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ENVIRONMENTAL MICROBIOLOGY - RESEARCH PAPER

Arbuscular mycorrhizal fungi associated with the rhizosphere of an endemic terrestrial bromeliad and a grass in the Brazilian neotropical dry forest

Antonio Marcos Miranda Silva[1] · Henrique Petry Feiler[2] · Gileno Vieira Lacerda-Júnior[3] · Paulo Ivan Fernandes-Júnior[4] · Saulo de Tarso Aidar[4] · Victor Araújo Vieira Prudêncio de Araújo[1] · Filipe Pereira Matteoli[5] · Arthur Prudêncio de Araújo Pereira[6] · Itamar Soares de Melo[3] · Elke Jurandy Bran Nogueira Cardoso[1]

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Abstract

Arbuscular mycorrhizal fungi form symbiotic associations with 80–90% of all known plants, allowing the fungi to acquire plant-synthesized carbon, and confer an increased capacity for nutrient uptake by plants, improving tolerance to abiotic and biotic stresses. We aimed at characterizing the mycorrhizal community in the rhizosphere of *Neoglaziovia variegata* (so-called `caroa`) and *Tripogonella spicata* (so-called resurrection plant), using high-throughput sequencing of the partial 18S rRNA gene. Both plants are currently undergoing a bioprospecting program to find microbes with the potential of helping plants tolerate water stress. Sampling was carried out in the Caatinga biome, a neotropical dry forest, located in northeastern Brazil. Illumina MiSeq sequencing of 37 rhizosphere samples (19 for *N. variegata* and 18 for *T. spicata*) revealed a distinct mycorrhizal community between the studied plants. According to alpha diversity analyses, *T. spicata* showed the highest richness and diversity based on the Observed ASVs and the Shannon index, respectively. On the other hand, *N. variegata* showed higher modularity of the mycorrhizal network compared to *T. spicata*. The four most abundant genera found (higher than 10%) were *Glomus*, *Gigaspora*, *Acaulospora*, and *Scutellospora*, with *Glomus* being the most abundant in both plants. Nonetheless, *Gigaspora*, *Diversispora*, and *Ambispora* were found only in the rhizosphere of *N. variegata*, whilst *Scutellospora*, *Paraglomus*, and *Archaeospora* were exclusive to the rhizosphere of *T. spicata*. Therefore, the community of arbuscular mycorrhizal fungi of the rhizosphere of each plant encompasses a unique composition, structure and modularity, which can differentially assist them in the hostile environment.

Keywords Environmental DNA sequencing · *Tripogon spicatus* · Mycorrhizal symbiosis · Glomeromycota · Mucoromycota · Glomeromycotina

Introduction

Caatinga, the Neotropical dry forests, also referred to as seasonally dry tropical forests (SDTFs), are one of the most threatened tropical forests in the world, with deforestation being the main threat, especially in Brazil, which comprises most of them [1–3]. SDTFs cover extensive areas from Mexico in Central America to Argentina in South America and throughout the Caribbean [4].

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The Brazilian Caatinga biome harbours the largest SDTFs, composed of a shrubland ecosystem that covers 844,453 km^2 and represents 10.1% of the Brazilian territory [5]. According to Teixeira et al. [6], only 1.3% of the Caatinga biome is protected, and conservation actions are urgently needed, as the Caatinga has unique biodiversity patterns. The evolutionary history confined to this biome converged to its uniqueness, presenting plant species restricted to it [7]. Alongside, it is known that a host microbiome co-evolving with endemic species is able to help them survive in a harsh environment [8]. Therefore, the Caatinga biome is a screening hotspot for microbes that may be employed to mitigate abiotic stresses [9–12]. However, little is known about the diversity and community composition of arbuscular mycorrhizal fungi (AMF)

associated with plants in dry forests, especially terrestrial bromeliads and resurrection grass, as revealed by our mini-review (Supplementary Note and Tables S1 and S2).

The mycorrhizal symbiosis plays a key role in maintaining plant growth and, compared to other known symbioses (e.g., nitrogen-fixing bacteria), it is the oldest, originated approximately 450 million years ago. AMF colonize about 80–90% of all plant species, and only very few plant families cannot generate mycorrhiza in symbiosis with AMF, such as *Brassicaceae*, *Chenopodiaceae*, *Cyperaceae* and *Juncaceae* [13]. According to Spatafora et al. [14], AMF have been included in the phylum Mucoromycota and subphylum Glomeromycotina, while, for Tedersoo et al. [15], they have been included in a single phylum, the Glomeromycota, but this has been controversial for years and it still is [16].

In the root system of SDTFs, some investigations have shown the AMF associated with epiphytic bromeliads (belonging to the family *Bromeliaceae*), which is considered one of the most species-rich and ecologically important plant families in the neotropics [17–20]. However, there are no studies on AMF communities associated with the rhizosphere of the terrestrial bromeliad *Neoglaziovia variegata* (Arruda) Mez, endemic to the Caatinga biome, only studies showing its gastroprotective, antibacterial and acaricidal potential [21–23]. Likewise, there are no studies investigating the AMF communities associated with the rhizosphere of *Tripogonella spicata* (Nees) P.M.Peterson & Romasch, the so-called resurrection plant. The term resurrection plant is due to its capacity to survive dehydration to an air-dried state for months, losing most of its cellular water, and quickly resume normal physiological activities after rehydration [24–26]. In addition, other plant species from the families *Myrothamnaceae*, *Selaginellaceae*, *Velloziaceae*, and *Scrophulariaceae* are equally known as resurrection plants [27]. Perhaps, the associated rhizosphere microbiota acts as the downstream agent modulating this upstream response.

Plant-associated AMF can be characterized using various molecular marker regions, such as small subunit rRNA (SSU), large subunit rRNA (LSU), and internal transcribed spacer (ITS), with distinct primer combinations [28]. Nevertheless, each marker region has its own set of advantages and drawbacks which must be considered when selecting a marker for a particular study [29, 30]. Among these markers, the SSU rRNA gene is one of the most widely used in studies related to mycorrhizal ecology [31–35].

Thus, this investigation has pioneered in revealing the arbuscular mycorrhizal fungi composition, structure, and modularity of the rhizosphere of *N. variegata* and *T. spicata,* using high-throughput sequencing of the partial 18S rRNA gene (SSU). Therefore, our study represents a significant contribution in the mycorrhizal ecology, especially in studies with terrestrial bromeliads and resurrection plants.

Materials and methods

Location site and characteristics

The investigation was conducted in the Caatinga biome in the State of Pernambuco located in northeastern Brazil (Fig. 1a and b). Rhizosphere sampling was carried out at the experimental stations of Brazilian Agricultural Research Corporation (Embrapa Semi-arid; 9° 03′ 58" S, 40 ° 19′ 14"W and 8° 48′ 11.6"S, 40° 14′ 48.4"W), located in the State of Pernambuco, Brazil (Fig. 1c). The climate is BSwh' according to the Köppen–Geiger classification, with an annual average temperature of 26.3 °C and rainfall of 577 mm. The soil is classified as red–yellow Ultisol [36], corresponding to Argissolo Vermelho-Amarelo in the Brazilian Soil Classification System [37] (Fig. 1d). Both experimental stations share the same soil physical and chemical characteristics as shown in Table 1. More information about those sampling areas can be found in [10, 12, 38]. Moro et al. [39] and Moro et al. [40] presented detailed information about the phytogeographical patterns of the Caatinga biome.

Sampling of the rhizosphere

Forty-eight native plants were studied, among which 24 rhizosphere samples were from *N. variegata* (Fig. 1e) and the other 24 rhizosphere samples from *T. spicata* (Fig. 1f) rhizosphere. Sampling was done in October 2018, in the late dry season. The rhizosphere soil was sampled according to Batista et al. [41]. Briefly, plants were removed from the soil using a shovel, followed by manual agitation and considering the aggregates adhered to the roots as rhizosphere soil. The samples were stored at the Embrapa Semi-arid until shipment to the University of São Paulo, in the municipality of Piracicaba, in the State of São Paulo, Brazil (22° 42′ 35" S, 47° 38′ 05" W), where they were stored at − 80 °C prior to molecular analysis. We used composite rhizosphere samples for the physicochemical soil characterization (Table 1).

Soil rhizosphere DNA extraction

Samples of freeze-dried soil (400 mg) were used for DNA extraction with the PowerSoil DNA Isolation kit (QIAGEN Inc., Valencia, CA, USA), according to the manufacturer. DNA concentrations were determined using the Qubit quantification platform with Quant-iT dsDNA BR Assay Kit (Invitrogen, Carlsbad, CA, USA). DNA quality was verified by electrophoresis in 1% agarose gel using tris–acetate-EDTA buffer (1 × TAE), 5 µl extracted DNA

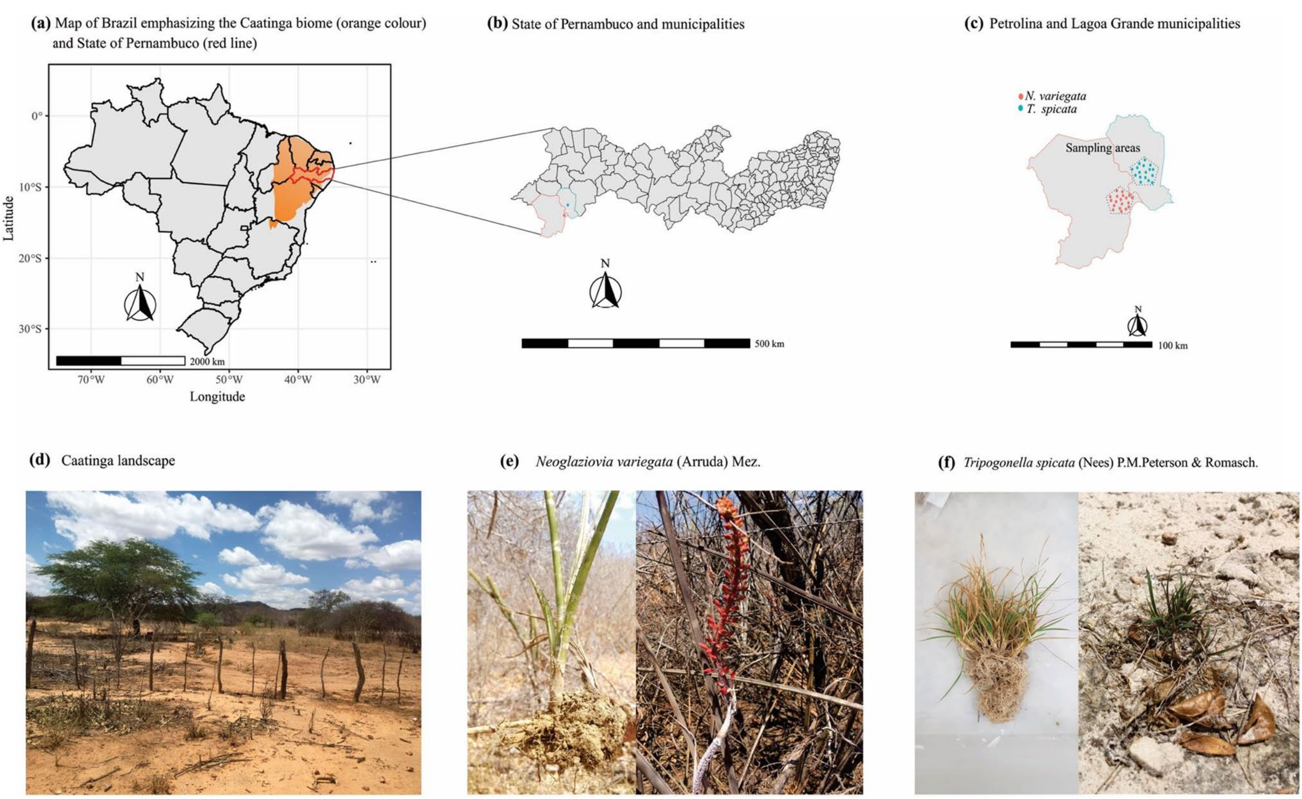

Fig. 1 Location of the sampling area and distribution of the Caatinga biome in Brazil, **a** map of the State of Pernambuco in Brazil, showing its municipalities, highlighting the municipalities where the sampling was carried out, **b** map of Petrolina and Lagoa Grande municipalities and sampling points, **c** a common landscape of the Caatinga biome during late dry season showing some *Mimosa tenuiflora* trees, **d** sampled plant *Neoglaziovia variegata* (Arruda) Mez., a bromeliad so-called "caroa", **e** sampled plant *Tripogonella spicata* (Nees) P.M. Peterson & Romasch., a grass so-called the resurrection plant, **f**

and 1 µl GelRed™ stained (0.5 µg mL^{-1}), followed by visualization on a UV transilluminator (DNR – Bio Imaging Systems/MiniBis Pro).

Arbuscular mycorrhizal fungi sequencing and data analyses

Only 19 samples of *N. variegata* and 18 samples of *T. spicata* presented enough DNA concentration and quality for sequencing. Sequencing was carried out using the MiSeq platform (250 bp paired-end) provided by the NGS Soluções Genômicas Facility (Piracicaba, São Paulo, Brazil), and libraries built using a 500-cycle V2 Sequencing kit. A nested PCR (polymerase chain reaction) was used to cover part of the 18S rRNA, a small subunit (SSU) ribosomal RNA gene [28]. For the first amplification step, the forward primer NS31 (5'-TTGGAGGGCAAGTCTGGT GCC-3') [42] and the reverse primer AML2 (5'-GAACCC AAACACTTTGGTTTCC-3') [43] were used. Whilst for the second amplification step were used the forward primer AMV4. 5NF (5'- AAGCTCGTAGTTGAATTTCG -3') and the reverse primer AMDGR (5'- CCCAACTATCCCTAT TAATCAT -3') [44]. According to van Geel et al. [28], these primers are widely used in surveys of AMF communities due to their higher complementary specificity (Fig. S1). Sequencing data were processed using QIIME2 [45] classify-sklearn command with sequences aligned against virtual taxa (VTs) using the *MaarjAM* database [46] followed by performing basic local alignment search tool (BLAST) searches against NCBI's non-redundant nucleotide database [47] of all amplicon sequence variants (ASVs) obtained, and then filtering the top 10 best hits. We provide both the classification obtained by *MaarJAM* with the best hit (Table S3) and a table containing the top 10 hits for each ASVs (Table S4). Our approach was similar to that of Edlinger et al. [35], who also employed BLAST searches to enhance the classification obtained from the *MaarjAM* database. The workflow used in our investigation is depicted in Fig. 2. Briefly, raw reads were demultiplexed, quality-filtered, joined, and grouped within ASVs using DADA2 [48], followed by BLAST search against VT in the *MaarjAM* database. Subsequently, the taxonomic, diversity, and abundance analyses were performed. Sequences were

Table 1 Chemical characterization of rhizosphere soil associated with Caatinga plants

RhizospherePlant	pH	SOM	P	S	K	Ca	Mg	B	Cu	Mn	Zn	Na	Al	H + Al	SB	CEC	Sand	Silt	Clay
	$CaCl_2$	g kg^{-1}	mg kg^{-1}		mmolc kg^{-1}			mg kg^{-1}					mmolc kg^{-1}				g kg^{-1}		
N. variegata	5.1a	11.0a	<3.0a	<5.0a	1.2a	11.0a	3.0a	0.3a	0.5a	10.5a	1.3a	9.0a	<0.02a	15.0a	15.2a	30.2a	726.0	226.0	49.0
T. spicata	5.4a	10.0a	5.0a	6.0a	2.5a	6.0a	3.0a	0.3a	0.3a	4.3a	0.7a	15.0a	<0.02a	12.0a	11.5a	23.5a			

pH: active acidity measured in 0.01 mol L^{-1} $CaCl_2$; SOM: soil organic matter measured by colorimetric method; P: phosphorus measured with anion exchange resin; S: sulphur measured with 0.01 mol L^{-1} calcium phosphate; K, Ca and Mg: potassium, calcium and magnesium measured in anion exchange resin; B: boron measured with hot water; Cu, Fe, Mn, Zn and Na: copper, iron, manganese, zinc and sodium measured with diethylenetriaminepentacetic acid (DTPA); Al: Aluminum measured in 1 mol L^{-1} KCl^{1}; H + Al: potential acidity in SMP buffer; SB: sum of bases (Ca, Mg and K); CEC: cation exchange capacity; $mmol_c$ kg^{-1}: millimoles of charge per kilogram of soil according to SI unit (International Standard of Units). Letters indicate differences between the chemical attributes of plant rhizospheres by Tukey's test at 5% ($p \leq 0.05$)

submitted to the NCBI and Sequence Read Archive (SRA) database with the BioProject PRJNA861682.

Alpha and beta diversity analyses were performed following Silva et al. [49]. Briefly, alpha diversity refers to organismal diversity within a sample, whereas beta diversity refers to organismal diversity between two or more samples [50]. The alpha diversity metrics used here were Shannon index (ASV diversity), Observed ASVs, Chao1 (ASV richness), and Faith's phylogenetic diversity (Faith PD). Differences were detected by Wilcoxon signed rank test, a non-parametric test [51]. Changes in beta diversity between the sampled plants were tested using principal coordinate analysis (PCoA) with Bray–Curtis distances coupled with a permutational analysis of variance (PERMANOVA, 999 permutations). We used a network analysis based on the Newman-Girvan algorithm for determining edge betweenness to detect mycorrhizal communities in the rhizosphere of the sampled plant species. For this method, high-betweenness edges are removed sequentially (recalculating at each step) and the best partitioning of the network is selected [52]. We used RNAseq pipeline edgeR [53] and limma voom [54], available from the Bioconductor project [55], to investigate differential abundances, revealing which mycorrhizal taxonomic groups were more or less predominant between sampled plants based on the log-fold changes (logFC). For these analyses, we considered the Benjamini–Hochberg false discovery rate correction (FDR < 0.10) [56].

For clarity, relative abundance considered the fraction of the taxa observed in the feature table relative to the sum of all taxa in the sample, and therefore varying between 0 and 100%. Whilst differential abundance considered the abundant taxa between two or more environments (in our case the rhizosphere of *N.variegata* and *T. spicata*) based on the log-fold changes [57]. Relative and differential taxonomic abundance results were presented at the order and genus level due to the wide use of the scientific community that investigates microbial communities with amplicon sequencing [58].

Results

Overview of amplicon sequencing

The total number of 527,246 high quality mycorrhizal sequences was generated by Illumina Miseq sequencing, with an average of 14,249.89 sequences per sample (Table S5). The rarefaction curves showed an adequate sequencing depth (Fig. S2a). Mycorrhizal sequences were grouped into 175 ASV. *Neoglaziovia variegata* (Arruda) Mez and *Tripogonella spicata* (Nees) P.M.Peterson & Romasch shared only four mycorrhizal ASVs (i.e., about 3%) (Fig. S2b).

Reads Obtainment

Sequencing raw data
Forward and reverse files
fastq.gz (final file type)

Pre-processing and sequence quality control

Importing data into QIIME 2
qiime tools import
'SampleData[PairedEndSequencesWithQuality]'
.qza (final file type)

Visualization of quality plots
qiime demux summarize
.qzv (final file type)

Denoise and dereplicate paired-end sequences
--p-trim-left-f 20 --p-trunc-len-f 0
--p-trim-left-r 22 --p-trunc-len-r 200
.qza (final file type)

Visualization of the quality summary
qiime metadata tabulate
qiime feature-table tabulate-seqs
qiime feature-table summarize
.qzv (final file type)

Database

Importing reference database
MaarjAM database (Öpik et al., 2010)
.fna (final file type)

Training classifier

Preparing classifier (sequence)
qiime tools import
'FeatureData[Sequence]'
.qza (final file type)

Preparing classifier (taxonomy)
qiime tools import
'FeatureData[Taxonomy]'
.qza (final file type)

Applying Naive Bayes algorithms
qiime feature-classifier
fit-classifier-naive-bayes
.qza (final file type)

Taxonomic classification

Assigning taxonomy
qiime feature-classifier classify-sklearn
.qza (final file type)

Outputs

Exporting data
qiime tools export
ASV table.qza
taxonomy table.qza
phylo-unrooted-tree.nwk

Blast

BLAST search on NCBI
ASVs subjected to a:
Basic local alignment search tool (BLAST)
Top 10 hits for each ASVs (Table S4.xlsx)

Fig. 2 Workflow of the pipeline used to analyse the AMF amplicon sequencing using nested PCR with NS31and AML2 as the first reaction and AMV4.5NF and AMDGR primers as the second round of PCR reactions

Differential abundance analyses between mycorrhizal communities

Regardless of the taxa level, the mycorrhizal composition and the specific taxa abundance shifted between the two plant species (*N. variegata* and *T. spicata*).

At the order level for *N. variegata,* the mycorrhizal composition was summarized by the predominance of Glomerales (71%), Diversisporales (21%), and Archaeosporales (8%), whilst for *T. spicata* the predominance was based on Glomerales (76%), Diversisporales (18%), and Paraglomerales (6%) (Fig. 3a). At the genus level for *N. variegata*, the mycorrhizal composition was composed of *Glomus* (68%), *Gigaspora* (11%), *Ambispora* (8%), *Diversispora* (7%), *Claroideoglomus* (3%), *Acaulospora* (2%), and *Scutellospora* (1%), while for *T. spicata*

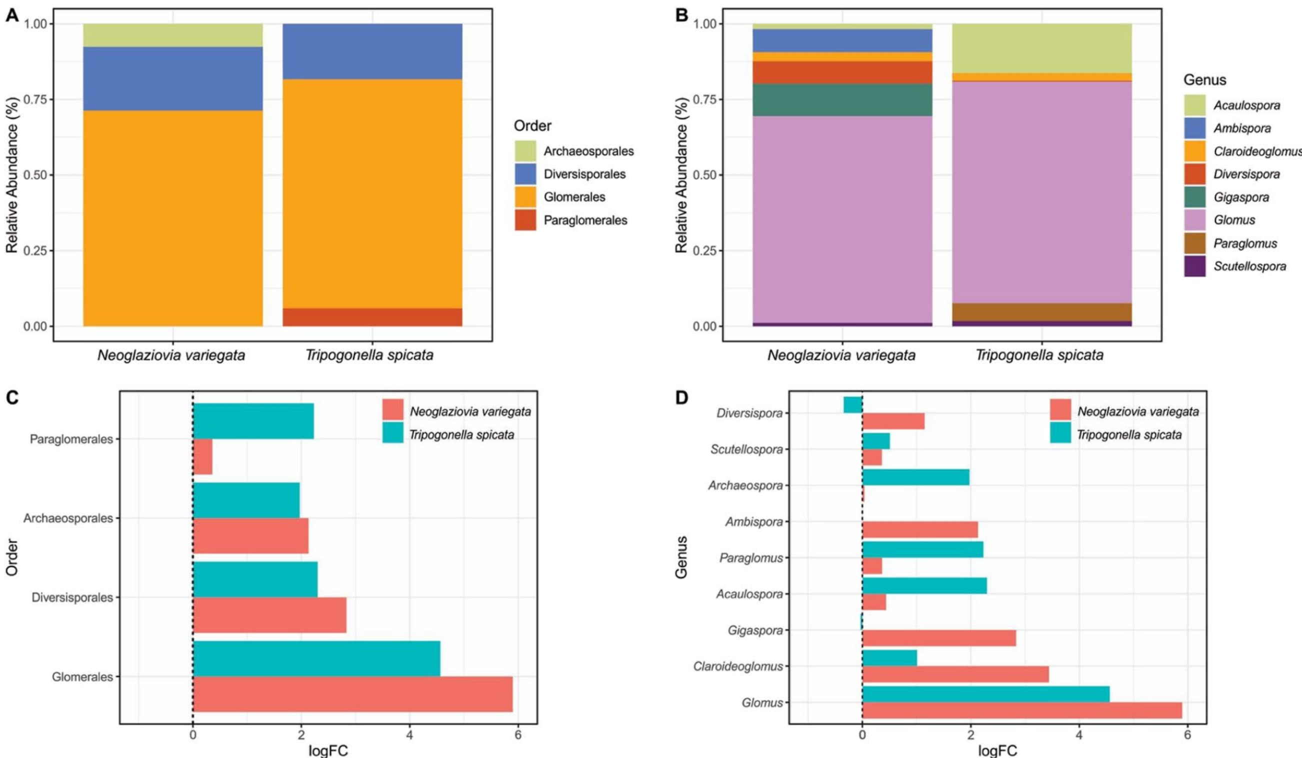

Fig. 3 Community composition of arbuscular mycorrhizal fungi (AMF) in two plants sampled in the Caatinga biome based on the relative abundance of order, **a** and genus, **b** taxa. Differential abundance analysis considering order, **c** and genus, **d** taxa of the AMF community for the plants with the results expressed by log-fold changes (logFC). logFC was calculated by subtracting the base mean counts of log ratios of each microbial taxa present at *Neoglaziovia variegata* from microbial taxa present at *Tripogonella spicata*. Analysis was performed using the edgeR and limma voom packages available from the Bioconductor project in R environment

the mycorrhizal composition was based on the presence of *Glomus* (73%), *Acaulospora* (16%), *Paraglomus* (6%), *Claroideoglomus* (3%), *Scutellospora* (1.5%), and *Diversispora* (0.5%) (Fig. 3b).

Overall, for *N. variegata,* the most predominant orders were Glomerales, Diversisporales, and Archaeosporales, while for *T. spicata* the most predominant order was Paraglomerales (Fig. 3c), according to the differential abundance analysis. At the genus level, substantial predominance was detected in *N. variegata* for the genera *Glomus*, *Claroideoglomus*, and *Gigaspora*, and *Ambispora*. Equally, substantial predominance was observed in *T. spicata* for the genera *Acaulospora*, *Scutellospora, Paraglomus*, and *Archaeospora*. There was a lower predominance of *Diversispora* in *T. spicata*, whereas in *N. variegata* this genus was the most predominant (Fig. 3d).

Alpha and beta diversity, and community detection

The alpha-diversity of the mycorrhizal community differed significantly according to the plants, with the highest Shannon diversity ($p < 0.05$), observed ASV ($p < 0.01$), Chao1 ($p < 0.01$), and Faith PD ($p < 0.05$) being found in the rhizosphere of *T. spicata* (Fig. 4). Likewise, beta-diversity showed higher dissimilarities of the mycorrhizal community between the plants based on Bray–Curtis distance, which was confirmed by the PERMANOVA ($p < 0.001$) (Fig. 5a, Table S6).

According to the algorithm to perform community detection based on edge betweenness (Newman-Girvan), we noticed a different pattern of sample clustering within the same plant, with the most pronounced differentiation in *N. variegata*. Overall, four different mycorrhizal groups of ASVs were detected within *N. variegata*, in which each one was composed of at least three samples. Higher modularity was found for *N. variegata* (0.240331), reflecting dense connections within groups of ASVs and sparse connections across communities (Fig. 5b). For *T. spicata* we observed a prevalence of only one group of ASV and lower modularity (0.005478) (Fig. 5c). In other words, the mycorrhizal community of the rhizosphere of *T. spicata* has strong similarity, clustering in the same module class, while the rhizosphere of *N. variegata* comprises different mycorrhizal communities strongly dissimilar to each other as evidenced by their distinct module classes.

Fig. 4 Alpha diversity indices considering the two plants sampled in the Caatinga biome, expressed by Shannon diversity, **a** observed ASV [amplicon sequence variant], **b** Chao1, **c** and Faith's phylogenetic diversity, **d**. Statistical differences are denoted as *($p < 0.05$) and **($p < 0.01$) by the Wilcoxon test. Heavy horizontal line within a box represents the median, the box represents the interquartile range, and whiskers indicate the variability outside the upper and lower quartiles

Discussion

Unravelling the composition of the mycorrhizal community associated with the rhizosphere of plants of hostile environments can be a step forward in field investigations of mycorrhizal ecology. Our investigation is the beginning of an ongoing project and, therefore, some limitations and future perspectives can be pointed out. Firstly, we must consider that the entire AMF community may not have been assessed due to limitations, when using the molecular

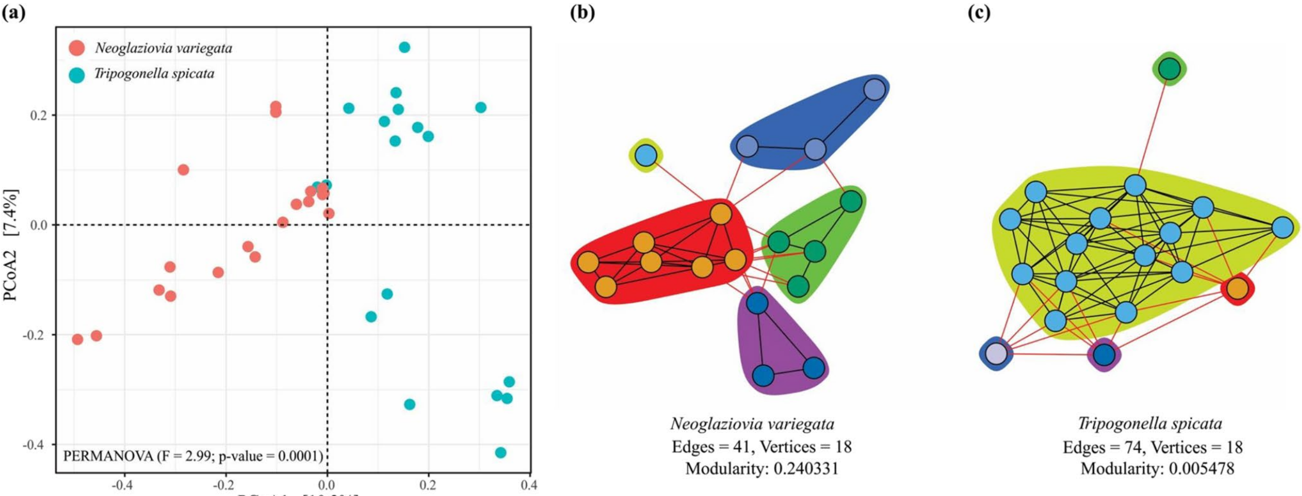

Fig. 5 Beta diversity expressed by principal coordinate analysis (PCoA) using Bray–Curtis distances, depicting mycorrhizal data from two plants sampled in the Caatinga biome, **a**. Network analysis for mycorrhizal community detection within *N. variegata*, **b** and *T. spicata*, **c** based on edge betweenness (Newman-Girvan). Each node represents the samples and colours represent the different mycorrhizal communities detected. Same colours between panels **b** and **c** represent similar mycorrhizal community

approach, i.e., biases from DNA extraction to low accuracy of the DNA reference databases [29, 30, 59, 60]. For example, the use of small subunit rRNA may not provide sufficient variability to fully resolve AMF species, as it is a slow-evolving gene, although it is still appropriate for higher phylogenetic ranks [61–63]. Furthermore, the bioinformatics pipeline used for analyzing the data can be subject to constant changes and improvements [31, 33, 46, 64, 65], as efforts in the mycology field of AMF phylogeny and taxonomy continue to increase, leading to many discoveries or reassigning of new genera and species, especially in the most abundant families in soil such as Glomeracea [66, 67]. Secondly, it is important to consider that precipitation and temperature regulate the composition and diversity of the AMF community [68–70]. Considering that our sampling strategy was done at the end of the dry season, we might have different results for the rainy season.

Undoubtedly, these issues do not discredit our investigations or the role of arbuscular mycorrhizal fungi (AMF) in providing essential ecosystem services [71]. Even though some authors disbelieve the necessity of considering the mycorrhizal community for the plant health under harsh environments or when managing crops in agriculture [72, 73], we firmly advocate that these ancient symbiotic groups are crucial for the soil–plant sustainability. We go further and argue that there are keystone taxa of AMF, which, combined with the physiological plant traits, are essential to help plants to overcome drought events. Notwithstanding, it is reassured that AMF is among the most ubiquitous plant mutualists that improve plant growth and yield by facilitating the uptake of phosphorus and water, besides other nutrients [74, 75].

In our investigation, the lack of information about the mycorrhizal ecology of the sampled plants was detected by our mini-review (Table S1 and Table S2), especially when they are considered as a host of microbes that can help crop plants to tolerate shortages of water in the soil. Overall, the AMF community found in the rhizosphere of *N. variegata* differs from the rhizosphere of *T. spicata* and this was reassured by the difference in network modularity observed. Briefly, modularity is a measure of network structure, where high modularity indicates that the network has dense connections within certain groups of nodes and sparse connections between the other groups [76].

Although the plants were sampled at two different sites, we observed that the soil chemical and physical characterization of both sites was similar, suggesting that the distinct mycorrhizal composition may be related to the host phylogeny rather than the sampled site (Table 1). Indeed, the two plants studied are not phylogenetically related and therefore may harbour a different AMF community and exploit their soil resources in different ways [77–79].

Although the AMF community differed between the rhizosphere of the plants species, more than 90% of the mycorrhizal community for both plants was composed of the order Glomerales and Diversisporales. Likewise, Leroy et al. [20], investigating the taxonomic and functional diversity of root-associated fungi in bromeliads (none of them being *N. variegata*), found the order Glomerales to be dominant, and *Rhizophagus*, *Funneliformis* and *Glomus* to be the main genera, while here for our bromeliad, the main genera found were *Glomus*, *Gigaspora*, *Ambispora* and *Diversispora*. These taxonomic differences may be expected, since

life forms, nutritional modes and environmental traits drive the root fungal community structure in bromeliads.

On the other hand, we can also find similar results with a distinct host, although it is known that the partner specificity in mycorrhizal symbiosis occurs at the level of ecological groups, rather than at the species level [80]. For example, dos Passos et al. [79], evaluating the composition of the AMF community of soil samples from the rhizosphere of *Mimosa tenuiflora* (legume), found the order Glomerales to be dominant and argued that some taxa of this order are recognised for colonising plants first, allowing their establishment in diverse environments. Several studies using native plants of the Caatinga have shown similar results [70, 81–84]. In addition, Davison et al. [32] have documented the worldwide predominance of Glomerales across a range of local environmental conditions and spatial configurations.

We observed that *T. spicata,* besides the highest diversity indices and predominance of different taxa, presented a well-structured AMF group according to the algorithm for community detection (i.e., lower modularity), and we raised the following questions: (1) could this structuring (presence of only a dense ASV group) result in benefits for the plant? (2) could the predominant taxa observed here (*Acaulospora*, *Scutellospora*, *Paraglomus*, and *Archaeospora*) play a crucial role in the desiccation tolerance trait of *T. spicata*?. Additionally, (3) could the structure of the AMF group observed in the network and the predominant taxa identified (*Glomus, Claroideoglomus, Gigaspora,* and *Diversispora*) contribute to the establishment of *N. variegata* in the harsh environment of the Caatinga biome?.

Indeed, there is evidence that certain species within the aforementioned genera can significantly impact a plant's response to abiotic stresses, such as saline stress and water shortage in the soil [85, 86]. This is due in part to their intrinsic stress-tolerant character and widespread geographical distribution, allowing them to adapt to adverse environmental conditions [87–90]. For example, Oliveira-Filho et al. [86] demonstrated that inoculating *Carica papaia* L. plants with *Scutellospora heterogama* (now known as *Dentiscutata heterogama*), *Gigaspora candida,* and *Acaulospora scrobiculata* increased the plant's tolerance to salt by enhancing leaf hydration and reducing biomembrane damage, with inoculation of *D. heterogama* and *G. candida* standing out. This finding is particularly interesting given that many soils in the Caatinga biome, where the plants studied were sampled, have high salt content [91].

Furthermore, Moreira et al. [85] found that *Coffea arabica* L. plants inoculated with *Rhizophagus clarus*, *Claroideoglomus etunicatum*, and *Dentiscutata heterogama* exhibited increased tolerance to water stress of up to 40% of field capacity. This may be due to the ability of AMF to mitigate the effects of drought stress by enhancing water transport, increasing the production of plant osmolytes, stomatal density, and gene expression related to plant hormones [90]. Other investigations have showed the positive effect of *Acaulospora* sp. on promoting the plant-growth response under water stress in soil, whilst little is known about how *Paraglomus* sp. and *Archaeospora* sp. can overcome the negative effects of drought in plants [92, 93].

Comparing the plants, we noticed a different mycorrhizal predominance for *N. variegata* for the genera *Claroideoglomus* (order Glomerales), *Gigaspora* (order Diversisporales), and *Ambispora* (order Archaeosporales). Among these genera, *Claroideoglomus* sp. has been the most studied in the Caatinga and has been shown to be promising to increase shoot dry weight of native plants due to its rapid establishment and symbiotic interactions with the host [68, 87]. Therefore, considering these results combined with the community detection algorithm for *N. variegata*, the C-R-S framework proposed by Chagnon et al. [87] fits very well. Briefly, it classifies AMF species into three functional groups, namely, competitor (C), ruderal (R), and stress tolerating (S). The aforementioned authors argued that species belonging to the genus *Gigaspora* sp. have competitive traits (higher soil hyphae density and stronger carbon-sink strength), and *Claroideoglomus* sp. have ruderal traits (higher growth rate and more efficient hyphae healing). *Ambispora* sp. appears to exhibit stress tolerating traits, such as low growth rate and long-lived mycelium [87, 94]. However, this was not completely true for *T. spicata*, given the lower modularity and predominance of other taxa observed. As the first investigation to describe the mycorrhizal community of the rhizosphere of these plants, we argue that studies evaluating the mycorrhizal community in the plant roots are necessary to understand the benefits of the rhizosphere community in the plant performance.

Conclusions

We concluded that, although arbuscular mycorrhizal communities found in the rhizosphere differ between *N. variegata* and *T. spicata*, both of them have *Glomus* sp. as the most abundant genus. Furthermore, we argue that the genera *Gigaspora*, *Diversispora*, *Ambispora*, *Scutellospora*, *Paraglomus*, and *Archaeospora* may be playing a key role for both plant species. Considering that the sampled sites shared the same soil chemical and physical traits, we concluded that the host species was the main driver for mycorrhizal diversity, richness and modularity in the rhizosphere.

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Data Availability The authors declare that the data will be available upon request.

Declarations

Competing interests The authors declare no competing interests.

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Authors and Affiliations

Antonio Marcos Miranda Silva[1] · Henrique Petry Feiler[2] · Gileno Vieira Lacerda-Júnior[3] · Paulo Ivan Fernandes-Júnior[4] · Saulo de Tarso Aidar[4] · Victor Araújo Vieira Prudêncio de Araújo[1] · Filipe Pereira Matteoli[5] · Arthur Prudêncio de Araújo Pereira[6] · Itamar Soares de Melo[3] · Elke Jurandy Bran Nogueira Cardoso[1]

✉ Antonio Marcos Miranda Silva
antoniomarcos@usp.br

Henrique Petry Feiler
feiler.1@gmail.com

Gileno Vieira Lacerda-Júnior
gilenolacerdajr@gmail.com

Paulo Ivan Fernandes-Júnior
paulo.ivan@embrapa.br

Saulo de Tarso Aidar
saulo.aidar@empraba.br

Victor Araújo Vieira Prudêncio de Araújo
victorlucas395@usp.br

Filipe Pereira Matteoli
matteolifilipe@gmail.com

Arthur Prudêncio de Araújo Pereira
arthur.prudencio@ufc.br

Itamar Soares de Melo
itamar.melo@empraba.br

Elke Jurandy Bran Nogueira Cardoso
ejbncard@usp.br

1 “Luiz de Queiroz” College of Agriculture, Soil Science Department, University of São Paulo, Piracicaba, São Paulo 13418-900, Brazil

2 Department of Agronomy, Purdue University, West Lafayette, IN 47906, USA

3 Brazilian Agricultural Research Corporation, Embrapa Meio Ambiente, Jaguariúna, São Paulo 13918-110, Brazil

4 Brazilian Agricultural Research Corporation, Embrapa Semiárido, Petrolina, , Pernambuco 56302-970, Brazil

5 Faculty of Sciences, Department of Biological Sciences, Laboratory of Microbial Bioinformatics, São Paulo State University, Bauru 17033-360, Brazil

6 Soil Science Department, Federal University of Ceará, Ceará 60356-000, Brazil