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# High diversity of arbuscular mycorrhizal fungi in natural and anthropized sites of a Brazilian tropical dry forest (Caatinga)

Frederico Marinho [a], Fritz Oehl [b], Iolanda Ramalho da Silva [c], Danny Coyne [d], Joana Suassuna da Nóbrega Veras [c], Leonor Costa Maia [c, *]

[a] Programa de Pós-Graduação em Ciências Biológicas, Universidade Federal de Pernambuco, Av. da Engenharia, s/n, Cidade Universitária, CEP 50740-600, Recife, PE, Brazil
[b] Agroscope, Competence Division for Plants and Plant Products, Ecotoxicology, Schloss 1, CH-8820, Wädenswil, Switzerland
[c] Programa de Pós-Graduação em Biologia de Fungos, Universidade Federal de Pernambuco, Av. da Engenharia, s/n, Cidade Universitária, CEP 50740-600, Recife, PE, Brazil
[d] International Institute of Tropical Agriculture (IITA), Oyo Road, Ibadan, Nigeria

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ABSTRACT

Arbuscular mycorrhizal fungi (AMF) establish symbiotic associations with higher plants, which support the establishment and maintenance of plant communities across a range of environments, including those adversely affected by anthropogenic activity as well as natural sites. This study aimed at determining the diversity and distribution of AMF in areas of the tropical semi-arid region of Caatinga, Brazil, and compare areas in a naturally preserved state with anthropized sites. We characterized AMF communities in soil samples (n = 108), based on morphological taxonomy, at three sampling occasions and from six areas (typical Caatinga, extremely sandy Caatinga, stony Caatinga, rocky Caatinga, and two typical Caatinga areas that had been modified by human activities), at the National Park of Catimbau, Northeast Brazil. Eighty AMF species were recorded, with *Glomus* and *Acaulospora* predominating at all sites. There were significant differences in the composition of AMF communities between natural and anthropized sites, and among sampling occasions. Habitat-types also influenced AMF communities in Caatinga. Extensive tropical dry forest areas, such as the Catimbau National Park possess distinct niches, which maintain diverse AMF communities that are determined by anthropogenic activities, as well as vegetation types and environmental conditions.



## 1. Introduction

Arbuscular mycorrhizas (AM) are the most widespread symbiotic associations between plant and fungi on Earth (Lekberg et al., 2015; Brundrett and Tedersoo, 2018). The majority of plant groups, including Bryophytes, Ferns, Lycophytes, Gymno- and Angiosperms, establish associations with AM fungi (AMF), phylum Glomeromycota, represented by ca. 300 species (Spatafora et al., 2016; MYCOBANK, 1997; Tedersoo et al., 2018; Turrini et al., 2018).

AMF associations offer numerous advantages for plants, including increased nutrient and water assimilation and uptake, which are indispensable for the establishment and stability of plant communities (Smith and Read, 2008). Thus, the AMF actively influence plant diversity and productivity (van der Heijden et al., 2008, 2015). Especially in semi-arid and arid regions and in soils of low fertility, plants become more dependent on mycorrhizal symbiosis to tolerate water stress and nutrient deficiencies (Frosi et al., 2016). For these reasons, non-mycorrhizal plant species tend to be exceptions in semi-arid ecosystems (Maia et al., 2010).

Extending over an area of 912,000 km$^2$, the Caatinga in Brazil is among the worlds valued area of drylands, which sustains a considerable species richness including a vast range of unique plant lineages (Silva et al., 2017). This biological diversity is influenced by climate, topography, and geological characteristics (Sampaio, 1995: Moro et al., 2016). Although interest in the conservation of the biodiversity of Caatinga has intensified during the 21st century, just 7.8% of the area is protected by law (Pacheco et al., 2018). Consequently, this Brazilian tropical dry forest domain is subject to exploitation and is currently among the domains most modified by human activity, for agricultural and forestry purposes. This has

* Corresponding author.
*E-mail address:* leonorcmaia@pq.cnpq.br (L.C. Maia).

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caused irreversible losses to biodiversity, soil cover and a profound decrease in edaphic fertility, with 80% of the Caatinga estimated to be in a vulnerable state and 62% in danger of desertification (Drumond et al., 2003; Sampaio and Batista, 2003), requiring special protection and scientific attention (Tabarelli and Vicente, 2003). Within the Caatinga, the Catimbau National Park is probably the most protected area, located in Pernambuco, Northeast Brazil (Jesus et al., 2006; Rito et al., 2017).

Although a number of ecological studies have been undertaken in the Caatinga (e.g. Mergulhão et al., 2010; Pagano et al., 2013; Silva et al., 2014; Pontes et al., 2017a) none have evaluated how soil AMF community composition varies in vegetation between unaffected natural and anthropized areas or among different habitat-types. In addition, AMF communities are mainly structured according to vegetation and soil type and so their assessment in the Caatinga will help to determine fundamental information regarding the ecology of Glomeromycotina communities, because in the Caatinga the same vegetation can establish itself on different types of soils (such as extremely sandy, stony and rocky soils).

National Parks such as Catimbau are vital repositories for biological conservation, but our understanding of the distribution of AMF species in these protected areas remains scarce (Turrini et al., 2010; Velázquez et al., 2013; Rodríguez-Echeverría et al., 2017). In the current study, we assessed the soil AMF communities from a variety of natural habitat types under both natural and anthropogenic disturbed conditions, at different times of the year in a semi-arid zone of the Catimbau National Park.

We hypothesized that AMF assemblages vary between natural and anthropogenic disturbed sites and that the diversity of these fungi will be lower in the anthropized environments. We also expected to register AMF community structure variation between habitat-types, which have different physiognomies and soil attributes. The results of this study will contribute to clarifying whether human disturbance to these semi-arid environments affects AMF assemblages, whether habitats with similar climatic conditions harbor different AMF assemblages and whether these assemblages are dependent upon the time of the year.

## 2. Materials and methods

### 2.1. Study area

The National Park of Catimbau is located in the center of Pernambuco State, in the micro-region of the Ipanema Valley, within the counties of Buíque, Tupanatinga and Ibimirim (MMA, 2002). The climate is tropical semi-arid classified as BShw, according to Köppen (Kottek et al., 2006), with annual rainfall between 650 and 1,100 mm and mean annual temperatures approximately 25 °C.

Six study sites were selected to each represent different phytophysiognomies: (a) an extremely sandy Caatinga, which has xerophytic vegetation (Supplementary Fig. 1A), dominated by spiny shrubs and bushes in soils of very high sand content ('*Trilha do Cânion*', 08°31′55.8″S; 037°15′06.2″W); (b) a Caatinga *stricto sensu* (typical Caatinga), with xerophytic vegetation (Supplementary Fig. 1B), dominated by spiny shrubs and bushes ('*Zé Bezerra*', 08°30′48.3″S; 037°14′57.8″W); (c) Carrasco, defined as non-spiny (spine-less Caatinga) with xerophytic vegetation (Supplementary Fig. 1C), ('*Serrinha*', 08°31′29.4″S; 037°14′17.3″W); (d) rocky Caatinga (Supplementary Fig. 1D), developed on rocks with extremely shallow, patchy soils ('*Serra Branca*', 08°32′25.9″S; 037°15′02″W); (e) anthropized Caatinga *stricto sensu* (Anthropogenic I - Supplementary Fig. 1E), deforested for cattle pastures ('*Pedra do Cachorro*', 08°34′25.8″S; 037°15′07.6″W); (f) a second anthropized Caatinga *stricto sensu* (Anthropogenic II - Supplementary Fig. 1F), used as goat pasture ('*Açude Velho*', 08°29′51″S; 037°19′58″W). The first five sites (a, b, c, d and e) are located in the county of Buíque and (f) in Tupanatinga.

### 2.2. Soil sampling

Soils were sampled on three occasions during the dry season: May 2012, September 2012 and March 2013 (sampling depth 0–20 cm). At each site, six field plot replicates of 1,000 $m^2$ were established within 10 m distance of each other. In each of these six plots, the six replicate samples were removed and mixed (~5 kg of soil per field plot) resulting in 108 sample units (six soil samples x six sites x three sampling times total). Soil samples were used to determine chemical and physical soil parameters, and to quantify, identify and propagate AMF species.

### 2.3. Chemical and physical soil analyses

Soil chemical and physical analyses were undertaken at the "Universidade Federal Rural de Pernambuco – Estação Experimental de Cana-de-Açúcar", in Carpina, Pernambuco, Brazil according to standard methods (Embrapa, 1997; Silva et al., 1998). Soil pH was determined from a soil:water suspension of 1:2.5 v/v. $Ca^{2+}$ and $Mg^{2+}$ contents were determined by atomic absorption; $K^{+}$, $Na^{+}$, P, Cu, Zn, and Mn were extracted using the Mehlich 1 method, with $K^{+}$ and $Na^{+}$ levels determined by flame photometry, P by colorimetry, and Cu, Zn, Mn, and Fe by atomic absorption spectrophotometry. The organic matter (OM) and C contents were determined by potassium dichromate oxidation and titration with ferrous ammonium sulfate. $H^{+}$ and $Al^{3+}$ contents were measured by the calcium acetate method and alkaline titration. SB is the sum of bases, CEC is the cation exchange capacity, V% is the percentage of base saturation, and m% is the percentage of aluminum saturation.

The pipette method was used for the evaluation of the soil texture (fine and coarse sand, silt, and clay). Humidity was determined by the difference between humid and dry soil (oven-dried). The soil density was evaluated by the graduated test tube method, particle density determined using the volumetric flask method, porosity was measured considering the percentage of soil water saturation, and natural clay was evaluated by the densimeter method.

### 2.4. AMF spore extraction

AMF spores were extracted from a 50 g air-dried soil subsample, using the wet-sieving method of Gerdemann and Nicolson (1963) followed by centrifugation in water and in a 50% sucrose solution (Jenkins, 1964 - modified) and quantified using a stereomicroscope at 40x magnification.

### 2.5. Trap cultures

Trap cultures were established to facilitate AMF species identification and to detect those species that were not sporulating at the time of sampling. Traps were carried out with a composite sample combining each sampling occasion and site. For each sampling time and site, three trap culture pots of 3 kg substrate were prepared, composed of 1 kg each from two of six replicate samples per site, and 1 kg of sterilized sand) totalling 54 trap culture pots for the study (three pots x six sites x three sampling times total). For each pot the 3 kg substrate was mixed thoroughly. Three host plant species: maize (*Zea mays*), sorghum (*Sorghum bicolor*) and peanut (*Arachis hypogaea*) were sown in each trap culture pot (five seeds of each host per pot). The pots were maintained under greenhouse conditions at 23.5–32.6 °C and air humidity of 80% for two growing

cycles of four months each and manually irrigated every day. After each cycle, AMF spores were extracted from 50 g sub-samples and morphologically identified.

### 2.6. Morphological identification of AMF species

AMF species were identified using spores and sporocarps extracted from field and trap cultures. These structures were fixed on slides with PVLG (polyvinyl alcohol lactoglycerol) and PVLG + Melzer's reagent (1:1 v/v) and observed under a compound microscope, referring to Schenck and Pérez (1990), Błaszkowski (2012) and all original and emended AMF species descriptions available.

### 2.7. Data analysis

For the analysis of the AMF communities, all AMF spores and sporocarps (counted as one unit) from field soil were quantified. The species richness and Shannon index were calculated for each sample. The species richness per habitat was also calculated (based on the first order Jackknife - Jackknife 1) (Magurran, 2004) to compare AMF species richness between habitats. Shannon's diversity index (H′) was calculated using formula H ' = - Σ (Xi/Xo) x log (Xi/Xo), where Xi is the number of spores per 50 g of soil and Xo is the total number of spores for all species (Shannon and Weaver, 1948). For statistical purposes, we used exponential values of Shannon diversity. The Pielou equitability index was obtained by applying the equation: J ' = H'/Log (S), where H′ is the diversity index of Shannon and S is the number of species (Pielou, 1975); and the Margalef index was calculated using the equation: d = S-1/LogN, where S is the number of species, and N is the total number of spores in the sample (Margalef, 1958).

The relative frequency of AMF occurrence (the number of samples in which a given species occurred divided by the total number of samples x 100), and relative AMF abundance (the number of spores of a given species to the total number of spores at the sites) were determined to evaluate the relative distribution and occurrence of AMF species.

One-way permutational multivariate analysis of variance (PERMANOVA), based on the Euclidean distance and 9999 permutations, was used to assess whether the soil chemical parameters differed between anthropized and natural environments, habitat-types, and sampling occasion. One-way rather than two-way PERMANOVA was used because the explanation of the variance in the composition of the soil parameters and AMF communities using both was similar. Before the analysis, soil attribute data were normalized to eliminate differences in the units of each edaphic variable. We also performed the permutational analysis for the multivariate homogeneity of dispersions (PERMDISP2) (Anderson, 2006).

The PERMANOVA, based on Bray–Curtis distances and 9999 permutations, were performed to partition variance in AMF community composition in relation to: (1) environment; (2) habitat-type; (3) sampling occasion. For this analysis, data of relative abundance of AMF were used and performed PERMDISP2 analysis before PERMANOVA. The variation in AMF community composition was visualized using non-metric multidimensional scaling (NMDS), based on Bray-Curtis distance with soil variables fitted to the ordination.

To identify the AMF species associated with each environment, habitat, and sampling occasion, we used indicator species analysis (Dufrene and Legendre, 1997) and considered only those species with an indication value of at least ≥ 25% and $p < 0.05$, as considered by Assis et al. (2016) and Moora et al. (2014).

Diversity and equitability indexes, richness registered and estimated for each sample were calculated using the Primer 6.0 program (Clarke and Gorley, 2006). The accumulation curves were constructed in Excel. Indicator species analysis was performed using PC-ORD version 6.0 (McCune and Mefford, 2011). The data of soil chemical and physical attributes, indexes of Shannon, Margalef, Pielou, species richness, and number of AMF spores were submitted for one-way analysis of variance, considering environment, habitat and sampling occasion, and Tukey test at 5% probability, when appropriate, using *agricolae* function in R. All other analyses were also performed in R: NMDS using function *metaMDS* (Oksanen et al., 2015) with soil attributes fitted to the NMDS ordination using *envfit* function, PERMDISP2 using the function *betadisper*, and PERMANOVA with the function *adonis*. Bonferroni correction was applied to adjust the statistical confidence measures based on the number of tests performed.

## 3. Results

### 3.1. Chemical and physical soil parameters

Soil pH ranged from 4.4 to 4.8 in the four natural Caatinga sites and 5.4–6.5 in the two anthropized Caatinga sites. The percentage of soil OM varied from 0.9 to 8.1 across study sites (Table 1). The soil textures varied from highly sandy (typical, sandy, rocky and anthropogenic Caatinga I), sandy (typical, rocky Caatinga) to loamy sandy with increased levels of silt and clay (spine-less and anthropogenic Caatinga II, Table 2).

Based on PERMANOVA and *post hoc* procedures, the soil composition differed significantly only between anthropized and natural environments ($df = 1$, $F = 21.18$, $R^2 = 0.17$, $P < 0.001$). This result was not attributed to heterogeneity among samples (PERMDISP; $df = 1$, $f = 0.14$, $P = 0.709$). Although the explanation for the variation in soil composition, based on habitat-type, had been high (PERMANOVA, $df = 5$, $F = 38.54$, $R^2 = 0.65$, $P < 0.001$; PERMDISP; $df = 5$, $F = 1.96$, $P = 0.091$), no difference was observed among habitats after Bonferroni correction.

### 3.2. Overall arbuscular mycorrhizal fungal species richness

Eighty separate AMF species were detected in the Catimbau National Park (Supplementary Tables 1) and 26 of which could not unequivocally be identified and presumably represent new undescribed species. The 80 species belong to 19 genera and nine families of the Glomeromycotina (Acaulosporaceae, Ambisporaceae, Dentiscutataceae, Entrophosporaceae, Intraornatosporaceae, Gigasporaceae, Glomeraceae, Racocetraceae and Scutellosporaceae). *Racocetra undulata* was not recovered from the field soil samples, but sporulated in one of the trap cultures.

*Acaulospora* (20 species) and *Glomus* (16) were the most abundant genera detected, followed by *Racocetra* (6), *Claroideoglomus* (5), *Gigaspora* and *Rhizoglomus* (4), *Scutellospora, Dentiscutata* and *Fuscutata* (3), *Ambispora, Entrophospora*, *Cetraspora*, *Dominikia*, *Paradentiscutata* and *Sclerocystis* (2), and *Bulbospora*, *Funneliformis*, *Intraornatospora* and *Orbispora* (1 taxon; Supplementary Table 1).

### 3.3. Frequent, dominant and rare AMF species

*Gigaspora albida, Gigaspora gigantea*, *Gigaspora margarita*, *Glomus glomerulatum*, *Glomus macrocarpum*, *Rhizoglomus intraradices*, *Rhizoglomus microaggregatum,* and *Sclerocystis coremioides* were each identified from all six study sites. The most frequently detected species were *Gi. albida, Gi. gigantea, Gi. margarita, Gl. glomerulatum, Gl. macrocarpum, Rh. intraradices, Rh. microaggregatum, Sc. coremioides*. Although *Acaulospora mellea* was identified at 71% of all field samples, it was not found in the Anthropogenic Caatinga

**Table 1**
Chemical soil parameters in the Caatinga study sites of the Catimbau National Park (NE Brazil).

| Sites | Times | Fe | Cu | Zn | Mn | P | pH | $K^+$ | $Na^+$ | $Al^{3+}$ | $Ca^{2+}$ | $Mg^{2+}$ | $H^+$ | SB | CEC | V | C | m | OM |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | (mg dm−3) | | | | | ($H_2O$) | cmolc $dm^{-3}$ | | | | | | | | (%) | | | |
| Typical Caatinga | 1st | 83.6 ± 2.4 | 0.4 ± 0.1 | 0.7 ± 0.2 | 5.1 ± 0.4 | 4.0 ± 0.8 | 4.4 ± 0.2 | 0.2 ± 0.0 | 0.0 ± 0.0 | 0.5 ± 0.0 | 1.4 ± 0.2 | 0.3 ± 0.0 | 5.9 ± 1.0 | 1.9 ± 0.2 | 8.3 ± 1.0 | 23.6 ± 3.5 | 1.6 ± 0.3 | 19.4 ± 1.5 | 2.7 ± 0.5 |
| Typical Caatinga | 2nd | 103.4 ± 7.1 | 0.0 ± 0.0 | 0.5 ± 0.0 | 4.8 ± 1.5 | 3.7 ± 0.5 | 4.7 ± 0.0 | 0.1 ± 0.0 | 0.1 ± 0.0 | 0.4 ± 0.0 | 1.1 ± 0.4 | 0.3 ± 0.0 | 6.2 ± 1.2 | 1.6 ± 0.4 | 8.2 ± 1.6 | 19.0 ± 2.4 | 1.7 ± 0.4 | 22.5 ± 5.0 | 2.9 ± 0.6 |
| Typical Caatinga | 3rd | 110.7 ± 1.2 | 0.0 ± 0.0 | 0.5 ± 0.0 | 6.1 ± 1.5 | 6.0 ± 2.2 | 4.9 ± 0.0 | 0.2 ± 0.0 | 0.1 ± 0.0 | 0.3 ± 0.0 | 1.3 ± 0.4 | 0.3 ± 0.0 | 6.3 ± 0.7 | 1.9 ± 0.4 | 8.5 ± 1.0 | 21.7 ± 2.3 | 1.5 ± 0.1 | 15.8 ± 4.7 | 2.5 ± 0.1 |
| Sand Caatinga | 1st | 15.3 ± 4.9 | 0.4 ± 0.1 | 1.1 ± 0.1 | 5.5 ± 1.2 | 7.0 ± 1.6 | 4.5 ± 0.0 | 0.1 ± 0.0 | 0.0 ± 0.0 | 0.4 ± 0.0 | 3.0 ± 0.6 | 0.3 ± 0.0 | 11.3 ± 1.8 | 3.4 ± 0.6 | 16.6 ± 0.4 | 22.6 ± 1.7 | 4.7 ± 1.1 | 11.5 ± 2.0 | 8.1 ± 1.9 |
| Sand Caatinga | 2nd | 14.7 ± 2.3 | 0.0 ± 0.0 | 1.0 ± 0.1 | 5.2 ± 1.6 | 5.3 ± 0.5 | 4.4 ± 0.1 | 0.1 ± 0.0 | 0.5 ± 0.0 | 2.5 ± 0.5 | 1.8 ± 0.2 | 0.3 ± 0.0 | 12.1 ± 0.9 | 2.9 ± 0.5 | 15.6 ± 1.4 | 18.7 ± 1.6 | 3.8 ± 0.4 | 16.6 ± 3.2 | 6.6 ± 0.7 |
| Sand Caatinga | 3rd | 46.6 ± 5.0 | 0.0 ± 0.0 | 0.5 ± 0.2 | 2.7 ± 0.8 | 4.0 ± 0.8 | 4.3 ± 0.1 | 0.1 ± 0.0 | 0.0 ± 0.0 | 0.4 ± 0.3 | 1.3 ± 0.4 | 0.3 ± 0.0 | 11.1 ± 3.6 | 1.7 ± 0.4 | 13.4 ± 3.6 | 13.8 ± 5.2 | 2.9 ± 0.8 | 25.9 ± 8.8 | 5.0 ± 1.4 |
| Spine-less | 1st | 130.8 ± 23.4 | 0.5 ± 0.1 | 0.6 ± 0.1 | 2.3 ± 0.4 | 5.3 ± 1.2 | 4.2 ± 0.1 | 0.1 ± 0.0 | 0.3 ± 0.1 | 0.8 ± 0.0 | 0.9 ± 0.1 | 0.3 ± 0.0 | 6.7 ± 0.4 | 1.7 ± 0.0 | 9.1 ± 0.4 | 18.2 ± 0.3 | 2.5 ± 0.3 | 31.6 ± 1.9 | 3.7 ± 0.4 |
| Spine - less | 2nd | 144.7 ± 17.2 | 0.0 ± 0.0 | 0.8 ± 0.1 | 5.0 ± 1.1 | 4.0 ± 0.8 | 4.6 ± 0.1 | 0.2 ± 0.0 | 0.2 ± 0.0 | 0.4 ± 0.0 | 1.2 ± 0.3 | 0.3 ± 0.0 | 5.1 ± 0.2 | 1.8 ± 0.2 | 8.4 ± 0.5 | 25.9 ± 2.5 | 2.0 ± 0.2 | 19.4 ± 2.0 | 3.5 ± 0.3 |
| Spine-less | 3rd | 153.2 ± 35.8 | 0.1 ± 0.0 | 0.6 ± 0.1 | 3.9 ± 0.6 | 5.3 ± 1.2 | 4.7 ± 0.2 | 0.2 ± 0.0 | 0.2 ± 0.0 | 0.5 ± 0.0 | 1.3 ± 0.2 | 0.3 ± 0.0 | 5.8 ± 0.7 | 2.0 ± 0.2 | 8.3 ± 0.9 | 24.2 ± 0.9 | 1.5 ± 0.3 | 19.2 ± 3.2 | 3.1 ± 0.4 |
| Rocky Caatinga | 1st | 55.5 ± 9.8 | 0.2 ± 0.2 | 1.1 ± 0.1 | 3.5 ± 0.3 | 8.7 ± 0.5 | 4.6 ± 0.1 | 0.1 ± 0.0 | 0.0 ± 0.0 | 0.4 ± 0.1 | 1.7 ± 0.1 | 0.5 ± 0.2 | 8.3 ± 0.4 | 2.4 ± 0.1 | 11.0 ± 0.4 | 21.6 ± 1.4 | 3.2 ± 0.2 | 14.5 ± 3.1 | 5.5 ± 0.4 |
| Rocky Caatinga | 2nd | 47.5 ± 10.6 | 0.0 ± 0.0 | 1.0 ± 0.1 | 3.1 ± 0.4 | 18.3 ± 11.1 | 4.8 ± 0.0 | 0.2 ± 0.0 | 0.0 ± 0.0 | 0.4 ± 0.1 | 1.7 ± 0.3 | 0.3 ± 0.0 | 8.5 ± 1.1 | 2.2 ± 0.3 | 11.1 ± 1.3 | 19.7 ± 1.8 | 2.6 ± 0.1 | 15.6 ± 3.4 | 4.7 ± 0.5 |
| Rock Caatinga | 3rd | 37.5 ± 5.0 | 0.0 ± 0.0 | 0.8 ± 0.2 | 2.4 ± 0.8 | 9.3 ± 0.9 | 5.0 ± 0.0 | 0.2 ± 0.0 | 0.1 ± 0.0 | 0.5 ± 0.0 | 1.4 ± 0.3 | 0.3 ± 0.0 | 8.9 ± 1.0 | 2.0 ± 0.3 | 11.4 ± 1.3 | 17.8 ± 1.5 | 2.7 ± 0.3 | 21.1 ± 3.7 | 4.7 ± 0.6 |
| Anthropogenic I | 1st | 35.2 ± 3.6 | 0.0 ± 0.0 | 0.6 ± 0.0 | 3.1 ± 0.1 | 4.0 ± 0.8 | 5.2 ± 0.1 | 0.0 ± 0.0 | 0.0 ± 0.0 | 0.1 ± 1.4 | 0.5 ± 0.1 | 0.3 ± 0.0 | 1.3 ± 0.1 | 0.9 ± 0.2 | 2.2 ± 0.3 | 38.4 ± 2.9 | 0.5 ± 0.0 | 10.7 ± 1.6 | 0.9 ± 0.0 |
| Anthropogenic I | 2nd | 60.3 ± 20.8 | 0.1 ± 0.0 | 1.3 ± 0.4 | 5.9 ± 2.7 | 14.7 ± 3.7 | 5.6 ± 0.5 | 0.1 ± 0.0 | 0.1 ± 0.1 | 0.1 ± 0.0 | 1.2 ± 0.3 | 0.3 ± 0.0 | 1.8 ± 0.5 | 1.8 ± 0.4 | 3.6 ± 0.6 | 48.8 ± 10.5 | 0.7 ± 0.0 | 4.1 ± 3.1 | 1.1 ± 0.2 |
| Anthropogenic I | 3rd | 53.5 ± 7.1 | 0.2 ± 0.1 | 1.0 ± 0.1 | 3.3 ± 1.8 | 9.0 ± 0.8 | 5.2 ± 0.6 | 0.2 ± 0.0 | 0.2 ± 0.1 | 0.3 ± 0.2 | 1.6 ± 0.4 | 0.5 ± 0.2 | 4.1 ± 2.5 | 2.3 ± 0.8 | 6.7 ± 3.5 | 41.4 ± 11.7 | 1.4 ± 0.9 | 7.9 ± 5.8 | 1.2 ± 0.2 |
| Anthropogenic II | 1st | 43.0 ± 15.8 | 0.1 ± 0.1 | 3.7 ± 0.5 | 20.8 ± 5.8 | 13.0 ± 3.6 | 6.2 ± 0.0 | 0.3 ± 0.2 | 0.0 ± 0.0 | 0.0 ± 0.0 | 6.3 ± 2.3 | 0.6 ± 0.2 | 1.3 ± 0.3 | 7.4 ± 2.3 | 9.0 ± 2.4 | 83.8 ± 7.8 | 1.1 ± 0.3 | 0.0 ± 0.0 | 2.0 ± 0.5 |
| Anthropogenic II | 2nd | 84.2 ± 2.38 | 0.2 ± 0.1 | 2.8 ± 0.1 | 154.0 ± 25.0 | 12.7 ± 0.5 | 6.3 ± 0.0 | 0.5 ± 0.1 | 0.1 ± 0.0 | 0.0 ± 0.0 | 5.3 ± 1.1 | 1.6 ± 0.5 | 1.5 ± 0.3 | 7.5 ± 1.7 | 8.9 ± 1.9 | 83.5 ± 2.5 | 0.8 ± 0.1 | 0.0 ± 0.0 | 1.4 ± 0.1 |
| Anthropogenic II | 3rd | 129.0 ± 20.9 | 0.6 ± 0.0 | 2.7 ± 0.7 | 19.8 ± 5.4 | 7.8 ± 0.5 | 5.93 ± 0.2 | 0.4 ± 0.1 | 0.2 ± 0.0 | 0.0 ± 0.0 | 13.5 ± 5.4 | 2.6 ± 2.3 | 4.2 ± 0.7 | 18.4 ± 4.9 | 21.0 ± 6.6 | 75.2 ± 14.0 | 3.6 ± 1.4 | 0.5 ± 0.8 | 6.2 ± 2.5 |

SB = sum of exchangeable bases; CEC=Cation exchange capacity; V=Base saturation; m = Al Saturation; OM=Organic Matter.

II. Only eight other species were recovered from at least 25% of all soil samples: *Gl. macrocarpum*, *Sc. coremioides*, *Rh. intraradices*, *Gl. glomerulatum*, *Gi. gigantea*, *Ambispora appendicula*, *Glomus brohultii* and *Glomus* sp. 7. The most dominant species recovered from the natural sites were *Ac. mellea*, and *Gl. macrocarpum* (Supplementary Table 1). Species with a higher abundance in at least one of the anthropogenic sites than the natural sites were *Sc. coremiodes*, *Rh. intraradices* and *Acaulospora scrobiculata*. Eighteen other species were recovered only from one of the six sites, with 11 of them in only one or two samples (field plot replicates) at their detection site (Supplementary Table 1).

### 3.4. AMF indicator species

Considering the environment, *Am. appendicula* was an indicator species for the anthropized areas. For the sampling occasion, *Acaulospora* sp.7, *Bulbospora minima, Claroideoglomus etunicatum*, and *Glomus* sp.1 were indicators for May 2012, while *Gi. albida* was associated with September 2012. In the case of habitat-type, *Acaulospora foveata* was an indicator for rocky Caatinga, and *Fuscutata heterogama* for anthropogenic Caatinga I site (Table 3).

### 3.5. AMF spore density, species richness and diversity

The AMF species richness varied from 37 to 56 species in the natural areas and from 25 to 42 species in anthropogenic areas (Supplementary Table 1). Higher richness of AMF species was observed in the natural than anthropized environment (Fig. 1A). Considering the habitat-type, the richness recorded in sand Caatinga differed from anthropized Caatinga I and II, and spine-less Caatinga; the AMF richness in rocky Caatinga also differed in relation to anthropized II and spine-less Caatinga, and between typical and anthropized II sites (Fig. 1B). For the sampling occasion, the richness of AMF differed between May 2012 and March 2013 samplings (Fig. 1C).

AMF spore density was higher in natural compared with anthropized environments (Fig. 1D). Considering natural habitats, the spore density differed only between sand Caatinga and spine-less Caatinga; the other differences found in spore density occurred between natural and anthropogenic sites (Fig. 1E); there was no difference among sampling occasions (Fig. 1F).

The Margalef diversity, which estimates species richness, was also higher in natural than in anthropized areas (Fig. 1G). Typical Caatinga had a higher Margalef index value than that registered in anthropized habitats (Fig. 1H). For the sampling occasion, the Margalef index differed between the May 2012 and March 2013 samplings (Fig. 1I).

The Pielou index followed an opposite pattern in relation to the richness, spore density, and Margalef index, being higher in the anthropized environment (Fig. 1J). There was no difference in the value of the Pielou index considering each habitat (Fig. 1K) or sampling occasion (Fig. 1L). For the Shannon index, there was a difference only for the sampling occasion (Fig. 1M, N and O), between the first (May 2012) in relation to other sampling occasions.

The species accumulation curves (according to the Jackknife index) showed that 80% of the estimated species occurred in the typical Caatinga, 77% in the sandy Caatinga, 73% in the spine-less Caatinga, 72% in the rocky Caatinga, 75% in the anthropogenic Caatinga I, and 72% in the anthropogenic Caatinga II (Supplementary Fig. 2).

### 3.6. Arbuscular mycorrhizal fungal communities

The NMDS analysis showed that the AMF communities from the natural sites grouped towards the center of the graph, whereas the

**Table 2**
Physical soil parameters in the Caatinga study sites of the Catimbau National Park (NE Brazil); all results were expressed as %.

| Sites | Times | Bulk Density | Particle Density | Total Porosity | Natural Clay | Degree Flocculation | Total Clay | Coarse Sand | Fine Sand | Silt | Clay |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | % | | | | | | | | | |
| Typical Caatinga | 1st | 1.4 ± 0.0 | 2.6 ± 0.0 | 43.5 ± 1.2 | 1.1 ± 0.9 | 85.9 ± 11.3 | 86.3 ± 0.7 | 51.2 ± 2.2 | 35.0 ± 1.6 | 5.6 ± 0.7 | 8.2 ± 0.0 |
| Typical Caatinga | 2nd | 1.4 ± 0.1 | 2.5 ± 0.0 | 46.0 ± 2.1 | 2.4 ± 1.6 | 69.8 ± 17.9 | 85.7 ± 2.0 | 57.8 ± 3.7 | 28.0 ± 3.3 | 7.3 ± 2.2 | 7.0 ± 1.9 |
| Typical Caatinga | 3rd | 1.5 ± 0.0 | 2.6 ± 0.0 | 40.0 ± 1.3 | 4.4 ± 0.0 | 65.5 ± 6.4 | 72.2 ± 3.9 | 44.7 ± 3.8 | 27.5 ± 0.68 | 14.7 ± 1.5 | 13.1 ± 2.5 |
| Sand Caatinga | 1st | 1.3 ± 0.0 | 2.4 ± 0.0 | 47.6 ± 1.5 | 0.5 ± 0.0 | 88.5 ± 0.8 | 87.2 ± 1.7 | 62.8 ± 2.4 | 24.4 ± 1.1 | 8.6 ± 1.8 | 4.2 ± 0.0 |
| Sand Caatinga | 2nd | 1.3 ± 0.0 | 2.5 ± 0.0 | 48.6 ± 1.3 | 1.7 ± 1.8 | 83.9 ± 9.9 | 80.3 ± 8.3 | 47.9 ± 16.2 | 32.4 ± 8.0 | 2.0 ± 3.6 | 7.6 ± 4.7 |
| Sand Caatinga | 3rd | 1.4 ± 0.0 | 2.5 ± 0.0 | 43.8 ± 0.2 | 2.0 ± 1.7 | 83.8 ± 9.0 | 79.0 ± 9.8 | 51.8 ± 5.3 | 27.2 ± 4.5 | 10.4 ± 5.7 | 10.6 ± 4.2 |
| Spine-less | 1st | 1.3 ± 0.0 | 2.5 ± 0.0 | 49.7 ± 0.8 | 5.8 ± 0.9 | 71.1 ± 5.5 | 58.4 ± 4.2 | 30.1 ± 2.0 | 28.3 ± 2.2 | 21.4 ± 2.6 | 20.2 ± 1.6 |
| Spine - less | 2nd | 1.4 ± 0.0 | 2.7 ± 0.1 | 49.1 ± 3.0 | 3.0 ± 1.9 | 77.4 ± 10.8 | 76.1 ± 8.6 | 41.9 ± 13.4 | 34.2 ± 5.5 | 12.9 ± 4.6 | 11.0 ± 4.7 |
| Spine-less | 3rd | 1.3 ± 0.1 | 2.5 ± 0.1 | 48.1 ± 1.8 | 1.1 ± 0.0 | 80.7 ± 4.3 | 85.2 ± 4.0 | 54.0 ± 3.8 | 31.2 ± 1.5 | 8.5 ± 4.1 | 6.3 ± 1.9 |
| Rocky Caatinga | 1st | 1.3 ± 0.0 | 2.5 ± 0.0 | 49.0 ± 0.8 | 1.8 ± 0.9 | 57.0 ± 22.6 | 89.2 ± 0.5 | 61.3 ± 2.2 | 27.9 ± 2.1 | 6.7 ± 0.5 | 4.2 ± 8.9 |
| Rocky Caatinga | 2nd | 1.4 ± 0.1 | 2.6 ± 0.0 | 46.2 ± 4.9 | 1.0 ± 0.9 | 82.2 ± 13.6 | 87.7 ± 4.1 | 64.5 ± 5.5 | 23.2 ± 3.3 | 7.3 ± 5.1 | 5.4 ± 1.0 |
| Rock Caatinga | 3rd | 1.4 ± 0.0 | 2.5 ± 0.8 | 45.6 ± 2.7 | 3.8 ± 1.9 | 69.9 ± 5.5 | 79.8 ± 8.1 | 49.6 ± 7.2 | 30.2 ± 2.0 | 8.6 ± 3.3 | 11.6 ± 4.7 |
| Anthropogenic I | 1st | 1.5 ± 0.0 | 2.7 ± 0.0 | 41.6 ± 0.7 | 1.1 ± 0.9 | 81.3 ± 14.5 | 94.3 ± 0.7 | 68.8 ± 0.9 | 25.5 ± 1.5 | 0.2 ± 0.2 | 5.5 ± 0.9 |
| Anthropogenic I | 2nd | 1.5 ± 0.0 | 2.6 ± 0.0 | 41.8 ± 1.7 | 0.4 ± 0.0 | 91.1 ± 0.6 | 94.3 ± 1.6 | 71.3 ± 6.6 | 23.0 ± 5.0 | 1.3 ± 1.8 | 4.4 ± 0.3 |
| Anthropogenic I | 3rd | 1.3 ± 0.0 | 2.4 ± 0.0 | 47.8 ± 0.8 | 2.4 ± 1.9 | 71.6 ± 8.0 | 81.2 ± 7.5 | 52.8 ± 9.1 | 28.4 ± 1.6 | 11.3 ± 3.9 | 7.6 ± 3.8 |
| Anthropogenic II | 1st | 1.5 ± 0.0 | 2.5 ± 0.0 | 40.4 ± 1.5 | 3.7 ± 0.9 | 66.0 ± 8.1 | 77.9 ± 6.6 | 48.8 ± 4.4 | 29.1 ± 2.7 | 11.2 ± 5.9 | 10.9 ± 1.0 |
| Anthropogenic II | 2nd | 1.5 ± 0.1 | 2.5 ± 0.0 | 40.7 ± 2.2 | 4.4 ± 0.0 | 70.6 ± 3.7 | 68.7 ± 3.9 | 43.8 ± 3.3 | 25.0 ± 3.0 | 16.2 ± 2.1 | 15.1 ± 1.9 |
| Anthropogenic II | 3rd | 1.5 ± 0.0 | 2.6 ± 0.1 | 42.2 ± 1.8 | 1.1 ± 0.0 | 86.4 ± 1.6 | 91.4 ± 0.6 | 57.7 ± 0.9 | 33.7 ± 0.6 | 0.3 ± 0.2 | 8.3 ± 0.9 |

**Table 3**
AMF indicator species analyses for the environments, habitats, and sampling times, at the Catimbau National Park (NE Brazil).

| AMF species | IndVal | *P* |
|---|---|---|
| **Anthropogenic Environment** | | |
| *Ambispora appendicula* | 43.0 | 0.0002 |
| **1st sampling time** | | |
| *Acaulospora* sp.7 | 27.8 | 0.0002 |
| *Bulbospora minima* | 27.8 | 0.0002 |
| *Claroideoglomus etunicatum* | 25.0 | 0.0002 |
| *Glomus* sp.1 | 33.3 | 0.0002 |
| **2nd sampling time** | | |
| *Gigaspora albida* | 36.1 | 0.0002 |
| **Rocky Caatinga habitat** | | |
| *Acaulospora foveata* | 30.8 | 0.0004 |
| **Anthropogenic I habitat** | | |
| *Fuscutata heterogama* | 33.3 | 0.0002 |
| **Anthropogenic II habitat** | | |
| *Ambispora appendicula* | 54.6 | 0.0002 |

*P* = significance level.

communities of the anthropogenic areas I and II were not grouped, possibly because most attributes of the soil are related to anthropized II (Fig. 2). However, the PERMANOVA showed a difference in the composition of AMF communities between anthropized and natural environments ($df = 1$, $F = 14.58$, $R^2 = 0.12$, $P < 0.001$, Table 4) and the structural difference was not related to the heterogeneity between environments (PERMDISP; $df = 1$, $F = 3.95$, $P > 0.053$).

Although the variation in AMF community structure was higher among habitat-type than for the environment (PERMANOVA, $df = 5$, $F = 7.92$, $R^2 = 0.21$, $P < 0.001$, Table 5), we did not find any difference among habitats after Bonferroni correction. This result was similar to that observed for the soil composition. Additionally, sample dispersion differed significantly among sites (PERMDISP; $df = 5$, $F = 6.89$, $P < 0.001$), with the composition of AMF communities from typical Caatinga differing from the sand Caatinga, rocky Caatinga, and anthropogenic II.

The composition of AMF communities differed among sampling occasion (PERMANOVA, $df = 2$, $F = 5.17$, $R^2 = 0.09$, $P < 0.001$, Table 6; PERMDISP, $df = 2$, $F = 5.17$, $R^2 = 0.35$, $P < 0.704$), with the communities collected in the first sampling (May 2012) different from the second (September 2012) and third (March 2013) occasions.

## 4. Discussion

This study provides the first known account of AMF at a landscape scale that considers habitat, anthropogenic disturbance, and time of the year (or dry season) in the Brazilian semi-arid Caatinga. To our knowledge, only Sousa et al. (2017) assessed AMF from various semi-arid sites within the Caatinga of NE Brazil but their sampling was performed once only at each site, and at specific localities ('Inselberg' sites) within the Caatinga. Thus, our work is a robust estimate of the AMF diversity in semi-arid Caatinga sites, and also in the Catimbau National Park, the primary conservation unit of the Caatinga (Brazilian tropical dry forest). The AMF species richness identified in our study was higher than recorded from other studies in the Caatinga area (12–50; Carneiro et al., 2012; Pagano et al., 2013; Silva et al., 2014; Pontes et al., 2017a). In other arid and semi-arid areas of the globe, Balázs et al. (2015) observed 31 AMF species in a semi-arid area of Hungary, Chaudhary et al. (2014) reported 42 AMF species from the semi-arid regions of the United States, and Uhlmann et al. (2006) identified just 12 AMF species from three arid sites in southern Namibia.

Even given the high heterogeneity of anthropized sites (soil conditions and land use type) in the Caatinga, we found that natural and anthropized environments harbor different AMF assemblages. These results were expected, since different studies have shown that disturbance affects the maintenance of AMF species/communities in ecosystems (Gavito et al., 2008; Mergulhão et al., 2010; Moora et al., 2014; Trejo et al., 2016; Birhane et al., 2017). The conversion from natural environments through the anthropogenic activity of deforestation and modern farming, among other factors, constitutes the major issue for tropical forests in Brazil. This may lead to a significant decline in and loss of AMF species, which are less able or unable to adapt, because some species are more sensitive to change and new conditions than others. Anthropogenic activity is consequently one of the most relevant factors for the loss of terrestrial biodiversity (Picone, 2000; Sala et al., 2000; Turrini et al., 2010; Trejo et al., 2016). It is possible that AMF species reproductivity is reduced by such anthropogenic activity, due to the lower viability of the reproductive propagules as a consequence of host-vegetation removal and burning, followed by the replacement of vegetation with agricultural crops, regular soil cultivation and the application of synthetic chemical products (Longo et al., 2014; Trejo et al., 2016; Pontes et al., 2017b). In semi-arid regions, the highest AMF richness has been associated with natural

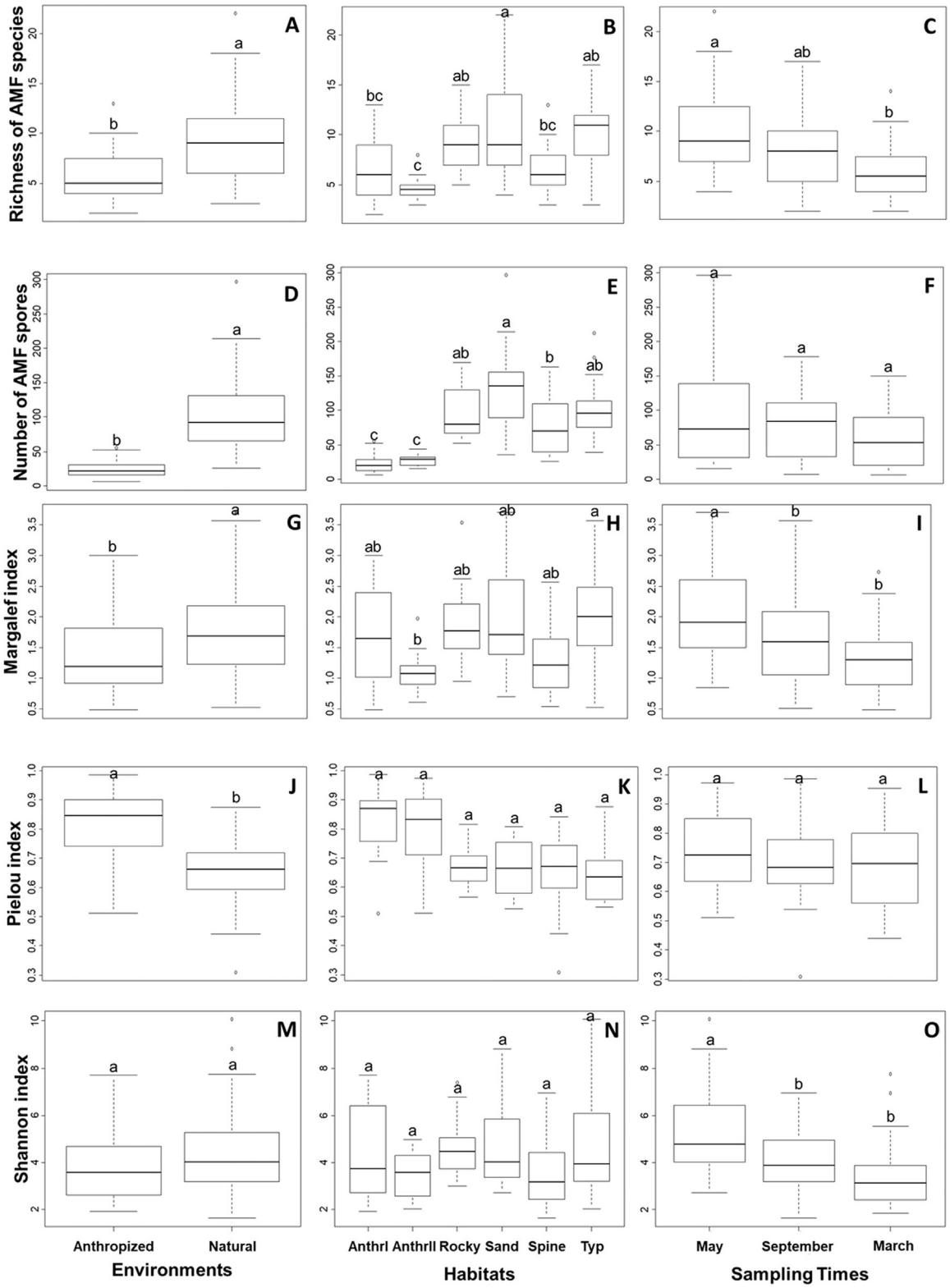


**Fig. 1. AMF species richness** (A) anthropized versus natural; (B) Anthropized Caatinga I (AnthrI), Anthropized Caatinga II (AnthrII), Rocky Caatinga (Rocky), Sandy Caatinga (Sand), Spine-less Caatinga (Spine) and Typical Caatinga (Typ); (C) Sampling times (May 2012, September 2012 and March 2013); **spore density (N, 100 $g^{-1}$) (**D) anthropized versus natural; (E) Anthropized Caatinga I (AnthrI), Anthropized Caatinga II (AnthrII), Rocky Caatinga (Rocky), Sandy Caatinga (Sand), Spine-less Caatinga (Spine) and Typical Caatinga (Typ); (F) Sampling times (May 2012, September 2012 and March 2013). **Margalef diversity (d) (**G) anthropized versus natural; (H) Anthropized Caatinga I (AnthrI), Anthropized Caatinga II (AnthrII), Rocky Caatinga (Rocky), Sandy Caatinga (Sand), Spine-less Caatinga (Spine) and Typical Caatinga (Typ); (I) Sampling times (May 2012, September 2012 and March 2013); **Pielou evenness (J′) (**J) anthropized versus natural; (K) Anthropized Caatinga I (AnthrI), Anthropized Caatinga II (AnthrII), Rocky Caatinga (Rocky), Sandy Caatinga (Sand), Spine-less Caatinga (Spine) and Typical Caatinga (Typ); (L) Sampling times (May 2012, September 2012 and March 2013) and **Shannon (H′) (**M) anthropized versus natural; (N) Anthropized Caatinga I (AnthrI), Anthropized Caatinga II (AnthrII), Rocky Caatinga (Rocky), Sandy Caatinga (Sand), Spine-less Caatinga (Spine) and Typical Caatinga (Typ); (O) Sampling times (May 2012, September 2012 and March 2013).

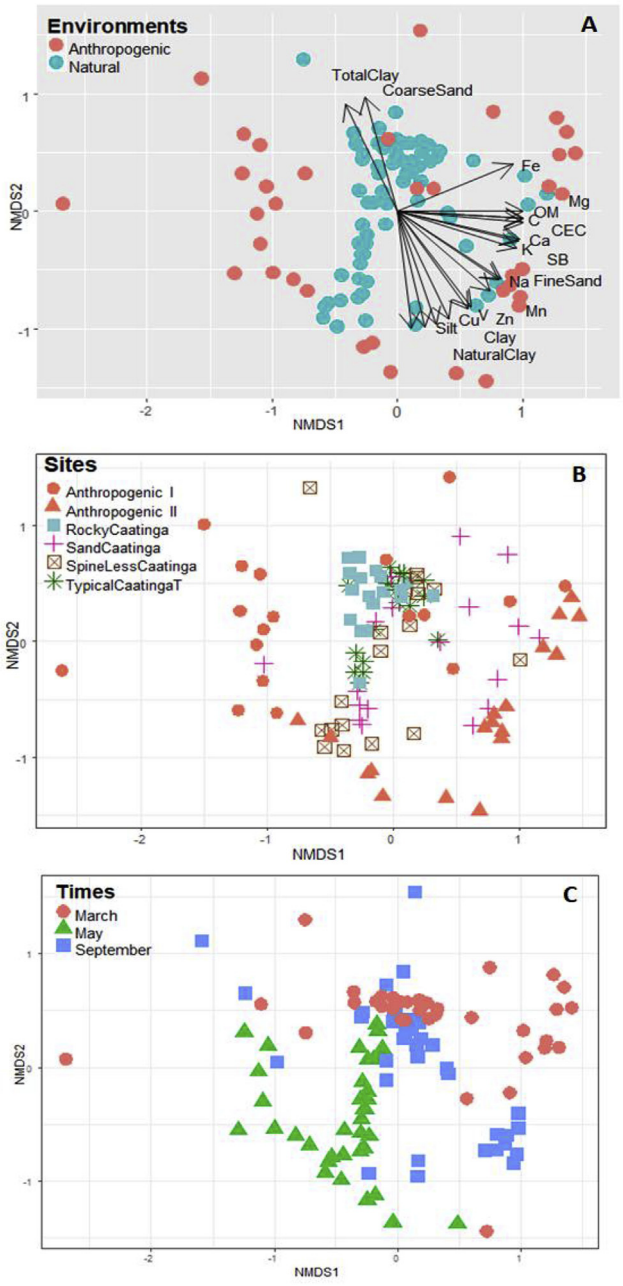


**Fig. 2.** NMS based on composition of AMF communities and soil attributes correlated to fungi groups. (A) Anthropogenic versus Natural areas, (B) Habitats and (C) Sampling times.

environments as opposed to anthropized environments, due to the presence of a diverse natural vegetation, larger amounts of organic matter and lower available phosphorus levels (Pontes et al., 2017a).

In the current study and in others (e.g., Gavito et al., 2008; Velázquez et al., 2013; Chaudhary et al., 2014; Silva et al., 2014; Sousa et al., 2017), the AMF community structure differed among sites with different soil conditions, microclimatic, and vegetation types. These results possibly are influenced by the plant communities, chemical and physical soil parameters at sites, rainfall, temperatures and altitudes (Vandenkoornhuyse et al., 2003; Lugo et al., 2008; Xu et al., 2017). The large differences in the Brazilian semi-arid for these parameters are major factors affecting the AMF communities in the Caatinga habitats, creating a mosaic of AMF

**Table 4**
Summary of one-way permutational multivariate analysis of variance (PERMANOVA) exploring how environment types (natural vs. anthropogenic) influence AMF community composition.

| | df | *F* value | $R^2$ | *P* value |
|---|---|---|---|---|
| Environment types | 1 | 14.58 | 0.12 | <0.0001 |
| Residuals | 106 | | | |
| Total | 107 | | | |

**Table 5**
Summary of one-way permutational multivariate analysis of variance (PERMANOVA) exploring how sites (sandy caatinga, typical caatinga, spine-less caatinga, rocky caatinga, anthropogenic caatinga I, anthropogenic caatinga II) influence AMF community composition.

| | df | *F* value | $R^2$ | *P* value |
|---|---|---|---|---|
| Sites | 5 | 7.92 | 0.21 | <0.001 |
| Residuals | 102 | | | |
| Total | 107 | | | |

| Comparison among sites | F Model | $R^2$ | *P* value | *P* adjusted |
|---|---|---|---|---|
| Anthropogenic I vs. Anthropogenic II | 3.65 | 0.10 | 0.001 | 0.015 |
| Anthropogenic I vs. Typical Caatinga | 8.83 | 0.21 | 0.001 | 0.015 |
| Anthropogenic I vs. Sand Caatinga | 8.92 | 0.21 | 0.001 | 0.015 |
| Anthropogenic I vs. Spine Less Caatinga | 7.00 | 0.17 | 0.001 | 0.015 |
| Anthropogenic I vs. Rocky Caatinga | 10.22 | 0.23 | 0.001 | 0.015 |
| Anthropogenic II vs. Typical Caatinga | 7.38 | 0.18 | 0.001 | 0.015 |
| Anthropogenic II vs. Sand Caatinga | 8.57 | 0.20 | 0.001 | 0.015 |
| Anthropogenic II vs. Spine Less Caatinga | 5.06 | 0.13 | 0.003 | 0.045 |
| Anthropogenic II vs. Rocky Caatinga | 8.49 | 0.20 | 0.001 | 0.015 |
| Typical Caatinga vs. Sand Caatinga | 2.86 | 0.08 | 0.019 | 0.285 |
| Typical Caatinga vs. Spine Less Caatinga | 0.75 | 0.02 | 0.637 | 1.000 |
| Typical Caatinga vs. Rocky Caatinga | 2.86 | 0.08 | 0.021 | 0.315 |
| Sand Caatinga vs. Spine Less Caatinga | 3.56 | 0.10 | 0.007 | 0.105 |
| Sand Caatinga vs. Rocky Caatinga | 3.68 | 0.10 | 0.005 | 0.075 |
| Spine Less Caatinga vs. Rocky Caatinga | 3.01 | 0.08 | 0.012 | 0.180 |

Significant when $p \leq 0.003$ considering the Bonferroni corrections.

community distribution, rather than uniformity (Pagano et al., 2013; da Silva et al., 2014). Such a mosaic was clearly recognized in our study at the Catimbau National Park, reflecting its diverse vegetation types and edaphic conditions, confirming the influence of habitat-type on AMF species richness and community composition.

In addition, we observed the influence of the time of sampling on species richness and AMF community composition, even though soil samples were collected on different occasions during only one single dry season. Seasonal variation has been indicated as a factor which influences AMF species groups and specific species, as some species can continuously sporulate throughout the year, while others are restricted to specific seasonal conditions, indicating the different sporulation strategies of different species. As sporulation is a stage of the fungal lifecycle and not all species will be in the same stage throughout the year, this contributes to seasonal differences of AMF communities. Favorable and even unfavorable environmental conditions may tend to stimulate sporulation as a survival strategy of fungi (Oehl et al., 2009; Velázquez et al., 2013; Silva et al., 2014).

We identified different indicator AMF species related to anthropized sites (*Am. appendicula*), sampling occasion (*Acaulospora* sp.7, *B. minima*, *Cl. etunicatum*, *Gi. albida*, and *Glomus* sp.1) and specific habitats (*Ac. foveata* and *F. heterogama*). *Am. appendicula* and *Cl. etunicatum* have been found in various ecosystems, and have been considered to be generalist species in Brazil (Moreira and Siqueira, 2006). However Pontes et al. (2017a), in a study performed in natural Caatinga and agroecosystems in Brazilian semi-arid, observed that *Am. appendicula* can also be sensitive to

**Table 6**
Summary of one-way permutational multivariate analysis of variance (PERMANOVA) exploring how sampling times influence AMF community composition.

| | df | *F* value | $R^2$ | *P* value |
|---|---|---|---|---|
| Sampling times | 2 | 5.17 | 0.09 | <0.0001 |
| Residuals | 105 | | | |
| Total | 107 | | | |
| Comparison among sampling times | *F* Model | $R^2$ | *P* value | *P* adjusted |
| 1st (May 2012) vs. 2nd (September 2012) | 3.39 | 0.05 | 0.002 | 0.006 |
| 1st (May 2012) vs. 3rd (March 2013) | 9.57 | 0.12 | 0.001 | 0.003 |
| 2nd (September 2012) vs. 3rd (March 2013) | 2.87 | 0.04 | 0.007 | 0.021 |

Significant when $p \leq 0.017$ considering the Bonferroni corrections.

agricultural practices.

In the present study, 80 AMF species were detected in the four natural and two anthropized sites of the Catimbau National Park in Pernambuco (NE Brazil). The number represents approximately 45% of the described AMF species recorded from Brazil (de Souza et al., 2010) and 69% of the described species previously recorded from the Caatinga (Goto et al., 2010; Maia et al., 2010). Although the AMF species richness was relatively high in at least five of the six study sites, the richness estimator used (Jackknife 1) indicates that 72–80% of the complete richness was registered; according to this estimate, 20–28% of the overall AMF species richness remained hidden.

Twenty-six AMF species were identified to the genus-level only. The majority of these likely represent as yet undescribed AMF species and will require further taxonomic investigations. According to Öpik et al. (2013) and Ohsowski et al. (2014), under natural vegetation systems, numerous species remain undescribed and can be detected. *R. undulata*, originally described from Taiwan, was recovered only from a single trap pot. This species has previously not been recorded from the Americas, while *Acaulospora gedanensis,* originally described from Poland, is here reported for the first time from the Caatinga.

The Shannon index was sufficiently sensitive to detect differences in AMF diversity among sampling occasions, although the values registered (3.3–4.6) were higher than previously reported for semi-arid areas, where values have varied from 0.54 to 2.83 (Dandan and Zhiwei, 2007; Ba et al., 2012; Sunil et al., 2012; Carballar-Hernández et al., 2013; Teixeira-Rios et al., 2013; Silva et al., 2014). For the Margalef index, which considers primarily the species richness, a difference in AMF species diversity was demonstrated between natural and anthropogenic areas, among habitats, and sampling occasions.

The dominance of Glomeraceae and Acaulosporaceae has commonly been observed in Brazilian ecosystems, such as in the Caatinga (Maia et al., 2010), Atlantic rainforests (Pereira et al., 2014), the Cerrado (Pontes et al., 2017b), sand dunes (Silva et al., 2015) as well as in other situations from across the world (Oehl et al., 2009; Birhane et al., 2017; Chaudhary et al., 2017). The dominance of these fungal groups is related to the high capacity of many of their species to adapt to new and different environments (Loss et al., 2009), their high tolerance to a wide range of soil pH (Maia and Trufem, 1990) and to a high production of small (usually) rather than few large spores (Dandan and Zhiwei, 2007). In the sandy sites in our study, a dominance of gigasporalean species was expected (e.g. according to Lekberg et al., 2007), although this was not clear, as only *Gi. gigantea*, *Gi. margarita* and *Scutellospora calospora* were frequently found. Nevertheless, the assemblage of AMF species belonging to the order Gigasporales accounted for 25% of all Glomeromycotina species isolated from across our study sites.

Overall, the high richness and diversity of AMF species in our study may relate to the high sampling intensity and taxonomic efforts (108 samples and 648 sub-samples collected on three occasions during the year) and the diversity of natural and anthropogenic sites covered, which likely enabled a broader range of communities, associated with different ecological niches, to be accessed (Whitcomb and Stutz, 2007; Dumbrell et al., 2010); the ecological theory predicts that heterogeneous landscapes harbor higher species diversity than homogeneous areas (Lekberg et al., 2007; Lumini et al., 2010).

## 5. Conclusions

Our findings show that the Catimbau National Park has a high diversity of AMF species. The variation in vegetation, soil and microclimatic conditions of this Park contribute to the maintenance of different Caatinga habitats, which in turn harbor diverse AMF communities. These AMF communities are influenced by anthropogenic activities, soil characteristics, vegetation types and other environmental conditions related to microclimate, habitat properties and seasonal changes, which are the main drivers of shifts in AMF communities in this semi-arid zone.

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## Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.funeco.2018.11.014.

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