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Ecological Processes

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Arbuscular mycorrhizal fungal community assembly in the Brazilian tropical seasonal dry forest

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Abstract

Introduction: Here, we compare the arbuscular mycorrhizal fungal (AMF) community composition in soils from the root zone of the exotic invasive species *Prosopis juliflora* (EXO soils) and soils from the root zone of the native species *Mimosa tenuiflora* (NAT soils) from five locations in the Brazilian tropical seasonal dry forest, Paraíba, Brazil, using morphological analyses.

Results: AMF community composition in EXO and NAT soils were dissimilar. Available phosphorus, diversity index, spore abundance, and species richness were the main factors differing between the EXO and NAT soils. In general, the most dominant order present in the soils were *Glomerales* (44.8%) and *Gigasporales* (41.4%). The most abundant AMF genus in all studied soils was *Funneliformis*.

Conclusions: Differences in AMF community composition were associated with (1) differences in the dominant plant species (*P. juliflora* vs. *M. tenuiflora*) and (2) changes in soil chemical factors (soil, pH, total organic carbon, total nitrogen, and available P) in EXO soils. These results contribute to a deeper view of the AMF communities in exotic soils and open new perspectives for ecological processes involving AMF species and exotic plant species in the Brazilian tropical seasonal dry forest.

Keywords: Glomeromycota, AMF community, AMF diversity, Native plant species, Exotic plant species, Caatinga

Introduction

The Brazilian tropical seasonal dry forest, also referred to as "Caatinga", was described by Santos et al. (2011) as a "type of desert vegetation, which consists of small, thorny trees that shed their leaves seasonally in interior northeastern Brazil." This ecoregion consists of a broad mosaic vegetation type that covers 850,000 km^2 (nearly 10% of Brazil's territory) in Brazilian Northeast. It has a unique biota that contains over 1000 endemic plant species, but unfortunately, it is poorly conserved, with only 1% of its territory in protection conservation areas (Alves et al. 2009; Andrade et al. 2009). Drought, intensive agriculture, excessive grazing, and biological invasion are recognized as the major threats with significative negative environmental impacts on plant diversity (Pegado et al. 2006; Andrade et al. 2008; Andrade et al. 2009).

Despite evidences of invasive exotic plant species introduction in the Brazilian tropical seasonal dry forest dating 516 years before present, when the Portuguese arrived in Brazil in 1500, Pegado and co-workers (2006) reported that invasive exotic plant species (e.g., *Prosopis juliflora* (Sw.) DC.) were introduced during 1942 as a result of a governmental program during that period. This governmental program was proposed to help the regional farmers during dry period providing them with a "tree of life" that would be used as an alternative to fodder and shelter for livestock. But, in fact, this "tree of life" became the most common troublesome invasive exotic plant species in the Brazilian tropical seasonal dry forests affecting native plant community composition and ecological processes in the invaded areas since 1942 (Alves et al. 2009; Andrade et al. 2009; Souza et al. 2016a).

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Many studies were done to shown how invasion by *P. juliflora* alter the native plant community (e.g., Pegado et al. 2006; Andrade et al. 2008; Andrade et al. 2009). These works showed negative impacts of *P. juliflora* on native plant diversity and plant community structure. But, it is still unclear if the biological invasion in Brazilian Northeast has negative impacts on arbuscular mycorrhizal fungal (AMF) diversity. Invasive plant species need AMF because these soil microorganisms increase nutrient acquisition, growth, and vitality of their hosts, independently if they are exotic or native plant species. In semi-arid conditions, as is in our case, AMF are also crucial for the protection of their hosts against abiotic (drought, salinity) stresses and have been found to determine plant community composition and function in other studies (Reinhart and Callaway 2006; Smith and Read 2008; Hodge and Storer 2014; Shah et al. 2009).

The consensus is that the biological invasion alters the dynamics of plant communities and soil characteristics (e.g., soil pH and nutrient availability), which may influence AMF community structure and functioning by three different mechanisms according to studies from elsewhere (Parkash and Aggarwal 2009; Rodríguez-Echeverría et al. 2009; Zhang et al. 2010; Kivlin and Hawkes 2011; Lekberg et al. 2013). First, invasive exotic plant species usually form large monospecific plant populations, thus reducing the diversity of host-plants available to the AMF community. Second, metabolites produced by invaders negatively affect native plants growth by disrupting their mutualistic associations with the AMF community from native soils (Zubek et al. 2016). Finally, the introduction of invasive exotic plant species might cause changes in soil chemical properties that may indirectly affect AMF community composition and, thus, contribute to a successful establishment and spread of invasive exotic plant species (Shah et al. 2009).

We examined the AMF community from *P. juliflora* root zone (EXO soils) and compared it with the AMF community from *Mimosa tenuiflora* root zone (NAT soils). Our study addressed the following questions. (1) Do invasive exotic plant species alter the composition of the AMF community in the studied areas? Based on the enhanced mutualisms hypothesis (Richardson et al. 2000; Reinhart and Callaway 2006), we expected to find evidence for changes in the original AMF community. (2) Is there evidence for differences in the relationship between invasive and native plants and the AMF community from NAT and EXO soils in field conditions? We hypothesized that invasive plants would experience a stronger interaction with a specific AMF community according to the invasion opportunity windows and resource enemy release hypotheses (Johnstone 1986; Agrawal et al. 2005; Blumenthal 2005; Kulmatiski and Kardol 2008). To accomplish this, we perform field sampling of two root zone types, i.e., invasive and native root zones, characterized by both the soil chemical properties and AMF communities.

Methods

Plant species and study sites

Field sampling was carried out in five different locations in the Brazilian tropical seasonal dry forest, Paraiba, Brazil (Algodão de Jandaíra, 06° 46′ 17.3″ S, 36° 01′ 55.3″ W; Esperança, 06° 56′ 45.7″ S, 35° 54′ 06.8″ W; Juazeirinho, 07° 06′ 33.3″ S, 36° 34′ 34.2″ W; Monteiro, 07° 48′ 19.8″ S, 37° 10′ 32.4″ W; and Natuba, 07° 37′ 34.9″ S, 35° 32′ 24.5″ W). These study areas are classified as Bsh following Köppen-Geiger climate classification, i.e., hot semi-arid with hot summers and mild to warm winters, annual precipitation and temperature of 600 mm and 30 °C, respectively. In these sites, rainfall is highly reduced, unpredictable, and irregular (Alves et al. 2009).

We selected the invasive exotic plant species *P. juliflora* and the native plant species *M. tenuiflora* which co-occur in a mixed plant community (well-mixed stand) in all studied areas. We also have selected these two plant species to perform our study because *P. juliflora* was introduced in 1942 and nowadays is the most common troublesome invasive exotic plant species in all studied areas and *M. tenuiflora* is highly abundant in Brazilian tropical seasonal dry forests (Pegado et al. 2006; Andrade et al. 2009; Souza et al. 2016b). The soil type of the studied areas was classified as a sandy loam Dystric Fluvisols (WRB 2006).

Field sampling and soil characterization

In each of the five study areas, we established 40 plots of 100 m^2 according to Fortin and Dale (2005). Within each plot, we selected one plant of each target species in a well-mixed stand (i.e., 2 plants per plot, thus 80 plants per study location, or 400 total plants across all locations) according to the following criteria: (1) the plant had a diameter near the soil surface of >3 cm and (2) no individuals from a different plant species were growing in a 3-m radius to the sampling point in all directions (Daubenmire 1968; Fortin and Dale 2005; Caifa and Martins 2007; Costa and Araújo 2007; Durigan 2009). Soil samples (including soil and root fragments) were collected near the drip line and beyond (0–20 cm deep), during the dry period, i.e., at the beginning of September 2012. By sampling during the dry season, we guaranteed that we sampled the largest number of AMF species because fungal sporulation is expected to be higher at this time of the year in semi-arid environments (Silva et al. 2014). Samples from each plant species in each plot were bulked, mixed, and stored at 4 °C until host-plant

bioassays. During sampling and handling of each soil sample, precautions (e.g., sterilization with ethanol and gloves) were undertaken to avoid cross contamination. Later, each sample collected from the field was divided into portions intended for chemical soil characterization and AMF community assessment.

To chemically characterize the soil from each plot, we analyzed soil pH, total organic carbon, total nitrogen, and available phosphorus ($N = 40$ by plant species). Soil pH was measured in a suspension of soil and distilled water (1:2.5 *v*:*v*, soil:water suspension) (Black 1965). Total organic carbon was estimated according to the methodology described by Okalebo et al. (1993). To quantify total nitrogen, soil samples were first digested with sulfuric acid plus potassium sulfate and we then followed the protocol described by Kjeldahl (Black 1965). Available phosphorus (Olsen's P) was determined colorimetrically using a spectrophotometer at 882 nm by extraction with sodium bicarbonate for 30 min (Olsen et al. 1954).

Arbuscular mycorrhizal fungi community characterization

AMF communities extracted from native and exotic soils were classified as "NAT" if they occurred in the root zone of *M. tenuiflora* and as "EXO" if they occurred in the root zone of the invasive exotic plant species *P. juliflora.* Spores from field were extracted by the wet sieving technique (Gerdemann and Nicolson 1963) followed by sucrose centrifugation (Jenkins 1964). For this, we used 100 g of field soil. Initially, the extracted spores were examined in water under a dissecting microscope and they were separated based on morphology. Subsequently, they were mounted in polyvinyl alcohol lactoglycerol (PVLG) with or without addition of Melzer's reagent (Walker et al. 2007). Species identification was based on the descriptions provided by Schenck and Perez (1987), publications with descriptions of new families and genera (i.e., Oehl et al. 2008), and by consulting the international culture collection of arbuscular mycorrhizal fungi database—INVAM (http://invam.caf.wvu.edu). In this work, we followed the classification proposed by Oehl et al. (2011), including recently new described taxa (i.e., Goto et al. 2012; Redecker et al. 2013; Sieverding et al. 2014). In addition to species identification, we also assessed spore abundance by counting the total number of spores, spore abundance of each AMF species by recording the number of spores of each AMF species recorded in the samples, and the species occurrence frequency (FOi) of each AMF species. FOi was calculated using the following equation:

$$\mathrm{FOi} = \mathrm{ni}/\mathrm{N}$$

where ni is the number of times an AMF species was observed and N is the total of AMF spores observed from each studied area.

Mycorrhizal root colonization assessment

Roots of *P. juliflora* and *M. tenuiflora* were examined for quantification of AMF colonization. The collected roots were stored in 50% ethanol until staining. Roots were cleared in 2% KOH for 1 h at 90 °C. Subsequently, they were left to acidify overnight in 1% HCl. Staining was done with blue ink (Parker Quink) for 30 min at 60 °C, followed by destaining in lactoglycerol. The amount of colonization was estimated using a grid-intersect method with examination of 100 intersects under a compound microscope at ×200 magnification (Phillips and Hayman 1970; McGonigle et al. 1990). All microscopic examinations were carried out by the same person. Root intersects that contained vesicles, arbuscules, and hyphae were scored as mycorrhizal. The decision to score hyphae as mycorrhizal was based on the associated presence of vesicles, arbuscules, spores, and the morphology of the mycelium. Roots that did not have cortex were excluded from the analysis. In total, 40 samples (20 samples from EXO soils plus 20 samples from NAT soils) per studied area were examined to score 100 intersections.

Glomalin analysis

To quantify total glomalin, soil samples (1.0 g) were used with 8.0 mL of 50 mmol L^{-1} sodium citrate at pH 8.0 over three cycles of autoclaving at 121 °C, for 1 h per cycle. The extractor was separated from the soil via protein centrifugation at 1720*g* for 15 min. The supernatant was quantitated in a mass spectrophotometer by the protocol described by Wright and Upadhyaya (1998).

Ecological indices and statistical analyses

After AMF species identification, we calculated the following ecological indices: diversity index (H) proposed by Shanon and Weaver (1949), and dominance index (C) proposed by Simpson (1949) for each studied AMF community.

Differences in soil properties and AMF community structure between EXO and NAT soil groups were determined by non-parametric *t* test followed by Monte Carlo test (100 replicates). Univariate analyses (*t* test, ANOVA, and Tukey's test) were performed using SAS 9.1.3 Portable, whereas multivariate analysis (principal component analysis) was performed using MVSP (MultiVariate Statistical Package) 3.1 (Kovach 2007). All data were checked for normality and homogeneity of variances before analyses. Count data and environmental variable values were transformed (function square root) before multivariate analysis. The relationships between the AMF community structure and soil properties were examined using the correlation analyses by the Pearson correlation coefficient.

Results

Soil properties

Significant differences ($p \leq 0.05$) between the EXO and NAT soils were found for soil chemical properties. On average, EXO soils were higher in soil pH, total organic carbon (TOC), total nitrogen (total N), and available phosphorus (P) (Table 1). Within the EXO soils, there were no significant differences among the EXO sites for soil pH, total organic carbon, and total nitrogen, but we found significant differences among EXO sites for available P. The Monteiro samples showed the highest soil pH and amounts of P, while the Natuba samples showed the highest amounts of TOC and total N, whereas in the NAT soils, we found significant difference from each studied site in soil pH, total organic carbon, total nitrogen, and available P. In the NAT soils, the Esperança and Juazeirinho soil samples showed the highest soil pH, while the Natuba samples showed the highest amounts of TOC, total N, and P (Table 1).

AMF abundance and community structure

For all study areas, the species richness, spore abundance, root colonization, total glomalin, diversity index, and dominance index were significantly different between the EXO and NAT soils (Table 2). The root colonization ($p \leq 0.01$), total glomalin ($p \leq 0.01$), and dominance ($p \leq 0.01$) were significantly higher in the EXO soils than in the NAT soils. Within the EXO soil, we found significant differences from each studied site in AMF abundance and community structure, except for diversity index that we did not find any difference between the EXO soils. The highest root colonization (43.74%) was found in the soil samples from Esperança, while the Monteiro samples showed the highest total glomalin (7.67 mg g^{-1} soil) and dominance index (0.97), whereas in the NAT soils, the species richness ($p \leq 0.01$), spore abundance ($p \leq 0.01$), and diversity index ($p \leq 0.01$) were significantly higher in the NAT soils than in the EXO soils. Within the NAT soil, we found significant differences among NAT sites for AMF abundance and community structure. The highest species richness (18 species) was found in the soil samples from Algodão de Jandaíra, while the Esperança and Monteiro samples showed the highest spore abundance (18.80 spores g^{-1} soil) and diversity index (2.98), respectively (Table 2).

The principal component analysis (PCA) showed two well-defined clusters segregating the soil attributes and fungal communities of EXO and NAT soils (Fig. 1). PCA also indicated that the EXO soils were correlated with higher soil pH, total organic carbon (TOC), total nitrogen (TN), available phosphorus (P), total glomalin (TG), root colonization (Col), and dominance index (*D*), whereas NAT soils were correlated with species richness (S), spore abundance (Spore), and diversity index (*H'*) (Fig. 1). Available P, diversity index, spore abundance, and species richness were the main factors differing between the EXO and NAT soils. The two axes explained 88.78% of the variation present in the samples.

The order *Glomerales*, specifically the family *Glomeraceae*, was the most abundant in all the soil samples (Table 3). *Funneliformis* was statistically significantly ($p \leq 0.01$) more abundant in all the studied soils, with exception of Natuba that was dominated by *Claroideoglomus* (60.5%) and *Glomus* (22.0%) in the EXO and

Table 1 Chemical soil attributes of exotic (EXO) and native (NAT) soils from the Brazilian tropical seasonal dry forest (mean ± SD, $N = 40$)

Soil type/site	Soil pH (H_2O)	Total organic carbon (g kg^{-1})	Total nitrogen (g kg^{-1})	Available *P* (ppm)
EXO				
Algodão de Jandaíra	6.64 ± 0.26 a	8.56 ± 0.55 a	0.86 ± 0.15 a	8.49 ± 0.07 c
Esperança	6.71 ± 0.20 a	8.44 ± 0.30 a	0.82 ± 0.10 a	8.42 ± 0.30 c
Juazeirinho	6.35 ± 0.46 a	8.99 ± 0.57 a	0.88 ± 0.09 a	6.97 ± 0.47 d
Monteiro	6.87 ± 0.26 a	8.81 ± 0.71 a	0.87 ± 0.07 a	10.70 ± 0.52 a
Natuba	6.50 ± 0.35 a	9.14 ± 1.78 a	0.92 ± 0.17 a	9.22 ± 0.22 b
NAT				
Algodão de Jandaíra	5.04 ± 0.03 b	2.78 ± 0.16 d	0.15 ± 0.04 d	1.93 ± 0.02 f
Esperança	5.20 ± 0.10 b	2.00 ± 0.10 e	0.21 ± 0.01 c	2.00 ± 0.10 f
Juazeirinho	5.20 ± 0.29	2.52 ± 0.59 d	0.22 ± 0.07 c	1.74 ± 0.26 f
Monteiro	4.87 ± 0.26 b	3.71 ± 0.15 c	0.28 ± 0.09 bc	2.78 ± 0.45 e
Natuba	4.27 ± 0.17 c	4.35 ± 0.17 b	0.45 ± 0.12 b	2.50 ± 0.09 e
EXO versus NAT[a]	9.73**	10.54**	25.01**	26.10**

Same letters represent no significant differences by Tukey's test ($p \leq 0.05$)
**$p \leq 0.01$
[a]Independent sample *t* test comparing EXO × NAT soil groups

Table 2 AMF community properties and ecological indexes for the AMF communities of exotic (EXO) and native (NAT) soils from the Brazilian tropical seasonal dry forest (mean ± SD, $N = 40$)

Soil type/site	Species richness	Spore abundance (spore g^{-1} soil)	Col. (%)	Total glomalin (mg g^{-1} soil)	*H'*	*D*
EXO						
Algodão de Jandaíra	11.0 ± 0.40 c[d]	5.91 ± 0.19 d	40.24 ± 3.10 ab	5.87 ± 0.81 b	1.73 ± 0.20 d	0.93 ± 0.02 a
Esperança	6.0 ± 0.60 f	6.12 ± 0.23 d	43.74 ± 1.11 a	6.35 ± 0.67 b	1.78 ± 0.12 d	0.95 ± 0.02 a
Juazeirinho	7.0 ± 0.30 e	5.14 ± 0.18 e	35.33 ± 2.32 b	5.90 ± 0.98 b	1.81 ± 0.11 d	0.90 ± 0.02 b
Monteiro	10.0 ± 0.50 c	5.12 ± 0.46 e	38.02 ± 1.56 b	7.67 ± 0.75 a	1.69 ± 0.12 d	0.97 ± 0.03 a
Natuba	9.0 ± 0.60 d	11.70 ± 1.42 b	40.20 ± 3.14 ab	6.35 ± 0.81 ab	1.80 ± 0.10 d	0.91 ± 0.01 b
NAT						
Algodão de Jandaíra	18.0 ± 0.80 a	7.80 ± 0.12 c	6.03 ± 0.12 f	0.55 ± 0.03 d	2.20 ± 0.02 c	0.86 ± 0.01c
Esperança	16.5 ± 0.30 b	18.80 ± 0.21 a	16.57 ± 1.12 d	0.81 ± 0.11 d	2.17 ± 0.01 c	0.85 ± 0.01 c
Juazeirinho	17.5 ± 0.20 a	12.27 ± 0.28 b	19.10 ± 0.98 c	0.67 ± 0.09 d	2.64 ± 0.02 b	0.68 ± 0.01 f
Monteiro	15.8 ± 0.80 b	11.38 ± 0.18 b	7.94 ± 0.67 e	0.69 ± 0.08 d	2.98 ± 0.04 a	0.76 ± 0.01 e
Natuba	17.2 ± 0.60 a	12.02 ± 0.19 b	14.83 ± 2.12 d	0.98 ± 0.11 c	2.58 ± 0.06 b	0.79 ± 0.02 d
EXO versus NAT[a]	12.34**	11.63**	16.32**	23.73**	12.65**	11.98**

Same letters represent no significant differences by Tukey's test ($p \leq 0.05$)
Col. (%) root colonization, *H'* diversity index, *D* dominance index
**$p \leq 0.01$
[a]Independent sample *t* test comparing EXO × NAT soil groups

NAT soils, respectively. The orders *Diversisporales* and *Gigasporales* were less abundant in the EXO soils at statistical significant level ($p \leq 0.01$) than the NAT soils. The EXO soils showed significant lower abundance of *Acaulospora* ($p \leq 0.01$), *Quatunica* ($p \leq 0.05$), *Gigaspora* ($p \leq 0.01$), *Racocetra* ($p \leq 0.01$), and *Scutellospora* ($p \leq 0.05$) than the NAT soils (Table 3).

The AMF community present in all soil samples was composed of 29 species, most of them classified as orders *Glomerales* (44.8%) and *Gigasporales* (41.4%) (Additional file 1). The EXO soil considering all sites was composed of 18 AMF species; of those, only one from the order *Diversisporales*, seven from the order *Gigasporales*, and ten from the order *Glomerales*

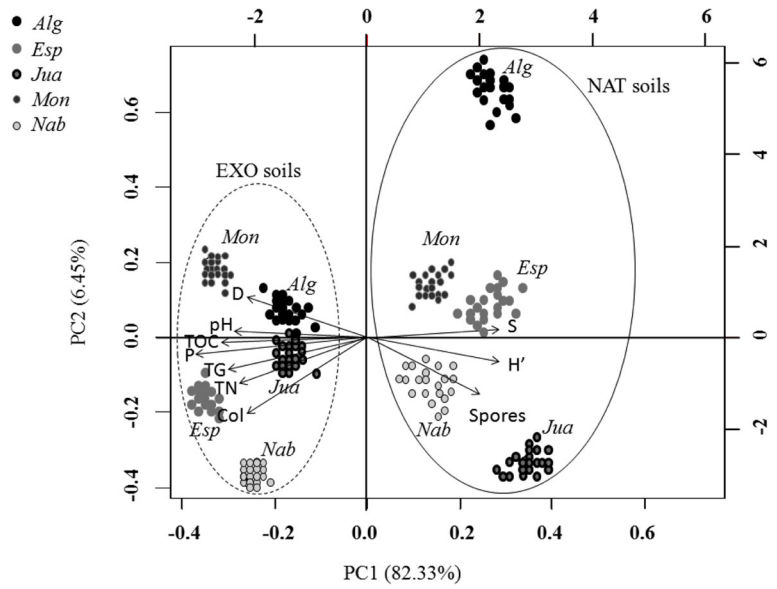

Fig. 1 PCA score plot of soil properties and AMF community structure for the five studied sites. *Alg* Algodão de Jandaíra, *Esp* Esperança, *Jua* Juazeirinho, *Mon* Monteiro, *Nab* Natuba. The points represent samples from each plot by exotic (EXO) native (NAT) soils. *S* species richness, *H'* diversity index, *Spores* spore abundance, *D* dominance index, *pH* soil pH, *TOC* total organic carbon, *P* available phosphorus, *TG* total glomalin, *TN* total nitrogen, and *Col* root colonization

(Additional file 1), whereas the NAT soil considering all sites was composed of 29 AMF species: 18 similar to EXO soil group, plus one from the order *Archaeosporales*, two from the order *Diversisporales*, five from the order *Gigasporales*, and three from the order *Glomerales* (Additional file 1).

Discussion

Up to date, the arbuscular mycorrhizal fungal (AMF) community in the EXO soils has been poorly described when compared to other sites, such as mining areas, desertic areas, and undisturbed habitats (Silva et al. 2005; Souza et al. 2003; Panwar and Tarafdar 2006; Mergulhão et al. 2007; Silva et al. 2014; Souza et al. 2016a). To our knowledge, this is the first study assessing the soil AMF composition and diversity of EXO soils in the Brazilian tropical seasonal dry forest compared to their respective NAT soils by using morphological characterization. As revealed by our study, soil properties (e.g., soil pH, total organic carbon, total nitrogen, and available P) were higher in the EXO soils compared with the NAT soils. These results are in agreement with previous work (Soumare et al. 2015; Majewska et al. 2015) that reported higher values of soil pH and available P in the root zone of invasive exotic plants, such as *Acacia senegal*, *Acacia seyal*, *Acacia albida*, *Eragrostis albensis*, and *Olpidium* spp. By altering the chemical properties of the soil below their canopy, invasive plant species may alter the nutrient cycle (Follstad Shah et al. 2010) and thus may be responsible for the modification AMF community composition in the EXO soils (Zubek et al. 2016; Zubek et al. 2013).

Significant differences in the species richness, spore abundance, root colonization, total glomalin, diversity index, and dominance index were observed between the EXO and NAT soils. These findings support our hypothesis that EXO soils have lower AMF diversity than NAT soils. Several studies (e.g., Richardson et al. 2000; Hawkes et al. 2006; Rodríguez-Echeverría et al. 2009; Oehl et al. 2010; Carneiro et al. 2015; Souza et al. 2016b) also showed a lower AMF diversity in disturbed soils by biological invasion of invasive exotic species (e.g., *A. senegal*, *A. seyal*, *A. albida*, *E. albensis*, *Olpidium* spp., *Cryptostegia madagascariensis*, *Sesbania virgata*, *P. juliflora*, and *Parkinsonia aculeata*) in comparison with soil in natural conditions.

These results are in agreement with previous studies (Soumare et al. 2015; Ayanu et al. 2015; Zubek et al. 2016; Callaway et al. 2008; Tanner and Gange 2013) and support our hypothesis that invasive plants are associated with specific AMF species. As a consequence, *P. juliflora* seemed to be in advantage comparing with *M. tenuiflora* by profiting from beneficial AMF species (e.g., AMF from the order *Glomerales*) (Shah et al. 2009). The differences in AMF community structure between EXO and NAT soils were revealed by the decreased AMF species richness in all studied sites from the EXO soils and a lesser root colonization of the NAT soils. According to studies from elsewhere (Shah et al. 2009; Callaway et al. 2008; Tanner and Gange 2013), we hypothesize that three different mechanisms may be involved in the detected changes in the AMF community. First, *P. juliflora* usually form large monospecific plant populations, as was the case in our

Table 3 Relative abundance (%) of the arbuscular mycorrhizal fungi (based on morphological classification) of exotic (EXO) and native (NAT) soils from the Brazilian tropical seasonal dry forest (mean ± SD, $N = 40$)

Order	EXO vs NAT[a]	Family	EXO vs NAT	Genera	EXO				
					Alg	Esp	Jua	Mon	Nab
Archaeosporales	2.13^{ns}	*Ambisporaceae*	2.13^{ns}	*Ambispora*	0.0 ± 0.0 b	0.0 ± 0.0 b	0.0 ± 0.0 b	0.0 ± 0.0 b	0.0 ± 0.0 b
Diversisporales	9.16**	*Acaulosporaceae*	9.16**	*Acaulospora*	0.0 ± 0.0 e	0.0 ± 0.0 e	0.0 ± 0.0 e	0.0 ± 0.0 e	0.0 ± 0.0 e
Gigasporales	15.33**	*Dentiscutataceae*	11.96**	*Dentiscutata*	9.0 ± 0.8 c	8.4 ± 0.6 c	7.5 ± 0.2 d	5.3 ± 0.1 e	28.0 ± 1.2 a
				Quatunica	2.5 ± 0.1 e	2.4 ± 0.3 e	5.4 ± 0.2 b	3.1 ± 0.1 d	0.0 ± 0.0 g
		Gigasporaceae	11.15**	*Gigaspora*	0.0 ± 0.0 f	0.0 ± 0.0 f	7.5 ± 0.2 b	0.0 ± 0.0 f	2.3 ± 0.1 d
		Racocetraceae	−9.37**	*Racocetra*	4.9 ± 0.2 c	4.4 ± 0.2 c	9.6 ± 0.8 b	4.2 ± 0.3 c	2.3 ± 0.1 d
		Scutellosporaceae	−8.99**	*Scutellospora*	0.5 ± 0.1 e	0.7 ± 0.3 e	1.7 ± 0.2 c	0.4 ± 0.1 e	0.0 ± 0.0 f
Glomerales	18.54**	*Entrophosporaceae*	14.75**	*Entrophospora*	0.0 ± 0.0 e	0.0 ± 0.0 e	0.0 ± 0.0 e	0.0 ± 0.0 e	0.0 ± 0.0 e
				Claroideoglomus	0.9 ± 0.1 f	3.0 ± 0.5 e	0.0 ± 0.0 g	7.5 ± 0.2d	60.5 ± 4.5 a
		Glomeraceae	16.76**	*Funneliformis*	60.7 ± 2.1 b	57.0 ± 1.7 b	67.9 ± 3.9 ab	75.6 ± 3.5 a	4.6 ± 0.9 g
				Glomus	5.0 ± 0.2 c	4.8 ± 0.1 c	0.4 ± 0.1 f	1.2 ± 0.3 e	0.0 ± 0.0 g
				Rhizoglomus	18.4 ± 0.9 a	19.3 ± 1.2 a	0.0 ± 0.0 e	2.7 ± 0.2 d	2.3 ± 0.1 d

Same letters represent no significant differences by Tukey's test ($p \leq 0.05$)
ns not significant
**$p \leq 0.01$
[a]Independent sample *t* test comparing EXO × NAT soil groups

Table 3 Relative abundance (%) of the arbuscular mycorrhizal fungi (based on morphological classification) of exotic (EXO) and native (NAT) soils from the Brazilian tropical seasonal dry forest (mean ± SD, $N = 40$) *(Continued)*

Order	NAT					EXO vs NAT
	Alg	Esp	Jua	Mon	Nab	
Archaeosporales	0.0 ± 0.0 b	0.0 ± 0.0 b	2.1 ± 0.1 a	3.0 ± 0.2 a	0.0 ± 0.0 b	2.13^{ns}
Diversisporales	5.3 ± 0.4 b	7.5 ± 0.3 a	3.2 ± 0.2 c	0.9 ± 0.4 d	1.8 ± 0.5 d	9.16**
Gigasporales	7.2 ± 0.4 d	9.0 ± 0.6 c	13.7 ± 1.2 b	1.4 ± 0.3 f	2.7 ± 0.2 f	10.13**
	0.7 ± 0.1 f	0.6 ± 0.2 f	3.9 ± 0.3 c	5.4 ± 0.3 b	11.0 ± 0.9 a	8.03*
	0.6 ± 0.2 e	20.0 ± 3.2 a	8.3 ± 0.8 b	3.7 ± 0.5 c	7.3 ± 0.2 b	11.15**
	2.3 ± 0.1 d	2.1 ± 0.2 d	18.2 ± 1.5 a	1.8 ± 0.3 d	10.1 ± 0.5 b	9.37**
	1.2 ± 0.2 d	1.0 ± 0.2 d	5.3 ± 0.4 b	6.3 ± 0.2 a	1.8 ± 0.3 c	8.99*
Glomerales	0.6 ± 0.0 d	0.6 ± 0.0 d	1.8 ± 0.1 c	0.0 ± 0.0 d	2.9 ± 0.3 a	4.15^{ns}
	18.9 ± 3.1 b	10.5 ± 0.9 d	0.0 ± 0.0 g	22.5 ± 2.5 b	14.6 ± 0.9 c	15.11**
	39.7 ± 1.2 c	28.3 ± 2.7 d	17.6 ± 0.9 e	39.2 ± 1.8 c	11.0 ± 1.1 f	13.72**
	5.1 ± 0.3 c	4.9 ± 0.4 c	7.4 ± 0.2 b	3.6 ± 0.4 d	22.0 ± 1.9 a	8.76*
	17.3 ± 2.9 a	10.5 ± 0.5 c	16.6 ± 0.8 ab	12.2 ± 1.7 b	13.8 ± 1.4 b	9.76**

study, thus reducing the diversity of host-plants available to the AMF community. Consequently, this changes soil organic carbon inputs (Andrade et al. 2009; Dandan and Zhiwei 2007; Oehl et al. 2010; Jansa et al. 2014; Silva et al. 2014; Carneiro et al. 2015; Sousa et al. 2011; Souza et al. 2016a) and decreases AMF's growth and proliferation in the absence of a diverse mycorrhizal plant community (Zubek et al. 2013).

Secondary metabolites produced by *P. juliflora* negatively affect native plants growth by disrupting their mutualistic associations with the unaltered AMF community (Andrade et al. 2009; Zubek et al. 2013). Studies by Stinson et al. (2006), Callaway et al. (2008) and Yuan et al. (2014) have provided evidence that invasive plant species produce metabolites that are novel for native AMF community in their introduced areas, and these secondary compounds directly limit AMF growth, spore germination, and root colonization (Callaway et al. 2008). Consequently, the most beneficial AMF (e.g., AMF species from the order *Glomerales*) from the native AMF community composition are favored, while the growth of the less favorable ones (e.g., AMF species from the order *Diversisporales*) is inhibited. Finally, the introduction of invasive exotic plant species might cause changes in soil chemical properties that may indirectly affect AMF community composition and thus contribute to a successful establishment and spread of invasive exotic plant species (Shah et al. 2009).

Previous studies revealed that Brazil is the diversification and dispersion center of species from the order *Gigasporales* (Goto et al. 2012; Marinho et al. 2014). In this study, we observed the same pattern for AMF communities from the NAT soils. But, we did not observe the same for the EXO soils. The biological invasion altered the composition of AMF communities in all studied EXO soils, promoting species from the order *Glomerales*, thus suggesting an effect of exotic plant species on the AMF community selection (Hausmann and Hawkes 2009; Jansa et al. 2014). Actually, the EXO soils showed disturbances and changes in soil properties and also showed the highest soil pH and the highest amount of total organic carbon, total nitrogen, and available P from the other NAT soils. Accordingly, the study done by Souza et al. (2016b) invasive plant species can directly affect the soil properties, which in turn can affect indirectly AMF community composition. We observed an increase in the relative abundance of AMF species from *Claroideoglomus*, *Glomus*, and *Funneliformis* in the EXO soils. So we can confirm that this effect was a result of the soil properties changes in response to biological invasion processes (Wetzel et al. 2014).

The low soil pH and low amounts of available phosphorus observed in the NAT soils could explain the high predominance of AMF species from *Acaulospora*, *Gigaspora*, *Quatunica*, *Racocetra*, and *Scutellospora.* Ramos et al. (2008) suggest that the AMF community composition in acid soils with low phosphorus availability is a result of enzymes (H^+-ATPase and H^+-pyrophosphatase) that act in the spore germination, and mycelium growth, improving absorption, translocation, and nutrient exchange utilization by the AMF species from the orders *Archaesporales*, *Diversisporales*, and *Gigasporales*.

Treseder and Turner (2007) have reported that the total glomalin is positively correlated with the primary productivity and soil organic matter, and according to the studies done by Comis (2002) and Rillig (2004), this

soil protein can improve soil quality due to its positive effects improving soil aggregate and decreasing soil erosion (Gillespie et al. 2011). In our survey, we observed a significantly higher amount of total glomalin in the EXO soils. We also observed a positive correlation with total glomalin and total organic carbon and total nitrogen in these sites. Based on these results, we hypothesize that the high amounts of total glomalin in the EXO soils are involved in the changes of soil properties (e.g., soil pH, soil total carbon, and soil organic matter) as described by King (2011) and Purin and Rillig (2007). However, the potential for higher total glomalin amounts by the biological invasion process influence cannot be discarded and should be investigated in the future. Controversial results are observed in the literature showing negative effect of land use on concentration of glomalin in soil (Rillig 2004; Rillig et al. 2003; Treseder and Turner 2007).

Conclusions

Our study revealed that AMF community composition in EXO and NAT soils were dissimilar. We find evidence for changes in the original AMF community and soil properties as we have hypothesized based on the enhanced mutualism hypothesis. Differences in AMF community composition were associated with (1) differences in the dominant plant species (*P. juliflora* vs *M. tenuiflora*) and (2) changes in soil chemical factors (soil, pH, total organic carbon, total nitrogen, and available P) in exotic soils. Soil properties, total glomalin, root colonization, and dominance index were correlated with EXO soils, while species richness, number of spores, and diversity index were correlated with NAT soils. The most abundant AMF order in all the soil samples was the order *Glomerales. Funneliformis*, *Claroideoglomus*, and *Glomus* species were more abundant in the EXO soils than the NAT soils, but the EXO soil showed lower abundance of *Acaulospora*, *Quatunica*, *Gigaspora*, *Racocetra*, and *Scutellospora* species than the NAT soils. Thus, future studies should include molecular studies of the functional diversity of arbuscular mycorrhizal fungi in the EXO soils and the relation with exotic plant species.

Additional file

Additional file 1: Table S1. Specific studied soil types (EXO and NAT) from Brazilian tropical seasonal dry forest followed by the arbuscular mycorrhizal fungi (AMF) taxonomical classification. (DOCX 25 kb)

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Authors' contributions
We declare that all the authors made substantial contributions to the conception, design, acquisition, analysis, and interpretation of the data. All the authors participate in drafting the article, revising it critically for important intellectual content; and finally, the authors gave final approval of the version to be submitted to Ecological Processes.

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Competing interests
The authors declare that they have no competing interests.

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