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Arbuscular mycorrhizal fungi community in soils under desertification and restoration in the Brazilian semiarid

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ABSTRACT

Soil desertification has a significant social, economic, and environmental impact worldwide. Mycorrhizal diversity remains poorly understood in semiarid regions impacted by desertification, especially in Brazilian drylands. More importantly, positive impacts of grazing exclusion on mycorrhizal communities are still incipient. Here, we hypothesized that overgrazing changes the structure of Arbuscular Mycorrhizal Fungi (AMF) community compared to native areas and, grazing exclusion is effective to restore the AMF community. Thus, we analyzed the status of AMF community in soils under desertification (overgrazing) and restoration (twenty-years of grazing exclusion) in the Brazilian semiarid. AMF-spores were extracted via humid decantation methodology, morphologically classified, and alpha diversity metrics were calculated. Soil samples were chemically, and physically characterized and multivariate statistical analyses were applied to verify the impact of soil degradation and restoration on AMF-community. Briefly, native, and restored areas presented higher contents of organic matter, phosphorus, microbial carbon, and β-glucosidase activity. However, degraded soil showed higher Al^{3+}, Na^{+}, and bulk soil density values. The abundance of AMF spores was higher in restored soil, followed by degraded and native vegetation, and Shannon's diversity index was significantly higher in restored soils, followed by native vegetation. AMF-spores were classified into four families (Gigasporaceae > Acaulosporaceae > Glomeraceae > Ambisporaceae). Ambisporaceae was closed correlated with degraded soil, mainly with Al^{3+}, Na^{+}, and bulk soil density properties. On the other hand, Acaulosporaceae and Glomeraceae were positively correlated with native vegetation and restored soil, respectively, thereby improving Shannon index, richness, enzyme activity, and soil respiration. Thus, grazing exclusion, in long term, can be a good strategy to restore AMF-diversity in soils in the Brazilian semiarid.

1. Introduction

Drylands comprise both arid and semiarid ecosystems and cover ~40% of the Earth's surface (Nickayin et al., 2022). However, the combined effect of natural and human activities leveraged soil degradation/desertification in these ecosystems (Araujo et al., 2022). Land degradation due to drought and desertification affects ~1.9 billion hectares and ~1.5 billion people globally (Albuquerque et al., 2020). The Brazilian semiarid presents a large area of 1.2 million km^2, being covered by soils with high vulnerability to desertification due to their

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geological and climatic environmental preconditions. In addition, the anthropogenic actions through unsuitable land use have contributed to accelerating the process of desertification (CGEE, 2016).

Among the several processes promoting desertification, the overgrazing of native vegetation has brought negative effects on soil health (Feltran-Barbieri and Féres, 2021; Vieira et al., 2021). Indeed, since overgrazing decreases the plant cover, it induces soil erosion and depletes nutrients and soil organic matter (SOM) (Oliveira Filho et al., 2019), therefore affecting the soil microorganisms and impairing their functions (Pereira et al., 2021). Recent studies demonstrated that overgrazing significantly intensifies soil desertification in the Brazilian semiarid, reducing richness, diversity, and functions of the soil bacterial community (Oliveira et al., 2021; Pereira et al., 2021).

As an important group of soil microorganisms, arbuscular mycorrhizal fungi (AMF) play several important functions in soil services (Genre et al., 2020) and plant growth, such as improving plant nutrition (Averill et al., 2019) and water absorption (Zhang et al., 2018), protecting against pathogens (Wehner et al., 2011) and ameliorating the contamination of heavy metals (Garcia et al., 2020). Particularly in degraded lands, AMF has been recognized to be a sensitive indicator of both degradation and restoration, which in turn affect the soil health (Vasar et al., 2021). In addition, AMF groups can play an important role to mitigate the ongoing climatic changes worldwide (Duarte and Maherali, 2022).

On the other hand, some restoration practices, such as grazing-exclusion, seem to be effective in ameliorating the negative impact of overgrazing (Pereira et al., 2021). Previous studies in the Brazilian semiarid have shown that grazing-exclusion can potentially restore the soil properties in long-term, increasing the content of SOM and nutrients (Oliveira-Filho et al., 2019), and recovering the bacterial richness and diversity (Pereira et al., 2021). Although the grazing-exclusion can be effective in restoring the soil properties worldwide(Liu et al., 2020; Xun et al., 2018; Zhang et al., 2021), little is known how AMF community responds to soil desertification and restoration, by overgrazing and grazing-exclusion, respectively, in the Brazilian semiarid.

Here, this study hypothesized that overgrazing changes the structure of AMF community compared to native areas and, more importantly, that grazing-exclusion is effective to restore the AMF community and, consequently, soil health. To address this hypothesis, we analyzed the status of AMF community in soils under desertification (overgrazing) and restoration (twenty-years of grazing exclusion) in the Brazilian semiarid.

2. Material and Methods

2.1. Location and experimental area

The study was carried out at Irauçuba municipality, Ceará state, Brazil (3°44′46"S e 39°47′00"W), ~152 m above sea level (Fig. 1). The mean annual precipitation in the last twenty years was 320 mm (Pereira et al., 2021), distributed mainly between January and May (Fig. S1). According to Köppen's classification system, the climate in this region is hot semiarid (BSh), with mean temperature ranging from 26ºC to 28ºC (Alvares et al., 2013). The predominant soil orders are Vertisols and Planosols (WRB/FAO) (Oliveira Filho et al., 2019).

Overgrazing is a common practice adopted by local farmers, which has contributed to soil desertification due to the removal of the Caatinga biome vegetation in the last 50 years. In 2000, several grazing-exclusion systems were set up in areas of 50 m x 50 m (2500 m^2), avoiding animal grazing (Fig. 2). However, to avoid border effects, we sampled in a 40 m x 40 m area. We sampled soil (0–10 cm), during February, the rainy season, in three different scenarios, as seen in Fig. 1, indicated as Native for native Caatinga vegetation, (Restored) for grazing exclusion and (Degraded) for overgrazed areas (Fig. 1). These three scenarios were present at three different sites, separated from each other by ~ 2 km. Thus, we analyzed a total of 27 samples (3 scenarios, 3 sites and 3 replications). The experimental design was detailed extensively in Pereira et al. (2021) and Oliveira et al. (2021).

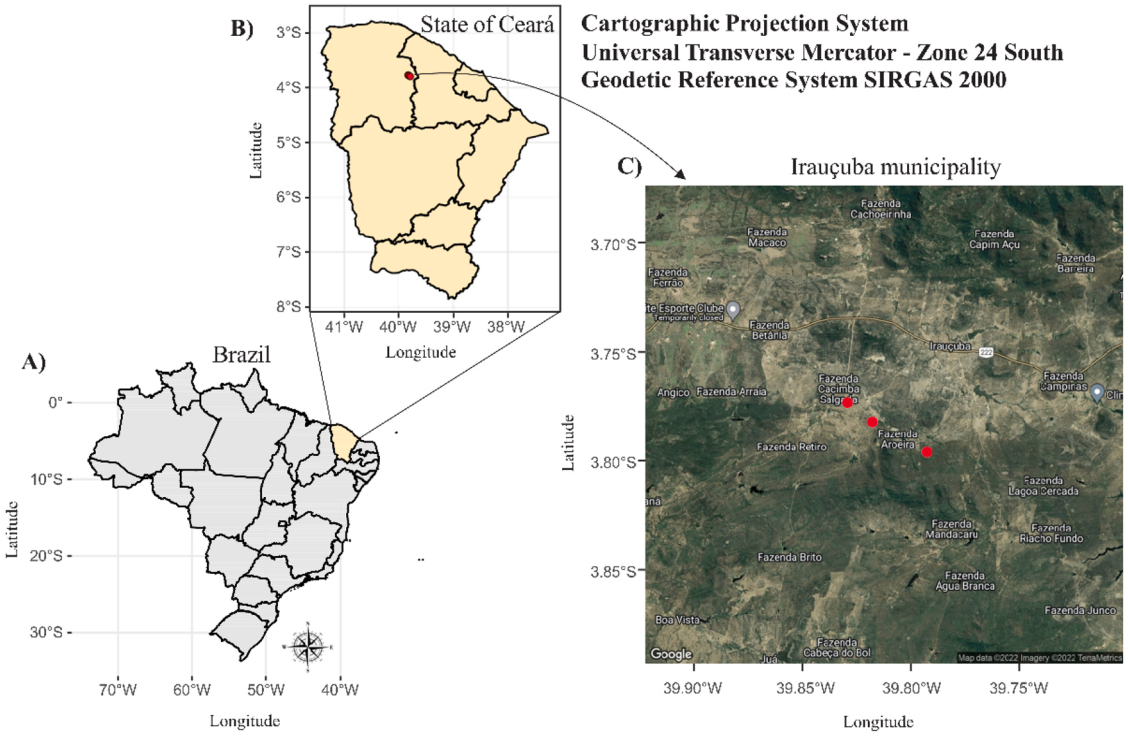

Fig. 1. Geographic location of Irauçuba municipality, Ceará State, Brazil. The map was drawn with QGIS (v. 3.12.1) software by the author. Red points symbolize the three analyzed sites.

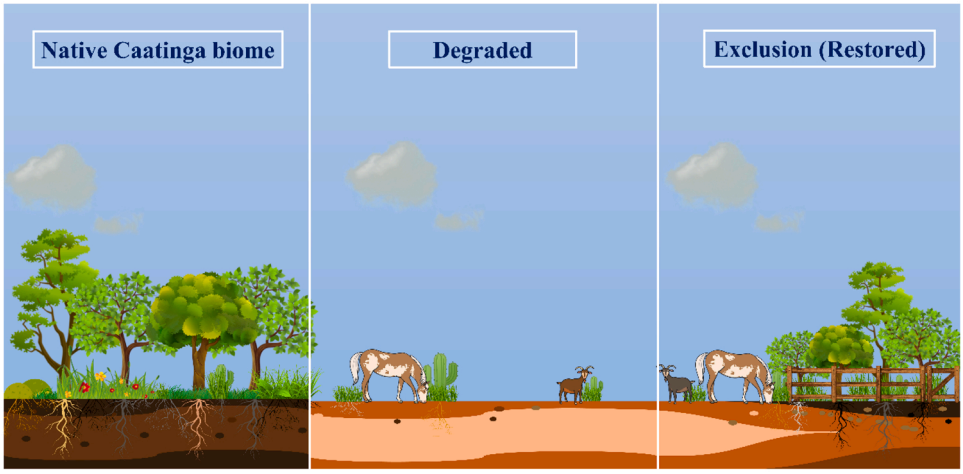

Fig. 2. Representation of native Caatinga vegetation, the soil degradation through overgrazing (suppression of vegetation and loss of soil layers) and grazing exclusion management by fencing.

2.2. Soil chemical and physical characterization

Soil pH was determined in $CaCl_2$ solution (0.01 mol L^{-1}). Total organic carbon (TOC) was extracted using dichromate ($K_2Cr_2O_7$) and determined by colorimetry. Available phosphorus (P) and potassium (K^+) were extracted through the ion exchange resin. Potential acidity (H+Al) via pH SMP (Shoemaker, MacLean, and Pratt, 1961) methodology. Aluminum (Al^{3+}), calcium (Ca^{2+}) and magnesium (Mg^{2+}) were extracted using KCl solution (1 mol L^{-1}), while sulfur was extracted by calcium phosphate solution (0.01 mol L^{-1}) (Raij et al., 2001). Sodium (Na^+) was extracted by Mehlich-1 solution (EMBRAPA, 2009), and electrical conductivity (EC) was read in a digital conductivimeter. The determinations of sum of base (SB), cation exchange capacity (CEC), base saturation (V%), exchangeable sodium percentage (ESP) and aluminum saturation (m%) were determined following the methods described by Raij et al. (2001) for tropical soils.

For the physical analyses, the disturbed soil was air-dried and passed through a sieve (2 mm). Particle-size analysis was performed as follows: the clay fraction was determined by the pipette method (Gee and Bauder, 1986); the sand fraction was determined by sieving; and the silt fraction by the difference between the total mass of the sample and the sum of the sand and clay fractions. Soil moisture was determined by the gravimetric method with oven drying (Gardner, 1986), as follows: wet soil samples were weighed and then dried in an oven, at a temperature of 105 °C, until reaching constant mass. After that, the samples were weighed again, and the mass difference represented the water mass. In sequence, the gravimetric moisture was evaluated by dividing the water mass by the solids mass. Finally, bulk density was determined with a 100 mL graduated cylinder (Tan, 2005), in which the mass of material needed to occupy its entire volume was measured. This methodology is well suited for the determination of bulk density of disturbed soil samples, especially for those with coarse texture.

2.3. Microbial activity (soil enzymes, microbial carbon, and respiration)

β-glucosidase (EC 3.2.1.21), and acid phosphatase (E.C. 3.1.3.2) activities were determined following Tabatabai's (1994) procedures. Briefly, 1 g of soil (dry weight) was incubated with ρ-nitrophenyl-β-D-glucoside and ρ-nitrophenyl phosphate for both β-glucosidase and acid phosphatase, respectively. Samples were incubated at 37°C for 1 h containing MUB (Modified Universal Buffer, pH 6.0 and 6.5, respectively). The reaction of β-glucosidase was paralyzed by $CaCl_2$ (0.5 M) and THAM (0.1 M, pH 12), while acid phosphatase by $CaCl_2$ (0.5 M) and NaOH (0.5). The extracts were filtered in Whatman's paper (nº 2), and the intensity of yellow color was analyzed in a spectrophotometer at 410 nm. Enzyme activities were estimated by using a ρ-nitrophenol solution as standard curve.

Microbial biomass C (Cmic) was estimated through the fumigation-extraction methodology proposed by Vance et al. (1987). Briefly, 10 g soil samples were fumigated with chloroform (99.8%) and digested with potassium dichromate for 30 min at 100 °C. Extracts were determined by titration using iron sulfate and ammoniacal ferrous sulfate (Brookes et al., 1985; Vance et al., 1987). Soil respiration (CO_2-C) was estimated by quantification of CO_2-C released during 31 days of incubation at 28 °C. Briefly, soil samples (100 g) were incubated in hermetic sealed flasks containing a (0.5 M) bottle trap with (0.5 M) NaOH. CO_2-C emitted was estimated by titration using (0.5 m) KCl (Cardoso et al., 2013). In both assays, soil moisture was maintained at 60% of maximum water retention capacity (MWC).

2.4. Exogenous easily extractable glomalin-related soil protein

Glomalin was extracted following the Wu et al. (2014) and Wright and Upadhyaya (1998) procedures. Briefly, soil samples (1 g – 2 mm) were incubated with 8 mL of 20 mM sodium citrate ($C_6H_5Na_3O_7.2\ H_2O$) buffer solution (pH 7.0) at 120 °C for 30 min, and latter centrifuged at 2800 RCF for 15 min. The supernatant was used for glomalin determination, which was analyzed in a spectrophotometer (595 nm) as per Bradford (1976), and contents were estimated by using bovine serum albumin as standard curve (He et al., 2020).

2.5. Spore extraction and classification

AMF spores were extracted through wet sieving and decanting of 50 g soil (Gerdemann and Nicolson, 1963) (Fig. S2). Sieves of 0.71 mm and 0.045 mm were used to collect AMF spores. Spores collected from the 0.045 mm sieve were purified by centrifugation in sucrose solution (70%) for 3 min at ~3500 rpm. The supernatant was rinsed with water, sieved at 0.045 mm, and counted individually in a stereoscopic microscope and later mounted on semi-permanent slides in polyvinyl alcohol with glycerol resin and Melzer's reagent (Morton et al., 1993). The numbers of potentially viable and non-viable spores were estimated by the presence of cellular content and apparently undamaged cell walls (Ramírez-Viga et al., 2020). Spores were taxonomically classified based on the International Collection of Arbuscular and Vesicular Mycorrhizal Fungi (INVAM) available at http://invam.wvu.edu (Stürmer et al., 2021) and Redecker et al. (2013). The most found AMF groups were classified taxonomically at species level, and in a few cases, spores were grouped only at family or genus levels.

Alpha diversity metrics were calculated, i.e., richness, total

abundance, and Shannon's diversity index. Briefly, richness was obtained counting the number of different AMF-species, while total abundance was the sum of all spores found per treatment, including potentially viable and non-viable spores. Shannon's index (H) was calculated using the formula $H = - \Sigma (p_i).(\text{Log}_2 p_i)$. In this case, $p_i = n_i/N$, in which n_i is the number of individuals in species i; N is the total number of individuals of all species (Hill, 1973).

2.6. Statistical analyses

Data were submitted to Levene and Shapiro–Wilk's tests, respectively, for homogeneity and normality of variances, and later we applied nested-ANOVA and groups of means were compared through Tukey's test (5%). We used distance-based redundancy analysis (db-RDA), coupled with forward selection (Monte Carlo permutation test - 499 random permutations), to assess correlation between chemical, physical and biological soil properties. To demonstrate whether the treatments present significant differences between AMF-groups, we used the permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001). AMF composition was analyzed by using family and species levels as input and relative abundance (%) through a histogram. In this case, p values were obtained using a two-sided Tukey-Kramer test with Benjamini-Hochberg correction (Benjamini and Hochberg, 1995). Finally, we applied a Spearman's rank correlation test to access the relationship between chemical and physical soil characteristics with AMF-groups and soil biological properties. Upstream analyses were made with R software (version 3.6.3) and Canoco® software for Windows (v. 4.5) (Leps, 2020; Leps and Smilauer, 2003).

3. Results

The values of TOC, P, CEC, Cmic, and β-glucosidase were higher in both soils under native vegetation and restored, while the values of Al^{3+}, Na^{+}, EC, PST, and bulk soil density were higher in the soil under degraded (Table 1; Fig. S3). The values of Ca^{2+}, SB, and acid phosphatase where higher and lower in soils under native vegetation and degraded, respectively, while the restored soil presented intermediate values.

The abundance of AMF spores was higher in restored soils, followed by degraded and native vegetation (Fig. 3a). Interestingly, we found similar proportions between the abundance of viable and non-viable spores. Shannon's diversity index (Log_2) was significantly higher in restored soils, followed by native vegetation and degraded (Fig. 3b). Morphologically, AMF spores were classified into four dominating families, being Gigasporaceae, Acaulosporaceae, Glomeraceae, and Ambisporaceae (Fig. 4a). Acaulosporaceae was more abundant in the soil under native vegetation, while Gigasporaceae and Ambisporaceae were higher in the degraded soil. Glomeraceae was dominant in both soils under native vegetation and restored. At a deeper taxonomical level, AMF spores were classified into five species (*Glomus etunicatum*, *Glomus fasciculatum*, *Ambispora. leptoticha*, *Ambispora appendicula,* and *Acaulospora foveata*) and two genera (*Funneliformis* spp. and *Acaulospora* spp.) (Fig. 4b). *Ambispora appendicula* was more abundant in the degraded soil, while *Glomus fasciculatum, Glomus etunicatum*, and *Acaulospora foveata* were abundant in the restored soil. Interestingly, *A. foveata* was not detected in the degraded soil.

AMF communities were clearly separated between native vegetation and restored from degraded (PERMANOVA $F = 3.4278$, $p = 0.002$) (Fig. 5). RDA clustered Al^{3+}, EC, PST, Na^{+}, bulk soil density, and Ambisporaceae in the degraded soil, while soil moisture, CEC, P, Ca^{2+}, and the biological parameters (Shannon's index, glomalin, richness, Acaulosporaceae and β-glucosidase) were clustered in the soil under native vegetation. Finally, Mg^{2+}, TOC, acid phosphatase, Glomeraceae, soil respiration, Cmic, and spore abundance were clustered in the restored soil (Fig. 5).

β-glucosidase and Cmic showed highest number of correlations (16 and 15, respectively), being 10 positive and 6 negative (β-glucosidase), and 10 positive and 5 negative (Cmic) (Fig. 6). TOC correlated positively with Glomeraceae, β-glucosidase, acid phosphatase, and Cmic. Interestingly, Na^{+} and PST presented positive correlations with Ambisporaceae and Gigasporaceae, and negative ones with Shannon's index and β-glucosidase. Glomalin content correlated positively with soil moisture

Table 1
Chemical, physical, and biological properties in soils under native vegetation, grazing exclusion, and overgrazing.

Parameters		Native	Restored	Degraded
pH	–	5.10 ± 0.18* ns	4.98 ± 0.13 ns	4.71 ± 0.59 ns
TOC	g dm^{-3}	22.71 ± 6.30 a	29.47 ± 4.07 a	11.89 ± 2.70 b
P	mg dm^{-3}	35.26 ± 15.61 a	20.48 ± 9.95 a	6.76 ± 1.22 b
S		9.00 ± 1.45 ns	9.19 ± 0.54 ns	8.13 ± 0.13 ns
Ca^{2+}	$mmol^{c}$ dm^{-3}	54.29 ± 15.91 a	43.94 ± 11.48 ab	19.65 ± 14.28 b
Mg^{2+}		24.71 ± 2.90 ns	24.41 ± 2.21 ns	13.59 ± 7.70 ns
K^{+}		2.64 ± 0.26 ns	2.62 ± 0.13 ns	1.87 ± 0.51 ns
Al^{3+}		0.48 ± 0.82 b	0.59 ± 0.55 b	2.57 ± 1.65 a
H+Al		21.13 ± 3.95 ns	24.54 ± 4.37 ns	18.43 ± 2.63 ns
Na^{+}		1.18 ± 0.35 b	2.09 ± 0.14 ab	3.55 ± 1.98 a
CEC		103.95 ± 20.24 a	97.82 ± 6.06 a	57.10 ± 23.48 b
SB		82.82 ± 18.03 a	72.97 ± 9.81 ab	38.67 ± 24.09 b
EC	μS cm^{-1}	39.46 ± 11.41 b	31.44 ± 24.49 b	138.91 ± 6.46 a
PST	%	1.33 ± 0.33 b	2.11 ± 0.50 b	5.22 ± 0.83 a
V		77.13 ± 4.91 ns	72.41 ± 3.21 ns	61.87 ± 17.38 ns
m		2.11 ± 3.65 ns	1.56 ± 1.34 ns	9.22 ± 7.01 ns
Bulk density	g cm^{-3}	1.52 ± 0.04 b	1.54 ± 0.02 b	1.62 ± 0.03 a
Sand	%	74 ± 3.01	68 ± 2.77	70 ± 4.72
Silt		18 ± 2.30	22 ± 3.55	19 ± 3.17
Clay		8 ± 0.86	10 ± 1.521	11 ± 1.68
Soil moisture		9.46 ± 2.18 ns	7.44 ± 2.63 ns	6.17 ± 0.12 ns
SR	mg CO_2-C g $soil^{-1}$ day^{-1}	2.85 ± 0.41 ns	4.53 ± 2.96 ns	2.67 ± 0.73 ns
Cmic	mg kg^{-1}	78.82 ± 8.41 a	93.46 ± 11.12 a	48.69 ± 6.34 b
Glomalin	mg g^{-1}	154.90 ± 48.4 ns	180.18 ± 57.3 ns	158.19 ± 20.9 ns
Textural class	–	Sandy loam	Sandy loam	Sandy loam

* Means followed by the same letter do not differ by Tukey's test at a significance level of 5% ($n = 9$). ns = not significant. TOC: total organic carbon, Na^{+}: sodium, PST: exchangeable sodium percentage, P: phosphorus, S: sulphur, Ca^{2+}: calcium, Mg^{2+}: magnesium, K^{+}: potassium, Al^{3+}: aluminum, H+Al: potential acidity, BS: Base sums, CEC: cation exchange capacity, V%: bases saturation; m%: aluminum saturation; EC: electrical conductivity; CO_2-C: soil respiration and Cmic: microbial carbon.

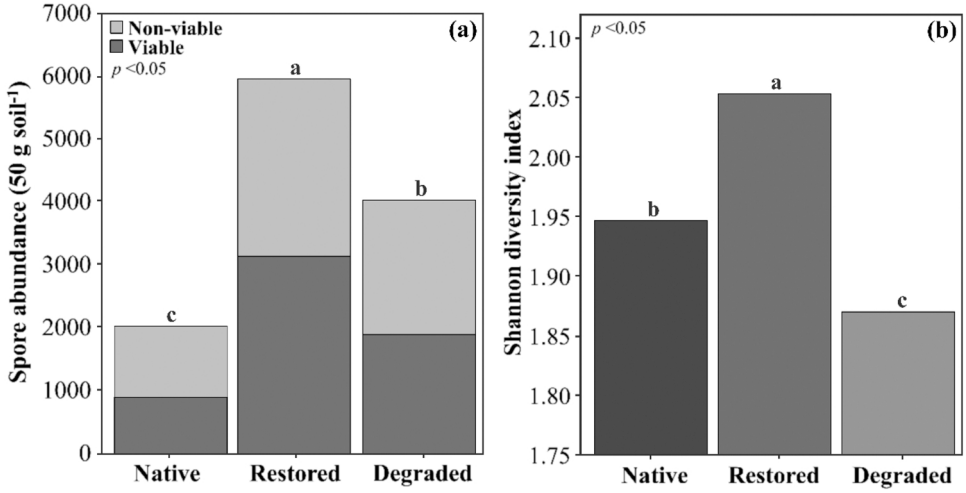

Fig. 3. Spore abundance (viable and non-viable) (a) and alpha diversity (b) alpha diversity, based on Shannon's index (Log_2), of arbuscular mycorrhizal fungi in soil under Native Caatinga vegetation, Exclusion and Grazed systems. Means followed by the same letter do not differ by Tukey's test at a significance level of 5% ($n = 9$).

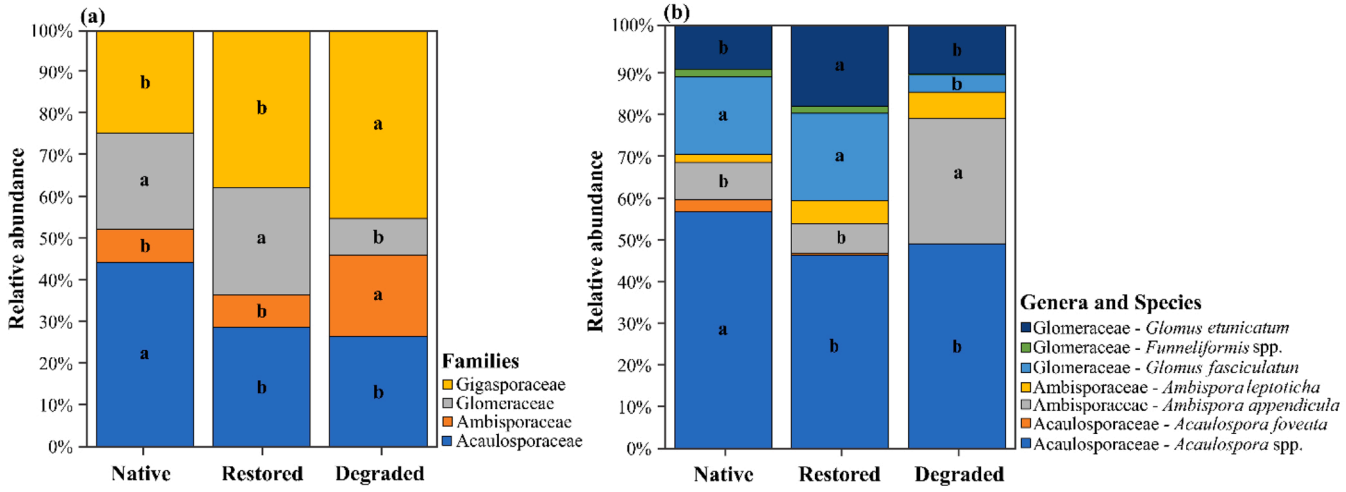

Fig. 4. Relative abundance (%) of arbuscular mycorrhizal families (ab), genera, and species (b) in soil under Native Caatinga vegetation, Exclusion and Grazed systems across three analyzed areas. Means followed by the same letter do not differ by Tukey's test at a significance level of 5% ($n = 9$).

(Fig. 6).

4. Discussion

This study assessed the status of AMF community in soils under desertification and restoration, by overgrazing and long-term grazing-exclusion, respectively, in the Brazilian semiarid. In line with the hypothesis, overgrazing changed the status of AMF community, in terms of abundance of spores, composition, and diversity. On the other hand, grazing-exclusion potentially improved the status of AMF community, being a suitable strategy to restore soil health as also reported in previous studies in the Brazilian semiarid (Pereira et al., 2021; Oliveira et al., 2021).

AMF are fundamental for ecosystem functioning (Ferlian et al., 2021; Genre et al., 2020). Thus, our findings reinforce the positive effect of grazing-exclusion in restoring semiarid soils under desertification. More importantly, AMF can induce plant tolerance to abiotic stresses related to climate changes events, which can decrease plant removal, and increasing its dispersal, adaptation, and survival capability. For example, AMF can mitigate the negative consequences of water stress via a huge hyphal system exploring the soil (Bennett and Classen, 2020; Hazzoumi et al., 2015).

Grazing-exclusion contributed to increase the values of TOC, P, CEC, Cmic, and β-glucosidase, which are indicators of improved soil quality/health, in terms of fertility and biology (Prommer et al., 2020). In contrast, overgrazing increased the values of Al^{3+}, Na^{+}, EC, PST, and soil density, which are indicators of soil degradation, since these parameters are indicators of acidity, salinity, and compaction (Nawaz et al., 2013; Shrivastava and Kumar, 2015). Andrews et al. (2004) and Cardoso et al. (2013) highlighted several indicators of soil health, including chemical, physical, and biological properties (e.g., organic matter, pH and enzymes activity) due to their important role to soil functioning. Therefore, our results confirm that grazing-exclusion is a suitable strategy to improve soil health in drylands soils, since TOC (and other nutrients), AMF diversity and enzymes activity were significantly improved. Interestingly, the activity of acid phosphatase was higher in native and restored areas. Bini et al. (2018) demonstrated that AMF could increase phosphatase activity in forest systems. Importantly, Ming and Hui (1999) demonstrated that AMF and phosphatase activity had a positive and strong effect in plant growth during drought events, conditions commonly found in semiarid systems; and phosphatase was closely related to the reduction of wilting of plants. The authors mentioned that the effect of AMF and phosphatase in the plant nutrition, mainly P, can improve the nutrient uptake and water conditions, and

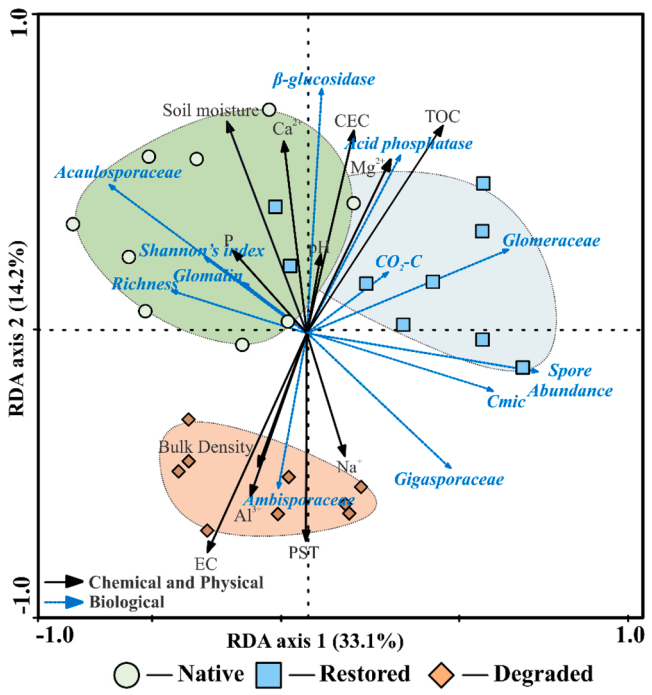

Fig. 5. Distance-based redundancy analysis (db-RDA) of soil chemical (dark arrows) and biological (blue arrows) properties in all analyzed areas. The db-RDA was based on the Monte Carlo permutation test (499 permutations), where only significant correlations were fitted in the ordination (Forward stepwise selection). Green circles mean AMF community groups under Native Caatinga vegetation, blue squares the grazing exclusion, and orange rhombs represent grazed system ($n = 27$). TOC: total organic carbon, Na^+: sodium, PST: exchangeable sodium percentage, P: phosphorus, Ca^{2+}: calcium, Mg^{2+}: magnesium, Al^{3+}: aluminum; CEC: cation exchange capacity, EC: electrical conductivity; CO_2-C: soil respiration and Cmic: microbial carbon.

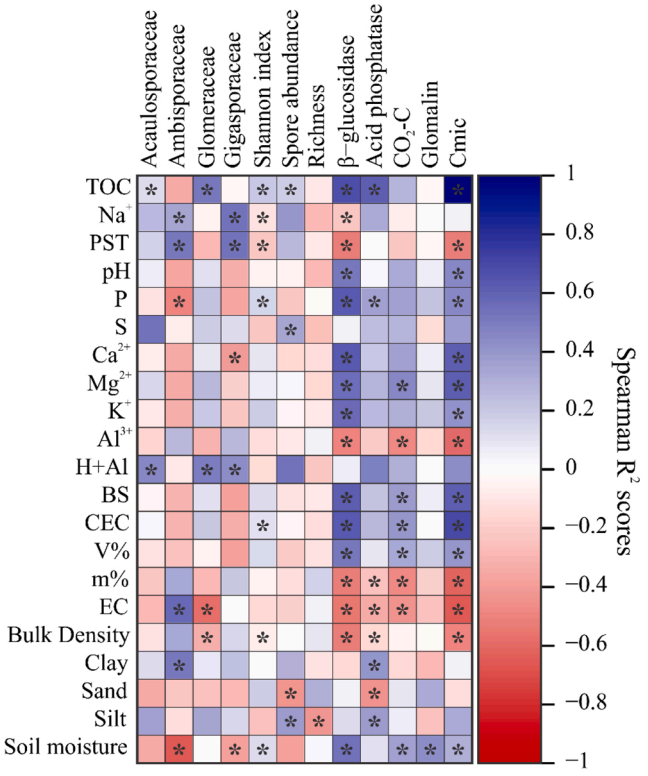

Fig. 6. Heatmap of Spearman's ranking correlation test between chemical (vertical) with biological (horizontal) soil properties. Blue and red colors indicate positive and negative correlations, respectively. Asterisk (*) indicates significant correlations by the Tukey's test ($p < 0.05$). TOC: total organic carbon, Na^+: sodium, PST: exchangeable sodium percentage, P: phosphorus, S: sulphur, Ca^{2+}: calcium, Mg^{2+}: magnesium, K^+: potassium, Al^{3+}: aluminum, H+Al: potential acidity, BS: Base sums, CEC: cation exchange capacity, V%: bases saturation; m%: aluminum saturation; EC: electrical conductivity; CO_2-C: soil respiration and Cmic: microbial carbon.

raise their drought-resistance. Thus, the increase of AMF diversity in drylands can improve the resistance of local-plant to support extreme conditions in Brazilian semiarid system and worldwide via improvements in native plant nutrition.

Interestingly, despite the degraded soil properties found in soil under overgrazing, the abundance of AMF-spores was not affected by degradation. AMF-spores are the most abundant infective propagules in the soil (Bueno and Moora, 2019) and can be produced in preserved and disturbed soils, and independently of any specific host plant (Kameoka et al., 2019). Thus, AMF-sporulation occurs naturally under stressed conditions since the spores act as structures of resistance to survive in extreme conditions (Bonfante and Genre, 2008), and it could explain the normal sporulation found in soil under overgrazing. Studying soils under dryland conditions, Mahmoudi et al. (2021) provided strong evidence that AMF traits (especially AMF spores abundance) are important indicators of multiple soil functions in these ecosystems during climate changes. Thus, although being a dynamic property, AMF sporulation can be a sensitive indicator of soil health under degraded soils.

On the other hand, our results have shown changes in AMF community due to overgrazing and grazing exclusion. Gigasporaceae and Ambisporaceae were dominant in the soil under overgrazing, while Glomeraceae was dominant in the soil under grazing exclusion. It confirms that the process of desertification in semiarid soils induces shifts on AMF groups as also observed in bacterial groups by Pereira et al. (2021).

Previous studies have reported Gigasporaceae as tolerant to stressed environments (Chagnon et al., 2013) and it has been found in degraded soils (Ríos-Ruiz et al., 2019), while Glomeraceae seems to be dominant under restored conditions (Becerra et al., 2019). Importantly, Gigasporaceae can increase its abundance in elevated CO_2 concentrations (Cotton et al., 2015). Thus, members of Glomeraceae should be include as key-stone species to mitigate climatic changes in drylands soils worldwide (Bennett and Classen, 2020).

We observed that *Ambispora appendiculata* abundant in the soil under overgrazing, and it agrees with a previous study in degraded soils (Ríos-Ruiz et al., 2019). On the other hand, *Glomus fasciculatum, Glomus etunicatum*, and *Acaulospora foveata* were abundant in the soil under grazing-exclusion. Species belonging to the genus *Glomus* present great adaptability and survival under varying soil conditions (Burni et al., 2011) and were highly abundant in enclosure or fenced soils in Northern Ethiopia (Birhane et al., 2017).

AMF diversity was found to be higher in the soil under grazing-exclusion, probably due to the presence of legume species, such as *Mimosa tenuiflora* (Oliveira Filho et al., 2019) that develop mutualistic interactions with AMF (de Souza et al., 2016). The redundancy analysis clearly separated AMF community between soil under overgrazing and grazing-exclusion, and this suggests that the process of restoration, by grazing-exclusion, can effectively change the structure of AMF community. Thus, the Spearman's rank correlation showed Ambisporaceae correlating with high acidity, salinity, and compaction in soil under overgrazing. Although both ecological and phylogenetic knowledge of Ambisporaceae still remain scarce (Oehl et al., 2011), this AMF-family seems to present resistance to drylands environments, being correlated positively with degraded lands (van der Heyde et al., 2017). In contrast, Acaulosporaceae and Glomeraceae communities were associated to SOM, microbial biomass, and enzyme activity under native vegetation or restoration. Interestingly, Acaulosporaceae and Glomeraceae predominate in native ecosystem or under undisturbed areas (Stürmer

et al., 2006) which could explain this association to soil properties in native or preserved ecosystems and reinforce its importance to maintain soil functioning/health. The correlation of AMF groups with SOM may indicate a participation of soil diversity to C-sequestration. Thus, increased SOM and AMF divert should be particularly important, since drylands stored more than 45% of the global terrestrial carbon (Mahmoudi et al., 2021).

5. Conclusions

This study confirms that AMF community in soils from Brazilian semiarid is sensitive to both processes of desertification and restoration. On the other hand, the process of desertification, by overgrazing, contributes to degrade soil chemical, physical, and biological properties, and change the structure, diversity, and composition of AMF community. Also, the grazing-exclusion, as an ecological practice to restore semiarid soils, present the potential in improving soil properties, and recovering the status of AMF community under ongoing climate changes globally. Thus, grazing-exclusion, in long-term, can be a good strategy to restore degraded soils in the Brazilian semiarid. Given the importance of AMF to soil health, future studies should test different AMF species and their interactions with native plant to restored degraded, improving its quality and functioning.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Arthur Prudêncio de A. Pereira reports financial support was provided by National Council for Scientific and Technological Development (CNPq). We confirm that this manuscript has not been published elsewhere and is not under consideration in whole or in part by another journal. All authors approved the manuscript, and they agree to the submission to Microbiological Research. The authors also declare that they have no conflict of interest regarding this study.

Data Availability

No data was used for the research described in the article.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.micres.2022.127161.

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