Acta Oecologica 79 (2017) 8–17

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Changes in arbuscular mycorrhizal fungal communities along a river delta island in northeastern Brazil

Iolanda Ramalho da Silva [a, *], Danielle Karla Alves da Silva [b], Francisco Adriano de Souza [c], Fritz Oehl [d], Leonor Costa Maia [a]

[a] Programa de Pós-Graduação em Biologia de Fungos, Universidade Federal de Pernambuco, Av. da Engenharia, s/n, Cidade Universitária, CEP 50740-600, Recife, PE, Brazil
[b] Laboratório de Microbiologia, Universidade Federal do Vale do São Francisco, Campus de Ciências Agrárias, Rodovia BR 407, Km 12, Lote 543, Projeto de Irrigação Nilo Coelho, s/n, "C1", Petrolina, PE CEP 56300-990, Brazil
[c] Embrapa Milho e Sorgo, Núcleo de Biologia Aplicada, Rod. MG 424 KM 45 - Bairro Esmeraldas, SN, Caixa Postal 285, CEP 35701-970, Sete Lagoas, MG, Brazil
[d] Agroscope, Ecotoxicology, Schloss 1, CH-8820 Wädenswil, Switzerland

ARTICLE INFO

Article history:
Received 28 July 2016
Received in revised form
20 December 2016
Accepted 30 December 2016

Keywords:
Arbuscular mycorrhiza
AMF community structure
Coastal ecosystems
Soil factors

ABSTRACT

Arbuscular mycorrhizal fungi (AMF) play a key role in the maintenance of the balance of terrestrial ecosystems, but little is known about the biogeography of these fungi, especially on tropical islands. This study aims to compare AMF community structure along a transect crossing a fluvial-marine island and relate these communities with soil and vegetation parameters to shed light on the forces driving AMF community structure on a local scale. We tested the hypothesis that the composition of AMF communities changes across the island, even within short distances among sites, in response to differences in edaphic characteristics and vegetation physiognomies. We sampled roots and soils in five different natural and degraded habitats: preserved mangrove forest (MF), degraded mangrove forest (MD), natural *Restinga* forest (RF), and two regeneration *Restinga* forests (RR1 and RR2) on Ilha da Restinga, northeastern Brazil. We determined the mycorrhizal colonization rate and AMF community structure based on morphological spore identification. The island soils were sandy with pH varying from acid to neutral; higher levels of organic matter were registered in RF and lower in MF; other chemical and physical soil attributes differed along the habitat types on the island. In total, 22 AMF species were identified, without any difference in species richness. However, the diversity and composition of AMF communities, spore abundance per families, and mycorrhizal colonization were statistically different among the habitats. The composition of AMF communities was strongly related to soil characteristics, especially the sum of exchangeable bases. Our results indicate that the different habitat types have diverse AMF communities even within short distances among habitats. In conclusion, islands with high spatial heterogeneity in soil parameters and diverse vegetation are potential refuges for the diversity conservation of AM fungi.

1. Introduction

Several factors may affect species community structure and distribution along spatial and temporal scales (Gotelli and Graves, 1996; Chase, 2003). On a local scale, environmental heterogeneity, abiotic, edaphic and micro-climatic factors are responsible for the maintenance of biological communities, while at larger scales, the historical-geological processes and regional climatic conditions are the main factors affecting community structure and influencing speciation, colonization and extinction of species (Buckley and Jetz, 2007; Dobrovolski et al., 2012).

Islands have been considered key environments to perform studies on ecological and evolutionary aspects of species. Terrestrial (or continental) islands are separated from the mainland environments by geographic barriers, decreasing accessibility and connection between island and mainland biological communities (MacArthur and Wilson, 1967; Walter, 2004). These islands

* Corresponding author. Departamento de Micologia, Universidade Federal de Pernambuco, Av. da Engenharia, s/n, Cidade Universitária, CEP 50740-600, Recife, PE, Brazil.
E-mail address: iolandaramalho@yahoo.com.br (I.R. da Silva).

http://dx.doi.org/10.1016/j.actao.2016.12.011
1146-609X/

sometimes have connections to the mainland, which contribute to sharing species between these environments; however, the species richness in islands is lower due to less diversity of niches, which can influence the establishment of some taxa (Triantis et al., 2012).

Arbuscular mycorrhizal fungi (AMF), ubiquitous mutualists of terrestrial plants, promote several benefits and ecosystem services that aid to maintain ecosystem balance, contributing to edaphic quality and providing nutritional and non-nutritional benefits to plant communities (Smith and Read, 2008; Gianinazzi et al., 2010). AMF also contribute to the maintenance of plant diversity, participate in successional ecological processes and promote plant colonization in different habitats including island environments (Allen and Allen, 1988; Koske and Gemma, 1990; Francis and Read, 1994).

Traditionally, AMF taxa have been identified based on spores morphology extracted directly from field samples. However, considering that sporulation is a part of AMF life-cycle, the establishment of trap cultures represents a strategy to recover spores from previously undetected taxa as well as to obtain healthy spores which can contribute to species identification (Morton et al., 1993; Douds and Millner, 1999).

Regarding ecological aspects of these microorganisms, some studies have indicated that AMF are influenced by the host plant (Kawahara and Ezawa, 2013; Pagano et al., 2013; Soteras et al., 2016) and abiotic characteristics, such as soil attributes and climatic factors (Bennett et al., 2013; Hazard et al., 2013; Pellissier et al., 2014). However, there is no consistent conclusion about factors shaping AMF communities (Xu et al., 2016), mainly because more information on distribution and diversity of these fungi is still needed.

Only a few studies on AMF diversity have been carried out in island environments and those have mainly been performed in large environments, for instance, in the Galapagos (Schmidt and Scow, 1986), Hawaii (Koske, 1988; Koske and Gemma, 1995, 1996a), and Great Nicobar, India (Kothamasi et al., 2006). In Brazil, research of this type has only been performed in two sites: Ilha do Cardoso, in the Southeast (Trufem et al., 1989, 1994; Trufem, 1990) and the island of Santa Catarina, in the South region (Stürmer and Bellei, 1994; Stürmer et al., 2013). Thus, information on AMF occurrence and distribution collected in other island environments can contribute to broaden knowledge about the biogeographical and ecological patterns of these fungi, especially in poorly studied environments such as tropical areas (Rodríguez-Echeverría et al., 2017).

This study aims to determine mycorrhizal colonization and to compare the AM fungi community structure along a transect crossing a fluvial-marine island, characterized by different environments in an area of only 530 ha, and relate the data to vegetation types and soil parameters to shed light on the forces driving AMF community structure. Considering that plant hosts and environmental factors are important drivers of AMF communities on a local scale (Li et al., 2010; Kawahara and Ezawa, 2013; Silva et al., 2015a), we tested the hypothesis that AMF community composition changes across the island, even within short distances among sites, in response to differences in the edaphic characteristics and vegetation physiognomies, with AMF community composition being more strongly determined by soil characteristics than by physiognomic conditions.

2. Material and methods

2.1. Study area

The study was performed on the Ilha da Restinga ('Restinga Island', 07°0′10.60″S and 34°51′32.01″W), located at the mouth of the Northern Paraíba River, in the municipality of Cabedelo, Paraíba, northeastern Brazil. With 530 ha and a relatively flat topography, ranging from 0 to 11 m above sea level, the island is part of the Atlantic Forest domain and the vegetation consists primarily of mangroves in flooded regions and sandbank woods, estuaries and lagoons (Farias, 1980). The formation of the island occurred through soil accumulation brought by the Paraíba River (Oliveira, 2012). The average annual temperature is 25 °C, the climate is As' - tropical hot and wet, according to the Köppen classification, and the average annual precipitation is 1764 mm (Alves, 2011).

A transect of approximately 1500 m was established across the island in the east-west direction, due to the impossibility to establishing north-south transect, because the island has lagoons and Atlantic Forest areas (Alves, 2011). At approximately every 350 m, we established a sampling area, which corresponded to a distinct vegetation type (Fig. 1 - Google Earth, 2016).

The transect went across the following habitats: 1 – a mangrove forest (MF; 07°0′15.66″S; 34°51′50.49″W; 5 m asl) representing a conserved mangrove forest area located in the west side of the island, which is frequently flooded; 2 – a regeneration *Restinga* forest 1 (RR1; 07°0′14.99″S; 34°51′40.93″W; 8 m asl), a *Restinga* forest area which was devastated and is currently still under a recover process; 3 – a natural *Restinga* forest (RF; 7° 0′10.60″S; 34°51′32.01″W; 8 m asl); 4 – a second regeneration *Restinga* forest 2 (RR2; 07°0′9.19″S; 34°51′19.30″W; 10 m asl), which was also devastated and is currently in a recovering process; 5 – a degraded mangrove forest (MD; 07°0′14.30″S; 34°51′2.35″W; 5 m asl), characterized by a mangrove area degraded for two years and currently presenting some exotic plant species. More information about the habitats can be found in Guedes (2002) and Alves (2011).

2.2. Soil and roots samplings

Soil and root sampling was conducted in August 2011 (end of wet season). We delimited three plots of approximately 3 m^2 at each habitat. In each plot, two subsamples were collected to form a composite sample, totaling three composite samples per habitat type. Each composite sample (about 3 kg) was placed in plastic bags and transported to the laboratories of the Department of Mycology (UFPE). About 300 g of soil were used to determine the soil chemical and physical attributes, 2 kg of soil were used to set up AMF trap cultures, and 100 g of soil were used for AMF spore extraction for morphological species identification. Samples of field roots were used to determine rates of mycorrhizal colonization.

2.3. Soil attributes

Three soil samples of each habitat type were used to determine the physical and chemical attributes of the soil. The analyses were performed at the "Estação Experimental de Cana-de-açúcar da Universidade Federal Rural de Pernambuco" in Carpina, Pernambuco.

The chemical attributes were evaluated following the methods described in Silva et al. (1999): the pH was measured in water (1:2.5; weight:volume); Ca^{2+} and Mg^{2+} were extracted with 1 M KCl and quantified by atomic absorption; K^{+}, Na^{+}, P, Cu, Zn and Mn were extracted using Mehlich 1 reagent (0,05 of HCl + 0,0125 of H_2SO_4), for the analysis of Cu, Zn, Mn and Fe a soil:reagent proportion of 1:5 was used, while for macronutrients a proportion of 1:10 was used. K^{+} and Na were determined by flame photometry, P by colorimetry, and Cu, Zn, Mn and Fe by atomic absorption spectrophotometry; organic carbon was evaluated by oxidation in potassium dichromate and titration of the excess potassium dichromate by ferrous ammonium sulfate; H^{+} and Al^{3+} were determined by the calcium acetate method and alkaline titration;

SB is the sum of bases (Na^+, K^+, Ca^{2+} and Mg^{2+}); CEC is the cation exchange capacity (SB + potential acidity H + Al); V is the base saturation (percentage of SB/CEC); m% is the percentage of aluminum saturation. The physical attributes (coarse sand, fine sand, silt and clay) were determined by the pipette method (EMBRAPA, 1997).

2.4. Mycorrhizal colonization rate

Fine roots were separated from the soil samples to estimate root colonization by AMF. The roots were washed in tap water, clarified with KOH (10%) and stained with Trypan blue (0.05%; Phillips and Hayman, 1970). Samples with highly pigmented roots were treated with H_2O_2 for 10 min before staining.

The mycorrhizal colonization rate was assessed using the magnified gridline intersection method (McGonigle et al., 1990 – modified) considering 250 intersections per sample to estimate the percentage of root length colonized by AMF. An intersection was considered colonized if intraradical hyphae, arbuscules, vesicles and/or spores were present. Many studies that have analyzed mycorrhizal colonization have not reported the presence of spores inside roots; however, in this study, we also considered these propagules since some AMF species sporulate within roots (Mergulhão et al., 2014; Sieverding et al., 2014).

2.5. Trap cultures

Trap cultures were prepared with 2 kg of soil samples from the field (three pots for each habitat type), using maize (*Zea mays* L.) as a host, due to its wide-ranging association with AMF and the production of large root biomass, and maintained in the greenhouse of the Department of Mycology (UFPE). These cultures were watered every other day and fertilized every fortnight with Hoagland solution (Hoagland and Arnon, 1950), as modified by Jarstfer and Sylvia (1992). At the end of the vegetative cycle (eight months), the plants were subjected to water stress during two weeks to favor sporulation of the fungi, and soil samples were collected for spore extraction and AMF species identification.

2.6. Glomerospore and sporocarp extraction, quantification and AMF species identification

Glomerospores and sporocarps were extracted from 100 g of soil samples by wet sieving (Gerdemann and Nicolson, 1963), and water and sucrose centrifugation (50%) (Jenkins, 1964 – modified), using sieves with openings of 850 μm and 45 μm. Glomerospores and sporocarps were quantified with the aid of a stereomicroscope (40x); sporocarps were counted as one unit. After quantification, the spores and sporocarps were separated according to spore size and color and mounted on glass slides using polyvinyl alcohol lactoglycerol (PVLG) and PVLG + Melzer's reagent for subsequent species identification based on spore morphology using identification manuals (e.g. Błaszkowski, 2012) and the most recent literature, following the classification proposed by Oehl et al. (2011) and updates (Goto et al., 2012).

2.7. Ecological and statistical analysis

We calculated spore abundance (*N*), AMF species richness (*S*), and the Shannon-Wiener diversity index (*H′*) for all samples.

Fig. 1. Map of the habitats studied across Ilha da Restinga (MF - Mangrove forest, RR1 - regeneration *Restinga* forest 1, RF - *Restinga* forest, RR2–regeneration *Restinga* forest 2, and MD - degraded mangrove forest), northeastern Brazil. Google Earth (2016).

Relative abundance of AMF spores per family was determined for each habitat. AMF species richness was determined as the number of species present in each sample and the first-order Jackknife index (Jackknife 1) was calculated to estimate the number of species. The Shannon-Wiener diversity index (*H'*) was calculated based on the equation H' = -∑(Pi ln (Pi)), where Pi = ni/*N*, ni = number of individuals of the species i, *N* = total number of individuals of all species (Shannon and Weaver, 1949). For statistical purposes, the values of *H'* were converted into Exp (H').

Permutation multivariate analysis of variance (PERMANOVA), using Euclidean distance, was applied to test whether soil composition differs along the habitat types on the island. Before analysis, the data were relativized in the column to eliminate differences among measured units of each edaphic attribute.

The multivariate analysis of AMF communities was performed using the relative abundance of AMF species. To investigate whether the habitat types of the island harbor distinct AMF communities, PERMANOVA analysis was applied using Bray-Curtis distance. Canonical correspondence analysis (CCA) was performed to test whether there is a relationship between the AMF community composition and soil variables. In addition to CCA, BIO-ENV was applied to investigate the relationship of the AMF community composition with soil parameters, and select which soil attributes have maximum correlation with the dissimilarities of the AMF communities (Clarke and Ainsworth, 1993).

Indicator species analysis (Dufrêne and Legendre, 1997) was performed to detect possible AMF species/habitat and AMF family/habitat relationships. Indication values (IndVal) were calculated for each species and the significance determined by the Monte Carlo test; a species was considered an indicator for a habitat type when it presented $p < 0.05$ and IndVal ≥25%.

Data of soil attributes, mycorrhizal colonization rates (total, arbuscules, vesicles, hyphae and spores), AMF species richness, spore abundance and diversity indices (Shannon-Wiener) of each sample over the five habitats along the transect were subjected to analysis of variance (ANOVA) followed by means of comparisons, when appropriate, using the Tukey test at 5% probability. We assessed relationships between soil variables and AMF data by calculating the Pearson's correlation coefficients. The univariate analyses (ANOVA) were performed using the Assistat software (Silva, 2014). Calculations of ecological indexes, species accumulation curves and BIO-ENV were determined with the aid of Primer 6.0 program (Clarke and Gorley, 2006). Indicator species analysis, CCA and PERMANOVA were performed using the PC-ORD 6.0 program (McCune and Mefford, 2011).

3. Results

3.1. Pedological attributes

The chemical characteristics of the soil differed significantly among the different habitats, especially between the natural *Restinga* (e.g. pH 4.0 and 47 g kg^{-1} soil organic matter) and the natural mangrove forest (e.g. pH 7.0 and 3 g kg^{-1} soil organic matter) (Table 1). The sandy soils differ to a lesser degree in terms of soil texture, with clay content ranging from 2 to 6% and <1% silt. Based on PERMANOVA analyses, soil composition differed among all sampled habitats ($F = 23.65$; $P < 0.001$). The sum of exchangeable bases, as well as sodium, copper and iron concentrations were higher in MF. The highest organic matter, Al-values, CTC were registered in RF, which represents the most developed soil of all five habitats. In general, the soils were eutric, but RF and RR2 were dystric (V%<50%). The phosphorus content was low (<10 mg dm^3) in all sampled habitats.

3.2. AMF root colonization

The AM root colonization differed in the collected root fragments from 1% in MF to 74% in RF (Table 2). The percentage of intraradical hyphae also differed greatly among the five habitats and was also highest in RF (63%), while it was only 2% in MF (Table 2). There was a significant difference also in vesicle formation, which was not detected in roots from MF, but in the other habitats it ranged from 4 to 11% (Table 2). Arbuscule formation was, as expected for field soil collected roots, generally low, and was higher in MD (6%), while it was 0–1% in the other habitats (Table 2). Intraradical spores were also found in the roots, with the exception of those collected from MD (Table 2).

There were positive correlations between percentage of arbuscules and Zn content ($r = 0.85$, $P<0.01$), H^+ ($r = 0.58$, $P < 0.05$), and CEC ($r = 0.55$, $P < 0.05$); percentage of vesicles and carbon content ($r = 0.54$, $P < 0.05$), and organic matter (OM) ($r = 0.54$, $P < 0.05$), and between the total colonization with carbon content ($r = 0.64$, $P < 0.01$) and OM ($r = 0.64$, $P < 0.01$). Negative correlations were registered between the percentage of hyphae and availability of soil Fe ($r = -0.54$, $P < 0.05$), Cu ($r = -0.54$, $P < 0.05$), Ca ($r = -0.57$, $P < 0.05$), base saturation ($r = -0.61$, $P < 0.05$), silt content ($r = -0.54$, $P < 0.05$), and pH ($r = -0.56$, $P < 0.05$), and between the total colonization and Fe ($r = -0.54$, $P < 0.05$), Cu ($r = -0.54$, $P < 0.05$), Ca ($r = -0.53$, $P < 0.05$), and base saturation ($r = -0.56$, $P < 0.05$).

3.3. AMF species richness

Twenty-two AMF species were identified, belonging to 9 genera: *Acaulospora* (6 species), *Ambispora* (1), *Cetraspora* (2), *Funneliformis* (1), *Gigaspora* (2), *Glomus* (7), *Paradentiscutata* (1), *Racocetra* (1) and *Sclerocystis* (1) (Table 3). Three species could not be identified to the species level: *Acaulospora* sp. 1, *Acaulospora* sp. 2, and *Glomus* sp. all of which might represent new species.

The AMF species accumulation curve did not reach the saturation point (Fig. 2), but at least 75% of the expected species were identified. Species richness ranged from four to nine species among the habitats (Table 3). Although richness was not statistically different among the habitats (Fig. 3a), diversity based in the Shannon-Wiener index was lower in the MF and RR2 habitats than in the other three habitats (Fig. 3b). *Glomus brohultii* was the most frequent species occurring in all habitat types, followed by *Ambispora appendicula* which occurred in 4 out of the 5 sampled habitats, and *Acaulospora* sp.2, *Gigaspora margarita, Racocetra coralloidea*, and *Glomus* sp.1 (all of which were found in 3/5). Most of the other species were found in only one of the five habitats: *Acaulospora morrowiae* and *Sclerocystis sinuosa* in MF, *Cetraspora gilmorei*, *Glomus glomerulatum* and *Glomus ambisporum* in RR1, *Acaulospora foveata* and *Glomus microcarpum* in RF, *Acaulospora scrobiculata* in RR2, and *Cetraspora pellucida* and *Gigaspora gigantea* in MD (Table 3).

In general, AMF spore abundance per family differed among some of the sampled habitats ($F = 3.9$, $P<0.05$). The habitats MF and RR2 did not differ and had the highest numbers of Acaulosporaceae spores (Fig. 4a), while RF and MD had higher numbers of Gigasporaceae spores (Fig. 4b). The other three AMF families (Ambisporaceae, Glomeraceae, Intraornatosporaceae, and Racocetraceae) had similar numbers of spores in the different habitats (data not shown).

3.4. AMF multiplication in trap cultures

Funneliformis halonatus, *Gigaspora margarita* and *Glomus brohultii* were detected in trap cultures from MD and *Racocetra*

Table 1
Physical and chemical properties of the soils along five natural and degraded habitats (MF - Mangrove forest, RR1 - Regeneration *Restinga* forest 1, RF - *Restinga* forest, RR2 - Regeneration *Restinga* forest 2, and MD - Degraded mangrove forest) on Ilha da Restinga, northeastern Brazil.

Attributes	Habitats					*F*
	MF	RR1	RF	RR2	MD	
pH (H_2O)	7.00 ± 0.1a	6.20 ± 0.5 ab	4.00 ± 0.1c	4.60 ± 0.3c	5.90 ± 0.3b	46.5**
Ca^{2+} ($cmol_c\ dm^{-3}$)	3.30 ± 0.0a	2.13 ± 0.3 ab	1.63 ± 0.6b	2.53 ± 0.8 ab	2.10 ± 0.0b	6.0*
Mg^{2+} ($cmol_c\ dm^{-3}$)	0.47 ± 0.3a	0.30 ± 0.0a	0.63 ± 0.3a	0.30 ± 0.0a	0.43 ± 0.1a	2.0^{ns}
K^{+} ($cmol_c\ dm^{-3}$)	0.36 ± 0.0a	0.06 ± 0.0b	0.09 ± 0.0b	0.08 ± 0.0b	0.10 ± 0.0b	131.8**
Na^{+} ($cmol_c\ dm^{-3}$)	1.46 ± 0.4a	0.15 ± 0.1b	0.15 ± 0.0b	0.06 ± 0.0b	0.09 ± 0.0b	29.3**
Al^{3+} ($cmol_c\ dm^{-3}$)	0.10 ± 0.0b	0.07 ± 0.0b	1.53 ± 0.4a	0.60 ± 0.4b	0.10 ± 0.0b	21.5**
P ($mg\ dm^{-3}$)	8.67 ± 1.2a	4.00 ± 0.0b	8.00 ± 1.0a	5.67 ± 1.5 ab	9.33 ± 2.5a	6.8**
C (%)	0.17 ± 0.1d	0.80 ± 0.1c	2.73 ± 0.8a	1.18 ± 0.2b	0.76 ± 0.1c	53.3**
OM (%)	0.29 ± 0.1c	1.37 ± 0.2b	4.71 ± 1.3a	2.04 ± 0.4v	1.30 ± 0.1b	53.8**
CEC ($cmol_c\ dm^{-3}$)	5.72 ± 0.6a	3.63 ± 0.4a	10.16 ± 0.8a	6.75 ± 1.0a	14.20 ± 17.5a	0.84 ^{ns}
SB ($cmol_c\ dm^{-3}$)	5.58 ± 0.6a	2.64 ± 0.2b	2.50 ± 0.3b	2.97 ± 0.8b	2.72 ± 0.2b	24.1**
Cu ($mg\ dm^{-3}$)	0.33 ± 0.1a	0.10 ± 0.0b	0.00 ± 0.0c	0.03 ± 0.0bc	0.10 ± 0.0b	38.2**
Fe ($mg\ dm^{-3}$)	79.80 ± 12.0a	24.47 ± 2.0b	8.27 ± 2.7c	4.53 ± 0.5c	8.60 ± 3.0c	72.1**
Mn ($mg\ dm^{-3}$)	5.57 ± 1.3 ab	4.10 ± 1.5 ab	1.70 ± 0.9c	8.43 ± 4.0 ab	8.53 ± 2.3a	5.0*
Zn ($mg\ dm^{-3}$)	0.97 ± 0.2b	1.57 ± 0.5 ab	1.27 ± 1.0 ab	1.27 ± 0.3 ab	3.77 ± 2.0a	3.7*
V (%)	97.49 ± 0.2a	73.03 ± 5.0b	24.77 ± 3.4d	43.59 ± 4.8c	47.07 ± 6.2b	40.4**
m (%)	0.90 ± 0.0b	1.75 ± 0.3b	37.76 ± 8.5a	17.37 ± 1.3b	1.80 ± 0.1b	17.9**
Total sand (%)	97.40 ± 0.7a	97.70 ± 0.3a	93.50 ± 1.3b	96.70 ± 0.2a	97.30 ± 0.2a	19.7**
Coarse sand (%)	79.85 ± 1.4b	87.50 ± 2.1a	78.70 ± 3.4b	87.20 ± 0.5a	84.40 ± 0.8 ab	13.7**
Fine sand (%)	17.55 ± 1.3a	10.20 ± 1.8b	14.80 ± 3.0 ab	9.50 ± 0.7b	12.90 ± 1.0 ab	10.7**
Silt (%)	0.00 ± 0.0a	0.00 ± 0.0a	0.60 ± 0.6a	0.00 ± 0.0a	0.00 ± 0.0a	4.0*
Clay (%)	2.60 ± 0.7b	2.30 ± 0.3b	5.90 ± 0.8a	3.30 ± 0.8b	2.70 ± 0.2b	24.6**

Average values of three samples. ns: not significant and represented by same letters based on ANOVA and Tukey test at 1% (**) and at 5% (*). CEC: denotes cation exchange capacity; SB: sum of exchangeable bases; m: aluminum saturation.

Table 2
Arbuscular mycorrhizal fungal colonization rates in plants of the habitats (MF - Mangrove forest, RR1 - regeneration *Restinga* forest 1, RF - *Restinga* forest, RR2 – regeneration *Restinga* forest 2, and MD - degraded mangrove forest) on Ilha da Restinga, northeastern Brazil.

Habitats	Mycorrhizal colonization %				
	Arbuscules	Vesicles	Hyphae	Spores	Total
MF	0.0 b	0.00 b	1.46 c	0.00 b	1.46 b
RR1	0.0 b	3.60 a	8.54 bc	2.86 a	21.60 ab
RF	0.0 b	10.69 a	62.86 a	0.39 a	73.93 a
RR2	1.11b	6.71 a	16.11 bc	1.11 a	25.05 ab
MD	6.14a	9.42 a	46.78 b	1.04 a	61.71 ab

% denotes percentage of intraradical arbuscules, vesicles, hyphae, spores, and total colonization. Means followed by the same letter in the columns do not differ significantly by the Tukey test at 5% probability.

coralloidea from RF samples, but these species were not registered previously in the field samples of these habitats. The species richness from the trap culture analyses was in general lower than or similar to that found in the field soil samples (Table 3) and did not differ among the habitats according to the ANOVA and Tukey test.

3.5. AMF community composition in relation to chemical and physical soil attributes

Positive correlations were registered between relative spore abundance of Acaulosporaceae and availability of soil Fe ($r = 0.84$, $P < 0.01$), Cu content ($r = 0.76$, $P < 0.01$), pH ($r = 0.59$, $P < 0.05$), exchangeable bases (BS) ($r = 0.93$, $P < 0.01$), silt ($r = 0.55$, $P < 0.05$), and clay content ($r = 0.63$, $P < 0.05$); a negative correlation was found with OM ($r = -0.52$, $P < 0.05$). The relative abundance of Glomeraceae spores was negatively correlated with Fe ($r = -0.60$, $P < 0.05$) and Cu availability ($r = -0.63$, $P < 0.05$), pH ($r = -0.60$, $P < 0.05$), BS ($r = -0.68$, $P < 0.01$), and silt content ($r = -0.62$, $P < 0.05$) and positively with Al content ($r = 0.56$, $P < 0.05$) and OM ($r = 0.54$, $P < 0.05$). The relative abundance of spores of Intraornatosporaceae was negatively correlated with soil Mn availability ($r = -0.60$, $P < 0.05$) and positively with Al availability ($r = 0.59$, $P < 0.05$) and soil organic matter ($r = 0.75$, $P < 0.01$).

There were significant differences in AMF community composition among the habitats based on the PERMANOVA analyses ($F = 5.3$; $P < 0.001$), with the exception of the RR2 habitat, which had similar composition to the two mangrove forests (MF and MD). In the CCA analysis a significant correlation between the AMF community composition and the soil was revealed ($P < 0.05$); the physicochemical attributes accounted for 47% of the AMF community and the variance explained by the two axes was 70% (Fig. 5).

Considering all chemical and physical soil attributes investigated, soil pH, sum of the exchangeable bases (BS), base saturation (V), fine sand, clay and silt content, and copper and iron availability had the greatest impact on the AMF community composition in habitat MF (Fig. 5), while coarse sand was most correlated with RR1, and the organic matter and available Al with RF (Fig. 5). The results of the BIO-ENV analysis showed that the sum of the exchangeable bases (BS) presented a high correlation with the AMF community composition ($r = 0.64$).

With the exception of RR2 and MD habitats, all others presented indicator species: *Acaulospora* sp. 1 was indicative for MF, *Acaulospora* sp. 2 for RR1, *Acaulospora foveata* and *Glomus macrocarpum* for RF. When considering the AMF families, Acaulosporaceae was indicative for MF and Gigasporaceae for the habitat MD (Table 4).

4. Discussion

Despite the short extent of the island (1500 m), AMF communities changed significantly across the five different habitat types sampled. As hypothesized, these changes are related to environmental characteristics, principally of soil and vegetation types.

Dunes and *Restinga* soils are very sandy and characterized by low nutrient availability, especially P and K (Błaszkowski and Czerniawska, 2011; Silva et al., 2015a). Considering that low soil fertility is one limiting factor for the establishment and maintenance of species-rich vegetation, the association between coastal plants and AM fungi is an important ecological strategy for both

Table 3
AM fungi in five island habitats (MF - Mangrove forest, RR1 - regeneration *Restinga* forest 1, RF - *Restinga* forest, RR2 — regeneration *Restinga* forest 2, and MD - degraded mangrove forest) identified from field soil samples and from AMF trap cultures.

	Field					Trap cultures				
	MF	RR1	RF	RR2	MD	MF	RR1	RF	RR2	MD
Glomeromycetes										
Diversisporales										
Acaulosporaceae										
Acaulospora foveata			x							
A. mellea		x		x						
A. morrowiae	x									
A. scrobiculata				x						
Acaulospora sp.1	x			x		x				
Acaulospora sp.2		x		x	x					
Gigasporales										
Gigasporaceae										
Gigaspora gigantea					x					
G. margarita			x		x	x				
Intraornatosporaceae										
Paradenstiscutata maritima			x		x					
Racocetraceae										
Cetraspora gilmorei		x								
C. pellucida					x					
Racocetra coralloidea		x			x			x		
R. tropicana	x		x							
Glomerales										
Glomeraceae										
Funneliformis halonatus			x			x				
Glomus ambisporum		x								
Glomus brohultii			x	x	x	x	x	x		
G. glomerulatum		x					x			
G. macrocarpum			x	x						
G. microcarpum.			x							
Glomus sp.1			x						x	x
Sclerocystis sinuosa	x									
Archaeosporomycetes										
Archaeosporales										
Ambisporaceae										
Ambispora appendicula		x	x	x	x			x		

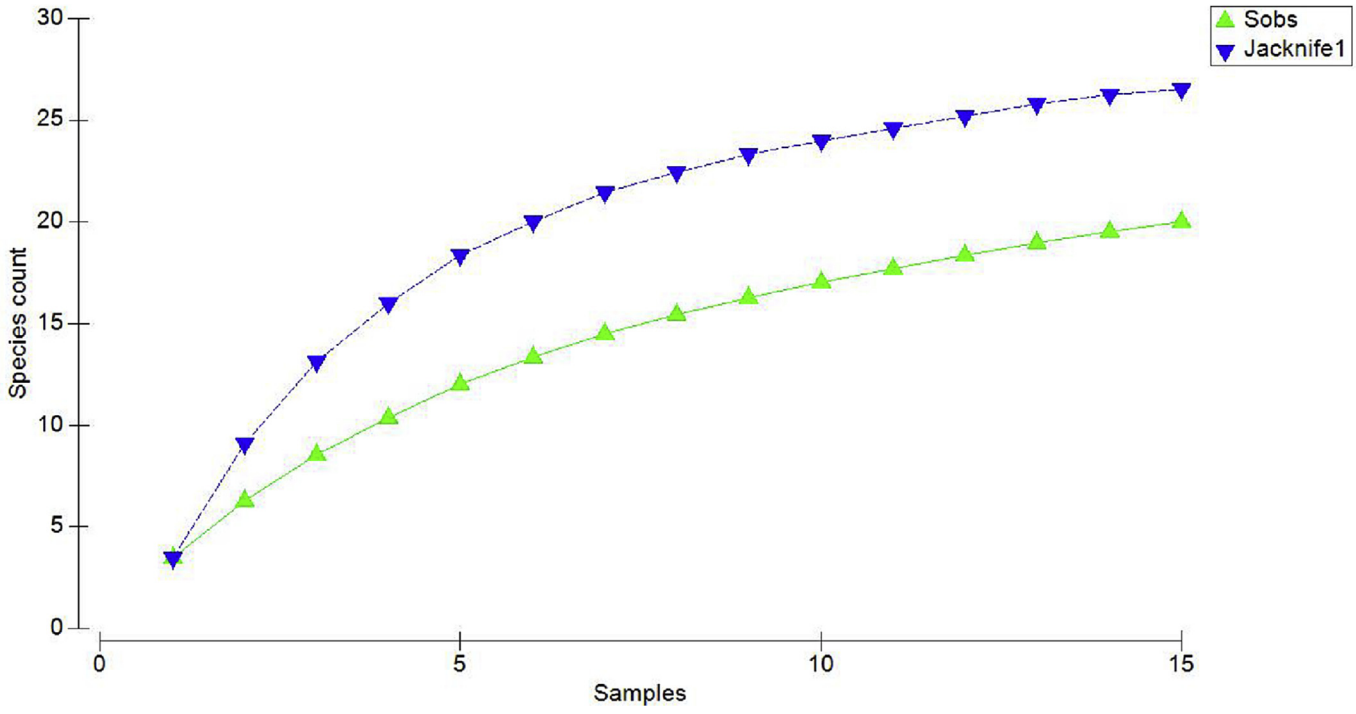

Fig. 2. Accumulation curve of AMF species (Sobs) and estimated richness based on the first-order Jackknife index (Jackknife 1) on Ilha da Restinga, northeastern Brazil.

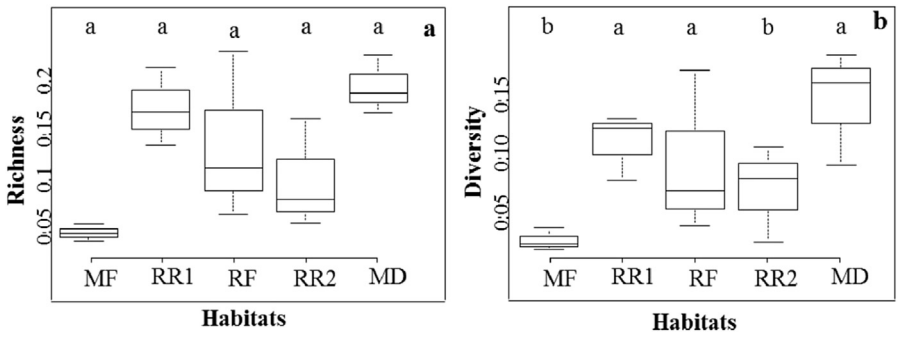

Fig. 3. Richness (a) and diversity (b) of AMF species along five natural and degraded habitats (MF - Mangrove forest, RR1 - regeneration *Restinga* forest 1, RF - *Restinga* forest, RR2 - regeneration *Restinga* forest 2, and MD - degraded mangrove forest) on Ilha da Restinga, northeastern Brazil.

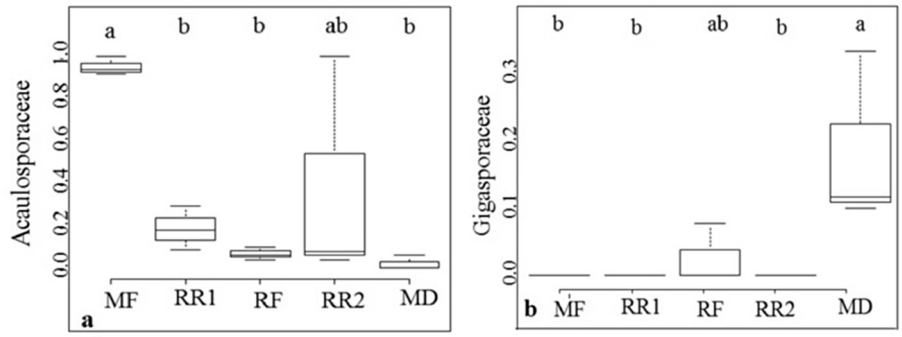

Fig. 4. Relative abundance of Acaulosporaceae (a) and (b) Gigasporaceae along five natural and degraded habitats (MF - Mangrove forest, RR1 - regeneration *Restinga* forest 1, RF - *Restinga* forest, RR2 - regeneration *Restinga* forest 2, and MD - degraded mangrove forest) on Ilha da Restinga, northeastern Brazil.

fungi and plants to overcome such extreme growing conditions (Willis and Yemm, 1961; Maun, 2009).

Root samples from the *Restinga* forest (RF) have the highest total AMF and AM hyphal colonization rates, while root samples from the other habitats showed a range of variation. The roots from the mangrove forest (MF) were almost free of AMF colonization, probably due to the anoxic condition of the soil. The degraded habitat types had intermediate values. This is the first study to include intra-radical spores as part of the quantification of mycorrhizal root structures. Although spores have been recognized as important propagules for the survival of AM fungi (Smith and Read, 2008) and many species regularly form spores inside roots (Mergulhão et al., 2014; Sieverding et al., 2014), they have usually not been considered or have been quantified erroneously as vesicles (Giovanetti and Mosse, 1980; McGonigle et al., 1990).

The number, intensity and structures of AMF colonization (hyphae, arbuscules or vesicles) can differ due to changes of the AMF community composition (Hart and Reader, 2002), as observed in our study. Differences in colonization rates are often related to other parameters such as the number of propagules (inoculum density), root growth, genetic compatibility between AMF and host plants, edaphic attributes and microbial activity (Camargo-Ricalde, 2002; Zangaro et al., 2013). In this study we found a correlation among mycorrhizal colonization and most chemical soil attributes.

The AMF species richness was rather low in our study, when compared to other coastal ecosystems in northeastern Brazil (e.g. Souza et al., 2011; Silva et al., 2015a, b). However, AMF species richness on islands has generally been considered relatively low in comparison with mainland habitats, due to difficulties for dispersal of AMF propagules (Koske, 1988). The AMF are obligatory biotrophic and in order to colonize, establish and maintain themselves in a new ecosystem, propagules need not only to arrive at the new

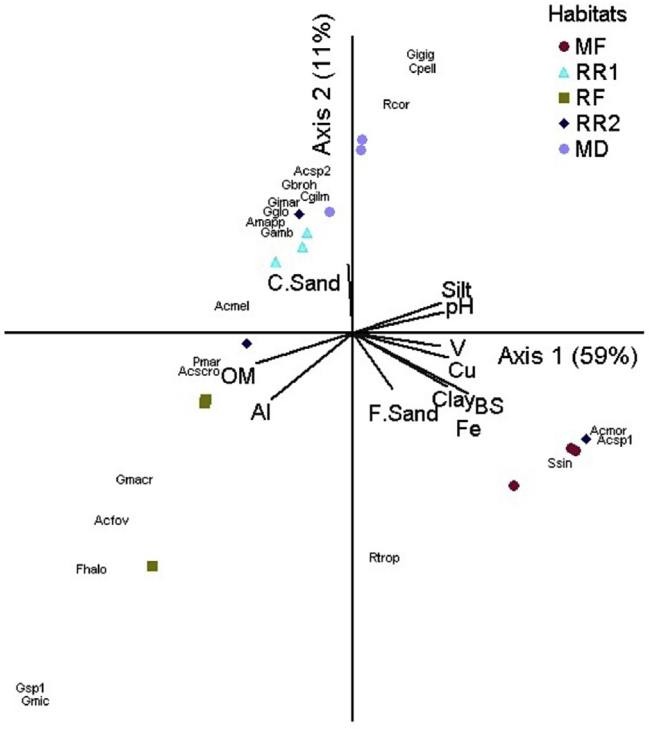

Fig. 5. Canonical correspondence analysis (CCA) of the relationship between AMF species and soil variables in five natural and degraded habitats (MF - Mangrove forest, RR1 - regeneration *Restinga* forest 1, RF - *Restinga* forest, RR2 - regeneration *Restinga* forest 2, and MD - degraded mangrove forest) on Ilha da Restinga, northeastern Brazil.

site, but they also must survive in edaphic conditions which are not always favorable, and find and colonize a compatible host plant before the exhaustion of their propagule resources.

All AMF genera and the majority of AMF species recorded in our study have already been reported from other *Restinga* areas (e.g. Silva et al., 2015a) suggesting that these species are adapted to such coastal living conditions. On *Ilha do Cardoso* (southeastern Brazil) AMF species richness ranged from 14 to 24 species in the coastal dunes and reached up to 35 at a humid forest site; the species in common with our study were *Ambispora appendicula, Acaulospora foveata*, *A. scrobiculata*, *Cetraspora gilmorei*, *Gigaspora gigantea*, *Glomus macrocarpum, G. microcarpum, Sclerocystis sinuosa* and *Racocetra coralloidea* (Trufem, 1990; Trufem et al., 1994). In dune areas of Santa Catarina State in southern Brazil, 12 species were registered, among them *Acaulospora scrobiculata* and *Racocetra coralloidea* (Stürmer and Bellei, 1994), which were also found in our study. In Hawaiian dunes 12–14 species were detected, among them *A. scrobiculata* and *Sclerocystis sinuosa* (Koske, 1988).

In general, *A. scrobiculata*, *Glomus macrocarpum* and *Gigaspora margarita* are considered generalist fungi in marine sand dune habitats, and are usually found in many environments (Kowalczyk and Błaszkowski, 2011), especially in tropical areas (Souza et al., 2003; Tchabi et al., 2010). The predominance of *Acaulospora* and *Glomus* species might be correlated with the ability of these taxa to adapt even to extreme conditions and to a wide range of soil pH (Maia and Trufem, 1990; Öpik et al., 2013). Furthermore, species belonging to *Glomus* and *Acaulospora* can establish root colonization from different types of propagule (hyphae, vesicles, and spores) while *Gigaspora* species are propagated exclusively by spores (Hart and Reader, 2002).

The mangrove forest (MF) and one regeneration *Restinga* forest (RR2) had lower AMF diversity despite having similar species richness to the other habitats, reflecting lower evenness, which is a characteristic of disturbed habitats. This might be expected in the specific environment of mangroves, which are frequently flooded by saline sea water, and by the disruption of the *Restinga* site, as both conditions might lead to the proliferation of specific AMF species which are also known from other extreme environments (Soka and Ritchie, 2014). Some AMF species are known to survive immersion in seawater for several days (Koske et al., 1996b).

The richness of AMF species from trap cultures was lower than AMF richness from samples directly collected in the field. This result might be related to the incompatibility between AMF taxa and the host plant (host preference) and/or AMF taxa and growing conditions (environmental preference) (Jansa et al., 2002, 2014; Trejo-Aguilar et al., 2013). Despite that, some species that had not been found in the respective field soil samples were detected from trap culture samples, indicating the complementarity of that approach to more comprehensively determine AMF species richness in an environment (Mergulhão et al., 2009; Błaszkowski and Czerniawska, 2011).

The changes in the AMF community composition across the habitats confirm the theory that different environments (especially related to vegetation and soil) significantly affect AMF communities (Walter, 2004; Triantis et al., 2012). Pagano et al. (2013) and Schechter and Bruns (2012) also observed that AMF species diversity and AMF community structure are correlated with habitat heterogeneity and soil attributes.

A strong impact of soil characteristics on the composition of AMF communities has been reported in recent literature (Oehl et al., 2010; Carvalho et al., 2012; Jansa et al., 2014; Silva et al., 2014). In the present study, soil attributes were important factors, among others, for differences in AMF community structure. Soil pH was one of these factors, as also reported in other studies (Dumbrell et al., 2010; Oehl et al., 2010).

Geographical factors may also affect AMF communities (Dumbrell et al., 2010; Jansa et al., 2014). In the present study, the mangrove forest (MF), which is periodically flooded, had a very distinct pattern when compared to the other habitats, which could be related to the periodic inundation by sea water (Sigüenza et al., 1996). The AMF species richness and diversity on Ilha da Restinga, although significantly lower than on the continental mainland (Souza et al., 2011; Silva et al., 2015a, b), is possibly well correlated with the dispersal of propagules deriving from continental sites.

The AMF spores might have arrived from the mainland by fluvial-marine water (Koske and Gemma, 1990; Harinikumar and Bagyaraj, 1994; Koehler et al., 1995; Koske et al., 1996b; Mangan and Adler, 2000) or even wind transport (Allen et al., 1989; Oehl et al., 2011). In AMF studies on the Galapagos islands, human and animal activities were also suggested to be important factors for AMF distribution over distances (Schmidt and Scow, 1986). Harner et al. (2009) observed that sediments deposited by flooding events had AMF propagules represented by hyphae and spores that were able to colonize sorghum roots. Spores of *Gigaspora gigantea*, a common AMF species in sand dunes, can tolerate immersion of several days in seawater and still germinate (Koske et al., 1996b).

5. Conclusions

On the fluvial-marine Ilha da Restinga the changes in AMF community structure were highly related to soil characteristics, especially to the sum of the exchangeable bases. The changes were evident even within the short distances among the habitats. Islands with high variability of soil attributes and diverse vegetation are potential refuges for diversity conservation of AM fungi.

Contributions

I. R. da Silva, D. K. A. da Silva, and F. A. de Souza designed the research; I. R. da Silva performed the research and analyzed the data; all authors discussed the results and wrote the manuscript.

Conflict of interest

The authors declare there are no conflicts of interest.

Acknowledgements

The authors are grateful to the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for providing a PhD scholarship to I.R. Silva, fellowship and research grants (INCT-Herbário Virtual Proc. 573.883/2008-4, Sisbiota Proc. 563342/2010-

Table 4
Results of AMF indicator species and respective indicator values for different island habitats.

Habitat	AMF species	Indicator Value (%)	p^*-value
Mangrove forest	*Acaulospora* sp.1	73.9	0.043
Regeneration *Restinga* forest 1	*Acaulospora* sp.2	79.2	0.012
Restinga forest	*Acaulospora foveata*	100	0.014
Restinga forest	*Glomus macrocarpum*	78.1	0.014

2, Universal Proc. 446.144/2014-2) to L.C. Maia and a Visiting Professor grant to F. Oehl. The authors also acknowledge a postdoctoral fellowship given to D.K.A. Silva by CNPq and Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco (FACEPE). The authors are indebted to Reginaldo Ferreira Neto and Camilla Pereira for help during the collection.

References

Allen, E.B., Allen, M.F., 1988. Facilitation of succession by the nonmycotrophic colonizer *Salsola-kali* (Chenopodiaceae) on a harsh site-effects of mycorrhizal fungi. Am. J. Bot. 75, 257–266. http://dx.doi.org/10.2307/2443892.

Allen, M.F., Hipps, L.E., Wooldridge, G.L., 1989. Wind dispersal and subsequent establishment of VA mycorrhizal fungi across a successional arid landscape. Landsc. Ecol. 2, 165–171. http://dx.doi.org/10.1007/BF00126016.

Alves, T.V.S., 2011. Impacto da degradação ambiental sobre a ictiofauna do estuário do Rio Paraíba – PB. Dissertation. Universidade Federal de, Pernambuco.

Bennett, A.E., Daniell, T.J., Öpik, M., Davison, J., Moora, M., Zobel, M., Selosse, M.A., Evans, D., 2013. Arbuscular mycorrhizal fungal networks vary throughout the growing season and between successional stages. PLoS ONE 8, e83241. http://dx.doi.org/10.1371/journal.pone.0083241.

Błaszkowski, J., Czerniawska, B., 2011. Arbuscular mycorrhizal fungi (Glomeromycota) associated with roots of *Ammophila arenaria* growing in maritime dunes of Bornholm (Denmark). Acta Soc. Bot. Pol. 80, 63–76. http://dx.doi.org/10.5586/asbp.2011.009.

Błaszkowski, J., 2012. Glomeromycota. W. Szafer Institute of Botany, Polish Academy of Sciences, Krakow.

Buckley, L.B., Jetz, W., 2007. Insularity and the determinants of lizard population density. Ecol. Lett. 10, 481–489. http://dx.doi.org/10.1111/j.1461-0248.2007.01042.x.

Camargo-Ricalde, S.L., 2002. Dispersal, distribution and establishment of arbuscular mycorrhizal fungi: a review. Bol. Soc. Bot. Mex. 71, 33–44.

Carvalho, F., de Souza, F.A., Carrenho, R., Moreira, F.M.S., Jesus, E.C., Fernandes, G.W., 2012. The mosaic of habitats in the high-altitude Brazilian rupestrian fields is a hotspot for arbuscular mycorrhizal fungi. Appl. Soil Ecol. 52, 9–19. http://dx.doi.org/10.1016/j.apsoil.2011.10.001.

Chase, J.M., 2003. Community assembly: when does history matter? Oecologia 136, 489–495. http://dx.doi.org/10.1007/s00442-003-1311-7.

Clarke, K.R., Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. Mar. Ecol. Prog. Ser. 92, 205–219. http://dx.doi.org/10.3354/meps092205.

Clarke, K.R., Gorley, R.N., 2006. Primer V6: User Manual/tutorial. PRIMER-E, Plymouth.

Dobrovolski, R., Melo, A.S., Cassemiro, F.A.S., Diniz-Filho, J.A.F., 2012. Climatic history and dispersal ability explain the relative importance of turnover and nestedness components of beta-diversity. Glob. Ecol. Biogeogr. 21, 191–197. http://dx.doi.org/10.1111/j.1466-8238.2011.00671.x.

Douds Jr., D.D., Millner, P.D., 1999. Biodiversity of arbuscular mycorrhizal fungi in agroecosystems. Agric. Ecosys Environ. 74, 77–93. http://dx.doi.org/10.1016/S0167-8809(99)00031-6.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366. http://dx.doi.org/10.1890/0012-9615.

Dumbrell, A.J., Nelson, M., Helgason, T., Dytham, C., Fitter, A.H., 2010. Idiosyncrasy and overdominance in the structure of natural communities of arbuscular mycorrhizal fungi: is there a role for stochastic processes? J. Ecol. 98, 419–428. http://dx.doi.org/10.1111/j.1365-2745.2009.01622.x.

EMBRAPA-Empresa Brasileira de Pesquisa Agropecuária, 1997. Manual de métodos de análise de solo. Centro Nacional de Pesquisas de Solos, Rio de Janeiro.

Farias, M.C.Q., 1980. Crustáceos decápodes da Ilha da Restinga. Bol. Inst. Oceanogr. 29, 169–172.

Francis, R., Read, D.J., 1994. The contributions of mycorrhizal fungi to the determination of plant community structure. Plant Soil 159, 11–25. http://dx.doi.org/10.1007/BF00000091.

Gerdemann, J.W., Nicolson, T.H., 1963. Spores of mycorrhizal *Endogone* extracted from soil by wet sieving and decanting. T Brit Mycol. Soc. 46, 235–244. http://dx.doi.org/10.1016/S0007-1536(63)80079-0.

Gianinazzi, S., Gollotte, A., Binet, M.N., van Tuinen, D., Redecker, D., Wipf, D., 2010. Agroecology: the key role of arbuscular mycorrhizas in ecosystem services. Mycorrhiza 20, 519–530. http://dx.doi.org/10.1007/s00572-010-0333-3.

Giovanetti, M., Mosse, B., 1980. An evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. New Phytol. 84, 489–500. http://dx.doi.org/10.1111/j.1469-8137.1980.tb04556.x.

Google Earth, May 22, 2016. Ilha da Restinga, PB, Brazil, 7.1.7.2606, 6° 59' 58.33"N, 34° 51' 06.98"W. (Accessed 8 11 2016).

Gotelli, N.J., Graves, G.R., 1996. Null Models in Ecology. Smithsonian Institution Press, Washington.

Goto, B.T., Silva, G.A., Assis, D.M.A., Silva, D.K.A., Souza, R.G., Ferreira, A.C.A., Jobim, K., Mello, C.M.A., Vieira, H.E.E., Maia, L.C., Oehl, F., 2012. Intraornatosporaceae (Gigasporales), a new family with two new genera and two new species. Mycotaxon 119, 117–132. http://dx.doi.org/10.5248/119.117.

Guedes, L.S., 2002. Monitoramento geoambiental do estuário do Rio Paraíba do Norte – PB por meio da cartografia temática digital e de produtos de sensoriamento remoto. Dissertação, Universidade Federal do, Rio Grande do Norte.

Harinikumar, K.M., Bagyaraj, D.J., 1994. Potential of earthworms, ants, millipedes, and termites for dissemination of vesicular-arbuscular mycorrhizal fungi in soil. Biol. Fertil. Soils 18, 115–118. http://dx.doi.org/10.1007/BF00336456.

Harner, M.J., Piotrowski, J.S., Lekberg, Y., Stanford, J.A., Rillig, M.C., 2009. Heterogeneity in mycorrhizal inoculum potential of flood deposited sediments. Aquat. Sci. 71, 331–337. http://dx.doi.org/10.1007/s00027-009-9198-y.

Hart, M.M., Reader, R.J., 2002. Taxonomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. New Phytol. 153, 335–344. http://dx.doi.org/10.1046/j.0028-646X.2001.00312.x.

Hazard, C., Gosling, P., van der Gast, C.J., Mitchell, D.T., Doohan, F.M., Bending, G.D., 2013. The role of local environment and geographical distance in determining community composition of arbuscular mycorrhizal fungi at the landscape scale. ISME J. 7, 498–508. http://dx.doi.org/10.1038/ismej.2012.127.

Hoagland, D.R., Arnon, D.I., 1950. The water-culture method for growing plants without soil. Calif. AES Bull. 347, 1–32.

Jansa, J., Mozafar, A., Anken, T., Ruh, R., Sanders, I.R., Frossard, E., 2002. Diversity and structure of AMF communities as affected by tillage in a temperate soil. Mycorrhiza 12, 225–234. http://dx.doi.org/10.1007/s00572-002-0163-z.

Jansa, J., Erb, A., Oberholzer, H.-R., Smilauer, P., Egli, S., 2014. Soil and geography are more important determinants of indigenous arbuscular mycorrhizal communities than management practices in Swiss agricultural soils. Mol. Ecol. 23, 2118–2135. http://dx.doi.org/10.1111/mec.12706.

Jarstfer, A.G., Sylvia, D.M., 1992. Inoculum production and inoculation strategies for vesicular–arbuscular mycorrhizal fungi. In: Metting, F.B. (Ed.), Soil Microbial Ecology: Applications in Agricultural and Environmental Management. Marcel Dekker, Inc., New York, pp. 349–377.

Jenkins, W.R., 1964. A rapid centrifugal-flotation technique for separating nematodes from soil. Plant Dis. Rep. 48, 692.

Kawahara, A., Ezawa, T., 2013. Characterization of arbuscular mycorrhizal fungal communities with respect to zonal vegetation in a coastal dune ecosystem. Oecologia 173, 533–543. http://dx.doi.org/10.1007/s00442-013-2622-y.

Koehler, H., Munderloh, E., Hofmann, S., 1995. Soil microarthropods (Acari, Collembola) from beach and dune: characteristics and ecosystem context. J. Coast Conserv. 1, 77–86. http://dx.doi.org/10.1007/BF02835564.

Koske, R.E., 1988. VA mycorrhizae of some Hawaiian dune plants. Pac Sci. 42, 217–229.

Koske, R.E., Gemma, J.N., 1990. VA mycorrhizae in vegetation of Hawaiian coastal strand: evidence for codispersal of fungi and plants. Am. J. Bot. 77, 466–474. http://dx.doi.org/10.2307/2444380.

Koske, R.E., Gemma, J.N., 1995. Vesicular-arbuscular mycorrhizal inoculation of Hawaiian plants: a conservation technique for endangered tropical species. Pac Sci. 49, 181–191 doi: 10125/2442.

Koske, R.E., Gemma, J.N., 1996a. Arbuscular mycorrhizal fungi in Hawaiian sand dunes: island of Kaua'i. Pac Sci. 50, 36–45 doi: 10125/2584.

Koske, R.E., Bonin, C., Kelly, J., Martinez, C., 1996b. Effects of sea water on spore germination of a sand dune-inhabiting arbuscular mycorrhizal fungus. Mycologia 88, 947–950. http://dx.doi.org/10.2307/3761057.

Kothamasi, D., Kothamasi, S., Bhattacharyya, A., Kuhad, R.C., Babu, C.R., 2006. Arbuscular mycorrhizae and phosphate solubilising bacteria of the rhizosphere of the mangrove ecosystem of Great Nicobar island, India. Biol. Fertil. Soils 42, 358–361. http://dx.doi.org/10.1007/s00374-005-0035-8.

Kowalczyk, S., Błaszkowski, J., 2011. Arbuscular mycorrhizal fungi (Glomeromycota) associated with roots of plants of the Lubuskie province. Acta Mycol. 46, 3–18. http://dx.doi.org/10.5586/am.2011.001.

Li, L.-F., Li, T., Zhang, Y., Zhao, Z.-W., 2010. Molecular diversity of arbuscular mycorrhizal fungi and their distribution patterns related to host-plants and habitats in a hot and arid ecosystem, southwest China. FEMS Microbiol. Ecol. 71, 418–427. http://dx.doi.org/10.1111/j.1574-6941.2009.00815.x.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography (Princeton, New Jersey).

Maia, L.C., Trufem, S.F.B., 1990. Fungos micorrízicos vesículo–arbusculares em solos cultivados no estado de Pernambuco, Brasil. Rev. Bras. Bot. 13, 89–95.

Mangan, S.A., Adler, G.H., 2000. Consumption of arbuscular mycorrhizal fungi by terrestrial and arboreal small mammals in a Panamanian cloud forest. J. Mammal. 81, 563–570. http://dx.doi.org/10.1644/1545-1542(2000)081.<0563:COAMFB>2.0.CO;2.

Maun, M.A., 2009. The Biology of Coastal Sand Dunes. Oxford University Press, Oxford.

McCune, B., Mefford, M.J., 2011. PC-ORD. Multivariate Analysis of Ecological Data. Version 6.0. MJM Software, Gleneden Beach, USA.

McGonigle, T.P., Miller, M.H., Evans, D.G., Fairchild, G.L., Swan, J.A., 1990. A new method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. New Phytol. 155, 495–501. http://dx.doi.org/10.1111/j.1469-8137.1990.tb00476.x.

Mergulhão, A.C.E.S., Figueiredo, M.V.B., Burity, H.A., Maia, L.C., 2009. Hospedeiros e ciclos sucessivos de multiplicação afetam a detecção de fungos micorrízicos arbusculares em áreas impactadas por mineração gesseira. Rev. Árvore 33, 227–236. http://dx.doi.org/10.1590/S0100-67622009000200004.

Mergulhão, A.C.E.S., da Silva, M.V., Lyra, M.C.C.P., Figueiredo, M.V.B., da Silva, M.L.R.B., Maia, L.C., 2014. Caracterização morfológica e molecular de fungos micorrízicos arbusculares isolados de áreas de mineração de gesso, Araripina, PE, Brasil. Hoehnea 41, 393–400.

Morton, J.B., Bentivenga, S.P., Wheeler, W.W., 1993. Germ plasm in the international

collection of arbuscular and vesicular-arbuscular mycorrhizal fungi (INVAM) and procedures for culture development, documentation, and storage. Mycotaxon 48, 491–528.
Oehl, F., Laczko, E., Bogenrieder, A., Stahr, K., Bösch, R., van der Heijden, M., Sieverding, E., 2010. Soil type and land use intensity determine the composition of arbuscular mycorrhizal fungal communities. Soil Biol. Biochem. 42, 724–738. http://dx.doi.org/10.1016/j.soilbio.2010.01.006.
Oehl, F., Sieverding, E., Palenzuela, J., Ineichen, K., Silva, G.A., 2011. Advances in Glomeromycota taxonomy and classification. IMA Fungus 2, 191–199. http://dx.doi.org/10.5598/imafungus.2011.02.02.10.
Oliveira, A.S., 2012. Análise de resíduos encalhados na Ilha da Restinga (análise de resíduos). Monografia, Instituto Federal de Educação, Ciência e Tecnologia da, Paraíba.
Öpik, M., Zobel, M., Cantero, J.J., Davison, J., Facelli, J.M., Hiiesalu, I., Jairus, T., Kalwij, J.M., Koorem, K., Leal, M.E., Liira, J., Metsis, M., Neshataeva, V., Paal, J., Phosri, C., Põlme, S., Reier, Ü., Saks, Ü., Schimann, H., Thiéry, O., Vasar, M., Moora, M., 2013. Global sampling of plant roots expands the described molecular diversity of arbuscular mycorrhizal fungi. Mycorrhiza 23, 411–430. http://dx.doi.org/10.1007/s00572-013-0482-2.
Pagano, M.C., Zandavalli, R.B., Araújo, F.S., 2013. Biodiversity of arbuscular mycorrhizas in three vegetational types from the semiarid of Ceará State, Brazil. Appl. Soil Ecol. 67, 37–46. http://dx.doi.org/10.1016/j.apsoil.2013.02.007.
Pellissier, L., Niculita-Hirzel, H., Dubuis, A., Pagni, M., Guex, N., Ndiribe, C., Salamin, N., Xenarios, I., Goudet, J., Sanders, I.R., Guisan, A., 2014. Soil fungal communities of grasslands are environmentally structured at a regional scale in the Alps. Mol. Ecol. 23, 4274–4290. http://dx.doi.org/10.1111/mec.12854.
Phillips, J.M., Hayman, D.S., 1970. Improved procedures for clearing roots and staining parasitic and vesicular arbuscular mycorrhizal fungi for rapid assessment of infection. T Brit Mycol. Soc. 55, 158–161. http://dx.doi.org/10.1016/S0007-1536(70)80110-3.
Rodríguez-Echeverría, S., Teixeira, H., Correia, M., Timoteo, S., Heleno, R., Öpik, M., Moora, M., 2017. Arbuscular mycorrhizal fungi communities from tropical Africa reveal strong ecological structure. New Phytol. 213, 380–390. http://dx.doi.org/10.1111/nph.14122.
Schechter, S.P., Bruns, T.D., 2012. Edaphic sorting drives arbuscular mycorrhizal fungal community assembly in a serpentine/non-serpentine mosaic landscape. Ecosphere 3, 1–24. http://dx.doi.org/10.1890/ES12-00059.1.
Schmidt, S.K., Scow, K.M., 1986. Mycorrhizal fungi on the Galápagos islands. Biotropica 18, 236–240. http://dx.doi.org/10.2307/2388491.
Shannon, C.E., Weaver, W., 1949. The Mathematical Theory of Communication. University of Illinois Press, Illinois.
Sieverding, E., Silva, G.A., Berndt, R., Oehl, F., 2014. *Rhizoglomus*, A new genus of the *Glomeraceae*. Mycotaxon 129, 373–386. http://dx.doi.org/10.5248/129.373.
Sigüenza, C., Espejel, I., Allen, E.B., 1996. Seasonality of mycorrhizae in coastal sand dunes of Baja California. Mycorrhiza 6, 151–157. http://dx.doi.org/10.1007/s005720050120.
Silva, F.C., Eira, P.A., van Raij, B., Silva, C.A., Abreu, C.A., Gianello, C., Pérez, D.V., Quaggio, J.A., Tedesco, M.J., Abreu, M.F., Barreto, W.O., 1999. Análises químicas para a avaliação da fertilidade do solo. In: Silva, F.C. (Ed.), Manual de análises químicas de solos, plantas e fertilizantes. EMBRAPA, Brasília, pp. 75–169.
Silva, F.A.Z., 2014. ASSISTAT. Version 7.7 Beta. DEAG-CTRN-UFCG.
Silva, I.R., Mello, C.M.A., Ferreira Neto, R.A., Silva, D.K.A., Melo, A.L., Oehl, F., Maia, L.C., 2014. Diversity of arbuscular mycorrhizal fungi along an environmental gradient in the Brazilian semiarid. Appl. Soil Ecol. 84, 166–175. http://dx.doi.org/10.1016/j.apsoil.2014.07.008.
Silva, D.K.A., Souza, R.G., Velez, B.A.A., da Silva, G.A., Oehl, F., Maia, L.C., 2015a. Communities of arbuscular mycorrhizal fungi on a vegetation gradient in tropical coastal dunes. Appl. Soil Ecol. 96, 7–17. http://dx.doi.org/10.1016/j.apsoil.2015.06.009.
Silva, D.K.A., Coutinho, F.P., Escobar, I.E.C., Souza, R.G., Oehl, F., da Silva, G.A., Cavalcante, U.M.T., Maia, L.C., 2015b. The community of arbuscular mycorrhizal fungi in natural and revegetated coastal areas (Atlantic Forest) in northeastern Brazil. Biodivers. Conserv. 24, 2213–2226. http://dx.doi.org/10.1007/s10531-015-0968-7.
Smith, S.E., Read, D.J., 2008. Mycorrhizal Symbiosis. Academic Press, London.
Soka, G., Ritchie, M., 2014. Arbuscular mycorrhizal symbiosis and ecosystem processes: prospects for future research in tropical soils. OJE 4, 11–22. http://dx.doi.org/10.15666/aeer/1301_229245.
Soteras, F., Moreira, B.C., Grillia, G., Pastora, N., Mendes, F.C., Mendes, D.R., Renison, D., Kasuya, M.C.M., de Souza, F.A., Becerra, A., 2016. Arbuscular mycorrhizal fungal diversity in rhizosphere spores versus roots of an endangered endemic tree from Argentina: is fungal diversity similar among forest disturbance types? Appl. Soil Ecol. 98, 272–277. http://dx.doi.org/10.1016/j.apsoil.2015.09.003.
Souza, R.G., Maia, L.C., Sales, M., Trufem, S.F.B., 2003. Diversidade e potential de infectividade de fungos micorrízicos arbusculares em área de caatinga, na Região de Xingó, Estado de Alagoas, Brasil. Rev. Bras. Bot. 26, 49–60. http://dx.doi.org/10.1590/S0100-84042003000100006.
Souza, R.G., Goto, B.T., Silva, D.K.A., Barbosa, F.S.B., Sampaio, E.V.S.B., Maia, L.C., 2011. The role of arbuscular mycorrhizal fungi and cattle manure in the establishment of *Tocoyena selloana* Schum. in mined dune areas. Eur. J. Soil Biol. 46, 237–242. http://dx.doi.org/10.1016/j.ejsobi.2010.04.004.
Stürmer, S.L., Bellei, M.M., 1994. Composition and seasonal variation of spore populations of arbuscular mycorrhizal fungi in dune soils on the Island of Santa Catarina, Brazil. Can. J. Bot. 72, 359–363. http://dx.doi.org/10.1139/b94-048.
Stürmer, S.L., Stürmer, R., Pasqualini, D., 2013. Taxonomic diversity and community structure of arbuscular mycorrhizal fungi (Phylum Glomeromycota) in three maritime sand dunes in Santa Catarina state, south Brazil. Fungal Ecol. 6, 27–36. http://dx.doi.org/10.1016/j.funeco.2012.10.001.
Tchabi, A., Coyne, D., Hountondji, F., Lawouin, L., Wiemken, A., Oehl, F., 2010. Efficacy of indigenous arbuscular mycorrhizal fungi for promoting white yam (*Dioscorea rotundata*) growth in West Africa. Appl. Soil Ecol. 45, 92–100. http://dx.doi.org/10.1016/j.apsoil.2010.03.001.
Trejo-Aguilar, D., Lara-Capistrán, L., Maldonado-Mendoza, I.E., Zulueta-Rodríguez, R., Sangabriel-Conde, W., Mancera-López, M.E., Negrete-Yankelevich, S., Barois, I., 2013. Loss of arbuscular mycorrhizal fungal diversity in trap cultures during long-term subculturing. IMA Fungus 4, 161–167. http://dx.doi.org/10.5598/imafungus.2013.04.02.01.
Triantis, K.A., Guilhaumon, F., Whittaker, R.J., 2012. The island species–area relationship: biology and statistics. J. Biogeogr. 39, 215–231. http://dx.doi.org/10.1111/j.1365-2699.2011.02652.x.
Trufem, S.F.B., Otomo, H.S., Malatinszky, S.M.M., 1989. Fungos micorrízicos vesículo-arbusculares em rizosferas de plantas em dunas do Parque Estadual da Ilha do Cardoso, São Paulo, Brasil. (1) taxonomia. Acta Bot. Bras. 3, 141–152. http://dx.doi.org/10.1590/S0102-33061989000300014.
Trufem, S.F.B., 1990. Aspectos ecológicos de fungos micorrízicoos vesículo-arbusculares em rizosferas de plantas da mata tropical úmida da Ilha do Cardoso, SP, Brasil do Cardoso, SP. Bras. Acta Bot. Bras. 4, 31–45. http://dx.doi.org/10.1590/S0102-33061990000200003.
Trufem, S.F.B., Otomo, H.S., Malatinszky, S., 1994. Fungos micorrízicos arbusculares em rizosferas de plantas de duna do Parque Estadual da Ilha do Cardoso, SP. Bras. Acta Bot. Bras. 8, 31–45. http://dx.doi.org/10.1590/S0102-33061994000200007.
Walter, H.S., 2004. The mismeasure of islands: implications for biogeographic theory and the conservation of nature. J. Biogeogr. 31, 177–197. http://dx.doi.org/10.1046/j.0305-0270.2003.00989.x.
Willis, A.J., Yemm, E.W., 1961. Braunton Burrows: mineral nutrient status of the soils. J. Ecol. 49, 377–390. http://dx.doi.org/10.2307/2257270.
Xu, T., Veresoglou, S.D., Chen, Y., Rillig, M.C., Xiang, D., Ondrej, D., Hao, Z., Liu, L., Deng, Y., Hu, Y., Chen, W., Wang, J., He, J., Chen, B., 2016. Plant community, geographic distance and abiotic factors play different roles in predicting AMF biogeography at the regional scale in northern China. Environ. Microbiol. Rep. 8, 1048–1057. http://dx.doi.org/10.1111/1758-2229.12485.
Zangaro, W., Rostirola, L.V., Souza, P.B., Alves, R.A., Lescano, L.E.A.M., Rondina, A.B.L., Nogueira, M.A., Carrenho, R., 2013. Root colonization and spore abundance of arbuscular mycorrhizal fungi in distinct successional stages from an Atlantic rainforest biome in southern Brazil. Mycorrhiza 23, 221–233. http://dx.doi.org/10.1007/s00572-012-0464-9.