

The community of arbuscular mycorrhizal fungi in natural and revegetated coastal areas (Atlantic Forest) in northeastern Brazil

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Abstract Soil fungi are the key elements in the maintenance of ecosystems, but they are not usually considered when assessing the impact of recovery practices. This study aimed to determine the community composition of arbuscular mycorrhizal fungi (AMF) in natural and revegetated coastal areas of the so-called ‘restingas’ on the borderline of the tropical Atlantic Forests and to provide information on the recuperation of the soil mycobiota in recovering environments. Soil samples were collected in two consecutive years at four sites (two natural and two revegetated ‘restinga’ areas), and the fungal communities were identified. Thirty AMF species were identified. Species of *Acaulospora* and *Glomus* prevailed in both areas, and the revegetated areas had a higher species richness than the natural areas. The BIO-ENV analysis did not select any soil characteristics that could affect the AMF communities, but the ANOSIM indicated that the AMF communities differed between the ‘restinga’ areas ($R_{\text{global}} = 0.621$; $p < 0.0001$). Because the physico-chemical soil factors do not directly influence this relationship, these differences may be due to the biological soil–plant interactions between the areas. *Funneliformis halonatus* was an indicator of natural ‘restinga’ areas, but no species was an indicator of the revegetated areas. These areas had a higher species richness, demonstrating that revegetation contributed to the recovery and increased the AMF diversity. The results emphasized the importance of biodiversity inventories in coastal areas subjected to natural and

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anthropic pressures. These areas have rarely been studied from the point of view of soil microorganisms, and this study highlighted the need for conservation policies.

Keywords Glomeromycota · Mycorrhiza · Restinga · SIMPER · ANOSIM

Introduction

Coastal areas occupy 80 % of the Brazilian littoral zone and have a significant richness of natural and environmental resources (Lacerda et al. 1993). These areas are included in the Atlantic Forest Dominion and are of great ecological importance when considering the associated ecosystem services. However, they are fragile environments with naturally restrictive conditions, and they suffer various anthropogenic disturbances (Emery and Rudgers 2010), including opencast mining, one of the main causes of landscape degradation of the coastal environment (Andres and Mateos 2006). The recovery of such areas is regulated by Brazilian environmental agencies (Article 225 of the Federal Constitution, and Decree 97.632/89) in order to maintain environmental stability.

The recovery of degraded areas implies that the area overcame obstacles, especially when the goals are to restore the functions, community structures and characteristics of the previous ecosystem (Banning et al. 2011; Bárcenas-Moreno et al. 2011). The process generally takes into account only the plant and animal communities above ground (Aumond et al. 2012), without assessing the impact of recovery practices on the soil microbial communities that are essential for the maintenance of ecosystems, as they provide many benefits to the environment. Soil studies indicate that the microbiota can contribute to the development of strategies used in the recovery of degraded areas (Haynes 2009).

Among the soil microorganisms, the arbuscular mycorrhizal fungi (AMF) stands out by offering several benefits to the ecosystem, such as nutrient cycling (Morgan et al. 2005), the reduction of the need for fertilizers (Chang and Yang 2009), the absorption of nutrients for plants (Smith and Read 2008), an increase in plant growth (Moreira and Siqueira 2006), improving the soil structure by the action of hyphae and/or through the aggregation mediated by glomalin (Purin and Rillig 2007), and contributing to increased water retention and the resistance of plants to drought, salinity, heavy metals in the soil and biotic stresses (Gianinazzi et al. 2010). The AMF, a key group of soil microbes, are essential for the establishment of plant communities, especially in coastal environments that are subjected to strong anthropic actions.

Fungal communities are affected by several factors, but on a global scale, the main factors that shape fungal communities are mean annual temperature, precipitation, pH and Ca content (Tedersoo et al. 2014). On a local scale, the communities are more influenced by soil properties and micro-climate differences than plant communities (Dreesens et al. 2014; Silva et al. 2014). The knowledge about fungal diversity and the factors that affect the community and species distribution in time and space has become important due to increasing shifts in climate, land use and biodiversity loss (Taylor et al. 2014).

To understand the changes on the soil fungal communities in environments subjected to complex disturbances, it is important to predict the ecosystem's response in future scenarios. Several studies on AMF in sand dunes were performed all over the world (e.g., Corkidi and Rincón 1997; Koske et al. 2004; Kowalchuk et al. 2002; Kulkarni et al. 1997; Rodríguez-Echeverría and Freitas 2006; Sridhar and Beena 2001). In Brazil, studies in the south (e.g., Cordoba et al. 2001; Cordazzo and Stürmer 2007; Stürmer et al. 2013) and

southeastern (e.g., Trufem et al. 1989, 1994) regions showed a high diversity of AMF, which was also reported in the northeast. In this region, investigations of coastal areas conducted by Silva et al. (2012) and Souza et al. (2013) demonstrated that revegetation practices contributed to the enhanced diversity and species richness of AMF in previously disturbed areas. The majority of the studies performed in coastal areas indicated that these environments exhibit great diversity, with new records for science and new occurrences of AMF species (Błaszowski et al. 2014; Goto et al. 2012a, b). The results of these studies provided additional information about the biodiversity in these areas and reinforced the need for conservation measures.

Studies of the soil mycota communities (those that are beneficial to plants and soils) in the coastal areas of tropical Atlantic rainforests are fundamental for the development of conservation programs and, when necessary, the revegetation of degraded areas. In this context, we tested three hypotheses: (i) coastal areas of Atlantic Forest have more AMF than coastal areas subjected to mining and later revegetation; (ii) it is possible to define AMF species that are indicators of natural and revegetated environments; and (iii) differences between AMF communities in disturbed and non-disturbed environments are due to changes in the physical and chemical soil characteristics. Our objective was to determine the composition of AMF communities in natural and revegetated coastal areas of the Atlantic Forest and to characterize the attributes of the soil in these areas, providing information about the regeneration of the soil mycota in environments undergoing the recovery process.

Materials and methods

Study area

The studied areas in the Atlantic Forest were located in the Municipality of Mataraca, north of the State of Paraíba, northeastern Brazil ($6^{\circ}28'20''$ – $6^{\circ}30'00''$ S, $34^{\circ}55'50''$ – $34^{\circ}57'10''$ W) and were the property of the Millennium Inorganic Chemicals Mining, a Cristal Company. Many heavy minerals (ilmenite, zircon, kyanite and rutile) are extracted from these areas, after the complete removal of vegetation and disassembly of the dunes. Details on the exploitation of ore deposits and the physical restoration of the dunes can be found in Souza et al. (2013). The local climate is tropical rainy (type Koppen Am), with an average temperature of 25.5 °C and an average rainfall of 1795 mm (Oliveira-Filho and Carvalho 1993). Figure 1 presents the precipitation data.

The study was conducted in the following coastal areas: (a) two areas of natural woody ‘restinga’ characterized by the presence of *Tabebuia roseo-alba*, *Ziziphus joazeiro*, *Psidium decussatum*, *Xylopia nitida*, *Buchenavia capitata*, *Duguetia gardneriana*, *Hymenia rubriflora* var. *glabra* Lee, *Apeiba tibourbou*, and others; (b) two woody/shrub areas replanted in 1989 and 2001 with approximately 80 native species, mainly Leguminosae, Anacardiaceae, Bignoniaceae, Rhamnaceae, Myrtaceae, Rubiaceae, Chrysobalanaceae, Annonaceae, Malvaceae, and Sapotaceae. The information regarding vegetation composition was based on Oliveira-Filho and Carvalho (1993).

Soil sampling and chemical analysis

In each of the areas (two natural and two revegetated), four plots of 100 m² (20 × 5 m) were delimited, and six subsamples were collected (at 0–20 cm deep) to form a composite

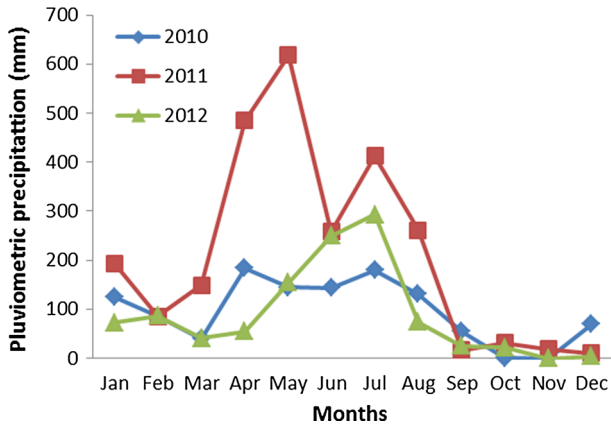


Fig. 1 Rainfall from January to December of 2010, 2011 and 2012 in the Municipality of Mataraca, State of Paraíba, northeastern Brazil

sample per plot, totaling four composite samples of rhizospheric soil per area. The samples were placed in plastic bags, transported to the laboratory within 48 h after collection and stored at 4 °C until processing. Altogether, six samplings were conducted considering three per year (March, July and November) in 2010 and 2011. Soil samples were analyzed in the soil laboratory of the Sugar Cane Experimental Station, Universidade Federal Rural de Pernambuco, Brazil.

Identification of AMF

Glomerospores were extracted from the soil (50 mL samples) by wet sieving (Gerdemann and Nicolson 1963) and sucrose centrifugation (50 %) (Jenkins 1964, modified). The spores were counted with the aid of a stereomicroscope (40×), mounted on slides with PVLG (polyvinyl-alcohol in lactoglycerol) and PVLG + Melzer's reagent (1:1 v/v) and observed under a microscope. Błaszowski (2012); Schenck and Perez (1990), INVAM (<http://invam.wvu.edu>) and the website Glomeromycota of the University of Agriculture of Szczecin—Poland (<http://www.zor.zut.edu.pl/Glomeromycota/index.html>) were consulted for species identification. We followed the classification proposed by Oehl et al. (2011) for Glomeromycota, including recently described new taxa (e.g., Błaszowski and Chwat 2013; Goto et al. 2012a, b). The slides of glomerospores from some of the studied AMF were deposited at URM Herbarium—Universidade Federal de Pernambuco, Brazil (URM—85905, 85906, 85907, 85908, 85909, 85910, 85911, 85912 and 85913).

Statistical analysis

An analysis of similarities (ANOSIM) based on the abundance of species data was performed to verify the differences between seasons (dry and wet) and groups (natural and revegetated), using the Bray-Curtis index. The value of R indicated whether the differences were more related to species composition ($R_{\text{global}} > 0.50$) or to differences in the frequency and abundance of species ($R_{\text{global}} < 0.50$). ANOSIM was also applied for the physico-chemical soil data to determine the differences and similarities between groups of samples. The similarity/dissimilarity percentage (SIMPER) was determined between

groups (natural and revegetated), according to Clarke (1993) and Clarke and Warwick (2001).

Indicator species values were calculated for each species in the area. This analysis took into account the relative frequency and abundance of the species (Dufrêne and Legendre 1997). The significance of the indicator value (IndVal) for each species was evaluated using the Monte Carlo test with 1000 permutations, and species were considered to be indicators when $p < 0.05$ and IndVal was greater than or equal to 40 % (Kubosova et al. 2010).

BIO-ENV analysis was performed to determine whether the community structure and soil characteristics were related and to define the set of environmental variables with a higher correlation with the dissimilarity of the communities of AMF using the Euclidean distance (Clarke and Ainsworth 1993).

To obtain a visual representation of the similarities among the areas, an ordination analysis (non-metric multidimensional scaling—MDS) based on the abundance of species was performed using the Bray-Curtis similarity (Kruskal 1964). The data of species abundance were transformed into the square root prior to analysis to minimize the effect of the dominance of single taxa, and a 0.05 significance level was used in all of the analysis.

The analysis of IndVal was performed with aid of the PC-ORD program version 5.0 (McCune and Mefford 2006). The PRIMER program version 6.0 (Primer-E Ltd. Plymouth, UK) (Clarke and Gorley 2006) was used for the ANOSIM, SIMPER, BIO-ENV and MDS analyses.

Results

The study areas had sandy soils, and the majority of the soil attributes were similar for both types of land use, with the natural areas presenting higher values of Mg, CEC, Mn and OM, and the revegetated areas having higher values of Fe, Zn and P (Table 1).

Thirty species of AMF belonging to eight families and 12 genera were identified (Acaulosporaceae, Ambisporaceae, Dentiscutataceae, Gigasporaceae, Glomeraceae, Intraornatosporaceae, Racocetraceae and Scutellosporaceae). Twenty-nine of these species were from revegetated areas, mostly represented by *Acaulospora* and *Glomus* (10 and 6 species, respectively), while only 17 species were from the natural areas (six *Acaulospora* and four *Glomus* species) (Table 2).

Sixteen of the 17 species identified in the natural areas were also found in the revegetated areas. Although these species occurred in both areas, 10 taxa (*Acaulospora foveata*, *A. mellea*, *A. morrowiae*, *A. scrobiculata*, *Ambispora* sp., *Cetraspora* sp.1, *Gigaspora gigantea*, *G. margarita*, *Glomus glomerulatum* and *Glomus* sp.) had higher abundances and

Table 1 Physical and chemical characteristics of soil samples collected from natural and revegetated coastal areas in Northeastern Brazil

Areas	pH –H ₂ O–	Na cmolc dm ⁻³	Al dm ⁻³	Mg	CEC	Mn mg dm ⁻³	Fe	Cu	Zn	P	OM g kg ⁻¹
Natural	5.42a	0.86a	0.96a	0.79a	5.80a	31.00a	37.00b	0.09a	3.56b	5.27b	2.11a
Revegetated	5.52a	0.74a	0.85a	0.54b	5.02b	18.23b	56.34a	0.09a	7.75a	11.42a	1.86b

Means followed by the same letter in the column do not differ according to the Tukey test ($p \leq 0.05$)

CEC cation exchange capacity, OM organic matter

Table 2 Relative abundance (RA), frequency of occurrence (FO) and AMF indicator species of natural coastal (N) and revegetated areas (R) in Northeastern Brazil

	Natural		Revegetated		Indicator species		
	RA	FO	RA	FO	Group	IV	p
<i>Acaulospora foveata</i>	2.60	16.67	6.05	64.58	–	–	–
<i>Acaulospora herrerae</i>	0.00	0.00	0.42	8.33	R	4.3	0.1189
<i>Acaulospora mellea</i>	6.54	20.83	29.18	93.75	–	–	–
<i>Acaulospora morrowiae</i>	2.60	8.33	4.70	62.5	–	–	–
<i>Acaulospora scrobiculata</i>	0.73	6.25	6.79	77.08	–	–	–
<i>Acaulospora sieverdingii</i>	0.00	0.00	0.60	10.42	R	10.4	0.0571
<i>Acaulospora</i> sp.1	0.00	0.00	0.53	10.42	R	10.4	0.0563
<i>Acaulospora</i> sp.2	0.00	0.00	1.56	22.92	R	22.9	0.0006
<i>Acaulospora spinosa</i> C.	1.25	6.25	0.64	16.67	R	13.6	0.0890
<i>Acaulospora tuberculata</i>	0.73	6.25	0.28	8.33	R	6.5	0.3147
<i>Ambispora appendicula</i>	0.00	0.00	1.17	16.67	R	16.7	0.0068
<i>Ambispora</i> sp.	0.31	2.08	2.97	22.92	R	22.6	0.0005
<i>Cetraspora</i> sp.1	1.25	6.25	2.02	20.83	R	19.5	0.0146
<i>Cetraspora</i> sp.2	0.00	0.00	2.62	20.83	R	20.8	0.0007
<i>Dentiscutata cerradensis</i>	0.00	0.00	0.56	18.75	R	18.8	0.0034
<i>Funneliformis halonatus</i>	24.09	50.00	0.18	8.33	N	47.0	0.0001
<i>Gigaspora gigantea</i>	12.56	41.67	1.70	45.83	R	24.9	0.6141
<i>Gigaspora margarita</i>	4.67	20.83	1.20	27.08	R	18.8	0.2284
<i>Glomus ambisporum</i>	0.00	0.00	0.46	6.25	R	6.2	0.2446
<i>Glomus glomerulatum</i>	12.56	31.25	2.86	43.75	–	–	–
<i>Glomus macrocarpum</i>	–	97.92	–	93.75	–	–	–
<i>Glomus microcarpum</i>	2.80	6.25	0.53	4.17	R	2.6	1.0000
<i>Glomus sinuosum</i>	0.00	0.00	3.82	47.92	–	–	–
<i>Glomus</i> sp.	19.83	35.42	23.73	45.83	–	–	–
<i>Orbispora pernambucana</i>	2.70	12.50	0.18	6.25	N	7.9	0.4130
<i>Paradentiscutata maritima</i>	0.00	0.00	0.42	10.42	R	10.4	0.0577
<i>Racocetra fulgida</i>	0.00	0.00	2.30	33.33	R	35.4	0.0001
<i>Racocetra tropicana</i>	0.00	0.00	1.17	27.08	R	27.1	0.0003
<i>Septoglomus constrictum</i>	0.00	0.00	1.34	29.17	R	29.2	0.0002
<i>Simiglomus</i> sp.	4.78	8.33	0.00	0.00	N	8.3	0.1196
Species richness	17		29				

IV indicator value

Species in bold are considered good indicators. $p < 0.05$ (significance to Monte Carlo permutation)

frequencies in the revegetated areas, and four species (*Funneliformis halonatus*, *Glomus macrocarpum*, *G. microcarpum* and *Orbispora pernambucana*) were more abundant and frequent in the natural areas. *Acaulospora spinosa* and *A. tuberculata* were less abundant but more frequent in the disturbed environments. Thirteen species were registered only in the revegetated areas, while only one (*Simiglomus* sp.) was exclusive of the natural areas.

The similarity analysis (ANOSIM) showed that the communities of AMF differed between the natural and revegetated areas ($p < 0.0001$ e $R_{\text{global}} = 0.621$). The ANOSIM performed between seasons revealed the differences among them ($p < 0.0001$ e $R_{\text{global}} = 0.166$). The SIMPER showed a mean dissimilarity of 88.72 % between the areas. The taxa that most contributed to this difference were *Acaulospora mellea* (18.96 %), *Glomus* sp. (9.94 %) and *Acaulospora scrobiculata* (8.25 %) (Table 3). The MDS analysis showed differences indicated by ANOSIM, allowing for the separation of AMF communities from natural and revegetated areas (Fig. 2).

Funneliformis halonatus ($IV = 47$, $p < 0.0001$) was characterized as an indicator of the natural ‘restinga’ areas (Table 2). The BIO-ENV procedure selected P content as a structuring factor of AMF communities ($p < 0.05$), but the correlation was very low ($r_s = 0.216$). The MDS analysis showed the differences indicated by ANOSIM, allowing for the separation of AMF communities from natural and revegetated areas (Fig. 2).

Table 3 Contribution of species (SIMPER) of AMF for similarity and dissimilarity between groups (natural and revegetated) based on the Bray-Curtis distance

Natural areas			Revegetated areas		
Species	Contrib.%	Cum.%	Species	Contrib.%	Cum.%
<i>Funneliformis halonatus</i>	37.11	37.11	<i>Acaulospora mellea</i>	39.68	39.68
<i>Glomus</i> sp.	19.63	56.74	<i>Acaulospora scrobiculata</i>	13.13	52.81
<i>Gigaspora gigantea</i>	17.32	74.06	<i>Acaulospora foveata</i>	9.2	62.00
<i>Glomus glomerulatum</i>	9.54	83.06	<i>Acaulospora morrowiae</i>	8.31	70.31
<i>Acaulospora mellea</i>	6.16	89.76	<i>Glomus</i> sp.	6.83	77.14
<i>Gigaspora margarita</i>	4.09	93.85	<i>Glomus sinuosum</i>	4.17	81.31
			<i>Glomus glomerulatum</i>	3.74	85.05
			<i>Gigaspora gigantea</i>	3.22	88.27
			<i>Racocetra fulgida</i>	2.65	90.92
Average similarity	19.85		Average similarity	37.49	
Dissimilarity: natural and revegetated groups					
Species	Contrib.%	Cum.%	Species	Contrib.%	Cum.%
<i>Acaulospora mellea</i>	18.96	18.96	<i>Racocetra fulgida</i>	3.51	72.43
<i>Glomus</i> sp.	9.94	28.90	<i>Gigaspora margarita</i>	2.75	75.18
<i>Acaulospora scrobiculata</i>	8.25	37.14	<i>Ambispora</i> sp.	2.67	77.85
<i>Acaulospora morrowiae</i>	6.65	43.79	<i>Septoglomus constrictum</i>	2.52	80.38
<i>Acaulospora foveata</i>	6.64	50.44	<i>Cetraspora</i> sp.2	2.43	82.80
<i>Glomus glomerulatum</i>	4.94	55.38	<i>Racocetra tropicana</i>	2.07	84.87
<i>Funneliformis halonatus</i>	4.73	60.10	<i>Cetraspora</i> sp.1	2.05	86.92
<i>Glomus sinuosum</i>	4.50	64.61	<i>Acaulospora</i> sp.2	1.81	88.73
<i>Gigaspora gigantea</i>	4.31	68.92	<i>Acaulospora spinosa</i>	1.78	90.52
Mean dissimilarity	88.72				

Contrib.% percentage of contribution of each species, Cum.% percentage of cumulative contribution to similarity/dissimilarity between groups

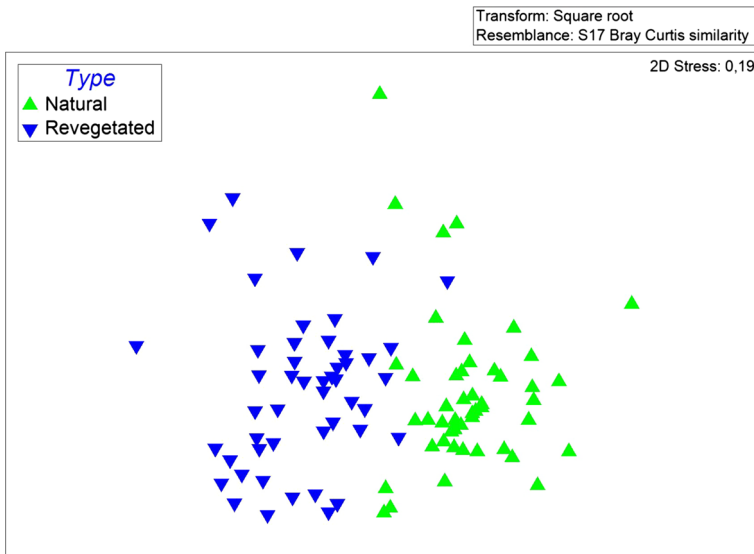


Fig. 2 Multidimensional scaling analysis based on the community of arbuscular mycorrhizal fungi in natural and revegetated ‘restinga’ areas in northeastern Brazil

Discussion

Although differences in some physico-chemical soil parameters (Mg, Mn, Fe, Zn, CEC, P and OM) were detected between the areas according to the type of land use, none of these were selected as a structuring factor of the AMF communities. BIO-ENV selected P content as a structuring factor ($p < 0.05$), but the correlation was very low ($r_s = 0.216$). Some studies showed the influence of soil attributes in the occurrence of fungi and highlighted pH as one of the main factors that shaped the communities of these soil organisms (Oehl et al. 2010; Sommerfeld et al. 2013; Taylor et al. 2014; Wang et al. 2014). However, other studies did not show the influence of soil physico-chemical properties in the AMF communities and attributed this lack of influence to other factors, such as type of vegetation and land use (Cutler et al. 2014; González-Cortés et al. 2012; Pereira et al. 2014), which may exert greater effects on fungal communities, as observed in this study. Beena et al. (2000) observed that changes in AMF communities in sand dunes were related to the degree of disturbance. The physico-chemical soil properties did not influence the communities of AMF in this study, which were more affected by the type of land use (natural or revegetated). The structure of microbial communities are not often well correlated with measurements of environmental variables (Talbot et al. 2014), and Bahram et al. (2015) stated that this may reflect “the existence of unknown environmental drivers or dispersal-driven neutral dynamics.”

Among the AMF, the prevalence of *Acaulospora* and *Glomus* is common in natural and disturbed environments (Aidar et al. 2004; Guadarrama et al. 2014; Silva et al. 2005, 2014; Stürmer et al. 2013). The large number of species described in these genera, together with their adaptability (Daniell et al. 2001) and high infectivity of propagules (Hart and Reader 2002), allow them to succeed in a variety of environments. Trufem et al. (1994) registered a higher abundance of spores of *Acaulospora*, *Gigaspora* and *Scutellospora* in comparison with those of *Glomus* in sand soils in the southeastern region of Brazil.

Our first hypothesis stated that the coastal areas of the Atlantic Forest are richer in AMF than mined, revegetated areas. However, the opposite occurred, with higher AMF richness being identified in the revegetated areas than in the natural areas. The highest number of exclusive species, which increased the richness of fungi in the revegetated areas, can be explained by the heterogeneity produced by the disruption of the soil structure when the areas were mined (Guimarães et al. 2002) as well as the introduction of fungi together with the substrates for the production of seedlings used for revegetation (Souza et al. 2010, 2012, 2013). Higher richness of AMF species in the revegetated areas demonstrated that this process contributed to the renewal and expansion of the diversity of microbial communities, which differed from the original.

Another explanation is that our analyses relied on sporulating fungi, and the natural areas could have had many species that were non-cultivable, impairing isolation and identification. Ohsowski et al. (2014) compared the proportion of cultivated taxa between natural and disturbed environments and found that disturbed areas presented higher proportions of taxa that could sporulate in trap culture, probably because the soil disturbance selected for species that were easily cultivable. Our study may somehow underestimate AMF richness because very small-spored species (<40 µm) were difficult to identify by classical methods (Błaszczowski et al. 2012) or may have been lost by the extraction method used.

AMF species common to both areas had increased abundance and/or frequency in the revegetated areas, as observed for most species of *Acaulospora*. This could be related to the life strategy of these genera. *Acaulospora* is known to have a good rate of infectivity and can regenerate from hyphae and spores. Cuenca et al. (1998) also found *Acaulospora* species more frequently in revegetated sites when compared with natural sites. The increased abundance and frequency of some species in the revegetated areas may be due to soil plowing (during disassembly of the dunes) and further spreading of the covering soil in these areas before planting the seedlings, with a more uniform distribution of fungal species in this environment (Silva et al. 2012; Souza et al. 2010, 2012, 2013).

Some AMF species showed increased abundance and frequency or exclusivity in natural conditions, possibly due to the stability/balance of these areas, enabling them to occupy specific niches (Frankland 1998), such as *Orbispora pernambucana*, which was reported primarily in natural areas (de Carvalho et al. 2012; Pereira et al. 2014; Silva et al. 2008).

Our second hypothesis was that it would be possible to find indicator species of the studied environments. We confirmed that selecting *Funneliformis halonatus* as an indicator of natural areas showed that these environments had optimal conditions for their growth, or that these species were more competitive in these environments. One species of *Simiglomus*, recorded only in natural areas, possibly represents a new species to science, underscoring the importance of biodiversity inventories and studies of the impact of human activities on soil microbial communities. With anthropic pressure and the loss of suitable substrates, many species could disappear before they are known. No indicator species were found for the revegetated areas, probably because this area was still changing.

Our third hypothesis stated that the differences in soil fungal communities between disturbed and undisturbed areas are related to changes in the chemical and physical properties of the soil. We could not confirm this in our study, as the BIO-ENV procedure, with the exception of type of land use (natural or revegetated), was not able to select abiotic factors that could be influencing the communities of AMF as indicated by ANOSIM. Thus, other factors were more important in the definition of the communities of soil fungi in 'restinga' areas. The spatial differences between the sites, as shown by MDS, appeared to be related to biological soil–plant interactions in the revegetated and natural

areas because the physical and chemical soil factors did not directly influence this relationship. Apparently, the difference between natural and revegetated areas was more related to the composition of their communities in these sites. Although a high diversity of plant species in natural woody ‘restinga’ was used for the revegetation of the disturbed areas, the community that would be established was not the same as that found in the natural areas. This difference in vegetation composition also accounted for a diverse AMF community between the areas. Even considering that the AMF were not host specific, the observations showed evidence that in the field, AMF growth rates were highly host specific (Bever et al. 2001). The occurrence of different species of AMF in association with different host species suggested the ecological specificity of these fungi (Trufem et al. 1994). Information regarding species occurrence and distribution is essential to develop conservation practices and policies, but as stated by Pimm et al. (2014), “although there has been rapid progress in developing protected areas, such efforts are not ecologically representative, nor do they optimally protect biodiversity.” The identification of species in an area provides additional information about the biodiversity, emphasizing the importance of inventories for guiding conservation policies for coastal areas exposed to natural and anthropogenic pressures that are also poorly studied from the soil microbial community standpoint.

The Atlantic Forest coastal areas are hotspots of biodiversity conservation based on the plant and animals communities (Conservation International do Brazil 2015), and considering our results, these areas may also be considered to be hotspots for the conservation of fungal communities. While information regarding the diversity of plants and animals for the Atlantic Forest is available, the knowledge about fungi is still very scarce and should be taken into account, considering the ecosystem services they contribute.

Studies showed that the species we know more about have broad geographical ranges and are usually common, but with most species, the opposite occurs. That is, the undescribed species are likely to have small distributions, are geographically concentrated and possibly already threatened (Pimm et al. 2014; Giam et al. 2012). For fungi, the situation is even more serious, as we do not know how many species are yet to be discovered. The last estimates, based on molecular methods, suggest that 5.1 million fungal species exist, but there is a large gap between the estimated and the known species, as only approximately 99,000 are described (Blackwell 2011). Specifically for the Glomeromycota, there are ca. 280 species described, but this number is underestimated, as new species are being continuously discovered. For example, in the last 10 years, more than 80 new species were described (www.mykobank.com) as more taxonomists work on the group and different regions and sites are visited.

Tropical regions are considered to have the highest diversity of fungi (Arnold and Lutzoni 2007), as is also the case for other groups of organisms. The greatest numbers of undescribed species are likely to be in tropical moist forests of the Neotropics, the Afrotropics and Indomalaya with minimal anthropogenic disturbance, and consequently, are less studied and scientifically explored in comparison with other biomes (Giam et al. 2012). Nevertheless, few areas are protected in many of these biomes. In Brazil, where the Atlantic Forest extended for 1.1 million km², today it covers approximately 300,000 km², from which only 7 % is included in Protection Units (http://www.mma.gov.br/estruturas/sfb/arquivos/livro_de_bolso__sfb_mma_2010_web_95.pdf). Most of this Atlantic Forest Dominion is now highly fragmented and under anthropogenic pressure. Therefore, undescribed species are subject to a greater risk of extinction in comparison with known species due to many factors, including their occurrence in small geographical ranges (Giam et al. 2012). Bever et al. (2001) emphasize the need to consider the below-ground

organisms as dynamic participants in plant community processes and their diversity as a key component of soil quality. Thus, more studies should be undertaken, especially in unexplored areas, to increase the knowledge on the diversity of those groups less known and to reinforce the need for conservation strategies.

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