3 of soil), while the lowest value was observed in the Open shrubby Caatinga (13.33 per cm^3 of soil). In the Brejo de altitude, the conditions of greater humidity, soil rich in organic matter and dense, stratified vegetation with medium to large trees and abundant leaf litter may have favor the activity of AMF, resulting in greater production of infective propagules. In contrast, in the Open shrubby Caatinga, aridity, limited water and nutrient availability, and sparse vegetation may have restricted the proliferation of these fungi, explaining the lower MPN observed.

Indicator species analysis is an approach that demonstrates the preference of a particular taxon in relation to the conditions of a given habitat (Cáceres & Legendre 2009). These taxa can be related to just one local factor (e.g. area), while others can be associated with more than one factor (e.g. vegetation and soil types) (Cáceres & Legendre 2009, Marinho et al. 2019), as seen in our study with *Acaulospora scrobiculata* (indicator of Open and Dense Caatinga areas). This species has a wide distribution and is adapted to different types of vegetation and soil, with records from all regions of the country (Maia et al. 2020). The same occurs with the species *Glomus glomerulatum* and *Gl. microcarpum* in the Brejo de altitude (Open shrubby Caatinga areas) and *Gl. macrocarpum* (Open shrubby Caatinga and Riparian Forest areas). These species of Glomeraceae are generalists and have been reported in all of Brazil's biomes (Maia et al. 2020). These taxa are commonly reported in dry and humid forest environments, such as *Glomus brohultii*, *Gl. glomerulatum*, and *Gl. microcarpum*, which in this study were identified as indicators of the Brejo de Altitude area (de Assis et al. 2018, da Silva et al. 2014). *Ambispora appendicula*, an indicator species of Open shrubby Caatinga, is commonly found in Caatinga ecosystems (Maia et al. 2020, Lima et al. 2022), highlighting its adaptation to semi-arid conditions.

Confirming our third hypothesis, Gigasporales was more abundant in areas with higher total sand contents; open shrubby Caatinga (sandy loam), riparian forest (sandy) and dense shrubby Caatinga (sandy loam soil), with the species *Gigaspora margarita* selected as an indicator of this last area. Representatives of Gigasporales typically prefer sandy environments (Lekberg et al.

2007), which is consistent with our observation while corroborating the findings of other studies (Pagano et al. 2013, dos Passos et al. 2021) in areas of Caatinga *sensu stricto*.

The composition of the AMF communities differed among the areas studied, confirming our fourth hypothesis. The seven soil attributes selected as structuring the composition of AMF communities among areas in this study (fine sand, coarse sand, phosphorus, hydrogen, aluminum, aluminum saturation and base saturation) have also been reported as determinants of AMF communities (de Mello et al. 2018, Marinho et al. 2019, dos Passos et al. 2021).

Macronutrients, especially phosphorus, and micronutrients, together with the distribution of particle sizes, influence soil properties, affecting its structure, porosity and water retention capacity (Chaudhary et al. 2008). These variables, in turn, shape the composition of AMF communities, as observed in other works (Lekberg et al. 2007, de Mello et al. 2018). This edaphic gradient, in interaction with the distinct phyto-physiognomies present in the four respective areas, are likely contributors in the creation of different niches for AMF communities. In agreement with the reports from previous studies (Pagano et al. 2013, Marinho et al. 2019, dos Passos et al. 2021) we conclude that the influence of edaphic characteristics, together with vegetation, act as to shape AMF communities of these Caatinga ecosystems.

This study contributes significantly to the understanding of the diversity, richness and distribution of arbuscular mycorrhizal fungi in different areas of the Caatinga domain, reinforcing the crucial role of soil and vegetation as a structuring factor of these communities.

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