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Community structure of arbuscular mycorrhizal fungi in fluvial and maritime dunes of Brazilian Northeast

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ABSTRACT

Arbuscular mycorrhizal fungi (AMF) are indispensable for the establishment of plant communities, which is essential for the stabilization of sediments in ecosystems, such as sand dunes. This study aimed at assessing the diversity and distribution of AMF in fluvial and maritime dunes, in order to verify if AMF community structure is influenced by physical and chemical soil characteristics. AMF species richness, diversity and community composition, spore density and mycorrhizal colonization were investigated in four natural dunes areas, i.e. two fluvial and two maritime dunes in Bahia State, northeastern Brazil. Soil samples were collected in September 2013 and March 2014. Spore density differed significantly among the dunes and sampling times, with the highest values recorded in the maritime dunes. Fifty-four AMF species were identified in the study areas, of which 51 were identified from field samples and three additional (*Acaulospora longula*,*Acaulospora spinosa* and *Rhizoglomus natalense*) after propagation in trap cultures. The most representative genera were *Acaulospora* (11), *Glomus* (10) and *Gigaspora* (8). *Gigaspora margarita* was the only species found in all areas at both sampling times. The AMF community composition significantly differed among the four dunes. There was a correlation between the AMF community composition and the soil characteristics. Highest species richness per sample was observed in the areas of maritime dunes. The fluvial and maritime dunes of Bahia showed high diversity of AMF and the soil is an important factor in the structure of the AMF community in sand dunes.

1. Introduction

Dunes are sand deposits formed in coastal regions (coastal or maritime dunes), or along river margins and deserts (inland dunes) that can be mobile or fixed, depending on the establishment of vegetation (Giannini et al., 2005). They are fragile and dynamic systems, subjected to natural (erosion) and anthropogenic (mining, tourism) disturbances, which affect the vegetation and physical substrate (Emery and Rudgers, 2010).

In Brazil, the category of plant communities covering dunes is called *restinga* and, having the function of "dune-fixing", it is protected by law (MMA, 2010). Due to the importance of *restingas* for the functional equilibrium of inland and coastal dune environments, it is important to elaborate management strategies that promote the maintenance of important stabilizing plant communities in these environments.

As key components of soil microbiota, arbuscular mycorrhizal fungi (AMF) play an important role in contributing to the maintenance of plant communities (Smith and Read, 2008). The AMF belong to the phylum Glomeromycota, which includes about 270 described species. These fungi are an important link in the soil-plant interface, because they form a mutualistic symbiosis with plant roots of over 80% of vascular plants and act as efficient facilitators for the absorption of nutrients by their host plants, including most inaccessible nutrients (e.g. phosphorous), increase in the complementarity of nutritional resources, ensures greater tolerance to biotic and abiotic stresses, and contribute to the

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stabilization of soils due to the formation of stable soil aggregates (Smith and Read, 2008). These fungi also influence the floristic composition and productivity of ecosystems (van der Heijden et al., 2008).

In dune areas, where environmental conditions are adverse and soils are predominantly sandy and have low nutrient contents, high salinity and low water availability, the arbuscular mycorrhizal symbiosis is an important strategy for plant species to support environmental stresses and be able to develop in these locations (Camprubí et al., 2010). In addition to the role of AMF in the greater availability of nutritional resources, AMF also play a significant role in the stabilization and rehabilitation of dunes. They accomplish this by actively participating in the control of soil erosion through the formation of aggregates, due to the production of glomalin and development of a vast network of hyphae (Aytok et al., 2013; Rillig and Mummey, 2006). The hyphae are also important for water retention and help to stabilize the substrate (Bedini et al., 2009). In these ways, these fungi contribute to the maintenance of habitats and ecological niches of different biological communities.

Knowledge of the AMF diversity present in natural soils is relevant for establishment of conservation strategies *in situ* of these beneficial microorganisms important for the equilibrium of terrestrial environments (Turrini et al., 2010). Given the above, there is a clear need for studies aiming at improving the knowledge of the structure and diversity of AMF communities (Montaño et al., 2012). Such data can be useful for the conservation policies and management of ecosystem processes (Beena et al., 2001).

Several taxonomic and ecological studies on AMF have been carried out in areas of sand dunes and *restingas*: in the USA (Koske and Gemma, 1997), Mexico (Ramos-Zapata et al., 2011), Poland (Błaszkowski et al., 2002), and elsewhere. In Brazil, there have been several studies in areas of maritime dunes (e.g. Silva et al., 2012, 2015; Souza et al., 2012; Stürmer et al., 2013; Stürmer and Bellei, 1994; Trufem et al., 1989, 1994), of which some have contributed to the knowledge of new AMF species (Goto et al., 2011, 2012), but no study of this kind has been carried out in dune areas formed by fluvial influence. Thus, we aimed to determine the diversity, composition and aspects related to the structure of AMF communities, and the mycorrhizal condition of the plant species present in the fluvial and maritime dunes belonging to protected areas in northeastern Brazil. We tested the hypothesis that the AMF diversity is influenced by abiotic factors.

2. Material and methods

2.1. Study areas

Our study sites were four environmental protection areas (EPA) in the state of Bahia, northeastern Brazil, of which two were fluvial dunes ('Lagoa de Itaparica EPA' and 'Dunas e Veredas do Baixo—Médio São Francisco EPA') and the other two maritime dunes ('Lagoas e Dunas do Abaeté EPA' and 'Litoral Norte do Estado da Bahia EPA'). In the following, these four dune areas are shortly called Veredas and Itaparica dunes (of fluvial origin; F) and Litoral Norte and Abaeté (of maritime origin; M) (Table 1).

The Itaparica fluvial dunes are located in the municipality of Xique-Xique, 0.3 km from the Itaparica Lagoon, where, in addition to *caatinga* vegetation, there is a grove of carnauba palms (Table 2; Jacomine et al., 1976). The sampling site of the Veredas dunes is in the municipality of Barra, near the village of Ibiraba, situated at a distance of 1.5 km from the São Francisco River. The vegetation of this area is sparse and open *caatinga*, with a shrubby tree layer and patches of cacti and bromeliads (Table 2; Barreto et al., 1999; Rodarte et al., 2008). In the Abaeté area, the collection site is located 1.3 km from the sea, the vegetation includes herbaceous, shrubby and arboreal plants (Table 2; Britto et al., 1993; Britto and Noblick, 1984). The Litoral Norte dunes are located in the municipality of Mata de São João, at a distance of 1 km from the sea, where the vegetation is composed of herbaceous, shrubby and arboreal species, with typical components of ecosystems associated with Atlantic Forest (Table 2; Dias and Menezes, 2007). The soils of the studied sites were classified as Alisol (Itaparica), Planosol (Veredas) and Arenosol (Abaeté and Litoral Norte) according to FAO (2014).

2.2. Sampling times

Soil samples were collected in September 2013 (corresponding to the end of dry season and start of dry season, in the fluvial and maritime dunes, respectively) and March 2014 (corresponding to the end of rainy season and start of rainy season, in the fluvial and maritime dunes, respectively). Eight plots were delineated in each dune area (with dimensions of 5×20 m), spaced 30 m apart. In each plot a sample was taken (10 sub-samples) of soil and roots in the rhizosphere of the plants at a depth of 0–20 cm, totaling eight composite samples (about 5 kg each) per area. Part of the soil (500 g from each collection point) was sent to the 'Estação Experimental de Cana-de-açúcar do Carpina, da Universidade Federal Rural de Pernambuco (UFRPE)' for chemical and physical analysis, while the remaining soil was used in the experiments and analysis of the AMF parameters.

2.3. Evaluation of root colonization

Fine roots were selected from the soil collected, washed with water, cleared with 10% KOH (25 °C/24 h), and stained with Trypan blue (0.05%) (Phillips and Hayman, 1970). Total mycorrhizal colonization was estimated by the method of McGonigle et al. (1990), with identification of the presence and type of mycorrhizal structures (arbuscules, vesicles or hyphae).

2.4. Extraction of glomerospores and identification of AMF species

The AMF spores and sporocarps were extracted from the samples of 50 g of soil from each collection point, via wet sieving (Gerdemann and Nicolson, 1963). Next, this material underwent

Table 1
Geographic position and climate characteristics of the study areas.

Dune areas	Geographical position	Mean annual Temperature	Mean annual Rainfall	Climate
Fluvial dunes				
Itaparica	11°02′36.69″S–42°47′39.59″W	25.5 °C	562 mm	Semiarid
Veredas	10°47′18.60″S–42°49′17.44″W	26.8 °C	747 mm	Semiarid
Maritime dunes				
Abaeté	12°56′16.56″S–38°20′49.57″W	25 °C	2000 mm	Tropical humid
Litoral Norte	12°27′15.55″S– 37°56′19.05″W	24.6 °C	1680 mm	Tropical humid

Source: Pigozzo et al., 2006; Almeida et al., 2013; Barreto et al., 1999; UFCG, 2014.

Table 2
Plant species in fluvial and maritime dunes in Bahia state, Brazilian northeast.

Plant species	Fluvial		Maritime	
	Itaparica[a]	Veredas[b]	Abaeté[c]	Litoral Norte[d]
Amaranthaceae				
Blutaparon portulacoides (A.St.-Hil.) Mears				X
Anacardiaceae				
Anacardium occidentale L.			X	X
Arecaceae				
Copernicia prunifera Miller.	X			
Asteraceae				
Argyrovernonia harleyi (H. Rob) MacLeish	X			
Bignoniaceae				
Clytostoma convolvuloides Bureau & K.Schum.	X			
Bromeliaceae				
Aechmea itapoana Morawetz & Morawetz			X	
Hohenbergia littoralis L.B.Smith			X	
Cactaceae				
Pilosocereus gounellei (Weber) Byles & Rowley		X		
Pilosocereus tuberculatus (Werderm.) Byles & Rowley		X		
Clusiaceae				
Kielmeyera reticulata Saddi			X	
Compositae				
Blainvillea rhomboidea Cass.			X	
Convolvulaceae				
Ipomoea pes-caprae (L.) R.Br.				X
Ipomoea stolonifera J.F.Gmel.				X
Ipomoea asarifolia (Desv.) Roem. & Schult.		X		
Curcubitaceae				
Apodanthera succulenta C.Jeffrey	X			
Cyperaceae				
Cyperus lanceolatus Poir.			X	
Killinga brevifolia Rottb.			X	
Remirea maritima Aubl.			X	X
Euphorbiaceae				
Chamaesyce alsinifolia (Boiss.)		X		
Chamaesyce hyssopifolia (L.) Small				X
Croton sonderianus Muell. Arg.		X		
Fabaceae				
Bauhinia petandra (Bong.) Vogel ex Steud.		X		
Geoffraea spinosa Jacq.	X			
Mimosa xiquexiquensis Barneby		X		
Lamiaceae				
Marsypianthes chamaedrys Kuntze				X
Poaceae				
Andropogon leucostachyus Kunth			X	
Cynodon dactylon L.			X	
Digitaria insularis Mez ex Ekman			X	
Panicum racemosum Spreng.				X
Sporobolus virginicus (L.) Kunth				X
Stenotaphrum secundatum (Walter) Kuntze				X
Polygalaceae				
Polygala cyparissias A.St.-Hil. & Moq.				
Rubiaceae				
Anisomeris spinosa Presl.			X	
Borreria verticillata Griseb.			X	
Sapotaceae				
Bumelia sartorum Mart.	X			
Total richness	6	7	14	11

Source: Barreto et al., 1999[b]; Britto et al., 1993[c]; Britto and Noblick, 1984[c]; Dias and Menezes, 2007[d]; Jacomine, 1976[a]; Rodarte et al., 2008[b].

centrifugation in water and 50% sucrose (Jenkins, 1964—modified) using sieves with meshes of 850 and 45 μm and quantified with the help of a stereomicroscope (40 times magnification). Subsequently, spores were mounted on slides using polyvinyl-lacto-glycerol (PVLG) and PVLG + Melzer's reagent (1:1 v/v). Sporocarps were counted as one unit. To calculate the diversity indices, we counting the individuals of each species. The identification of AMF species was based on their spore morphology under a compound microscope, according to the morphological characteristics described in AMF identification manuals (Schenck and Pérez, 1990; Błaszkowski, 2012), in addition to consulting the species descriptions in recent publications.

2.5. Trap culture

The trap cultures were set up with samples from each collection point to obtain new glomerospores. A layer of 500 g of field soil was placed on top of 500 g of sterilized sand in plastic pots. Sorghum (*Sorghum bicolor* (L.) Moench), corn (*Zea mays* L.) and peanut (*Arachis hypogaea* L.) were sown into these pots as host plants. The pots were kept in a greenhouse for two cycles of four months each, with watering every other day and biweekly addition of a nutrient solution (Hoagland) without phosphorus (Hoagland and Arnon, 1950—modified). At the end of each cycle, an aliquot (50 g) of soil

was removed from each pot for glomerospores extraction and morphological identification of AMF species.

2.6. Statistical and ecological analyses

For the analysis of the AMF communities, the richness and Shannon index were calculated for each sample. For the calculation of diversity indices all individuals of AMF from field soil were counted (spores and sporocarps) at the AMF species level. The Shannon diversity index (H') was calculated using the following equation: $H' = -\Sigma$ (Pi ln [Pi]), where Pi = ni/N, ni = number of individuals by species i, and N = total number of individuals (spores) in all species (Shannon and Weaver, 1949). For statistical purposes Exp (H') values were used.

The multivariate analysis was performed using the relative abundance of AMF species. A PERMANOVA, based on Bray-Curtis distance, was applied to test whether the AMF communities differ among areas, sampling times and dune types. The Bonferroni's correction was applied to the p values of the comparison among sites, and the p was considered significant when $p < 0.008$. Canonical correspondence analysis (CCA) was used to explore whether there is a significant relationship between the composition of the AMF community and abiotic factors related to soil parameters, the significance of this variable was determined by Monte Carlo test ($p < 0.05$). Rare species were removed for this analysis. A indicator species analysis was performed to determine species, genera and spore type formation indicator for sites, sampling times and dunes types. This analysis is a combination of relative abundance and relative frequency of species and the significance of these values was determined by the Monte Carlo test using 9999 permutations (Dufrene and Legendre, 1997). Species were considered indicators when indicator value (IV) was >25% and p was <0.05.

For the soil chemical attributes, AMF spore number and colonization data, a two-way analysis of variance (ANOVA) was applied to compare sampling times and areas. For the physical attributes, one-way ANOVA was applied only among areas. The AMF spore number data were transformed to log (x + 1), colonization data were transformed to arcsine $\sqrt{x}/100$, the Shannon index was transformed into Exp (M') and values of soil chemical and physical properties were transformed into log 10 before to analysis of variance (ANOVA), when significantly different the means were compared by Tukey test ($P \leq 0.05$) using the Assistat program 7.6 (Silva and Azevedo, 2002). The PERMANOVA, CCA, indicator species analyses and the construction of the graphics box plot were performed using the PC-ORD version 6.0 program (McCune and Mefford, 2006).

3. Results

3.1. Physical and chemical soil parameters

The soils of the areas showed significant differences in most chemical properties, except for Cu and Al (Table 3). The soil of all four study areas was acidic with pH (H_2O) ranging from 5.5 to 6.3, and the fluvial dunes present higher pH (Table 3). The highest levels of phosphorus and potassium were detected in the areas of fluvial dunes, while the soil of maritime dunes had higher sodium content and greater amount of coarse sand (Tables 3 and 4). Itaparica site (fluvial dunes) showed higher amount of clay (Table 4).

3.2. Root colonization

In all areas, only the colonization by arbuscules did not differ between sampling times, while the colonization by hyphae, vesicules and total differed between sampling times and were greater at the first sampling time. In general, the mycorrhizal colonization was greater in the maritime dunes; however, significant differences were observed only in relation to the Veredas area (fluvial dunes) (Table 5).

Table 4
Soil particle size analysis in fluvial and maritime dunes of four study areas.

Areas	Particle size composition (%)		
	Coarse sand	Fine sand	Clay
Fluvial dunes			
Itaparica	39.3c	59.0a	5.20a
Veredas	25.6d	71.4a	5.12ab
Maritime dunes			
Abaeté	84.3a	36.0b	5.00c
Norte	61.1b	15.0c	5.10b

Means followed by the same letters in a row did not significantly differ from each other (*P < 0.05) among areas by ANOVA.

Table 3
Chemical soil analyses in fluvial (Itaparica e Veredas) and maritime (Abaeté and Litoral Norte) dunes of four study areas and two collection dates.

Attributes		Fluvial				Maritime			
		Itaparica		Veredas		Abaeté		Litoral Norte	
		1st	2nd	1st	2nd	1st	2nd	1st	2nd
Fe	mg dm^{-3}	19.00Bb	50.70Aa	47.90Aa	18.50Bb	7.20Ac	3.70Bc	6.60Ac	3.70Ac
Cu		0.54Aa	0.09Ba	0.36Aa	0.13Aa	1.81Aa	0.52Aa	0.59Aa	0.22Aa
Zn		1.22Aa	0.62Aab	0.36Ab	0.90Aa	0.65Aab	0.52Bab	0.31Ab	0.26Ab
Mn		12.00Aa	2.10Bb	2.30Bb	7.70Aa	2.20Ab	2.40Ab	1.60Ab	1.80Ab
P		9.00Aa	5.90Aa	4.40Bb	9.00Aa	1.50Ac	1.50Ab	1.30Ac	1.30Ab
pH	H_2O	5.50Bb	6.30Aa	5.90Aa	5.60Bb	5.60Ab	5.60Ab	5.60Ab	5.60Ab
K	mg dm^{-3}	23.40Aa	27.30Aa	19.50Aa	19.50Aa	3.90Bb	7.80Ab	7.80Ab	3.90Ab
Na		2.30Bb	9.20Aa	0.00Ab	2.30Ab	2.30Ba	4.60Aa	6.90Aa	4.60Aa
Al		3.60Aa	0.00Ba	0.90Aa	0.00Ba	0.90Aa	1.80Aa	1.80Aa	1.80Aa
Ca		202.00Aa	158.00Aa	174.00Aab	130.00Aab	78.00Ac	70.00Ab	98.00Abc	74.00Ab
Mg		43.76Ab	32.80Aa	57.13Aa	37.68Aa	32.82Ac	49.80Aa	42.55Ac	32.82Aa
CEC	%	2.60Aa	1.60Ba	1.80Aab	2.10Aa	1.00Bc	1.60Aa	1.50Ab	1.50Aa
OM		0.75Aa	0.14Bb	0.22Bb	0.68Aa	0.26Bb	0.54Aab	0.28Ab	0.24Ab

EC: cation exchange capacity; OM: organic matter. Capital letters compare periods in the same area and lower-case letters compare areas at the same collection data. Means followed by same letters in a row indicate non-significant differences (*P < 0.05) between areas by ANOVA.

Table 5
Percentage of arbuscular mycorrhizal root colonization, by arbuscules, hyphae, vesicles, and total AMF colonization, in fluvial and maritime dunes of four study areas in two sampling times (1st and 2nd sampling events).

Areas	Arbuscules		Hyphae		Vesicles		Total	
Fluvial dunes	1st	2nd	1st	2nd	1st	2nd	1st	2nd
Itaparica	0.0aA	0.1aA	39.0aA	20.2bB	4.8aA	1.9abB	43.8aA	22.2abB
Veredas	0.0aA	0.0aA	16.2bA	6.3cB	2.7aA	0.5bA	18.8bA	6.8bB
Maritime dunes	1st	2nd	1st	2nd	1st	2nd	1st	2nd
Abaeté	0.75aA	0.14aA	53.8aA	35.1aB	9.1aA	6.0aA	63.7aA	41.3aA
Norte	0.92aA	1.23aA	44.2aA	27.0abB	7.9aA	6.2aA	53.0aA	34.4aA

Means followed by the same lower-case letters (between dune areas, in column) or capital letters (collection dates; in row), did not significantly differ from each other by Tukey test (*$P < 0.05$).

3.3. AMF species richness, diversity and community composition

The AMF spore density differed significantly among the sampling times (Table 6). There was a significant difference in the number of spores between the two maritime dunes, and both differed significantly from the areas of fluvial dunes in the two sampling times. At each sampling date, no significant variation was observed in the number of glomerospores between the fluvial dune areas. However, there was a significant difference between sampling times for the maritime dunes. Higher AMF spore density was observed in the Abaeté area when compared to the Litoral Norte area.

Higher total AMF species richness was observed in the Abaeté, followed by Itaparica, Norte and Veredas, and the species accumulation curves reached the *plateau* only for Veredas site (Fig. 1). There was a significant difference in species richness per sample between the dunes types and sites, while there was no significant difference in diversity by Shannon index (Fig. 2 and Supplementary material). Higher species richness was found in the maritime dunes type when compared to the fluvial ones (Fig. 2a). The richness differed among sites, and the lowest richness was observed in Itaparica site (Fig. 2c). The Shannon index did not differ and the values ranging from 0.56 to 0.58 for sampling times; from 0.52 to 0.62 for dunes type and from 0.44 to 0.64 for sites (Supplementary material).

We also detected differences for the predominance of spore type formation among areas and dunes types, with Gigasporoid-type spores (IV = 63.3; $p < 0.0007$) predominating in the fluvial dunes and Glomoid-type spores (IV = 66.2; $p < 0.0001$) in the maritime dunes. Considering the differences among sites, we observed that Glomoid-type spores (IV = 43.3; $p < 0.0001$) prevailed in the Abaeté, while Acaulosporoid-type spores (IV = 51.9; $p < 0.0001$) predominated in the Litoral Norte and Gigasporoid-type spores (IV = 53.1; $p < 0.0001$) were more related to the Itaparica site.

Altogether, there were 54 AMF species detected, belonging to 19 genera in ten families (Table 7). Of the species, 47 were recorded in the first sampling time and 35 in the second. Fifteen taxa were identified only to genus level, as specimens did not show enough morphological characteristics to determine them unequivocally to species level. The largest number of identified species belonged to the genus *Acaulospora* (11) and *Glomus* (10), followed by *Gigaspora* (eight). The predominance of genera differed among the dune areas. According to the indicator species analysis, in the Abaeté, *Glomus* was considered an indicator genus (IV = 51.1; $p < 0.0001$); while *Acaulospora* (IV = 56.0; $p < 0.0001$) was indicator of Litoral Norte. The genera *Fuscutata* (IV = 38.5; $p < 0.0019$) and *Racocetra* (IV = 56.2; $p < 0.0001$) were considered indicator of Itaparica, and *Corymbiglomus* (IV = 25.0; $p < 0.0125$), *Claroideoglomus* (IV = 26.5; $p < 0.030$), *Dominikia* (IV = 25.0; $p < 0.0096$), *Rhizoglomus* (IV = 35.6; $p < 0.0002$) and *Sclerocystis* (IV = 25.0; $p < 0.0116$) were indicator of Veredas.

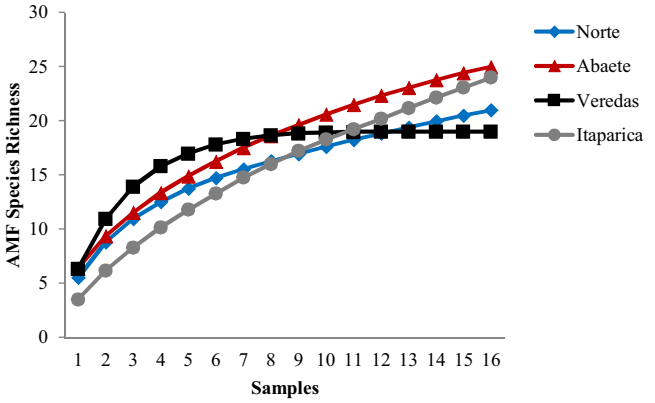

Fig. 1. Species accumulation curve in fluvial (Veredas and Itaparica) and maritime (Norte and Abaeté) dune areas of Bahia state, Brazilian Northeastern.

Gigaspora margarita was found in all areas at both sampling times, *Glomus macrocarpum* was found in all areas at the first sampling time, while at the second sampling time, *Claroideoglomus etunicatum* and *Glomus glomerulatum* were present in all study areas. In this study, it was also possible detect indicator species for sampling time, dune types and for each studied area (Table 7). *Glomus macrocarpum* and *Glomus glomerulatum* were selected as indicator for the first and second sampling time, respectively (Table 7). Six species were considered indicator of the dunes types, four species related to the maritime type (*Acaulospora scrobiculata, Glomus brohultii, Glomus glomerulatum, Glomus microcarpum* and *Glomus* sp.2) and one in the fluvial type (*Fuscutata heterogama*) (Table 7). Twelve species were indicator of one of the areas: *Glomus brohultii*, *Glomus glomerulatum*, *Glomus microcarpum* and *Glomus* sp.1 were indicator of Abaeté site; *Acaulospora scrobiculata* in Litoral Norte; *Fuscutata heterogama* and *Racocetra fulgida* in the Itaparica; and *Fuscutata* sp.1, *Claroideoglomus etunicatum*, *Corymbiglomus* sp., *Gigaspora decipiens*, *Gigaspora* sp.2, *Dominikia aurea* and *Funneliformis mosseae* were indicator of the Veredas site (Table 7).

Trap cultures allowed for the registration of three species that had not been identified in field samples in three of the four study

Table 6
AMF spore density (100 g^{-1} soil) in fluvial and maritime dunes at two sampling times (1st and 2nd) in Bahia.

	Fluvial dunes		Maritime dunes	
	Itaparica	Veredas	Abaeté	Norte
1st	10.2 cA	9.0 cA	67.5 aA	41.0 bA
2nd	6.5 cB	6.5 cB	41.7 aB	23.2 bB

Means followed by the same capital letters (collection dates, in columns) and lower-case letters (dune areas; in rows) do not significantly differ according to Tukey test at 5% probability.

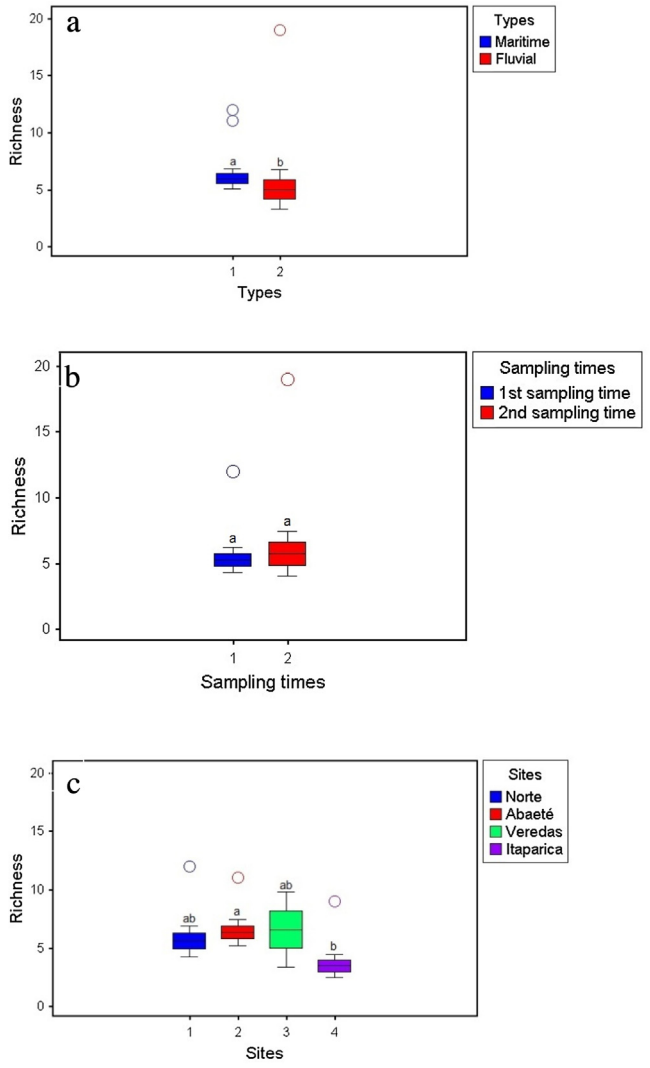

Fig. 2. Species richness for dune type (maritime and fluvial) (a), sampling time (1st and 2nd) (b) and sites (Norte, Abaeté, Veredas and Itaparica) (c).
Means followed by the same letter do not differ statistically by Tukey test at 5% probability. Error bars shows standard deviation and spheres represent outliers.

areas. These were *Acaulospora longula*, *Acaulospora spinosa* and *Rhizoglomus natalense*. From the Abaeté dune, five species were recovered (*Ambispora appendicula* – collected only in the first sampling time, *Acaulospora longula*, *A. mellea*, *A. scrobiculata* and *Rhizoglomus natalense*; Table 7). In the Litoral Norte dune two species were recovered (*Acaulospora spinosa* and *R. natalense*) and in Itaparica *Acaulospora morrowiae* and *A. scrobiculata* were additionally found.

The PERMANOVA analysis showed that the AMF community composition differed among sites ($F = 5.9762$; $p = 0.0001$), dune types ($F = 6.4463$; $p = 0.0001$) and sampling time ($F = 2.5473$; $p = 0.008$). All sites differed from each other, and the p values were lower than 0.004. The canonical correspondence analysis (CCA) explained 15.8% of the total variance of the data, and there were differences related to dune types (Fig. 3a), areas (Fig. 3b) and in the distribution of AMF species (Fig. 3). The CCA selected Ca, Fe, P, K, pH, Na, clay, coarse and fine sand as soil factors that determined the AMF communities in the studied areas ($p < 0.05$).

According to CCA analysis, the content of coarse sand was correlated with the occurrence of *Acaulospora scrobiculata* (Acascrob), *Gigaspora* sp.1 (Gigsp1), *Glomus brohultii* (Globro), *Glomus macrocarpum* (Glomac), *Glomus microcarpum* (Glomic), *Glomus* sp.2 (Glosp2), *Glomus trufemii* (Glotruf) and *Intraornatospora intraornata* (Intint); while the content of K, P, Ca, Fe, pH, Na, Clay and fine sand influenced the occurrence of the following AMF species: *Acaulospora mellea* (Acamel), *Acaulospora foveata* (Acafov), *Ambispora appendicula* (Ambapp), *Claroideoglomus etunicatum* (Claetu), *Funneliformis halonatus* (Funhal), *Fuscutata heterogama* (Fushet), *Fuscutata rubra* (Fusrub), *Gigaspora gigantea* (Giggig), *Gigaspora margarita* (Gigmar), *Gigaspora rosea* (Gigros) and *Racocetra fulgida* (Racful) (Fig. 3).

4. Discussion

The highest percentage of hyphae colonization in dune areas from this study is similar to the results observed by Rodríguez-Echeverría et al. (2008) in European sand dunes. According to Yang et al. (2008), hyphae comprise the main colonization structure of AMF and are widely distributed in plant roots. Arbuscules are ephemeral structures that are difficult to detect in field samples as they are lost within a short time (about 4–15 days), but their presence in field samples suggests that a transfer of nutrients occurs from the fungus to the host (Dennett et al., 2011), indicating that the symbiosis is active.

The absence (almost total) of arbuscules in the roots of the fluvial dune areas may be due to degradation or could indicate a lower exchange of substances between plant and fungus. Besides, we can consider the bias related to the evaluation method and/or difficulty to see or finding arbuscules from field roots, especially as we sampled at the beginning and the end of wet and dry seasons, which corresponded to the beginning and end of the growing seasons. According to Rodríguez-Echeverría et al. (2008), low percentage of vesicles might possibly indicate lower acquisition of new resources and increased use of stored carbohydrates. The values observed in this study are within the range observed by these authors (3–18%).

During the second sampling time, reductions in colonization by hyphae and vesicles were observed in all areas. In coastal dunes in Venezuela a low intensity of mycorrhizal colonization (3–15%) was attributed to the constant disturbance produced by wind in these environments (Alarcón and Cuenca, 2005). It is possible that factors related to wind are also responsible for the reduction in the colonization rate observed in the study areas, although this parameter was not measured.

In general, low AMF spore density was recorded in the two sampling times in all studied areas. This is a common trend in dune environments, where only low numbers of spores are usually recovered (Camprubí et al., 2010). The significant variation in the number of glomerospores observed between the two maritime dunes was unexpected, as they are similar. However, this might be explained by differences in the plant host, AMF communities at the sites, and the sporulation patterns of the AMF species (Gemma et al., 1989). Variations in the production of these structures may be related to several factors, including seasonality, nutrient levels in the soil, associated plant species and host physiology (Sylvia and Will, 1988).

The significant difference in the spore densities observed between the maritime and fluvial dunes may be related to the distinct vegetation between the two types of dunes, since the fluvial dunes are inserted in areas of *Caatinga* (a Brazilian type of tropical dry forest biome) and the maritime dune areas which are part of the Atlantic Forest (included in the tropical rain forest biome). Glomerospore density in the semiarid region is in general much lower when compared to (semi-)humid Atlantic Forest (Maia et al., 2010; Zangaro and Moreira, 2010).

Veredas showed the lowest AMF species richness; however, only in this area the species accumulation curve reached the plateau, which indicate that the sampling effort was sufficient to

Table 7
AMF species in fluvial and maritime dunes of Bahia State with their indication values (IV) and group indicated for the dune types (Maritime – M; Fluvial – F), Sites (Abaeté – A; Litoral Norte – LN; Itaparica – I; Veredas – V) and Sampling times (first – 1st and second – 2nd sampling time).

Species	Fluvial		Maritime		Type			Sites			Sampling time		
	Itaparica	Veredas	Abaeté	Litoral Norte	group	IV	*p*	group	IV	*p*	group	IV	*p*
Acaulosporaceae													
Acaulospora foveata Trappe & Janos	X		X	X	M	16.2	0.07	LN	23.9	0.01	1st	14.9	0.13
Acaulospora lacunosa J.B. Morton	X			X	M	2.2	1.00	LN	4.3	1.00	1st	6.2	0.49
Acaulospora longula Spain & N.C. Schenck			TC										
Acaulospora mellea Spain & N.C. Schenck	X	X	X	X	F	19.2	0.35	LN	16.9	0.24	2nd	16.5	0.59
Acaulospora morrowiae Spain & N.C. Schenck	X				F	3.1	1.00	I	6.2	1.00	1 st	3.1	1.00
***Acaulospora scrobiculata* Trappe**		X	X	X	**M**	**36.4**	**0.00**	**LN**	**66.6**	**0.00**	2nd	17.1	0.82
Acaulospora sp.1			X	X	M	6.2	0.49	A	4.4	1.00	1 st	6.2	0.49
Acaulospora sp.2	X			X	F	2.9	1.00	I	5.8	1.00	1 st	6.2	0.49
Acaulospora sp.3	X				F	3.1	1.00	I	6.2	1.00	1 st	3.1	1.00
Acaulospora spinosa Walker & Trappe				TC				-	-	-	-	-	-
Acaulospora spinosissima Oehl, Palenz., Sánchez-Castro, Tchabi, Hount. & G. A. Silva			X		M	3.1	1.00	A	6.2	1.00	1st	3.1	1.00
Kuklospora sp.			X		M	3.1	1.00	A	6.2	1.00	1 st	3.1	1.00
Ambisporaceae													
Ambispora appendicula(Spain, Sieverd. & N.C. Schenck) C. Walker		X	X	X	F	12.4	0.68	V	24.9	0.03	1 st	10.2	0.97
Dentiscutataceae													
***Fuscutata heterogama* Oehl, F.A. Souza, L.C. Maia & Sieverd.**	X	X	X		**F**	**48.8**	**0.00**	**I**	**42.7**	**0.00**	1 st	17.3	0.61
Fuscutata rubra (Stürmer & J.B. Morton) Oehl, F.A. Souza & Sieverd.	X		X		F	24.2	0.01	V	20.4	0.08	1 st	17.9	0.09
***Fuscutata*sp.1**		X			F	12.5	0.11	**V**	**25.0**	**0.01**	2nd	12.5	0.12
Diversisporaceae													
***Corymbiglomus* sp.**		X			F	12.5	0.11	**V**	**25.0**	**0.01**	2nd	12.5	0.12
Entrophosporaceae													
***Claroideoglomus etunicatum*(W.N. Becker & Gerd.) C. Walker & A. Schüßler**	X	X	X	X	F	17.3	0.52	**V**	**26.5**	**0.02**	2nd	14.1	0.89
Gigasporaceae													
***Gigaspora decipiens* R. Hall e L.K. Abbott**		X			F	12.5	0.11	**V**	**25.0**	**0.01**	2nd	2.6	1.00
Gigaspora gigantea (T.H. Nicolson & Gerd.) Gerd. & Trappe	X		X	X	M	13.6	0.58	LN	11.8	0.56	1 st	10.9	0.87
Gigaspora margarita W.N. Becker & I.R. Hall	X	X	X	X	M	24.0	0.99	LN	15.4	0.92	2nd	34.1	0.23
*Gigaspora ramisporophora*Spain, Sieverd. & N.C. Schenck	X			X	F	2.7	1.00	I	5.5	1.00	1 st	2.7	1.00
Gigaspora rosea T.H. Nicolson & N.C. Schenck	X		X		M	2.7	1.00	A	5.3	0.61	1 st	9.4	0.24
Gigaspora sp.1			X	X	M	12.5	0.11	A	6.8	0.46	2nd	8.8	0.23
Gigaspora sp.2		X			F	12.5	0.11	**V**	**25.0**	**0.01**	1 st	2.7	1.00
sp.3	X				F	3.1	1.00	I	6.2	1.00	1 st	3.1	1.00
Glomeraceae													
Dominikia aurea (Oehl & Sieverd.) Błaszk., Chwat, G.A. Silva & Oehl 2015		X			F	12.5	0.10	V	25.0	0.01	1 st	2.4	1.00
Funneliformis mosseae (T.H. Nicolson & Gerd.) C. Walker & A. Schüßler		X			F	12.5	0.10	V	25.0	0.01	2nd	12.5	0.11
Funneliformis halonatus (S.L. Rose & Trappe) Oehl,G.A. Silva & Sieverd.				X	M	9.4	0.23	LN	18.8	0.05	2nd	2.1	1.00
Glomus ambisporum G.S. Sm. & N.C. Schenck				X	M	3.1	1.00	LN	6.2	1.00	2nd	3.1	1.00
Glomus brohultii Sieverd.& R.A. Herrera			X		M	34.4	0.00	A	54.3	0.00	1 st	10.0	0.78
Glomus glomerulatum Sieverd.	X	X	X	X	M	46.9	0.00	A	43.1	0.00	2nd	47.9	0.00
Glomus macrocarpum Tul. & C. Tul	X	X	X	X	M	28.3	0.36	A	16.0	0.73	1 st	39.8	0.02
Glomus microcarpum Tul. & C. Tul.		X	X	X	M	58.2	0.00	A	55.0	0.00	1 st	23.8	0.78
Glomus sp.1				X	M	34.4	0.00	A	68.8	0.00	1 st	15.5	0.25
Glomus sp.2			X		M	3.1	1.00	A	6.2	1.00	2nd	3.1	1.00
Glomussp.3		X			M	3.1	1.00	A	6.2	1.00	1 st	3.1	1.00
Glomus spinuliferum Sieverd. & Oehl			X		M	3.1	1.00	LN	6.2	1.00	1 st	3.1	1.00
Glomus trufemii B.T. Goto, G.A. Silva & Oehl			X		M	6.2	0.48	A	12.5	0.23	2nd	2.2	1.00
Rhizoglomus natalense (Błaszk., Chwat & B.T. Goto) Sieverd., G. A. Silva & Oehl			TC	TC				–	–	–	–	–	–
Rhizoglomus intraradices N.C. Schenck & G.S. Sm		X			F	18.8	0.02	V	37.5	0.00	1st	7.3	0.60
Rhizoglomus irregulare Blaszk., Wubet, Renker & Buscot			X		M	3.1	1.00	A	6.2	1.00	2nd	3.1	1.00
Rhizoglomus sp.	X				F	12.5	0.10	V	25.0	0.01	1 st	2.4	1.00
Sclerocystis sinuosa R.T. Almeida & N.C. Schenck		X			F	12.5	0.11	V	25.0	0.01	2nd	2.6	1.00
Intraornatosporaceae													
Intraornatospora intraornata (B.T. Goto & Oehl) B.T. Goto, Oehl & G.A. Silva			X	X	M	10.4	0.22	A	6.2	0.75	2nd	6.0	0.74
Paradentiscutata maritima B.T. Goto, D.K. Silva, Oehl & G.A. Silva	X				F	3.1	1.00	I	6.2	1.00	1 st	3.1	1.0000
Racocetraceae													
Cetraspora sp.1	X				F	3.1	1.00	I	6.2	1.00	1 st	3.1	1.00
Racocetra coralloidea (Trappe, Gerd. & I. Ho) Oehl, F.A. Souza & Sieverd.	X				F	6.2	0.49	I	12.5	0.23	1 st	2.0	1.00
Racocetra fulgida (Koske & C. Walker) Oehl, F.A.Souza & Sieverd.	X				F	21.9	0.01	I	43.8	0.00	2nd	13.8	0.11
Scutellosporaceae													
Bulbospora minima Oehl, Marinho, B. T. Goto & G. A. Silva			X		M	3.1	1.00	A	6.2	1.00	1 st	3.1	1.00

Table 7 (*Continued*)

Species	Fluvial		Maritime		Type			Sites			Sampling time		
	Itaparica	Veredas	Abaeté	Litoral Norte	group	IV	*p*	group	IV	*p*	group	IV	*p*
Orbispora pernambucana (Oehl, D.K.Silva, N. Freitas & L.C. Maia) Oehl, G.A. Silva & D.K. Silva			X		M	9.4	0.23	A	18.8	0.05	2nd	9.4	0.23
Scutellospora aurigloba (I.R. Hall) C. Walker & F.E. Sanders	X			X	F	2.0	1.00	I	4.1	1.0	1 st	2.0	1.00
Scutellospora calospora (T.H. Nicolson & Gerd.) C. Walker & F.E. Sanders	X				F	3.1	1.00	I	6.2	1.00	2nd	2.0	1.00
Scutellospora sp.1	X				F	6.2	0.49	I	12.5	0.24	2nd	2.6	1.00

IV is the indicator value; Type is referred to the dune type (maritime – M or Fluvial – F); Sites represent each location evaluated (Abaeté – A; Litoral Norte – LN; Itaparica – I; Veredas – V); Sampling times refers to two sampling events (first – 1st and second – 2nd sampling time). $p < 0.05$ (significance to Monte Carlo permutation). Species in bold are considered indicators.

recovery all species of this community. In this study, high species richness was observed, compared with the data obtained in other areas of dunes and *restinga* in Brazil (Trufem et al., 1989, 1994; Stürmer and Bellei, 1994; Santos et al., 1995; Silva et al., 2012; Stürmer et al., 2013; Souza et al., 2013), which recorded 5–47 species. In other countries, 16–31 species were identified in dunes in India (Beena et al., 2000, 2001; Selvaraj and Kim, 2004) and 7–23 in dunes in Spain (Camprubí et al., 2010; Estrada et al., 2013). Most taxa reported here have been previously reported in dune areas in Brazil (e.g. Silva, 2013).

The higher richness per sample in maritime when compared to the fluvial dunes, may be related to the ecosystems in which these dunes are inserted, once maritime dunes are associated ecosystems of Atlantic Forest Domain, while fluvial dunes are ecosystems associated to the *Caatinga* biome. Interestingly, the Shanon index take into account the evenness and richness, and it did not differ among sites, dune types or sampling times.

Indicator species analysis is an index that combines the relative abundance and the frequency of occurrence of species (Dufrene and Legendre, 1997). The detection of indicator species in the study areas shows that the conditions of these environments favored the sporulation and distribution of these species, while variations in the abundance and frequency of these taxa may reflect changes in these locations. Considering the types of spore formation, it was observed that Glomoid-type is more related to the maritime dunes, while Gigaporoid-type is related to the fluvial dunes.

When comparing the spore type formation among sites, we found the Glomoid-type as indicator of Abaeté site, Acaulosporoid-type related to the Litoral Norte site and Gigasporoid-type as indicator of Itaparica site. The Glomoid-type spore formation is related to the areas of maritime dunes, AMF species with this type of spore formation (mainly species of the genus *Glomus*) are known to be more abundant in maritime dunes in Brazil (Souza et al., 2013), USA (Sylvia and Will, 1988) and Poland (Błaszkowski, 1994). On the other hand, spores with Gigasporoid-type formation was related to areas of fluvial dunes, this result was also recorded in dunes in the USA (Friese and Koske, 1991).

These differences may reflect the function of these fungi in each environment where they were found. AMF species have different strategies for colonization and production of spores. Species of Gigasporales (Gigasporoid-type spore formation) invest in greater production of extra-radicular mycelium which are important for soil aggregation and acquisition of nutrients, while Glomeraceae *sensu lato* (Glomoid-type spore formation) species colonize plant roots more rapidly (Hart and Reader, 2002). These features are important to colonize and survive in such extreme environments.

Glomus and *Acaulospora* had the most species and together accounted for almost 40% of the taxa registered. These genera are commonly referred to as the most representative in different environments, probably because they have the highest number of described species which also favors a greater recovery of taxa. The AMF communities of the four studied areas were different as to the predominance of genera. *Acaulospora* was selected as indicator in the Litoral Norte area and *Glomus* in the Abaeté area (both sites of maritime dunes), the predominance of these genera in maritime dunes of Brazilian northeast was also observed by Silva et al. (2012, 2015) and Souza et al. (2013).

The high occurrence of members of the genus *Glomus* reveals the good adaptation of these fungi to different environmental conditions (Błaszkowski and Czerniawska, 2011). The predominance of *Glomus* species is commonly observed in studies of maritime dune environments (Błaszkowski et al., 2002; Estrada et al., 2013), and this may be due to fact that many *Glomus* species are more adapted for sporulation in hot and dry environments. Species of this genus are commonly reported as the dominant taxa in desert areas presenting resistance to high soil temperatures, conditions that are quite similar to the dune areas (Estrada et al., 2013; Mohammad et al., 2003; Mathur et al., 2007). The presence of species of the genus *Acaulospora* has also been frequently reported in studies conducted in areas of maritime dunes (Koske and Gemma, 1997; Trufem et al., 1994), but rarely as the dominant genus in AMF communities (Błaszkowski and Czerniawska, 2011).

Corroborating with the prevalence of Gigasporoid-type formation in fluvial dunes, *Fuscutata* and *Racocetra* were selected as indicator of Itaparica site; while *Corymbiglomus*, *Dominikia*, *Claroideoglomus*, *Rhizoglomus* and *Sclerocystis* were the indicator genera for the Veredas site. Similar results were obtained by Friese and Koske (1991), who registered only taxa with Gigasporoid-type formation in dunes of USA.

Glomus microcarpum was selected as indicator species in the Abaeté site. In a previous study performed in the same area, this specie was also considered the most common species (Santos et al., 1995). *A. scrobiculata* was an indicator species for maritime dunes and for the Litoral Norte. Silva et al. (2015) also registered *A. scrobiculata* as indicator species for maritime dunes in Northeastern Brazil, and this species was also found with high abundance and frequency of occurrence in dunes of Southern Brazil (Stürmer and Bellei, 1994). *Gigaspora decipiens* and *C. etunicatum* were selected as indicator species in the fluvial dune of Veredas (site within *Caatinga* ecosystem). These species were also registered as indicator in Caatinga areas (Silva et al., 2014). *Fuscutata heterogama* was considered indicator for fluvial dunes and for Itaparica site, showing that this species is well suited to the soil conditions at this site. The presence of *G. margarita* species in all sites and sampling times indicates that this taxon is of widespread occurrence in the environments of the dunes studied, which was also observed by Silva et al. (2012).

Seven species were recovered in the trap culture, from which five belongs to *Acaulospora*. Some species were observed only at the end of the second multiplication cycle (*A. longula* and *A. mellea*), which highlights the importance of maintaining successive cycles for multiplication, allowing the identification of more

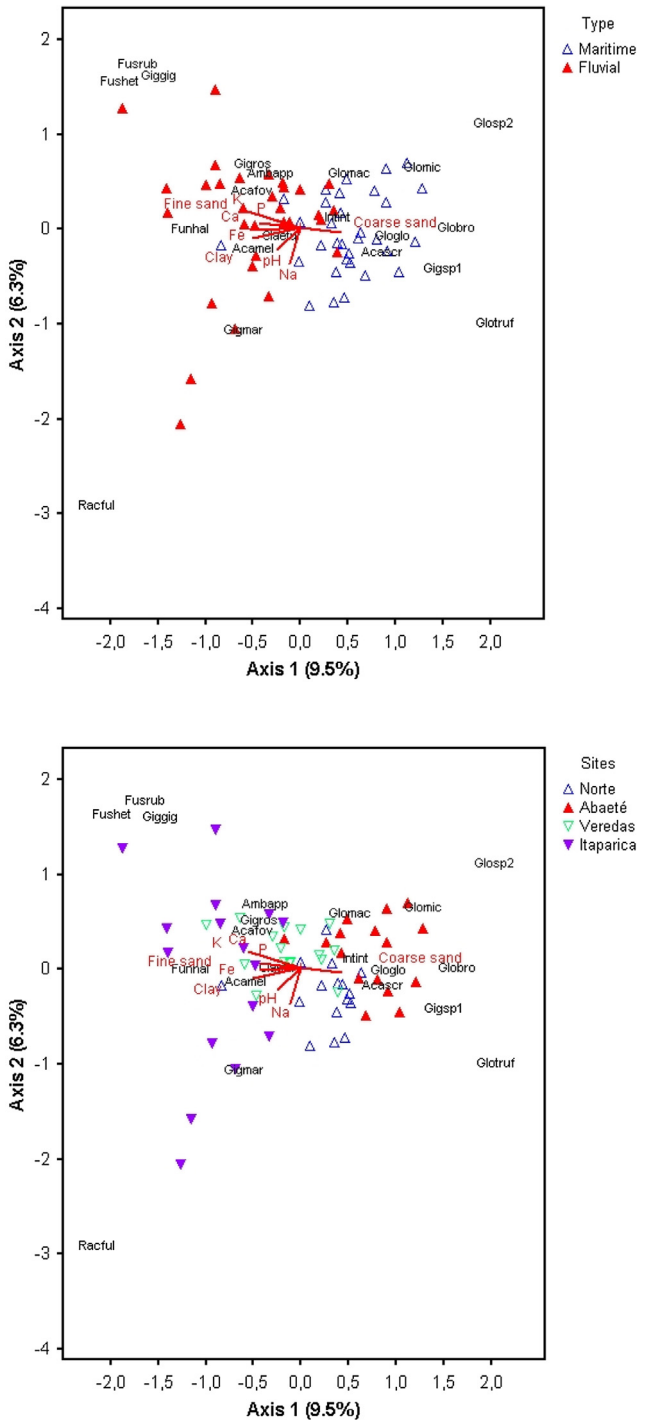

Fig. 3. Canonical correspondence analysis based on the similarity between the communities of arbuscular mycorrhizal fungi and correlated with physical and chemical soil properties by (a) type of area (fluvial and maritime) and (b) sites (Itaparica, Veredas, Abaeté and Norte).
Acaulospora foveata (Acafov), *Acaulospora mellea* (Acamel), *Acaulospora scrobiculata* (Acascrob), *Ambispora appendicula* (Ambapp), *Claroideoglomus etunicatum* (Claetu), *Funneliformis halonatus* (Funhal), *Fuscutata heterogama* (Fushet), *Fuscutata rubra* (Fusrub), *Gigaspora gigantea* (Giggig), *Gigaspora margarita* (Gigmar), *Gigaspora rosea* (Gigros), *Gigaspora* sp.1 (Gigsp1), *Glomus brohultii* (Globro), *Glomus macrocarpum* (Glomac), *Glomus microcarpum* (Glomic), *Glomus* sp.2 (Glosp2), *Glomus trufemii* (Glotruf), *Intraornatospora intraornata* (Intint) and *Racocetra fulgida* (Racful).

species. The identification of *R. natalense* in the trap cultures of the maritime dunes areas was an important result, considering that this taxon was originally described from a similar environment in Northeastern Brazil, which suggests that this species may be commonly detected in maritime dunes after trap culturing (Błaszkowski et al., 2014).

The absence of most of the species extracted from the field soil in the cultivation vessels may be an adaptation to the environment, since the pot conditions are different from those originally found in nature (Trejo-Aguilar et al., 2013). Taking this into consideration, among the factors that could be influencing the AMF in cultivation vessels are the type of substrate used, low viability of spores, incompatibility with the host plant, and selective pressure due to the different characteristics of the soil, humidity, light and temperature. These factors may be allowing only the survival of the species able to cope with these conditions, preventing the spread of other species present in the initial inoculum (Błaszkowski et al., 2002; Turrini et al., 2010). Alternatively, some species may not sporulate under controlled conditions (Lee et al., 2013).

Canonical correspondence analysis (CCA) was applied to understand, which environmental factors influence the AMF communities in the study areas. The differences in physical and chemical properties of the soil between the areas of maritime and fluvial dunes are reflected in the composition of AMF communities. The differences between the types of dunes and among the areas may be a result of local factors. In this study, the soil of each area was found to influence the fungi in each environment (local scale), affecting community structure, even in areas that are geographically close, as also observed by Silva et al. (2015).

The AMF diversity was related to local soil heterogeneity, the majority of chemical attributes were related to fluvial dunes, while the coarse sand was the main factor influencing the maritime dunes. The soil is a strong driver of AMF communities (de Carvalho et al., 2012; Jansa et al., 2014; Silva et al., 2014 Jansa et al., 2014; Silva et al., 2014), and soil texture had great influence on the AMF communities, as observed in other studies (de Carvalho et al., 2012; Silva et al., 2015 Silva et al., 2015).

The areas of maritime and fluvial dunes studied had a high richness of AMF species compared to richness registered in studies carried out in other dunes. AMF communities' structure differed between maritime and fluvial dune area, as well as the community composition with predominance of different genera of AMF. The physical and chemical properties of the soil are important factors affecting AMF communities in dune areas. This was the first study of AMF diversity in fluvial dunes areas in Brazil comparing AMF communities in maritime dunes.

Studies on AMF communities' structure and composition in natural environments, especially in protected areas, provide basis data which can help in conservation and managements policies, considering that AMF are a key ecological group for the maintenance of terrestrial ecosystems. Such areas are important genetic resources of these fungi *in situ* (Turrini et al., 2010). Our results reinforce the importance of conservation and maintenance of dune and *restinga* areas, considering that these environments harbor distinct AMF communities, and each area has an important role for AMF species. Furthermore, based on data of AMF species recorded in areas of sand dunes and *restinga*, future studies can use these species as inoculum for mycorrhizal seedlings in re-vegetation programs in sand dunes areas, which are endangered ecosystems by anthropogenic pressures, in order to enhance the recovery of plant diversity and guarantee the functional equilibrium of these ecosystems.

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Resources) of Bahia for its support, as well all managers of the study areas. The authors thank Iolanda Ramalho da Silva for her suggestions and help with statistical analysis.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2016.07.018.

Shanonn index for dune type (maritime and fluvial) (a), sampling time (1st and 2nd) (b) and sites (Norte, Abaeté, Veredas and Itaparica) (c). Means followed by the same letter do not differ statistically by Tukey test at 5% probability.

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