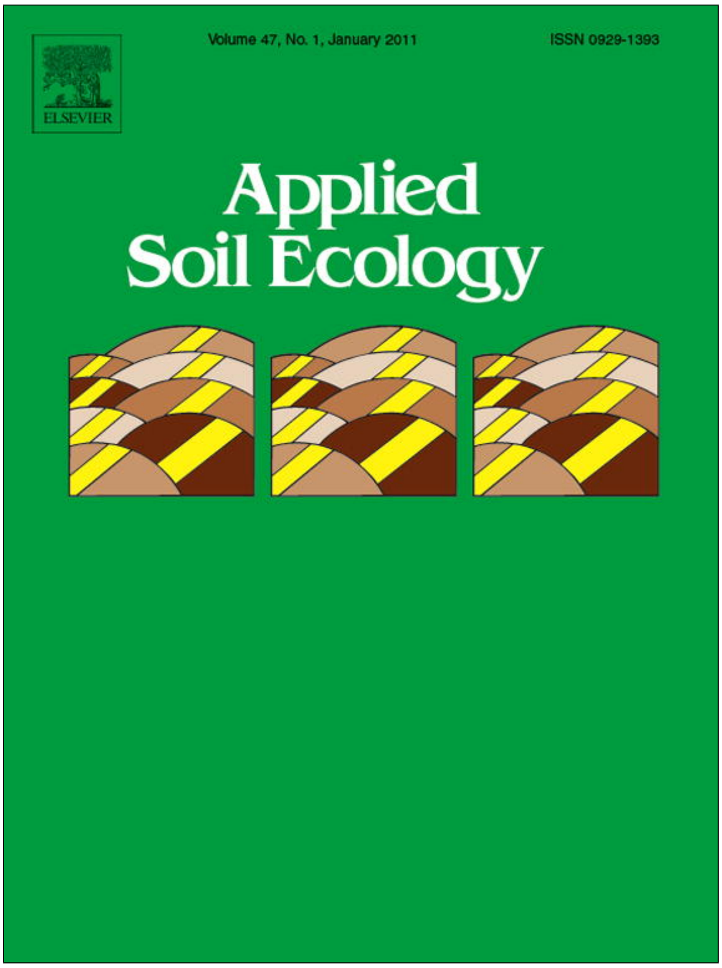
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The mosaic of habitats in the high-altitude Brazilian rupestrian fields is a hotspot for arbuscular mycorrhizal fungi

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ABSTRACT

The high diversity in rupestrian field vegetation has been attributed to the mosaic of environments formed by several soil classes, rugged relief and microclimatic variation. Although advances in the knowledge of some biological areas in rupestrian fields have been made, little is known about the relevance of soil microorganisms and their relationships with the vegetation. Symbiosis with arbuscular mycorrhizal fungi (AMF) is one of the most studied interactions between microorganisms and plants, because they are ubiquitous and contribute to the sustainability of ecosystems. This study aimed to investigate the occurrence and diversity of AMF species and to evaluate their relationship with soil physicochemical attributes and plant diversity in different habitats of the rupestrian fields from the Cadeia do Espinhaço, Serra do Cipó, Brazil. These rupestrian fields were delimited into five distinct habitats: rock outcrop, quartz gravel fields, sandy bogs, peat bogs and the Cerrado. Forty-nine AMF species were identified as belonging to nine families and twelve genera. Among them, *Acaulospora colossica* and *Pacispora dominikii* were found for the first time in Brazil. The results of this study suggest that the diversity of AMF is related to the heterogeneity of habitats and that the soil texture (coarse sand, gravel and silt) is better related to the structure of these fungi communities than to the soil chemical attributes. Plant species richness was related to AMF richness only in the quartz gravel field, rocky outcrop, and sandy bog habitats. Considering these habitats constitute one of the most menaced ecosystems on the planet, our survey provides information to improve knowledge about rupestrian field biodiversity, thus supporting policy actions for its conservation and preservation.

1. Introduction

The mechanisms and processes that determine the structure and function of ecosystems, as well as changes in these, are not yet fully understood, especially those found in some tropical mountains. The Cadeia do Espinhaço in Brazil is about eleven hundred kilometers long, with an average width from 50 to 100 km and a wealth of plants and animals. It contains formations of at least three biomes, including the Caatinga, Atlantic Forest and Cerrado (Brazilian savanna) phytophysiognomies. Located in the southern part of Cadeia do Espinhaço, Serra do Cipó is generally credited as belonging to the Cerrado biome. With an altitude above 900 m, this region is dominated by rupestrian fields, which comprise a unique ecosystem and are known for their great diversity of species, mostly plants, and its high endemism index (Joly, 1970; Giulietti et al., 2000; Menezes and Giulietti, 2000; Vitta, 2002; Conceição and Pirani, 2007). The number of plant species in this area is estimated at 4000, with approximately 30% from exclusive taxa (Giulietti et al., 1997). The rupestrian fields are composed of a rich mosaic of habitats, which are distinguished by the substrate configuration, continuity of vegetation, floristic composition, proportion of exposed rock, and presence of rock blocks and sand sediments; they can remain dry or periodically waterlogged in the rainy season

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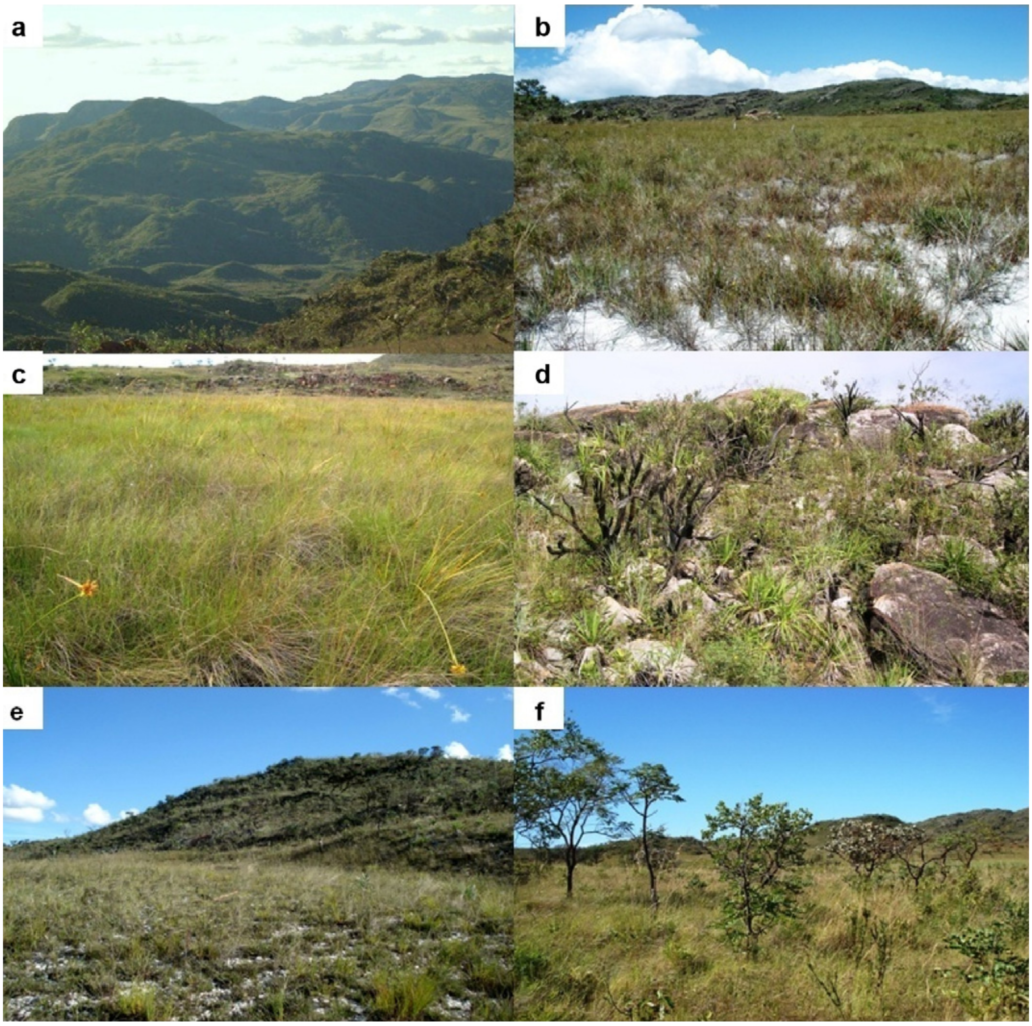

Fig. 1. Habitats found in the Serra do Cipó area studied. (a) Rupestrian field mountains, (b) Sandy Bogs; (c), Peat bogs; (d), Rocky outcrops (d), Quartz gravel fields (e) and the Cerrado (f).

(Conceição, 2000; Conceição and Pirani, 2005, 2007) between the months of November to March. In the rupestrian fields of Serra do Cipo 5 main phytophysiognomies occur: (1) Sandy bogs; (2) Peat bogs; (3) Rocky outcrops; (4) Quartz gravel field; and (5) Cerrado. The soil, poor in nutrients and thin (Benites et al., 2003), is one of the factors modulating the different types of habitats within the rupestrian fields.

The involvement of arbuscular mycorrhizal fungi (AMF) on the ecosystem diversity and function is mainly due to its effect on plant diversity and productivity. Several studies have reported positive relationships between plant diversity and AMF diversity (e.g., Grime et al., 1987; van der Heijden et al., 1998). Therefore, the presence of AMF may be essential for ecosystem sustainability, plant development and maintenance of biological diversity. However, such knowledge is not available for the ecosystems of the rupestrian fields.

The AMF (Glomeromycota) are the most common microsymbionts of plant roots (Smith and Read, 2008). These fungi establish mutualistic relationships with approximately 80% of plant species, acting as an extension of the plant root system, thereby leading to greater absorption and utilization of soil nutrients (Siqueira et al., 2002; Moreira and Siqueira, 2006). They assist in the acquisition and translocation of nutrients (de Souza et al., 2008), enhances water absorption capacity and increases the resistance of the plant root system to pathogen attacks (Jeffries et al., 2003; de Souza et al., 2008).

The Glomeromycetes origin was estimated to have occurred 300 Ma before the appearance of the land plants (Heckman et al., 2001). Nevertheless, the glomeromycotan diversity is surprising low as compared to the terrestrial plant diversity, this result is explained by difficulties to access the underground diversity and to distinguish closely related species (de Souza et al., 2008). Indeed, only approximately 217 species have been described so far worldwide and from these the occurrence of 119 has been recorded for Brazil (de Souza et al., 2010). There is a clear gap of studies in this field. However, previous studies carried out in Brazil have been limited to certain vegetation types or ecosystems (Stürmer and Siqueira, 2008; Carrenho et al., 2010; Oliveira and Oliveira, 2010; Zangaro and Moreira, 2010; Maia et al., 2010; Stürmer et al., 2010).

Considering that the rupestrian fields are composed of different habitats with high diversity and are rich in endemic species, they are also expected to harbor large numbers of AMF. Therefore, we evaluated the specific composition of AMF communities and then to evaluate the relationship of the diversity of these organisms with the soil physical–chemical attributes and the plant diversity in different habitats of the rupestrian fields of Serra do Cipó, Minas Gerais State, Brazil.

2. Materials and methods

2.1. Site location and characteristics

This study was conducted at the Reserva Natural Particular Vellozia (lat 19°16′45.7″S, long 43°35′27.8″W), Serra do Cipó, Minas Gerais, Brazil. The climate of the region is tropical, with mild summers and well-defined dry seasons from May to September, with a mean annual temperature and rainfall of 21.2 °C and 1622 mm, respectively.

Five distinctive rupestrian habitat types of the region were selected for evaluation of AMF (Fig. 1 and Table 1). For each habitat type, three plots of 1000 m^2 (50 m × 20 m) were set. To account for the high spatial variability, five sub-plots of 25 m^2 (5 m × 5 m) were randomly set within each selected plot.

2.2. Plant diversity

To determine the floristic composition and diversity of each habitat, the richness and abundance of plant species were recorded monthly for each sub-plot, due to different flowering periods throughout the year. Plants were identified with the help of botanical experts and by comparison with herbarium specimens deposited at the Universidade Federal de Minas Gerais – BHCB and Universidade Federal de Lavras – HESAL. The plant diversity was calculated by using the Shannon index.

2.3. Soil sampling, chemical and physical analyses

During the dry season in September 2007, five soil samples were collected from the superficial layer (0–0.2 m depth) of each sub-plot. These samples were combined and homogenized to form a composite sample. In total, three composite samples were taken from each habitat.

The soil samples were divided into two parts. One part was used to determine the physical–chemical attributes of the soil while the other was stored at 6 °C until AMF spore extraction. The samples were air-dried and sieved to 2.0 mm for analysis of the texture, nutrient and C content. The soil texture was characterized by particle size class separation, using the pipette method, as described in Embrapa (1997). The following attributes of the soil were analyzed: pH in water (1:2.5 (v:v) soil:water suspension); exchangeable Al, Ca and Mg extracted with 1 M KCl; and exchangeable P, K, Na, Zn, Fe, Mn and Cu extracted with a double acid solution (0.025 M sulfuric acid and 0.05 M hydrochloric acid–Mehlich-1 extractor), according to the standard methods compiled by Embrapa (1997). The total N was determined by Kjeldahl digestion as described by Tedesco et al. (1995). The organic matter and carbon (C) content were determined using the method of Walkley and Black (1934).

2.4. AMF spore extraction, counting and species identification

AMF spores were extracted from 50 ml of dried soil in triplicate for each sub-sample by wet-sieving and decanting (Gerdemann and Nicolson, 1963). The particles retained in the 32-μm sieve were transferred to a centrifuge tube with water and centrifuged at 1400 × *g* for 4 min. The supernatant was discarded, and the pellet was resuspended in a water–sucrose solution (60% [w/v]) and centrifuged at 900 × *g* for 1 min. The supernatant was recovered in the 32-μm sieve and washed with tap water until removal of the sucrose. Next, the spores were transferred to dishes with concentric rings and counted under a stereo microscope at 40–100× magnification. After counting, the spores were mounted on slides with polyvinyl-lacto-glycerol (PVLG) and 1:1 (v/v) PVLG + Melzer's reagent. The taxonomic characteristics of the spores were distinguished under a light microscope by using bright field and

Table 1
Principal characteristics of different habitats in the rupestrian fields of Serra do Cipó, Brazil.

Sampling sites/samples	Principal characteristics	Geographical position		Altitude (m)
		S	W	
Sandy bogs (Sb)				
Sb1	Suffer periodic flooding during the rainy season and remains dry during the dry season. The herb layer is continuous. Predominance of Poaceae, Eriocaulaceae, Cyperaceae, Asteraceae and Melastomataceae families. Dominant species: *Lagenocarpus rigidus* (Cyperaceae)	19°16′50.2″	43°35′27.7″	1158
Sb2		19°16′47.5″	43°35′24.2″	1173
Sb3		19°16′46.1″	43°35′23.2″	1154
Peat bogs (Pb)				
Pb1	Remains constantly wet during the rainy season and retains moisture in the dry season. There was a predominance of the herbaceous layer, with members of Poaceae, Asteraceae and Cyperaceae. Melastomataceae also frequent. Dominant species: *Axonopus siccus* (Poaceae)	19°16′53.0″	43°35′26.6″	1138
Pb2		19°16′54.4″	43°35′29.0″	1146
Pb3		19°17′10.4″	43°35′34.0″	1179
Rocky outcrops (Ro)				
Ro1	Predominance of herbaceous species of the Poaceae, Asteraceae and Cyperaceae families, and shrubs and subshrubs of the Velloziaceae and Rubiaceae families. These shrubs grow roots in rock crevices or agglomerate into small depressions within the same outcrop, where there may be greater deposition of sand. Dominant species: *Trachypogon spicatus* (Poaceae)	19°17′15.2″	43°35′39.2″	1163
Ro2		19°17′07.9″	43°35′44.8″	1175
Ro3		19°17′04.1″	43°35′39.9″	1121
Quartz gravel field (Qf)				
Qf1	Habitat peculiarity of soil surface coverage by small fragments of quartzite rocks. Predominance of herbaceous plants of the Eriocaulaceae, Poaceae, Asteraceae, and Cyperaceae families. Dominant species: *Vellozia* sp. (Velloziaceae)	19°17′09.0″	43°35′20.0″	1182
Qf2		19°17′10.0″	43°35′15.1″	1194
Qf3		19°17′04.1″	43°35′37.7″	1192
Cerrado (Ce)				
Ce1	Predominance of tree and shrub species. Poaceae, Fabaceae and Asteraceae are among the most representative families. Dominant species: *Schizachyrium tenerum* (Poaceae)	19°16′55.0″	43°35′35.8″	1150
Ce2		19°16′57.7″	43°35′40.0″	1173
Ce3		19°17′04.1″	43°35′37.7″	1192

Table 2
Chemical soil attributes of the different habitat types studied in the rupestrian fields from Serra do Cipó.

Chemical soil attributes	Habitats types from rupestrian fields					F
	Sandy bogs	Peat bogs	Rocky outcrops	Quartz gravel field	Cerrado	
pH (H_2O)	4.2 ± 0.1 b	4.9 ± 0.2 a	4.1 ± 0.2 b	4.4 ± 0.1 b	5.0 ± 0.1 a	7.4^{**}
Ca^{2+} (cmolc/kg)	0.2 ± 0 b	0.4 ± 0.1 a	0.2 ± 0 b	0.2 ± 0 b	0.3 ± 0.1 a	4.1^{*}
Mg^{2+} (cmolc/kg)	0.2 ± 0 b	0.4 ± 0.1 a	0.2 ± 0 b	0.2 ± 0 b	0.3 ± 0.1 a	4.1^{*}
K^{+} (cmolc/kg)	0.04 ± 0.1 a	0.08 ± 0 a	00.7 ± 0 a	0.05 ± 0 a	0.11 ± 0 a	3.6^{*}
Na^{+} (cmolc/kg)	0.01 ± 0 a	0.02 ± 0 a	0.01 ± 0 a	0.01 ± 0 a	0.02 ± 0 a	1.2^{ns}
Al^{3+} (cmolc/kg)	1.93 ± 0.2 a	0.93 ± 0.3 b	0.97 ± 0.4 b	0.90 ± 0.1 b	0.66 ± 0.1 b	3.4^{*}
P (mg/kg)	2 ± 0.6 a	3 ± 0.9 a	2 ± 0 a	3 ± 0.8 a	2 ± 0.3 a	1.4^{ns}
C (g/kg)	8.3 ± 1.8 a	19.9 ± 7.5 a	11.8 ± 0.5 a	13.7 ± 1.5 a	19.7 ± 3.4 a	2.2^{ns}
OM (g/kg)	13.5 ± 3.2 a	34.6 ± 12.9 a	20.3 ± 0.9 a	23.2 ± 2.6 a	26.1 ± 5.9 a	2.2^{ns}
N (mg/kg)	0.7 ± 0.1 b	1.5 ± 0.5 a	0.9 ± 0.1 b	0.8 ± 0.1 b	1.7 ± 0.1 a	3.3^{*}
Cu (mg/kg)	1.05 ± 0.7 a	0.52 ± 0.2 a	0.21 ± 0.1 a	0.26 ± 0 a	1.26 ± 0.2 a	1.8^{ns}
Fe (mg/kg)	79.73 ± 18.7 b	152.33 ± 29.5 a	66.33 ± 15 b	59.30 ± 10.3 b	44.70 ± 5.5 b	5.6^{*}
Mn (mg/kg)	0.35 ± 0.0 b	1.27 ± 0.3 b	0.47 ± 0 b	0.82 ± 0.1 b	5.92 ± 1.1 a	21.7^{**}
Zn (mg/kg)	1.85 ± 1.7 a	0.32 ± 0.1 a	0.32 ± 0.1 a	0.88 ± 0.8 a	0.37 ± 0 a	0.7^{ns}

Data are reported as averages for three replicate plots per vegetation types. Non-significant (ns) differences between vegetation types are shown by identical letters, determined using Tukey test at the1% level (**) and 5% level (*) following one-way ANOVA.

immersion objectives. The spores were counted and identified to the species level based on current species descriptions and identification manuals (Schenck and Pérez, 1990).

2.5. Statistical analyses

We estimated the AMF diversity by the Shannon index and the Spearman correlation coefficient was applied to identify correlations between AMF richness and plant species. Analyses of variance (ANOVA) were applied to test differences in soil attributes, spore densities and diversity. The means were compared with Tukey's tests at 5% significance using the *R*. Principal Component Analysis (PCA) was applied to demonstrate the ordination of the AMF species into the five rupestrian habitat types and to identify which soil attributes were related with AMF species. The five habitats, the physical and chemical attributes of soil, and the 49 AMF species were transformed into ordinates corresponding to their projection on the ordination axes, or eigenvalues, representing the weight of each variable on each component (axis) and with a correlation coefficient ranging from −1 to +1. These analyses were performed using CANOCO version 4.5 software (Ter Braak and Smilauer, 1998). PCA was performed after Detrended Correspondence Analysis (DCA) to determine the length of the gradient. PCA was used as it presented a gradient value below 3. In this work, we considered an eigenvalue ≥0.4 to indicate high association for interpretation of the principal components. A simple correlation analysis between AMF richness and soil physical attributes was made with the help of *R*.

3. Results

3.1. Soil attributes

Soils from all five habitats were dystrophic, acidic and with medium values of organic matter (Table 2). However, peat bogs and the Cerrado showed higher levels of N, $Ca^{2+}$and Mg^{2+} than the other habitats studied. The Cerrado showed higher levels of Mn^{2+} and peat bogs showed higher levels of Fe. All soils showed medium levels of Al^{3+} except for sandy bogs, which showed higher levels of Al^{3+} than the others (Table 2). The soil texture of the majority of the plots was sandy loam, except for the Cerrado plots, which have clay loam (Table 3). The silt fraction was the only fraction that did not show statistical differences among the habitats studied, whereas the gravel fraction was the most discriminatory (Table 3).

3.2. AMF spore densities and species diversity

The AMF spore densities were consistently higher in the quartz gravel fields than in the other habitats studied (Fig. 2). In total, 49 AMF species were identified in the 15 samples taken from the five rupestrian habitats in Serra do Cipó (Table 4). The average species richness found in the quartz gravel field was significantly higher when compared with the other rupestrian fields studied (Fig. 3a). *Glomus* was the genus with the highest number of species recovered (19), followed by *Acaulospora* (13), *Scutellospora* (4), among others, see (Table 4).

The AMF diversity of the different rupestrian field habitats of Serra do Cipó showed no statistical differences based upon the Shannon diversity index (Fig. 3b). Nevertheless, the AMF communities showed interesting features. Only 5 out the 49 species found were common to all of the studied rupestrian field habitats (*Acaulospora morrowiae*, *Scutellospora calospora*, *Glomus etunicatum*, *G. invermaium* and *G. macrocarpum*), while other species were found only in one habitat (Table 5). Some AMF species found in our study had not been previously recorded in Brazil (*A. colossica*, *G.* aff. *pellucidum* and *Pacispora dominikii*). Potentially undescribed species were also found in our study (Table 5). The identities of *G.* aff. *pellucidum* and *A.* aff. *bireticulata* could not be confirmed

Table 3
Granulometric characterization and soil texture of the different habitats studied in the rupestrian fields from Serra do Cipó, State Minas Gerais, Brazil.

Habitats types from rupestrian fields	Gravel, g/kg	Coarse sand, g/kg	Fine sand, g/kg	Silt, g/kg	Clay, g/kg	Soil texture
Sandy bogs	122 ± 63.9 c	293 ± 51.1 a	487 ± 41.6 a	198 ± 19.9 a	20 ± 0 b	Sandy loam
Peat bogs	70 ± 27.1 d	172 ± 30.9 b	529 ± 26.5 a	271 ± 48.5 a	27 ± 7 b	Sandy loam
Rocky outcrops	226 ± 78.3 b	107 ± 8.6 b	507 ± 16.2 a	352 ± 21.7 a	33 ± 13.3 b	Sandy loam
Quartz gravel field	470 ± 121.8 a	266 ± 10.1 a	470 ± 22.9 a	243 ± 25.4 a	20 ± 0 b	Sandy loam
Cerrado	7 ± 7 e	183 ± 16.8 b	270 ± 50.5 b	293 ± 64.5 a	299 ± 100.5 a	Clay loam
F	162.9^{**}	23.2^{**}	9.5^{**}	2.1ns	7.3^{**}	

Data are reported as averages for three replicate plots per habitat types. Averages followed by the same letter in columns did not differ by Tukey's test at 1% (**) significance level. Non-significant (ns) difference between treatments.

Table 4
Arbuscular mycorrhizal fungal genera and species richness found at 15 sites in five habitats in the rupestrian fields of Serra do Cipó, Brazil.

	Sb	Pb	Ro	Qf	Ce	Species richness
Acaulosporaceae						
Acaulospora	4	7	4	7	5	13
Kuklospora	0	1	0	0	0	1
Ambisporaceae						
Ambispora	1	2	0	2	0	2
Dentiscutataceae						
Dentiscutata	1	0	1	1	1	1
Fuscutata	0	1	1	0	2	2
Gigasporaceae						
Gigaspora	0	0	1	1	1	2
Glomeraceae						
Glomus	9	8	10	15	9	19
Pacisporaceae						
Pacispora	2	0	0	1	1	2
Paraglomeraceae						
Paraglomus	0	0	1	1	0	1
Scutellosporaceae						
Scutellospora	2	2	2	4	2	4
Racocetraceae						
Racocetra	0	0	1	1	1	1
Cetraspora	0	0	0	0	1	1
Total species richness	19	21	21	33	23	49

Sb: Sandy bogs; Pb: Peat bogs; Ro: Rocky outcrops; Qf: Quartz gravel field; Ce: Cerrado.

because the number and quality of the spores did not allow for accurate identification, which is a well-known problem in AMF spore identification from field samples. Four potentially undescribed species were found. Two species with acaulosporoid morphologies were found in the peat bogs. One species with scutellosporoid morphology was found in the rocky outcrops. The other species possesses a glomoid morphology and was found in the rocky outcrops and quartz gravel fields.

3.3. Plant diversity

We recorded 171 species of plants, which were classified in 110 genera and 44 families, in the studied area. The plant species richness and Shannon diversity index were similar between the habitat types except for the rocky outcrops, which showed significantly higher richness (Fig. 3c), and the sandy bogs, which exhibited the lowest diversity index (Fig. 3d).

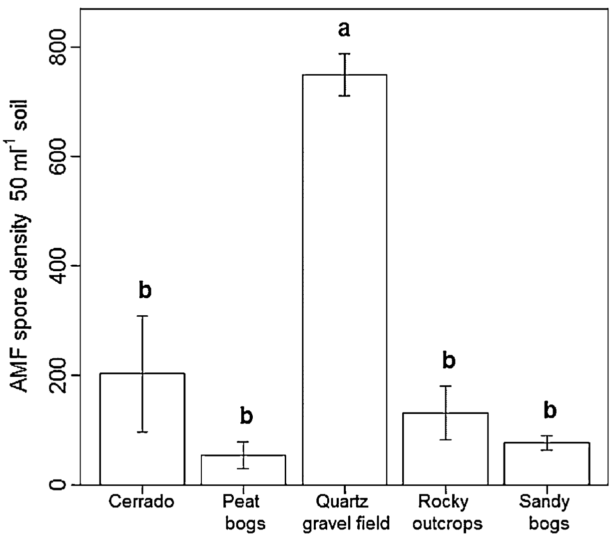

Fig. 2. AMF spore density of different habitats in the rupestrian fields of Serra do Cipó, Brazil (±SD). Values in the columns followed by the same letter are not different based on Tukey's tests ($P < 0.05$).

3.4. AMF species and soil attributes

Considering the soil attributes, the first two components of PCA explain 67.1% of the total variability in the data. Of this total, 52.1% is explained by axis 1 and 15% by axis 2 (Fig. 4a and b). Except for the content of fine sand and clay, the variables pH, Ca, Mg, K, Na, Al, P, OM, N, Cu, Fe, Zn, and Mn are not to be related to the ordination axes (Table 6). The first axis is directly related to the variable content of gravel (0.90) and coarse sand (0.62) and inversely related to the silt content (−0.46). Axis 2 is inversely correlated with gravel (−0.40). The silt and sand variables are not correlated with this axis.

PCA analysis has shown soil physical attributes have presented a greater influence on AMF occurrence than soil chemical attributes. Before this, a simple correlation analysis between AMF richness and soil physical attributes was made. This correlation has shown to be significant only for gravel ($r = 0.51$, p-value = 0.00278, $P < 0.01$).

The occurrence of *G. macrocarpum* (Gmac), *G. invermaium* (Ginv), *A. morrowiae* (Amo), *S. pernambucana* (Spe), *A. delicata* (Ade), *A.* aff. *bireticulata* (Abi), *Dentiscutata biornata* (Dbi), *G.* aff. *multiforum* (Gmu), *G. diaphanum* (Gdi) and *Scutellospora* sp. 1 (Ssp1) are directly related to the coarse sand and gravel content (Fig. 4b). The other AMF species did not show a correlation with the physical and chemical attributes of the soil.

3.5. Plant diversity × AMF diversity

The diversity of plant species was not significantly correlated with the diversity of AMF ($r = 0.167$; $P > 0.05$) (Fig. 5). However, considering the five habitats individually, the samples from sandy bog, quartz gravel field and rocky outcrop habitats remained clustered, showing three distinct patterns of organization. In sandy bogs, the communities of plants and AMF showed low species richness. In quartz gravel fields, the plant communities showed low richness while the AMF communities had high species richness. In the rocky outcrops, the plant communities showed high species richness and the AMF communities exhibited low richness (Fig. 3a and c).

Table 5
AMF species recorded of different habitats in the rupestrian fields of the Serra do Cipó, State of Minas Gerais, Brazil.

Abbrev.	AMF species	Sandy bogs	Peat bogs	Rocky outcrops	Quartz gravel field	Cerrado
Acaulosporaceae						
Abi	*Acaulospora* aff. *bireticulata* Rothwell & Trappe				+	
Aca	*A. cavernata* Blaszkowski	+		+	+	+
Aco	*A. colossica* Schultz, Bever & Morton		+			
Ade	*A. delicata* Walker, Pfeifer & Bloss				+	
Ako	*A. koskei* Blaszkowski	+	+	+	+	
Alo	*A. longula* Spain & Schenck	+	+			
Ame	*A. mellea* Spain & Schenck		+		+	+
Amo	*A. morrowiae* Spain & Schenck	+	+	+	+	+
Aru	*A. rugosa* Morton				+	
Asc	*A. scrobiculata* Trappe			+		+
Asp	*A. spinosa* Walker & Trappe					+
Asp1	*Acaulospora* sp. 1		+			
Asp2	*Acaulospora* sp. 2		+			
Kco	*Kuklospora colombiana* (Spain & Schenck) Oehl & Sieverd.		+			
Ambisporaceae						
Aap	*Ambispora appendicula* (Spain, Sieverd.ing & Schenck) Walker	+	+		+	
Abr	*Ambispora brasiliensis* Goto, Maia & Oehl		+		+	
Dentiscutaceae						
Dbi	*Dentiscutata biornata* (Spain, sieverd. & Toro) Sieverd, Souza & Oehl	+		+	+	+
Dhe	*Fuscutata heterogama* Oehl, Souza, Maia & Sieverd.ing		+	+		+
Fru	*Fuscutata rubra* (Stürmer & Morton) Oehl, souza & Sieverd.ing					+
Gigasporaceae						
Gide	*Gigaspora decipiens* Hall & Abbott					+
Gima	*G. margarita* Becker & Hall			+	+	
Glomeraceae						
Gcla	*Glomus claroideum* Schenck & Smith		+	+	+	
Gcl	*G. clarum* Nicololson & Schenck			+	+	+
Gco	*G. constrictum* Trappe		+			
Gdi	*G. diaphanum* Morton & Walker		+		+	
Get	*G. etunicatum* Becker & Gerdemann	+	+	+	+	+
Gfa	*G. fasciculatum* (Thaxter) Gerdemann & Trappe emend. Walker & Koske	+			+	+
Gge	*G. geosporum* (Nicolson & Gerdemann) Walker	+				
Ggl	*G. glomerulatum* Sieverding	+	+		+	+
Gin	*G.* aff. *insculptum* Blaszkowski	+			+	+
Ginv	*G. invermaium* Hall	+	+	+	+	+
Gla	*G. lamellosum* Dalpé, Koske & Tews				+	
Gma	*G. macrocarpum* Tul.asne & Tul.asne	+	+	+	+	+
Gmi	*G. microaggregatum* Koske, Gemma & Olexia	+	+	+	+	
Gmic	*G. microcarpum* Tul.asne & Tul.asne			+	+	+
Gmu	*G.* aff. *multiforum* Tadych & Błaszkowski	+		+	+	
Gmo	*G. mosseae* (Nicolson & Gerdemann) Gerdemann & Trappe				+	
Gpe	*G.* aff. *pellucidum* McGee & Pattinson			+		
Gve	*G.* aff. *verruculosum* Blaszkowski					+
Gsp	*Glomus* sp.			+	+	
Pacisporaceae						
Pdo	*Pacispora dominikii* Blaszkowski emend. Sieverding & Oehl	+				
Pro	*(cf) P. robiginia* Sieverding & Oehl	+			+	+
Paraglomeraceae						
Poc	*Paraglomus occultum*			+	+	
Scutellosporaceae						
Sca	*S. calospora* (Nicolson & Gerdemann) Walker & Sanders	+	+	+	+	+
Sdi	*S. dipurpurescens* Morton & Koske	+			+	
Spe	*S. pernambucana* Oehl, Silva, Freitas & Maia		+	+	+	+
Scu	*Scutellospora* sp. 1				+	
Racocetraceae						
Rfu	*Racocetra fulgida* (Koske & Walker) Oehl, Souza & Siverding			+	+	+
Cgi	*Cetraspora gilmorei* (Trappe & Gerdemann) Oehl, Souza & Sieverding					+

+ Indicates presence.

4. Discussion

4.1. AMF richness from rupestrian fields of Serra do Cipo

The rupestrian fields of the Serra do Cipó contains specimens classified in 12 out of the 18 known genera of AMF (Table 7). The genus *Glomus* had the highest number of species. However, *Glomus* has 111 described species, which represent more than 50% of all known AMF species worldwide (216 in total, Table 7). By contrast, genera, such as *Kuklospora*, are represented by only two described species. The collector's curve indicated that our sampling effort did not reach saturation for these sites (Fig. 6), thus the richness of these fields might be higher than we estimate here. Results of this research revealed that rocky fields shelter 23% AMF species described all over the world and 41% of identified species in Brazilian ecosystems (Stürmer and Siqueira, 2008; de Souza et al., 2010) (Table 7) and therefore suggest that rupestrian fields is a hotspot for glomeromycetes, or else a prioritary place for conservation, with high diversity and threatened in the highest degree (Myers et al., 2000; Rapini et al., 2002; Ribeiro et al., 2009).

Although remarkable, the AMF diversity in rupestrian fields may be underestimated, as the collector's curve indicates that the samples were insufficient to detect all of the diversity present. Due to

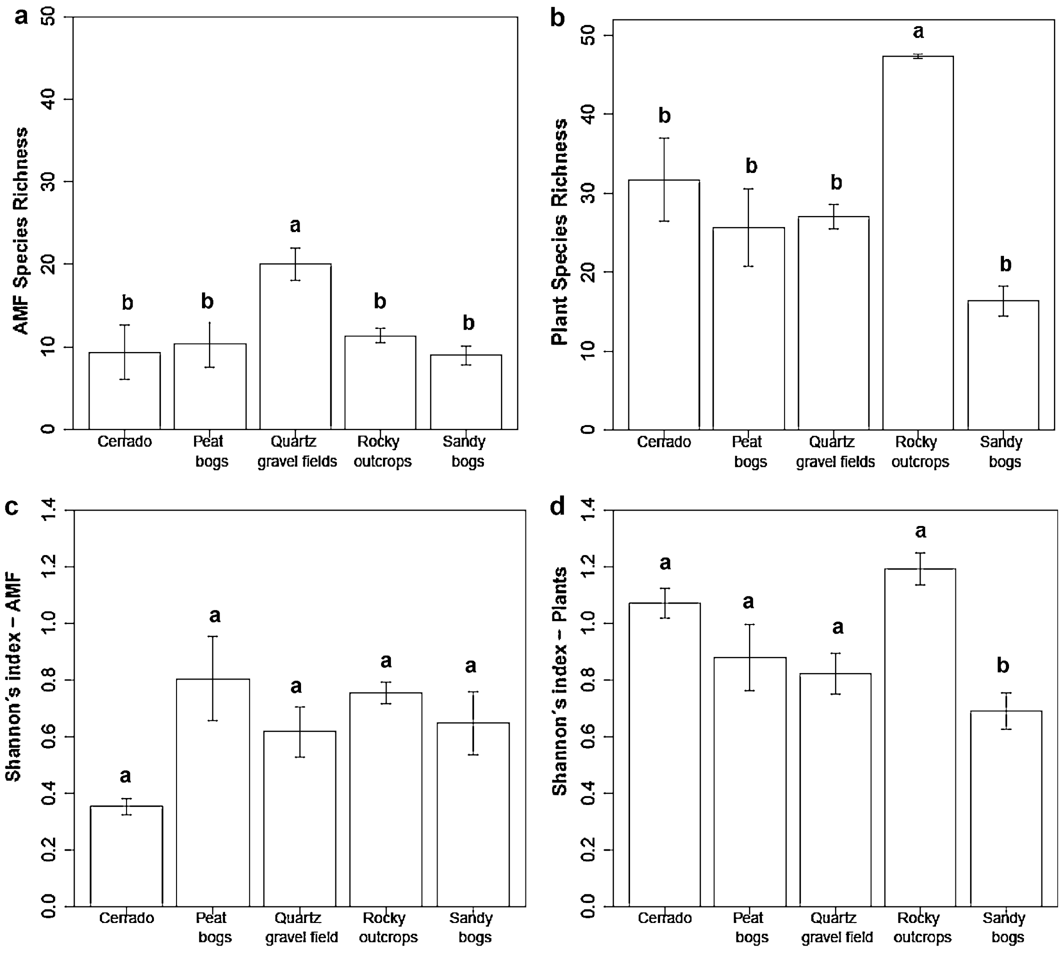

Fig. 3. Species richness of AMF (a) and plants (b) and Shannon Diversity Index (base ln) of AMF (c) and plants (d) of five different habitats in rupestrian fields of Serra do Cipó, State of Minas Gerais, Brazil (±SD). Values in the columns followed by the same letter are not different based on Tukey's tests ($P < 0.05$).

the lack of information about the diversity of AMF in this ecosystem, we opted for samples that would cover the five habitats instead of performing a more detailed evaluation for only one of them. In fact, usually not all components of the mycorrhizal community are in the form of spores in a given sampling time (Bartz et al., 2008). This study assessed the occurrence of AMF in a single seasonal period; therefore, not all of the species present in the ecosystem had sporulated at the time of sampling (dry season). However, the dry season has been described by some authors as the time when the highest AMF species richness could be detected (Caproni et al., 2003; Souza et al., 2003; Tchabi et al., 2008). Moisture along with the growth of plants favors vegetative growth of the fungus, resulting in root

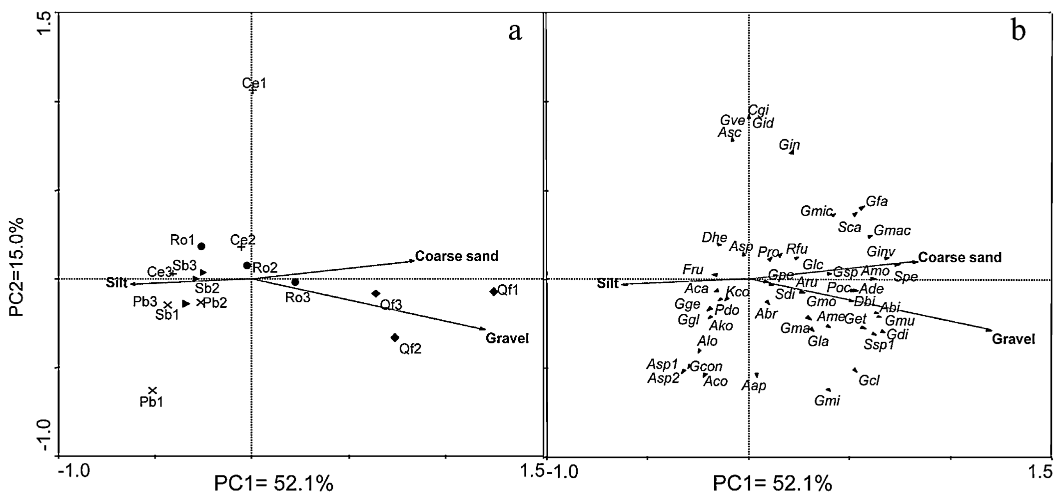

Fig. 4. Ordination diagram (PCA) of five different habitats in rupestrian fields (S = sandy bogs; Pb = Peat bogs, rocky outcrops Ro = , Qf = Quartz gravel field, Ce = Cerrado) with the soil attributes (coarse sand, gravel and silt) related to the ordination axes (eigenvalue ≥0.4, Table 6) (a) and with 49 AMF species found in five different habitats in rupestrian fields (b). The AMF species are abbreviated, and the full list is in Table 5.

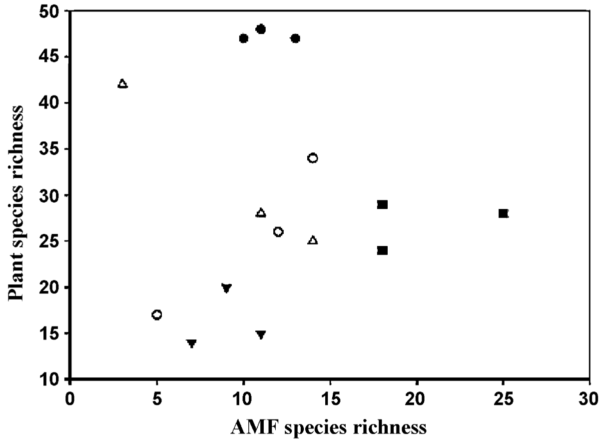

Fig. 5. Relationship between plant and AMF species richness recorded in each sample from different habitats in rupestrian fields: ▼ = Sandy bogs; ○ = Peat bogs; ● = Rocky outcrops; ■ = Quartz gravel fields; △ = Cerrado.

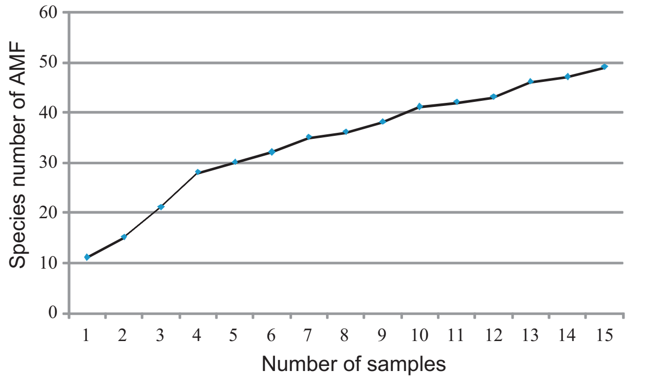

Fig. 6. Collector's curve of AMF based on total number of samples analyzed for all five rupestrian sites.

Table 6
Loading for PC1 and PC2 of Principal component analysis of the attributes of 19 soil chemical and physical variables measured at different habitats in the rupestrian fields of the Serra do Cipó, Minas Gerais State, Brazil.

Variables	Factor 1	Factor 2
pH	−0.08	0.26
Ca^{2+}	−0.16	0.18
Mg^{2+}	−0.12	0.18
K	−0.04	0.14
Na	−0.14	0.11
Al	−0.08	0.26
P	−0.02	−0.22
OM	−0.08	0.16
N	−0.08	0.18
Cu	−0.05	0.24
Fe	−0.14	0.11
Zn	−0.08	0.14
Mn	−0.12	−0.22
Gravel	**0.90***	**−0.40**
Fine sand	−0.15	0.12
Coarse sand	**0.62**	−0.15
Clay	−0.08	0.18
Silt	**−0.46**	−0.04

(*) Values in bold ≥ 0.4 indicate high association for interpretation of the principal component analysis (see Fig. 4).

colonization and reduction of the number of spores present in the soil (Guadarrama and Álvarez-Sánchez, 1999).

Among the 49 AMF species, four are probably undescribed species and likely belong to the genera: *Acaulospora* (2), *Scutellospora* (1) and *Glomus* (1). Although glomoid morphology is shared by several genera (*Glomus*, *Paraglomus*, *Diversispora* and *Pacispora*), molecular identification might be necessary for proper classification of a glomoid spore (de Souza et al., 2008).

The discovery of undescribed species in areas considered vulnerable, such as the rupestrian fields (Menezes and Giulietti, 2000; Ribeiro and Fernandes, 2000; Viana et al., 2005), reinforces the urgent need for more research on the ecology and diversity of these fungi in this environment. Comparison of the richness of AMF found in this study with other Brazilian ecosystems (Stürmer and Siqueira, 2008) reveals that AMF are highly diverse in these rupestrian fields. The glomeromycotan species richness reported in our study was higher than the rainforests in Costa Rica (13 spp.) (Lovelock et al., 2003), the hot-dry valley of the Jinsha River, southwest China (43 spp.) (Dandan and Zhiwei, 2007), boreal forests (34 spp.) (Öpik et al., 2008), Mongolia's steppes (27 spp.) (Tian et al., 2009), and ecosystems in India (35 spp.) (Karthikeyan and Selvaraj, 2009). However, the diversity reported in these studies is based on more than one

Table 7
AMF phylogenetic classification according to order, family and genus; the number of species described by genera in the world, in Brazil (% of species found in Brazil in comparison to those described in the world) and in the rupestrian fields (% of species found in rupestrian fields in comparison to those described in the world and in Brazil).

Order	Family	Genera	Number of AMF species		
			Described in the world	Recorded in Brazil	Recorded in this study Rupestrian fields
Archaeosporales	Archaeosporaceae	*Archaeospora*	1	1 (100%)	0
		Intraspora	1	1 (100%)	0
	Ambisporaceae	*Ambispora*	8	5 (63%)	1 (13; 20%)
Diversisporales	Acaulosporaceae	*Acaulospora*	34	23[a] (68%)	14 (41; 61%)
		Kuklospora	2	2 (100%)	1 (50; 50%)
	Diversisporaceae	*Diversispora*	2	1 (50%)	0
		Otospora	1	0	0
	Entrophosporaceae	*Entrophospora*	2	1 (50%)	0
	Gigasporaceae	*Gigaspora*	8	6 (75%)	2 (25; 33%)
	Scutellosporaceae	*Scutellospora*	10	6 (60%)	4 (40; 67%)
	Dentiscutataceae	*Dentiscutata*	7	6 (86%)	2 (29; 33%)
		Fuscutata	4	2 (50%)	1 (25; 50%)
		Quatunica	1	1 (100%)	0
	Racocetraceae	*Cetraspora*	5	2 (40%)	1 (20; 50%)
		Racocetra	9	8 (89%)	1 (11; 12%)
	Pacisporaceae	*Pacispora*	7	3[a] (43%)	2 (28; 67%)
Glomerales	Glomeraceae	*Glomus*	111	52 (47%)	19 (17; 37%)
Paraglomerales	Paraglomeraceae	*Paraglomus*	3	2 (67%)	1(33; 50%)
Total = 4	12	18	216	122 (56%)	49 (23; 40%)

[a] Include species of that study.

sampling period or the AMF species were determined with the help of a trap crop.

Notably, when the AMF diversity in agroecosystems was evaluated only with field samples, Bever et al. (2001) identified 11 AMF species; after five years of sampling and attempts to isolate AMF in a trap cultures, the number of AMF species increased to 37.

4.2. What are the driving forces that shape the diversity of AMF in the rupestrian fields of Serra do Cipo?

The high diversity found in the rupestrian fields of Serra do Cipó can be attributed to heterogeneity within the habitats of these fields, with soil physical attributes (grain size and texture) having the greatest influence on the occurrence of AMF species and the presence of dominant plant species, suggesting distinct patterns in the constitution of AMF communities (Table 1).

Texture is a property closely related to soil structure, it is directly linked to several soil physical and chemical attributes, such as capacity to Exchange cations, retaining and soaking water, draining, erodibility, among others (Meurer, 2007). Several works have reported the importance of AMF for soil structure (Rillig and Steinberg, 2002; Rillig and Mummey, 2006), however there are no works which describe the influence of soil texture over diversity or even related to AMF occurrence. Nevertheless we should consider that fungi may potentially influence soil aggregation in different levels by means of plant community, individual host and by means of AMF mycelium (Rillig and Mummey, 2006). Products from AMF mycelium such as glomalin protein have important roles in aggregation and stabilization of aggregate (Moreira and Siqueira, 2006) and studies simulating little aggregate soil (as the case of gravelly soil present in quartz gravel fields habitat) which has shown greater glomalin concentration, hence revealing an important feedback between fungal growth and soil structure (Rillig and Mummey, 2006).

Most studies on the occurrence of AMF in Cerrado natural ecosystems have been performed in areas covered by Cerrado *stricto sensu*. Only one study was done in rupestrian fields (Pagano and Scotti, 2009); these authors found only three AMF species, among which, *D. biornata* is the only species common to this study. They also reported two undescribed species (*Acaulospora* sp. and *Glomus* spp.), supporting our hypothesis that rupestrian fields are a hotspot for Glomeromycetes.

Thirty-eight percent of the species found in this study were reported in other studies conducted in the Cerrado (Bononi and Trufem, 1983; Schenck et al., 1989; Siqueira et al., 1989) among them *Ambispora brasiliensis*, which was recently described and so far is only found in the Cerrado of Serra do Cipó, MG (Goto et al., 2008).

S. pernambucana, another recently described species (Silva et al., 2008), was isolated in areas of the Caatinga and Atlantic Forest in the Pernambuco state and now in the rupestrian fields of Minas Gerais, which suggests that it widely occurs in different types of ecosystems.

A. morrowiae, *S. calospora*, *G. etunicatum*, *G. invermaium* and *G. macrocarpum*, species widely present in the five habitats investigated in the rupestrian fields, have been reported in several studies in different ecosystems and with various conservation statuses (Mehrotra, 1998; Stürmer and Siqueira, 2008).

The occurrence of exclusive species suggests a higher affinity of these AMF species with specific conditions of the habitat (Table 4). However, only *A. bireticulata* and *Scutellospora* sp.1 were related to the physical attributes of the soil (Fig. 4b), indicating that other environmental factors may be influencing the establishment and fixation of these species (Table 1).

4.3. AMF diversity × plant diversity

The habitats that make up the rupestrian fields presented different compositions of AMF species (Table 4). These natural habitats are heterogeneous, which has been attributed to several abiotic factors (Giulietti et al., 1987; Giulietti and Pirani, 1988; Vitta, 2002; Benites et al., 2003), such as soil texture. However, the different compositions of AMF in this study may also contribute to the heterogeneity of these environments, especially considering that the diversity and productivity of the plant communities are closely linked with the AMF diversity. Moreover, the plant communities regulate AMF progress in terms of occupation and exploitation of niches (Grime et al., 1987; van der Heijden et al., 1998, 2006), as different species of host plants create their own habitat around their roots and may lead to the establishment of distinct AMF species (Carrenho et al., 2001). Despite the presence of a positive correlation between plant diversity and AMF diversity, distinct patterns of organization in accordance with the type of habitat studied could be observed. These patterns are shown in Table 4, where the smallest number of AMF was observed in the sandy bogs and rock outcrops. The dominant plant species in sandy bogs is *Lagenocarpus rigidus*, which is a species of the Cyperaceae family, which is recognized as non-mycorrhizal (Trappe, 1987) or mycorrhizal with low incidence (Muthukumar et al., 2004). In rocky outcrops the dominant species is *Trachypogon spicatus*, a slow-growing climax Poaceae, whose seral stage in tropical regions is slightly dependent on AMF association (Zangaro et al., 2002; Pasqualini et al., 2007). Conversely, high AMF richness was found in gravel fields, with *Vellozia* sp. as the dominant plant species in this habitat. This species is a monocotyledon, which ceases photosynthetic activity under drought deficit conditions (Owoseya and Sanford, 1972). As in the present study, data were collected during the dry season, so the greater richness may reflect the physiological changes of the dominant species, which may have stimulated the sporulation of AMF associated with their roots, thereby contributing to the richness.

4.4. AMF spore density

The density of spores in this study is higher than that observed in degraded areas of the Cerrado for the same sampling season (dry season) (Martins et al., 1999).

The AMF density is related to the aggregated form of spores found in soil and to the distribution, morphology and physiological age of the roots (Anderson et al., 1983; Zangaro et al., 2008). Moreover, the concentration of AMF propagules is usually strongly correlated with vegetation cover and soil conditions (Sieverding, 1991).

Therefore, the soils evaluated in this study likely provided conditions for the establishment of the AMF, as the limitation of mineral resources interferes with plant growth, conditions that favor mycorrhizal associations (Moreira and Siqueira, 2006). Species such as *A. scrobiculata*, *G. macrocarpum*, *G. mosseae*, *G. fasciculatum* and *G. claroideum* are considered indifferent to the levels of soil fertility (Siqueira et al., 1989; Jonhson, 1993; Weber and Oliveira, 1994), and others are restricted by factors such as soil acidity. According to Stümer (1999), *Acaulospora* species are more prevalent in acidic soils. The highest occurrence of the genera *Glomus* and *Acaulospora* observed in this study corroborates data obtained from other Brazilian ecosystems as reviewed in (de Souza et al., 2010). Future studies on the effects of AMF on the growth of native species present in the rupestrian fields are essential to the preservation and maintenance of this tropical montane ecosystem, and will contribute to the knowledge of AMF diversity and function not only in Brazil but also worldwide.

5. Conclusions

The results of this study indicate that the rupestrian fields are an AMF biodiversity hotspot. This diversity is related to the variability among the mosaic of habitats composing the rupestrian fields. Among these variabilities, soil texture (content of gravel, sand and silt), which is more related to AMF richness than the chemical attributes of soil, should be highlighted. The plant species richness was related to AMF species richness in the quartz gravel field, rocky outcrop, and sandy bog habitats.

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