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Original Article

Arbuscular mycorrhizal fungal communities associated with coffee intercropped with grevillea

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ABSTRACT

Arbuscular mycorrhizal fungi (AMF) communities in coffee-cultivated areas in the northeastern region of Brazil have been insufficiently studied when compared to other Brazilian regions. This study determined AMF occurrence and richness in coffee-cultivated soils under different management systems and in soils from surrounding areas with pasture and native forest (control areas), all of them located in the southwest region of Bahia, Brazil. Physicochemical soil characteristics in the different study areas were also evaluated. A total of 43 AMF spore morphotypes in 14 genera belonging to six families were recovered from soil samples from all study areas: Glomeraceae (35%), Acaulosporaceae (35%), Gigasporaceae (21%), Ambisporaceae (5%), Archaeosporaceae (2%) and Diversisporaceae (2%). *Rhizophagus fasciculatus*, *Acaulospora mellea* and *Glomus* sp. 1 were the most frequent fungi found in all areas. In the coffee-cultivated areas, 12 genera were identified, two of which (*Dominikia* and *Fuscutata*) had not yet been reported in association with coffee plants in Brazil. We concluded that soil physicochemical properties and AMF occurrence can distinguish study areas based on land use. The different coffee management systems did not influence AMF species richness, but the occurrence was influenced by both management and soil factors.

Keywords: Agroforestry, *Coffea arabica* L, Fungal communities, Glomeromycota, Sustainability.

Introduction

Soil microorganisms play an important role in several processes responsible for the sustainability of ecosystems, which makes soil microorganisms essential elements in management practices in low-input agricultural systems. Among soil microorganisms, arbuscular mycorrhizal fungi (AMF - phylum Glomeromycota) have been widely studied due to the benefits they provide to their hosts when forming a mutualistic arbuscular mycorrhizal (AM) symbiosis. In this association, plant growth and nutrition are usually improved due to higher P uptake by the fungal mycelium at the same time the plants provide the fungi with products from photosynthesis (Walder *et al.*, 2012; Keymer *et al.*, 2017).

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AMF hyphae, which originate from the roots of their hosts, extend into the soil, increasing the surface area and volume explored to capture phosphorus (P) (Javot, 2007). This effect is relevant for agricultural systems in weathered tropical soils, in which mineral components have a strong interaction with P (fixation), decreasing P availability in the soil solution for plants and increasing the need for phosphate fertilization (Faquim & Andrade, 2004; Souza *et al*., 2010). In addition to this nutritional effect, AMF improves water-host plant relations (Smith & Read, 2008), reduces damage caused by pathogens (Abarca *et al*., 2024), increases the plants' tolerance to environmental stresses, such as herbicides and organic pollutants (Carvalho *et al*., 2014), and improves soil aggregation and accumulation of bioactive substances (Rilling & Mummey, 2006; Melloni *et al*., 2013).

These functions prove the potential application of AMF for sustainable agriculture, especially when considering that they are ubiquitous in terrestrial environments and capable of associating with roots of 72% of plant species (Brundrett & Tedersoo, 2018), including crops of economic importance such as coffee (Arias *et al*., 2012; Marins & Carrenho, 2017). Coffee plants (*Coffea arabica* L. and *C. canephora* Pierre — Rubiaceae) have high mycorrhizal dependence, especially seedlings under nursery conditions (Fernandes & Siqueira, 1989). A compilation carried out by Cogo *et al*. (2017) showed that 70 AMF species have been recorded in association with coffee plantations.

Coffee plantation management systems include selecting shade-providing plant species and determining appropriate spacing for the afforestation of coffee plantations. In Brazil, *Grevillea robusta* A.Cunn. is recognized as one of the most used trees for shade due to less competition with coffee (Pezzopane *et al*., 2011). Considering the tree's height, deep root system, and thin canopy allowing light penetration, the grevilleas protect coffee plantations against winds and other inclement weather without compromising the development and productivity of coffee plants (Tscharntke *et al*., 2011). In Brazil, the world's largest coffee producer, coffee cultivation is mostly practiced as monoculture under full sun because most coffee growers believe that shading using tree species decreases productivity and shaded cultivation represents a greater need for labor, in addition to the difficulty of using machines (Ricci *et al*., 2006). However, shade-grown coffee has been shown to be efficient in increasing the supply of organic matter, conserving soil moisture, reducing N losses, increasing water holding and infiltration capacity, reduction of the risk of erosion and the emergence of invasive plants, and stimulation of biological activity (Ricci *et al*., 2006; Campanha *et al*., 2007; Jaramillo-Botero *et al*., 2010). Agroforestry systems in coffee cultivation have also shown relevant results regarding the maintenance of the occurrence and diversity of AMF species, which also shows the importance of this consortium during the growth of coffee plants with others when compared to conventional cultivation systems (Muleta *et al*., 2007; Dobo *et al*., 2017; Prates Júnior *et al*., 2019).

The analysis of AMF communities based on the morphological analysis of the spores is an initial step for better understanding of the effects of different land use systems on the community structure of these fungi (Overby *et al*., 2015; Säle *et al*., 2015). This represents an advance in the conservation and selection of AMF species or communities within an ecosystem or geographic region that could contribute to the development of sustainable agricultural production. The present study aimed to determine the occurrence of AMF in coffee-cultivated soils under different management systems and the effects of physicochemical characteristics on AMF communities. We tested the hypothesis that AMF species richness is higher in shade-grown coffee systems than in those grown in full sun.

Materials and methods

Study site

Soil samples were collected at the Vidigal Farm, located from the municipality of Barra do Choça, in the southwest region of the State of Bahia, Brazil. The geographic coordinates are 14º 52' 52" S, 40º 34' 46" W, and elevation 847 m above sea level. According to Köppen & Geiger (1936), the characteristic climate of the region is tropical highland, with rain during the winter, and average air temperature in the hottest month > 22 °C. According to the National Institute of Meteorology (INMET, 2018), the average rainfall in the region is 758 mm per year, while the average annual temperature ranges from 16.4 to 26.2 °C, with a relative humidity of 78.4%.

Soil samples were collected from five different systems: coffee plantation intercropped with grevillea (CG), full sun coffee plantation with 2.5 x 0.5 m spacing (CS1), full sun coffee plantation with 1.70 x 0.70 m spacing (CS2), pasture (PS), and native forest (NF). We included PS and NF for comparison as they represent degraded and conserved areas, respectively, and both were located adjacent to the coffee plantations (Table 1). The representation of management involving full sun- and shade-grown coffee is illustrated (Fig. 1).

Soil sampling procedure

Soil samples from each study area were collected during the dry season (June/ 2018). A 25 m transect was determined within each area and four points per transect, equidistant from each other, were marked as sampling points. At each sampling point, three soil samples were obtained and homogenized, collected at a depth of 20 cm with an auger. For each study area (n = 5), four composite samples were collected from three simple soil samples. Therefore, a total of 20 soil samples were obtained (representative for the study

Table 1. Characteristics of the systems surveyed for arbuscular mycorrhizal fungi in the Vidigal farm, Bahia, Northeast Brazil.

Systems	Composition	Area (ha) and spacing	Planting Time
CG	Catuaí coffee crop (IAC 144) intercropped with *Grevillea robusta* in order to protect coffee plants from strong winds and minimize strong sunlight	12 hectares of planted area with spacing of 2.0 x 0.50 m between coffee plants and 20.0 x 4.0 m between grevillea plants	The grevilleas were planted 20 years ago and the coffee culture was implemented 10 years later.
CS1	Catuaí coffee grown in full sun	4 hectares of planted area with spacing of 2.50 x 0.50 m.	10 years
CS2	Catuaí coffee grown in full sun	5 hectares of planted area with spacing of 1.70 x 0.70 m.	12 years
PS	Cultivation of *Brachiaria brizantha* used to raise beef cattle.	30 hectares of planted area	10 years
NF	Native vegetation of Montana seasonal semideciduous forest. Composed of medium-sized woody plants (10 to 20 m), with markedly deciduous characteristics, presence of lianas, and Fabaceae dominance.	Fragment consisting of 10 hectares	20 years

CG: Coffee combined with grevillea; CS1: Coffee in full sun with 2.50 x 0.50 m spacing; CS2: Coffee in full sun with 1.70 x 0.70 m spacing; PS: Pasture cultivated with *Brachiaria brizantha*; NF: Native Forest (Mata de Cipó).

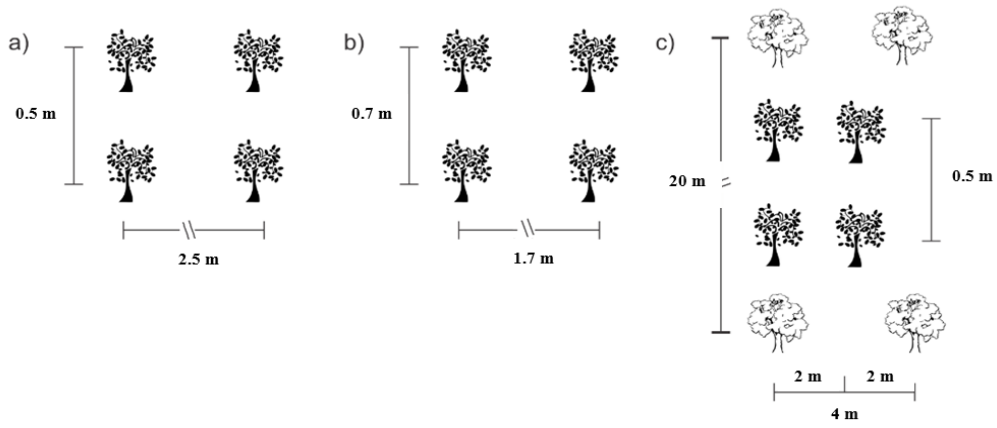

Figure 1. The representation of management involving coffee cultivation. a) CS1: Coffee in full sun with 2.5 x 0.5 m spacing, b) CS2: Coffee in full sun with 1.7 x 0.7 m spacing, c) CG: Coffee combined with grevillea, planted area with a spacing of 2 x 0.5 m between coffee plants and 20 x 4 m between grevillea plants.

areas), packed in plastic bags, stored in a Styrofoam box, and transported to the laboratory. Soil samples were stored at 4º C in a cold room for up to two months prior to processing.

Chemical and physical characterization of soil samples

From each sample, 300 cm^3 of soil underwent chemical analysis. Soil acidity was estimated as pH in water (1: 2.5 v:v). Aluminum (Al^{3+}), calcium (Ca^{2+}), and magnesium (Mg^{2+}) were extracted using KCl 1mol L^{-1} and determined by atomic absorption spectrometry (Ca and Mg) and titration with NaOH (Al). Phosphorus (P) and potassium (K^{+}) were extracted using Mehlich^{-1} solutions and determined by flame photometry (K) and spectrometry (P). The proportions of clay, silt, and sand (soil texture) were obtained using the pipette method.

Extraction and identification of AMF species

From each soil sample, AMF spores were extracted from a 50 g subsample by the wet sieving procedure (Gerdemann & Nicolson, 1963) followed by sucrose gradient centrifugation (20% and 60%). The spores were retained on two overlapping sieves with 710 and 45 µm opening each. The material retained on the 710 µm sieve was placed on a Petri dish, analyzed under a dissecting microscope, and inspected for the presence of sporocarps. The material retained on the 45 µm sieve was transferred to tubes containing a sucrose

gradient (20 and 60%) and centrifuged at 2000 rpm. The supernatant was again passed through a 45μm sieve and gently washed in running water to remove excess sucrose. The retained spores were transferred to a Petri dish and counted using a dissecting microscope.

AMF spores were separated by morphotype and mounted on slides with polyvinyl-lacto-glycerol (PVLG) and PVLG mixed with Melzer's reagent. Spore shape, color, size, and spore wall phenotypic characteristics were identified at the genus and species levels. Taxonomic identification was based on a comparative description available at the International Culture Collection of (Vesicular) Arbuscular Mycorrhizal Fungi (INVAM) on the website (http://invam.ku.edu) and Blaszkowski (2012). Vouchers for the sampled spores used to identify species were deposited at the International Culture Collection of Glomeromycota (www.furb.br/cicg) (slides #PLL001 to PLL138).

Occurrence and richness of AMF

Differences in AMF communities between areas were investigated using a set of community descriptors. Frequency of occurrence (FO) of each species was calculated, considering the proportion (%) of samples that a given species was found in relation to the total number of samples. FO was used to classify AMF species as dominant (FO> 50%), most common (30% <FO ≤ 50%), common (10% <FO <30%), and rare (FO ≤ 10%) according to Zhang *et al*. (2004). AMF species richness (S) was determined by counting the number of species in each soil sample.

Statistical analysis

Differences in chemical and physical soil properties and species richness of arbuscular mycorrhizal fungi in different coffee plantation, pasture, and native forest areas were evaluated using analysis of variance (ANOVA) followed by Tukey's test (5%) using the SISVAR statistic software 22.

Presence/absence data of AMF were submitted to qualitative multicategorical dissimilarity using the simple index of arithmetic complement by coincidence. The Sørensen coefficient (SC) was used to assess the degree of similarity of AMF communities between sites. The relationship of AMF species with the physical and chemical characteristics of soil was analyzed using Principal Component Analysis (PCA). For this analysis, we used only the most contrasting soil attributes between the reference sites and the coffee plantations (Al, Ca, Mg, K^+, P, and pH) and excluded AMF species with FO <0.50. PCA was used to summarize the information and two-dimensionally visualize the distribution of the samples using information from the variables in the study. PCA was performed on R software (R CORE TEAM, 2019) using the packages FactoMineR (Lê *et al*., 2008) and factoextra (Kassambara & Mundt, 2020) to achieve a biplot PCA, showing the distribution of the samples, how much each variable influences principal components (loadings), and their correlations.

Results

Chemical and Physical Analysis of Soil

Soils in all areas showed acid pH ranging from 4.4 in NF to 5.8 in PS (Table 2). Soil pH ranged from 4.6 to 4.84 in coffee plantations, but values were not significantly different ($p < 0.05$). The CG area showed P values of 9 mg/dm^3, and this value was at least twice as high as those found in CS1 and CS2. K concentration ranged from 0.08 to 0.20 cmolc/dm^3 of soil, with no difference among areas (Table 2).

The availability of Ca ranged from 2.75 to 3.65 cmolc/dm^3 for all areas, except NF, which had 0.67 cmolc/dm^3 of Ca and differed ($p < 0.05$) significantly from other systems. Soil Mg concentration in PS was 2.77 cmolc/dm^3 of soil and differed significantly from other systems. The highest Al^{3+} concentration was found in NF and this value differed significantly ($p < 0.05$) from other systems (Table 2).

All areas under coffee cultivation had effective cation exchange capacity values (t) greater than 4.6 cmolc/dm^3 of soil, and among the control areas, the highest value was recorded in PS (6.72 cmolc/dm^3 of soil). Considering SB values, there was no difference between the coffee cultivated areas (3.35 - 4.45 cmolc/dm^3 of soil). SB values in coffee areas were higher than those found in NF (1.45 cmolc/dm^3 of soil) and lower than those recorded in PS (6.60 cmolc/dm^3 of soil). Base saturation (% V) and aluminum saturation (m) values did not differ from coffee management systems, with higher %V in PS (52.0%) and higher m in NF (66.0%) (Table 2).

Regarding physical attributes, soils had a predominance of coarse sand fraction with values ranging from 365 g kg^{-1} in CS1 to 402 g kg^{-1} in NF, while clay fraction ranged from 410 g kg^{-1} in CS2 to 515 g kg^{-1} in CS1 (Table 3). Soils in all systems were classified as sandy clay.

Composition of the AMF community

Spores of 43 AMF morphotypes were recovered from field samples, 29 of them were identified at the species level and 14 at the genus level (Table 4). The AMF species were distributed across 14 genera belonging to six Glomeromycota families: Glomeraceae (35%), Acaulosporaceae (35%), Gigasporaceae (21%), Ambisporaceae (5%), Archaeosporaceae (2%), and Diversisporaceae (2%) (Table 4).

Considering the number of species, *Acaulospora* was the dominant genus with 34.8% of the species, followed by *Glomus* with 16.27% of the total number of species recorded. Only one to three species were recorded as belonging to *Dominikia*, *Sclerocystis*, *Rhizophagus*, *Funneliformis*, *Diversispora*, *Scutellospora*, *Racocetra*, *Gigaspora*, *Cetraspora*, *Fuscutata*, *Archaeospora*, and *Ambispora*. *Glomus* sp. 1 was the

Table 2. Soil chemical properties, at a depth of 0-20 cm, under three coffee management systems, a pasture area, and a native forest area.

Systems	pH	P	K^+	Ca^{2+}	Mg^{2+}	Al^{3+}	H^+	S.B	t	T	V	m
		mg/dm^3				$cmol_c/dm^3$					%	
CG	4.60 b	9.0 a	0.13 a	3.20 a	1.12 b	1.02 b	8.82 b	4.45 b	5.47 b	14.20 a	33.50 b	19.50 b
CS1	4.67 b	4.5 b	0.20 a	2.75 a	0.95 b	1.15 b	9.57 b	3.50 b	4.65 b	14.22 a	24.75 b	24.75 b
CS2	4.84 b	2.7 b	0.15 a	2.75 a	0.97 b	0.92 b	9.10 b	3.35 b	5.15 b	14.25 a	31.25 b	19.50 b
PS	5.82 a	2.7 b	0.14 a	3.65 a	2.77 a	0.12 c	5.95 b	6.60 a	6.72 a	12.67 a	52.00 a	2.00 c
NF	4.42 b	1.0 b	0.08 a	0.67 b	0.67 b	2.82 a	14.12 a	1.45 c	4.27 b	18.40 a	8.00 c	66.00 a
CV%	5.32	32.68	34.38	26.61	33.65	42.24	25.67	31.32	16.29	17.59	29.09	34.32

Means followed by the same letter in the column are not significantly different according to Tukey test ($p < 0.05$). CG: Coffee combined with grevillea; CS1: Coffee in full sun with 2.50 x 0.50 m spacing; CS2: Coffee in full sun with 1.70 x 0.70 m spacing; PS: Pasture cultivated with *Brachiaria brizantha*; NF: Native Forest (Mata de Cipó). S.B: Sum of bases; t: effective CEC; T: CEC in pH 7; V: Base saturation; m: Aluminum saturation. CV = Coefficient of variation.

Table 3. Physical characteristics of the soil, at a depth of 0-20 cm, under three coffee management systems, a pasture area, and a native forest area.

Systems	Cs	Fs	S	C	Textural Class
			$(g\ kg^{-1})$		
CG	367 a	70 b	77 bc	485 a	Sandy clay
CS1	365 a	75 ab	45 c	515 a	Sandy clay
CS2	390 a	82 a	117 a	410 b	Sandy clay
PS	400 a	77 ab	87 ab	435 b	Sandy clay
NF	402 a	72 b	110 ab	415 b	Sandy clay
VC (%)	6.16	4.93	13.96	3.83	--------

Cs: Coarse sand; Fs: Fine sand; S: Silt; C: clay. CG: Coffee combined with grevillea; CS1: Coffee in full sun with 2.50 x 0.50 m spacing; CS2: Coffee in full sun with 1.70 x 0.70 m spacing; PS: Pasture cultivated with *Brachiaria brizantha*; NF: Native Forest (Mata de Cipó). Means followed by the same letter in the column are not significantly different according to Tukey test ($p < 0.05$).

only species detected in all areas, and 18 species were detected exclusively in only one management system (Table 4).

AMF species richness was 22 and 27 in CG and PS, respectively, while this value ranged from 11 to 15 for the other systems. No significant differences in mean species richness ($p < 0.05$) were observed among the systems (Fig. 2).

Based on the frequency of occurrence, most AMF species were classified as common or very common (Table 4). *Rhizoglomus microaggregatum*, *Acaulospora mellea,* and *Glomus* sp. 1 were the only species classified as dominant in this study, and 11 species were considered rare. The highest number of rare species was detected in PS: *Glomus glomerulatum*, *Acaulospora alpina*, *A. foveata*, *A. rehmii*, *A. sieverdingii*, and *Scutellospora calospora*.

The highest Sørensen coefficient was detected between CG and CS1 (0.64), and the lowest between PS and CS1 (0.23), while similarity between the other combinations of systems ranged from 0.31 to 0.49 (Table 5).

Multivariate analysis

Results from PCA showed that the first and second components explained 60.8% and 20.0% of total variance respectively (Fig. 3). It was observed that the physicochemical properties and the AMF occurrence allowed for distinction between the study areas, revealing that among the coffee management systems, CG and CS1 showed a strong relationship. Pasture and Native Forest were considerably different from each other, as well as from coffee management systems (Fig. 3).

NF showed a positive relationship with H^+, Al^{3+}, aluminum saturation (m), and effective CEC (t), and *Glomus* sp. 3 was the only AMF associated with this study area. Conversely, CS1 was associated exclusively with the AMF species *Sclerocystis coremioides*, *Dominikia* sp. 1, and *Rhizoglomus microaggregatum* (Fig. 3).

CG and CS2 coffee cultivation systems showed a positive relationship between P, K, and Ca^{2+} levels with *Acaulospora mellea*, *Acaulospora scrobiculata*, *Glomus* sp. 2, and *Rhizoglomus microaggregatum* (Fig. 3). Finally, PS was associated with the sum of bases (SB), base saturation (V), pH and Mg^{2+}, and with *Ambispora reticulata*, *Diversispora* sp. 1, and *Sclerocystis sinuosa* (Fig. 3).

Discussion

Physical, chemical, and biological properties of the soil are strongly influenced by land use systems, such as agricultural management practices. In this study,

Table 4. Species of arbuscular mycorrhizal fungi (AMF) associated with coffee plants under distinct management systems, a pasture area and a native forest area, in the Vidigal farm, Northeast of Bahia state, Brazil.

	Systems †					
AMF Families/species	**CG**	**CS1**	**CS2**	**PS**	**NF**	**FO**
Glomeraceae						
Dominikia sp.1	x	x			x	MC§
Sclerocystis coremioides cf. Berk. & Broome	x	x	x		x	MC
Sclerocystis sinuosa Gerd. & B.K. Bakshi	x		x	x	x	MC
Sclerocystis rubiformis Gerd. & Trappe		x				C
Glomus sp.1	x	x	x	x	x	D
Glomus sp.2			x	x		C
Glomus sp.3	x		x	x		MC
Glomus sp.4		x		x	x	C
Glomus glomerulatum Sieverd.	x			x	x	R
Glomus cf. *majewskii* Blaszk.	x	x			x	MC
Rhizoglomus microaggregatum (Koske, Gemma & P.D.Olexia) Sieverd., G.A.Silva & Oehl	x	x	x	x		D
Rhizophagus fasciculatus (Thaxter) C. Walker & A. Schüssler		x			x	C
Rhizophagus clarus (Nicolson & Schenck) C. Walker & A. Schüssler	x		x			C
Rhizophagus sp.1	x					C
Funneliformis mosseae (Nicolson & Gerd.) C. Walker & A. Schüssler					x	C
Diversisporaceae						
Diversispora sp.1	x			x		MC
Acaulosporaceae						
Acaulospora alpina Oehl, Sykorova & Sieverding				x		R
Acaulospora mellea Spain & N.C. Schenck	x	x	x			D
Acaulospora morrowiae Spain & N.C. Schenck	x			x		C
Acaulospora foveata Trappe & Janos				x		R
Acaulospora lacunosa J.B. Morton	x		x			C
Acaulospora rehmii Sieverding & S. Toro				x		R
Acaulospora scrobiculata Trappe	x	x	x	x		MC
Acaulospora sieverdingii Oehl, Sýkorová, Blaszk. & G.A. Silva				x		R
Acaulospora tuberculata Janos & Trappe		x	x			C
Acaulospora sp.1				x	x	C
Acaulospora sp.2				x		C
Acaulospora sp.3	x					R
Acaulospora sp.4	x					C
Acaulospora sp.5		x				R
Acaulospora sp.6		x				C
Gigasporaceae						
Scutellospora pernambucana Oehl, D.K. Silva, N. Freitas, L.C. Maia					x	C
Scutellospora calospora (T.H. Nicol. & Gerd.) C. Walker & F.E. Sanders				x		R
Scutellospora sp.1					x	R
Racocetra fulgida (Koske & C. Walker) Oehl, F.A. Souza & Sieverding	x				x	C
Racocetra verrucosa (Koske & C. Walker) Oehl, F.A. Souza & Sieverding			x	x		C

Table 4. Cont.

	Systems †					
AMF Families/species	**CG**	**CS1**	**CS2**	**PS**	**NF**	**FO**
Gigaspora decipiens I.R. Hall & L.K. Abbott					x	R
Gigaspora cf. *margarita* W.N. Becker & I.R. Hall	x	x	x	x		C
Cetraspora pellucida (Nicol. & Schenck) Oehl, F.A. Souza & Sieverding				x		C
Fuscutata aurea Oehl, C.M. Mello & G.A. Silva		x				R
Archaeosporaceae						
Archaeospora cf. *myriocarpa* (Spain, Sieverd. & N.C. Schenck) Oehl, G.A. Silva, B.T. Goto & Sieverd.	x					R
Ambisporaceae						
Ambispora leptoticha (N.C. Schenck& G.S. Sm.) R.J. Bills & J.B. Morton	x		x	x	x	C
Ambispora reticulata Oehl & Sieverd.	x		x	x		MC
Total	22	15	15	27	11	

† CG: Coffee combined with grevillea; CS1: Coffee in full sun with 2.50 x 0.50 m spacing; CS2: Coffee in full sun with 1.70 x 0.70 m spacing; PS: Pasture cultivated with *Brachiaria brizantha*; NF: Native Forest (Mata de Cipó). § Species classified according to their frequency of occurrence index (FO), where: Dominant (D) = FO > 50%; Most common (MC) = 30% < FO ≤ 50%), Common (C) = 10% < FO ≤30%; and Rare (R) = FO ≤ 10%.

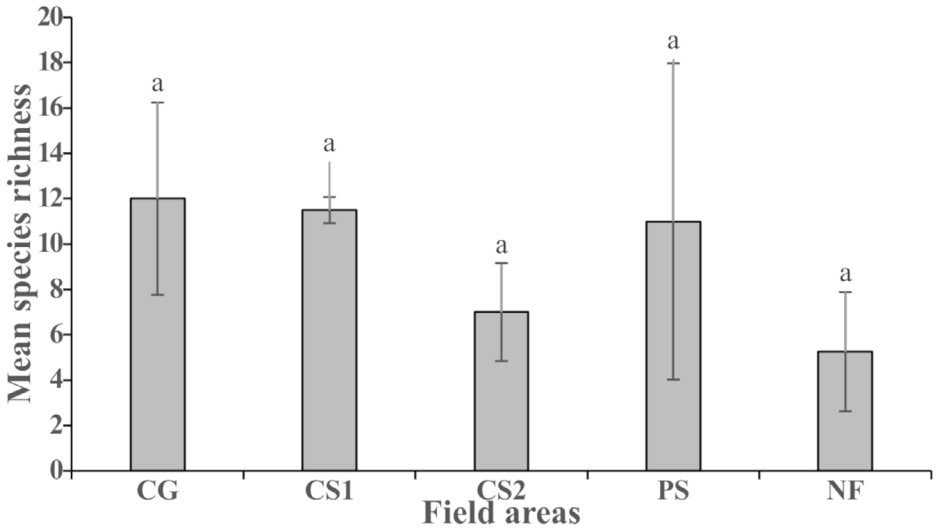

Figure 2. Mean species richness of arbuscular mycorrhizal fungi in different coffee plantations, pasture, and native forest areas. Bars followed by the same letter indicate means that are not significantly different according to Tukey ($p < 0.05$). CG: Coffee combined with grevillea; CS1: Coffee in full sun with 2.5 x 0.5 m spacing; CS2: Coffee in full sun with 1.7 x 0.7 m spacing; PS: Pasture cultivated with Brachiaria brizantha; NF: Native Forest (Mata de Cipó).

Table 5. Pairs comparisons of the Sorensen coefficient between coffee plants under distinct management systems, a pasture area, and a native forest area.

Systems	NF	PS	CG	CS1	CS2
NF	-	-	-	-	-
PS	0.31	-	-	-	-
CG	0.48	0.49	-	-	-
CS1	0.46	0.23	0.43	-	-
CS2	0.38	0.47	0.64	0.46	-

CG: Coffee intercropped with grevilea; CS1: Coffee in full sun with 2.50 x 0.50 m spacing; CS2: Coffee in full sun with 1.70 x 0.70 m spacing; PS: Pasture cultivated with *Brachiaria brizantha*; NF: Native Forest (Mata de Cipó).

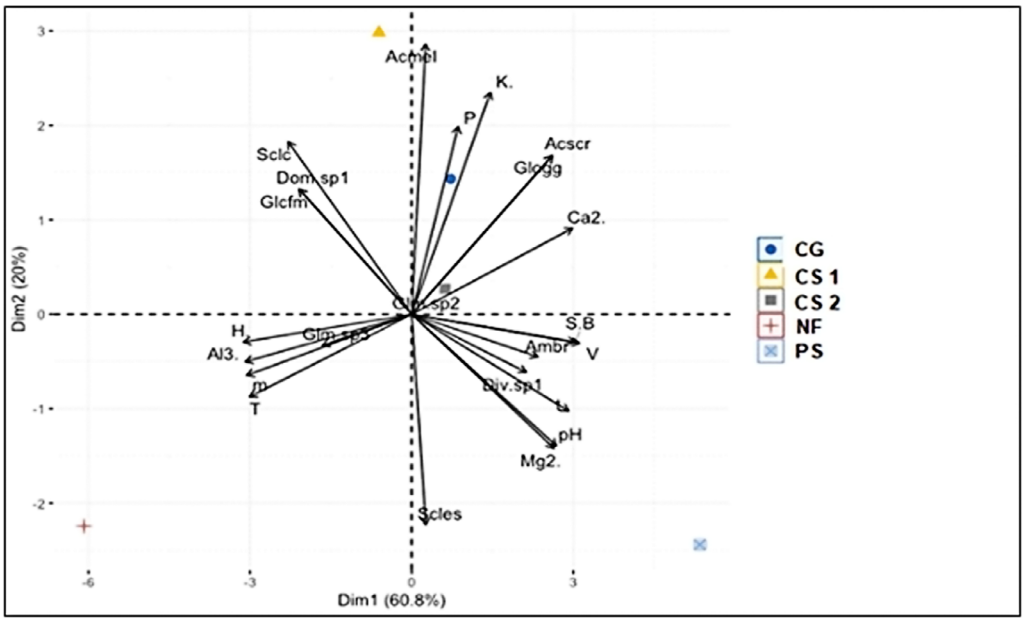

Figure 3. Analysis of major components for the frequency of AMF and chemical attributes of the soil in study areas [CG (coffee intercropped Grevillea); CS1 (coffee in full soil with spacings of 2.50 x 0.5 m); CS2 (coffee in full soil with spacings of 1.7 x 0.7 m); NF (Native Forest) and PS (Pasture). Where Mg2: *Magnesium*, pH: *Hydrogen potential*, Ca2: Calcium, K: Potassium, Al3: Aluminum, P: Phosphorus, H: Potential acidity; Sun: Sum of base; m: Aluminum saturation; t: Effective CEC; V: Base saturation; Acscr: *Acaulospora scrobiculata*; Glogg: *Glomus glomerulatum*; Acmel: *Acaulospora mellea*; Div sp1: *Diversispora* sp1, Glm sp2: *Glomus* sp2; Glm sp3: *Glomus* sp3; Scles: *Sclerocystis sinuosa*; Sclc: *Sclerocystis coremioides*; Glcfm: *Glomus cf majewskii*; Dom sp1: *Dominikia* sp1.; Ambr: *Ambispora reticulata*.

we characterized the composition of AMF community and physicochemical properties in cultivated soils with coffee, under different managements (agroforestry and full sun), and compared them with native forest (natural system) and pasture (anthropized system) in one of the main coffee producing regions in Northeast of Brazil.

Soil chemical analysis of the different study areas, in general, showed coffee cultivation systems shared close values for most chemical attributes, differentiating them from PS and/or NF (Table 2). However, some exceptions were observed, such as the high P content found in CG and the high SB and %V values observed in PS. Agroforestry systems (AFS), such as CG, are recognized for benefits to P availability in soil, especially through the contribution of plant residues to the soil surface (Prates Júnior *et al*., 2021). Some studies even suggest that AMF contribute to the construction of the organic P pool in soil, including forms with greater lability, which is important for P cycling in tropical soils (Cardoso *et al*., 2003, Xavier *et al*., 2011). The high values of SB and %V found in PS are probably due to the fertilizers commonly applied to these systems, in addition to the deposition of animal excreta.

In relation to attributes related to the AMF community, qualitative differences in the composition of the AMF community were important to demonstrate the effect of soil use and its characteristics on the structure of AMF communities (Table 4). One limitation of our study is that the data are based on spores collected only from the field, thus representing the sporulating species at the time of sampling. The use of trap culture techniques could have revealed additional species that were not sporulating in the field (Stutz & Morton, 1996), although this technique can act as a filter, and might not necessarily reveal non-sporulating species (Leal *et al*., 2018). It is important to note that this study represents the first to evaluate AMF communities in coffee plantations in the northeastern Brazil because most studies in Brazil were carried out in the South and Southeast regions (Fernandes & Siqueira, 1989; Oliveira *et al*., 1990; Balota & Lopes, 1996; Colozi-Filho *et al*., 2000; Theodoro *et al*., 2003; Prates Júnior *et al*., 2019).

Our results show a richness of AMF associated with coffee plantations and adjacent areas equal to 43 taxa, 29 morphotypes identified at the species level, and 14 identified at the genus level, which may indicate the occurrence of new fungal species. This total of AMF taxa identified at the species level (n=29) recorded in the present study represents approximately 41% of the total diversity reported by Silva *et al*. (2014) in a survey on the diversity of AMF in soils in the Bahia, including natural and agricultural areas.

Of the total 43 AMF morphotypes found in the land use systems, 31 of them were detected in coffee-cultivated areas. These values are similar to other studies carried out

in coffee plantations. In Mexico, Arias *et al*. (2012) found 32 AMF morphotypes in five coffee production systems while Dobo *et al*. (2017) found 28 morphotypes by analyzing nine agroforestry systems with coffee plants, in Ethiopia. Prates Júnior *et al*. (2019) detected 43 AMF morphotypes in coffee-cultivated soils under different agroecological managements in Brazil. It is also interesting to highlight that, considering only the number of AMF morphotypes identified at the species level (n=21) in coffee-cultivated areas in this study, the species richness value corresponds to approximately 30% of that reported by Cogo *et al*. (2017) for coffee grown in different regions of Brazil.

Considering the number of species, the dominant genera were *Acaulospora* and *Glomus*, similar to other studies of occurrence in coffee systems in the Americas and Africa (Muleta *et al*., 2008; Jefwa *et al*., 2009; Arias *et al*., 2012; Beenhouwer *et al*., 2015). Both genera have been considered widely distributed in different forest ecosystems (Oehl *et al*., 2003; Zhao *et al*., 2003) and agricultural systems (Oehl *et al*., 2009; Pereira *et al*., 2014), including coffee plantations (Cogo *et al*., 2017). This demonstrates the high adaptability of these genera to the prevailing climate and soil conditions in coffee agroecosystems, as reported by Colozzi-Filho & Cardoso (2000) and Theodoro *et al*. (2003). Furthermore, another 12 genera were identified in our study, two of them (*Dominikia* and *Fuscutata*) representing the first report of association with coffee in Brazil (Cogo *et al*., 2017).

No significant difference in AMF species richness was detected in coffee cultivation systems (CG, CS1, and CS2) compared to control systems (PS and NF) (Fig. 2). However, AMF community composition differed among management systems, despite some overlap among systems (Fig. 3). These results indicate that land use systems, especially those under coffee cultivation, impact the AMF community composition at a local scale because CG, CS1, and CS2 were related to distinct groups of AMF species (Fig 3.).

Therefore, qualitative differences in the composition of the AMF community were important to demonstrate the effect of coffee management. *Rhizoglomus microaggregatum*, *Acaulospora mellea*, *Acaulospora scrobiculata,* and *Gigaspora margarita* were present in all areas under coffee cultivation, but they were absent in native forest soils. These species, especially the last three, are widely mentioned in the scientific literature in association with coffee plants (Jefwa *et al*., 2009; Arias *et al*., 2012; Beenhouwer *et al*., 2015).

Results of the multivariate analysis indicated that the occurrence of some fungal species can be used to distinguish the CS1 system from the other coffee-cultivated areas. This area had a positive relationship with *Sclerocystis coremioides*, *Dominikia* sp. 1, and *Glomus* cf. *majewskii* (Fig. 3), all belonging to Glomeraceae. *Sclerocystis coremioides* is not commonly found associated with coffee plantations (Cogo *et al*., 2017), despite being recorded in northeastern Brazil (Goto & Maia, 2005). *Dominikia* was described by Błaszkowski *et al*. (2015) and includes species that form small spores (usually < 40-50 µm). This genus was never recorded associated with coffee plantations, and the detection of *Dominikia* in this study is possibly due to the use of a 25 µm sieve during the spore extraction procedure. The presence of *Glomus* cf. *majewskii* also represents an indication of the first record of this species associated with coffee plants.

It is interesting to note that AMF species richness was similar between study areas. The grevillea used in the CG system is a highly mycotrophic plant, similar to *Brachiaria decumbens*, a grass dominant in PS, which can contribute to maintaining AMF diversity in both systems (Leal *et al*., 2013). Conversely, forest systems such as NF are more stable than other soil use systems when regarding to the presence of host plants and the absence of variation in soil characteristics. This could act as a selection pressure in AMF communities with reduced sporulation (Leal *et al*., 2009). The low number of species in both full-sun coffee cultivated areas was expected because this system had conventional management, with a high input of fertilizers, which generally results in a fewer associated AMF species (Muleta *et al*., 2007; Durazzini *et al*., 2016; Dobo *et al*., 2017).

In this study, all systems were located under the same soil and climate conditions, and adjacent to each other, which allowing us to observe the effect of the vegetation cover on the composition of the AMF community. Overall, Sørensen coefficients were considered low (on average, Cs <0.5), suggesting that changes in soil cover and agricultural practices, in addition to the physicochemical properties of the soil, influenced the composition of AMF communities. Although the structure of AMF communities can be affected by geographic conditions (Davison et al., 2015), edaphic factors can be the main drivers of AMF communities (Jansa *et al*., 2014; Alguacil *et al*., 2015) at a local level.

We observed that in addition to the composition of AMF communities, soil chemical characteristics were important to distinguish the effects of land use. For NF, high values of potential acidity (H + Al), Al^{3+}, saturation by Al^{3+} (m) and total cation exchange capacity (T) may have been determinants of the association of *Glomus* sp. 3 with this area. It is known, that Al reduces the availability of P in soil because Al binds easily to P. This is a considerable factor in the distribution of AMF species among communities, with the most versatile and adaptable species to the most stressful conditions prevailing, such as the species of the genus *Glomus* (Sousa *et al*., 2014).

Soil pH has been considered an environmental filter for AMF communities (Jansa *et al*., 2014; Bainard *et al*., 2015). In our study, PCA demonstrated an association of *Ambispora reticulata*, *Diversispora* sp. 1, and *Sclerocystis sinuosa* with PS, the system with the highest soil pH value. *Ambispora reticulata* has been described by Oehl *et al*. (2011), but there are still few reports of this species in natural ecosystems. On the other hand, *S. sinuosa* has a wide distribution in tropical soils with low pH values in Brazil (Carrenho & Trufem, 2001; Souza *et al*., 2003;

Yano-Melo *et al*., 2003), while *Diversispora* spp. has been commonly found in pasture cultivated soils in Brazil (Leal *et al*., 2013; Cristo *et al*., 2018), New Zealand (Wakelin *et al*., 2012), China (Shi *et al*., 2016), and Mexico (Álvarez - Lopeztello *et al*., 2020).

It is interesting to note that studies carried out in the northern Minas Gerais, Brazil considered *Acaulospora scrobiculata* and *Acaulospora mellea* as dominant (Siqueira *et al*.,1989) and both species were frequent in the coffee areas. Siqueira *et al*. (1989) suggested the predominance of these species does not depend on either coffee cultivation or the type of management because the species are also found in coffee seedlings growing in commercial nurseries; instead, the predominance is influenced by the ecosystem's characteristics and by the combination with the coffee plant.

The results of this study showed that full sun- and shade-grown coffee plants are hosts of a wide range of AMF in the Northeast of Brazil. However, these management practices and spacings of coffee plants had no impact on total AMF species richness, thus contradicting the hypothesis of this study. The most dominant genera found among the systems were *Acaulospora* and *Glomus*. This was expected for agricultural systems, considering the high number of species described for both genera. Furthermore, this was the first report of the species *Dominikia* and *Fuscutata* in a coffee-growing area, highlighting the importance of sampling AMF communities in regions that have not been previously surveyed.

In general, the agricultural systems studied here differed significantly from the natural systems in terms of the physicochemical properties of soil and the composition of AMF communities, showing that changes in natural systems can impact the structure of AMF communities. Our results represent a first step towards the identification of the main AMF species associated with coffee in the northeastern Brazil, serving as a support for future research on the management of these populations or the isolation of these fungi for the formulation of mycorrhizal inoculants.

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Authors' contribution

PLL, RSS, and DLM participated in conceptualization, data curation, formal analysis, investigation, methodology, project administration, supervision, validation, visualization, writing – original draft and writing – review & editing. LMF, FGVA, VDT, SLS, and KK participated in formal analysis, investigation, methodology, visualization, writing – original draft, and writing – review & editing. All authors approved for publication and agreed to be responsible for the word conducted.

Conflict of interest

The authors declare no conflicts of interest (personal, scientific, commercial, political, or financial) in the submitted manuscript.

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