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Research Article

Seasonal variation of arbuscular mycorrhizal fungi in ecotone forests of the northern region of Brazilian Amazonia

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Abstract

The ecotone forests in the northern region of Brazilian Amazonia are important areas representing transition zones between forest and non-forest ecosystems. These areas have soils nutrient-poor that poorly drain. Under these environmental conditions, *Peltogyne gracilipes* (Leguminoseae), an endemic tree species, can form natural monodominant forests. Here, we assessed the arbuscular mycorrhizal fungi (AMF) community in three forest types on the eastern side of Maracá Island and the relationship of these microorganisms with the monodominance of *P. gracilipes.* In this study, soil samples were collected in two seasons (dry and rainy). The samples were collected in 9 plots, in rich areas, poor areas and areas without *P. gracilipes*. Soil samples were evaluated for chemical and particle size analysis, spore density and morphology, and identification of AMF. AMF species were identified using two approaches: spores collected in the field and trap cultures. Eighteen and 13 AMF species were identified in the dry and rainy seasons, respectively, for spores extracted from the field. Six total species were detected exclusively in trap cultures in the dry season. AMF communities were co-dominated by members of the Gigasporaceae, Acaulosporaceae and Glomeraceae families. Redundancy analyses indicated that several soil attributes, such as pH, Fe, Mg, and sand content associated with the AMF species richness in both seasons. We conclude that the ecotone forests in the eastern region of Maracá Island are home to important richness and diversity of AMF species and that various soil factors influence the composition of the AMF community in this ecosystem.

Keywords: Amazonian; Maracá Island; monodominant; Mycorrhiza; taxonomy

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Introduction

Mechanisms that influence the monodominance of a plant species in tropical forests are usually studied from an above-ground perspective (Ghazoul and Sheil, 2010), while less attention has been given to the below ground soil community (Aime and Brearley, 2012). Monodominance of some tropical forest species has been attributed to the presence of ectomycorrhizal associations, but the role of arbuscular mycorrhizal fungal communities has yet to be elucidated. Dominance of *Gilbertiodendron dewevrei* and *Julbernardia seretii* in a tropical forest in the Democratic Republic of the Congo (Torti and Coley, 1999) and of *Oreomunnea mexicana* in Panama (Corrales *et al.*, 2016) are closely linked to the presence of ectomycorrhizae. Considering that soil microbiota performs several key functions to maintain productivity, diversity, and structure of plant communities (Van der Heijden *et al.*, 2008), studies of target fungal groups that influence plant growth and nutrition such as arbuscular mycorrhizal fungi (AMF) might contribute to understanding how monodominant plant species use their resources for establishment and reproduction (Rodríguez-Echeverría *et al.*, 2017).

In the Brazilian Amazon rainforest, patches dominated by a single tree species, considered monodominante, can occur (ter Steege *et al.*, 2019). In the extreme northern portion of the Amazon rainforest, *Peltogyne gracilipes* Ducke (Leguminoseae) can form monodominant forests on eastern Maraca Island (Nascimento *et al.*, 2017). This species is dispersed in areas defined as ecotone forests, where depending on its abundance and dominance, it may represent a bioindicator of different forest types: (i) ombrophiluss, where individuals of *P. gracilipes* are rare or non-existent; (ii) seasonal/semideciduous, where *P. gracilipes* occurs in low abundance, and (iii) seasonal/deciduous, where *P. gracilipes* occurs abundantly and, when in high dominance, can form large conglomerates of monodominant forests (Nascimento and Villela, 2010; Nascimento *et al.*, 2017). Monodominance of *P. gracilipes* has been studied over the years, and factors identified to be associated with this monodominance include soil factors (topographic characteristics and physical-chemical analysis) (Nascimento *et al.*, 2017), the dynamic variation in floristic composition (Nascimento *et al.*, 2014), the phylogenetic structure associated with the tree community to which *P. gracilipes* belongs (Nascimento and Proctor, 1997), and properties of this species that allow survival in low nutrient, poorly drained soils (Nascimento *et al.*, 1997; Nascimento *et al.*, 2017). According to Nascimento (1994), *P. gracilipes* has an established association with AMF, however the author did not quantify that association and was unable to associate arbuscular mycorrhizal colonization with the monodominance of this species.

Arbuscular mycorrhizal fungi are distinguished by their ecological function and the ecosystem services they provide, such as increasing soil stabilization, improving plant growth and nutrition, protecting plants against biotic and abiotic stresses, and impacting plant community structure (Gianinazzi *et al.*, 2010; House and Bever, 2018). These fungi are distributed among 11 families and 40 genera (CICG, 2020) within the subphylum Glomeromycota, establishing the arbuscular mycorrhizal association with 72% of plant species (Brundrett and Tedersoo, 2018). AMF communities in undisturbed tropical regions are complex and species-rich (Alexander and Selose, 2009). Within the Brazilian Amazon Forest floristic domain, surveys of AMF communities have been performed in agroecosystems (Azevedo *et al.*, 2014; Araújo *et al.*, 2019), forest areas (Stürmer and Siqueira, 2011; Leal *et al.*, 2013; Freitas *et al.*, 2014), and savannas (Stürmer *et al.*, 2018). These studies have contributed to the knowledge of AMF distribution in distinct land use systems but have not addressed the occurrence of AMF species in monodominant plant species.

In this study, we assessed AMF community and soil factors in an ecotone forest in the extreme north of the Brazilian Amazon Forest in Maracá Island, where *P. gracilipes* forms monodominant forests. Our goal was to assess the occurrence and diversity of AMF communities in three areas with or without the presence of *P. gracilipes* and to investigate the relationship of AMF species occurrence with soil properties and seasonality. We hypothesized that AMF community structure is a factor contributing to the monodominance of *P. gracilipes* in these forests.

Materials and Methods

Study area and sampling design

This study was located in the eastern part of the Biological Reserve Maracá Island (3°15′54″N, 61°22′50″W) in the state of Roraima, Brazil. Formation of this island is associated with two tectonic faults that divert the normal flow of the Uraricoera River between the Santa Rosa and Maracá holes. The geographic relief is quite variable, ranging from areas with altitudes between 250 and 330 m to areas subject to flooding (Milliken and Ratter, 1989; Barbosa *et al.*, 2007). Soils in the island are defined by variations in three factors, material of origin, relief, and water regime, and can be extremely dystrophic or eutrophic, with textures that vary from very sandy to clayey (Robison and Nortcliff, 1991). The island is located in the southern portion of the Guiana Shield, where mosaics of ombrophilous and seasonal forests are found in contact with the large area of savanna in the northern Brazilian Amazon (Milliken and Ratter, 1989). According to Köppen's classification, Maracá is a humid tropical climate (A) and represents a transition from the subtype savanna or tropical climate with a dry winter season (Aw) to the monsoon subtype (Am) (Barbosa, 1997). Based on data from the Maracá agrometeorological station (1984-2005), the average annual temperature is 26 °C, and annual precipitation is 2,086±428 mm, with the wettest months (>300 mm month^{-1}) are from May to August and the driest months (<100 mm month^{-1}) from December to March (Carvalho *et al.*, 2018).

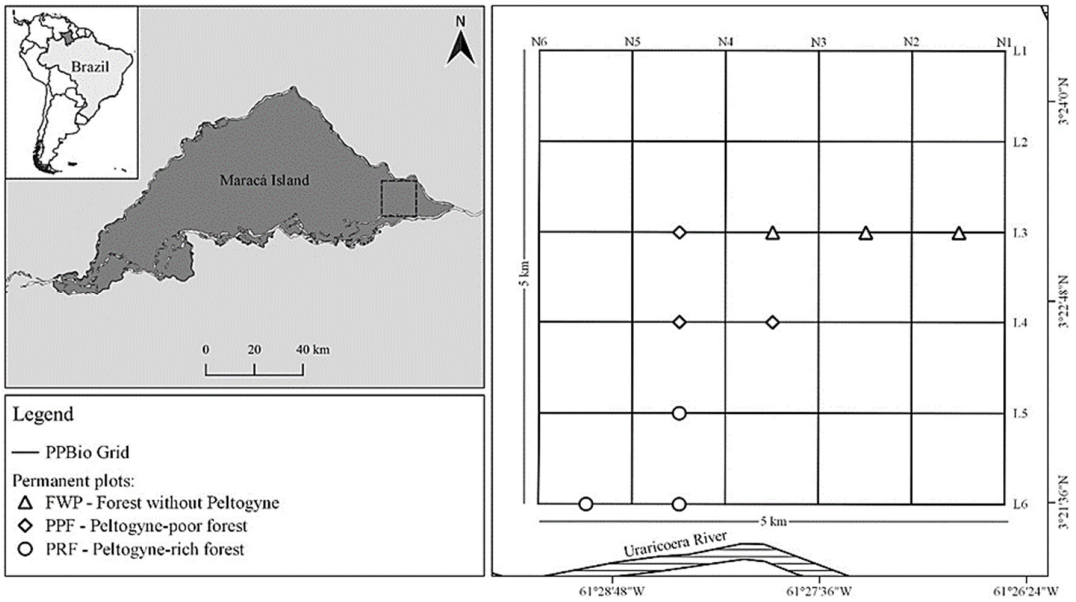

Figure 1. Location of the PPBio trail network in Maracá Ecological Station, Roraima, Northern Brazilian Amazon

Sampling was performed inside the grid of permanent plots of the Biodiversity Research Program (PPBio). The PPBio research grid spans an area of 25 km^2 and is composed of 12 trails of 5 km each organized in a North-South and East-West direction with 30 permanent plots of 1 ha (250 m x 40 m), each regularly distributed along the trails (Magnusson *et al.*, 2005; Pezzini *et al.*, 2012). According to Nascimento (1997), three forest types were selected: (i) *Peltogyne* Rich Forest (PRF) - occurrence of *P. gracilipes* representing greater than 50% of the total species; (ii) *Peltogyne* Poor Forest (PPF) - *P. gracilipes* occurs with in less than 50% of total species, and (iii) Forest without *Peltogyne* (FWP) - area without *P. gracilipes*. For each forest type, three permanent plots of the PPBio grid were sampled (Figure 1) in the dry and rainy season of 2017 to determine the effect of seasonality on the AMF community. In each of the 9 plots, 5 soil samples were collected (1 kg each) at 25, 75, 125, 175 and 225 meters from the starting point of the plot (45 samples in the dry season

and 45 in the rainy season). Each soil sample was composed of 5 subsamples collected uniformly in an area of 1 m2 with a Dutch auger at a depth of 0-10 cm. The auger was cleaned with 70% ethanol between collections to avoid cross contamination. Soil samples were packed in plastic bags, stored in thermal boxes containing ice for transportation to the Soil Microbiology Laboratory at EMBRAPA-Roraima and stored at 4 °C for chemical, physical and microbiological analysis.

Physical and chemical soil analysis

An aliquot of 300 cm^3 of each soil sample was sent to the soil laboratory of EMBRAPA-Roraima. Soil texture was determined by the pipette method (Teixeira *et al.*, 2017). Soil pH was measured with distilled water (1:1), and P K, Cu, Fe, Zn, and Mn were extracted in a $Mehlich^{-1}$ solution. The elements of Ca, Mg, H+Al, and Al were extracted with a solution of $(CH_3COO)_2CaH_2O$. Sulfur was extracted in the SO_4 solution. Boron was extracted in hot water. Organic matter was evaluated by the oxidation of soil samples with a sulfochromic solution and determined using the Black Method (Teixeira *et al.*, 2017). Except for texture which was only made in the rainy season, all analyses were made in the dry and rainy seasons, and values are presented as the mean (± standard deviation) of 5 samples in each of the 9 plots for both seasons.

AMF spore extraction and identification

AMF spores were extracted from 100 g of each soil sample by the wet sieving method (Gerdemann and Nicolson, 1963) followed by centrifugation in a sucrose gradient (20 and 60%). For the wet sieving, we used nested sieves with 400, 200, 100 and 50 μm openings. Material trapped on the 400 μm sieve was transferred to a Petri dish and inspected under a dissection microscope (Quimis Q7714Z) to detect and collect large spores and sporocarps. Materials collected on the other sieves were transferred to Falcon tubes containing the sucrose gradient and centrifuged at 3000 rpm for 3 minutes. The supernatant from the centrifugation was decanted into a 50 μm sieve, washed with sterile distilled water to remove excess sucrose, and transferred to Petri dishes for further inspection of AMF spores under a dissection microscope.

Phenotypic characteristics of the spores, such as spore size, colour, shape and hyphal attachment, were used to distinguish the different morphotypes. Spores of each morphotype were permanently mounted on slides with polyvinyl-lacto glycerol (PVLG) and PVLG mixed with Melzer's reagent (1:1, v/v) and examined under a compound and camera-mounted microscope (Leica DM 2500).

Spores were identified at the genus and species level based on analysis of spore wall structure, Melzer's reaction and other characteristics that are taxonomically informative. Comparisons with original protologue of species description, with those described in Blaszkowski (2012), and with online photos of reference cultures from INVAM (http://invam.wvu.edu – West Virginia University, USA) were made to identify AMF spores at the genus and species level. Gigasporoid spores differentiating two or more germinal walls and glomoid spores that could not be attributed to species were allocated in *Scutellospora* and *Glomus*, respectively. The classification followed herein is that proposed by Redecker *et al.* (2013). Total AMF spore abundance (per 100 g of soil) was obtained by counting spores for each soil sample. The number of samples from which spores of a particular species were detected was used to calculate the frequency of occurrence (FO), expressed as a percentage. AMF species richness (S) was determined by counting fungal species per soil sample. The number of spores of each species was used as a measure of species abundance to calculate Shannon-Wiener (H) diversity index, and the ratio of observed diversity to maximum expected diversity between forest types was determined based on AMF species composition by the equitability index of Pielou (J).

Trap cultures

We used trap cultures to recover AMF species that were not sporulating in the field at the time of sampling following methods by Vestberg (1995). Trap cultures were established by mixing 200 g of soil and roots of each soil sample with a substrate consisting of a sterilized washed sand and dark red latosol (1:2, v/v). The mixture of field soil and roots with the substrate was placed in 1.5 kg pots to establish three pots per soil

sample. Seeds (50-70) of *Urochloa brizantha* were sown, and plants were maintained in a greenhouse and watered as needed, *U. brizantha* was used because it is a mycotrophic plant, fast growing and resistant to pests and diseases. After 120 days, two 50 mL metal cylinders were used to remove a sample from each pot to extract and identify spores as indicated above.

Mycorrhizal colonization of P. gracilipes roots from the field

Mycorrhizal colonization of *P. gracilipes* was evaluated in the field from plants occurring only in the PRF forest type. In the 3 plots of PRF, 300 g of roots from 5 adult individuals of *P. gracilipes* were collected in each plot, totaling 30 root samples (15 in the dry season and 15 in the rainy season). Roots were washed under running water for cleaning and stored in flasks containing 50% alcohol until analysis of mycorrhizal colonization. Roots were stained in Trypan blue following Koske and Gemma (1989), placed in Petri dishes and inspected under a dissection microscope (Quimis Q7714Z) for evaluation of the percentage of root length colonized using the grid line method (Giovannetti and Mosse, 1980).

Statistical analysis

The data on total abundance of spores were log $(x + 1)$ transformed before analysis to meet the requirements of normality and homogeneity of variance, the Kolmogorov-Smirnov normality test and Levene's homogeneity test were performed. Differences in total spore abundance and species richness between sites were tested using a unidirectional analysis of variance (ANOVA) followed by a Tukey post hoc test ($P < 0.05$).

Values of the percentage of mycorrhizal colonization in the roots of *P. gracilipes* were transformed into arcsin $\sqrt{x + 1}$ before analysis. Differences in root colonization between the dry and rainy seasons were compared using a student's t-test.

To examine whether the AMF community composition differed between forest types and seasons, a PERMANOVA test was performed using the Bray-Curtis dissimilarity index with presence-absence data using 999 permutations of group association. ANOVA, mean comparison tests and PERMANOVA were performed using the VEGAN package of the R software platform (R Core Team, 2015).

Two matrices were obtained to correlate AMF community compositions with soil physical and chemical properties. The first matrix was obtained with spore abundance for AMF species in each forest type by season, and these data were submitted to Hellinger transformation prior to analysis. Rare species (those comprising <10% of the total frequency) were removed from the analysis as the ordering power of the data decreased (Hill and Gauch, 1980). The second matrix of soil properties was obtained, and collinear variables were removed based on an inflation factor of variance (VIF) ≥ 10. Both matrices were subjected to discriminant redundancy analysis (RDA) followed by a step forward selection (Blanchet *et al.*, 2008) analyzed to determine the proportion of variance of the AMF community explained by soil properties, followed by ANOVA test ($P < 0.05$). All multivariate analyses were performed using the "for" (Dray *et al.*, 2016) and "vegan" (Oksanen *et al.*, 2015) packages in the R software platform (R Core Team, 2015).

Results

Physical and chemical soil analysis

Soil pH ranged from 4.85 to 4.98 in the dry season and from 4.37 to 5.14 in the rainy season. Organic matter (OM), B, Ca, Mg and Mn were all significantly higher ($P < 0.05$) in FRP compared to other sites in the dry season. OM and K values were significantly higher in the dry season compared to the rainy season. Sand concentration was not significantly different between forest type. Silt values were similar between PPF and PRF, being higher than in FWP (Table 1).

Table 1. Physical and chemical properties of the soil where AMF communities were studied at Maracá Ecological Station, Brazil

Soil properties	FWP		PPF		PRF	
	Dry	Rainy	Dry	Rainy	Dry	Rainy
pH	4.85±0.27a	4.37±0.23b	4.98±0.22a	5.14±0.58a	4.96±0.14a	4.93±0.39a
B	0.18±0.07b	0.30±0.08b	0.21±0.08b	0.42±0.07a	0.28±0.05a	0.45±0.1a
Ca	2.27±0.80b	3.13±1.19b	3.0±1.31b	4.87±2.59ab	4.4±1.96a	6.4±2.47a
Cu	0.43±0.15a	0.43±0.18b	0.5±0.18a	0.63±0.30ab	0.43±0.16a	0.49±0.15a
Fe	37.6±25.67b	36.56±26.37b	113.73±46.97a	238.87±152.99a	96.2±49.71a	148.85±104.76a
P	4.67±3.29a	5.33±1.29b	4.67±2.13a	6.27±0.96ab	6.2±1.61a	7.13±1.69a
H+Al	26.27±7.81b	23.87±7.76b	30.27±5.71ab	29.67±8.41b	36.67±10.64a	42.87±16.87a
K	56.42±14.51b	30.68±9.07b	68.9±24.96ab	47.06±15.07a	83.98±43.52a	53.3±11.85a
Al	2.6±0.99a	2.33±1.35a	2.73±1.1a	1.73±1.16a	2.8±1.61a	2.2±1.42a
Mg	1.8±0.41c	1.6±0.74c	3.8±1.70b	3.67±1.8b	5.4±1.99a	5.47±1.1a
Mn	6.12±4.44b	6.68±3.94b	8.99±5.28b	15.69±15.88b	25.54±21.98a	35.65±26.25a
OM	15.07±7.20c	6.53±2.64b	23.0±7.49b	14.67±6.13a	30.47±9.67a	17.6±6.93a
S	6.8±3.61a	5.07±1.28b	5.87±2.80a	5.13±1.06b	5.2±2.70a	6.53±0.83a
Zn	0.46±0.12b	0.48±0.07b	0.78±0.28ab	0.72±0.29b	1.1±0.80a	1.15±0.75a
Texture						
Clay	N/A	106.8±56.85a	N/A	119.8±41.19a	N/A	121.07±20.81a
Silt	N/A	45.2±31.39b	N/A	95.53±65.02a	N/A	74.93±29.27ab
Sand	N/A	848.0±72.62a	N/A	784.67±101.76a	N/A	804.0±41.02a

Different letters between seasons denote significant differences (Tukey test, $P < 0.05$)

AMF community analyses and mycorrhizal colonization

Overall, 18 AMF morphotypes were recovered and identified from all forest types, five of which were detected exclusively in the dry season (Table 2). Spores identified belonged to *Glomus* (Glomeraceae), *Acaulospora* (Acaulosporaceae), *Gigaspora*, *Dentiscutata* and *Scutellospora* (Gigasporaceae), and *Archaeospora* (Archaeosporaceae). *Glomus* sp1, *Glomus* sp2, *Acaulospora mellea*, *Acaulospora* sp1, *Acaulospora* sp2, *Scutellospora* sp1 and *Scutellospora* sp2, which were detected in all forest types and in both seasons, but their abundance varied according to each forest type and sampling time. Gigasporaceae and Acaulosporaceae were represented by six species, Glomeraceae by five species and Archaeosporaceae by one species.

Table 2. AMF species and families and spore abundance per species in dry and rainy seasons in forest without *Peltogyne* (FWP), forest poor in *Peltogyne* (PPF) and forest rich in *Peltogyne* (PRF). This list of species does not include those found in the trap cultures

Code	Families / AMF species	Dry Season			Rainy Season		
		FWP	PPF	PRF	FWP	PPF	PRF
	Family Glomeraceae						
Glo1	*Glomus* sp1	109	107	279	120	166	186
Glo2	*Glomus* sp2	85	95	93	39	48	70
Glo3	*Glomus* sp3	-	2	327	22	99	96
Glo4	*Glomus* sp4	-	6	249	-	-	-
Glo5	*Glomus* sp5	137	115	166	-	-	-
	Family Acaulosporaceae						
Acol	*Acaulospora colombiana* (Spain & Schenck) Kaonongbua, Morton and Bever	-	9	17	-	-	-
Amell	*A. mellea* Spain and Schenck	1	46	122	8	21	62
Ascro	*A. scrobiculata* Trappe	-	13	226	-	3	108
Aspin	*A. spinosa* C. Walker and Trappe	14	-	79	4	102	20

Acau1	*Acaulospora* sp1	27	29	23	6	16	16
Acau2	*Acaulospora* sp2	13	5	72	16	16	35
	Family Gigasporaceae						
Gmarg	*Gigaspora margarita* Becker and Hall	242	153	90	-	-	-
Giga1	*Gigaspora* sp1	-	-	76	-	8	268
Dbior	*Dentiscutata biornata* (Spain, Sieverd. and S. Toro) Sieverd., F.A. Souza and Oehl	176	146	176	-	-	-
Dhete	*D. heterogama* (T.H. Nicol. and Gerd.) Sieverd., F.A. Souza and Oehl	-	70	64	1	42	60
Scut1	*Scutellospora* sp1	160	36	2	60	4	0
Scut2	*Scutellospora* sp2	113	115	173	84	107	75
	Family Archaeosporaceae						
Artra	*Archaeospora trappei* (Ames & Linderman) J.B. Morton and D. Redecker	30	12	-	15	-	-

AMF species richness varied according to the season and forest type, and species richness was higher in the dry season in all forest types than in the rainy season (Table 3). The highest values of richness were found in PRF (13.5 in the dry season and 9.1 in the rainy season), while the lowest values were reported in FWP (9.40 in the dry and 5.33 in the rainy season). The average number of AMF spores per 100 g of soil was significantly different between seasons, with the highest counts observed in the dry season in PRF. The Shannon index was significantly higher in the dry season compared to the rainy season in all three forest types, with the highest Shannon index value detected in the PRF dry season (H = 2.52). No significant differences were found for the Pielou equitability index between seasons.

Table 3. Total number of AMF spores (in 100 g of soil), mean species richness (S) per sample, Shannon index (H) and Pielou equitability index (J) in the dry and rainy seasons at Maracá Ecological Station, Brazil

	FWP		PPF		PRF	
	Dry	Rainy	Dry	Rainy	Dry	Rainy
Spore number	73.8 ± 0.85a	25.0 ± 0.42b	63.93 ± 0.67 a	42.13 ± 0.64b	148.93 ± 1.21 a	66.4 ± 0.81b
S	9.40 ± 1.35a	5.33 ± 1.23b	9.53 ± 1.19 a	6.93 ± 1.58b	13.46 ± 1.30 a	9.13 ± 1.06b
H	2.13 ± 0.15a	1.55 ± 0.23b	2.16 ± 0.12 a	1.80 ± 0.27b	2.52 ± 2.53 a	2.12 ± 0.13b
J	0.95 ± 0.1a	0.94 ± 0.3a	0.96 ± 0.1 a	0.94 ± 0.3b	0.97 ± 0.1a	0.96 ± 0.12a

Different letters between seasons denote significant differences (Tukey test, $p < 0.05$)

Overall, 19 species were detected sporulating in the dry season, 13 of which were previously recorded in field samples. *Acaulospora morrowiae*, *Claroideoglomus etunicatum*, *Gigaspora* sp2, *Rhizophagus clarus*, *Cetraspora pellucida*, and *Glomus* sp6 were detected sporulating exclusively in trap cultures of FWP and PPF. In the rainy season, 16 species were detected sporulating in trap cultures, four of which (*Acaulospora morrowiae*, *Rhizophagus clarus*, *Cetraspora pellucida* and *Glomus* sp6) were recovered exclusively in FWP and PPF traps. Traps established with soils from PRF yielded the same species detected in field samples (Figure 2). Mycorrhizal colonization of *P. gracilipes* was 63.7% in the dry season, which was significantly higher compared to colonization measures in the rainy season (18.7%).

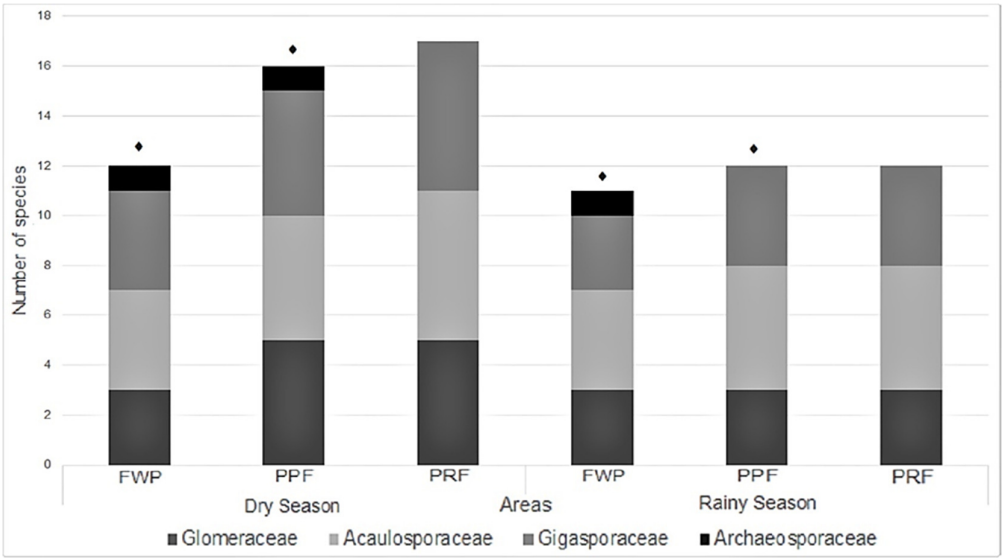

Figure 2. Redundancy Analysis (RDA) of AMF communities with soil parameters and forest types in the dry season at Maracá Ecological Station, Brazil
Abbreviation of species are as shown in Table 2

Relationship between soil characteristics and the density and richness of AMF species

AMF spore abundance and species richness were positively correlated with several soil chemical attributes (Table 4). The largest correlation coefficients were with Mg, Mn, Ca, B and OM ($P < 0.01$) in the dry season, while in the rainy season, spore abundance was positively correlated with all soil chemical parameters, except for Cu and Al (Table 4). No correlation was detected between soil physical attributes and species abundance and richness.

Table 4. Correlation coefficient (r) between soil physical and chemical attributes with AMF species richness and abundance at Maracá Ecological Station, Brazil

Soil parameters	Dry Season		Rainy Season	
	Spore abundance	Species richness	Spore abundance	Species richness
	r	*r*	*r*	*r*
pH	0.232ns	0.136ns	0.476***	0.410**
B	0.436**	0.442**	0.420**	0.350**
Ca	0.472***	0.520***	0.592***	0.549***
Cu	-0.164ns	-0.077ns	0.144ns	0.087ns
Fe	0.185ns	0.049ns	0.362**	0.333ns
P	0.225ns	0.296*	0.442**	0.368ns
H+Al	0.272ns	0.189ns	0.376**	0.297ns
K	0.218ns	0.206ns	0.431**	0.329**
Al	-0.085ns	-0.095ns	-0.201ns	-0.135ns
Mg	0.495***	0.458***	0.615***	0.559***
Mn	0.357**	0.477***	0.610***	0.457***
OM	0.396***	0.274ns	0.534***	0.431**
S	-0.196ns	-0.236ns	0.380**	0.368**
Zn	0.313ns	0.219ns	0.375**	0.327*
Texture				
Clay	0.075ns	0.117ns	0.246ns	0.291*
Silt	-0.087ns	0.067ns	0.296*	0.268ns
Sand	0.014ns	-0.103ns	-0.313*	-0.319*

*, ** and *** indicate statistical significance at $P<0.05$; $P<0.01$ and $P<0.001$, respectively; ns: not significant.

In the dry season, the soil properties that were significant in the RDA model were pH, Fe, H + Al, Mn, Ca, sand and silt (P <0.001). The RDA analyses resulted in seven canonical axes in the dry season and five in the rainy season, explaining 12% of the total variance by the Monte Carlo permutation test. In the dry season, results showed that *Dentiscutata heterogama* was positively correlated with pH, Fe, and silt and associated with PPF, and *Acaulospora mellea* was positively correlated with H+Al and sand in PRF. *Acaulospora scrobiculata*, *Glomus* sp3, and *Glomus* sp4 were positively correlated with Mn and associated with FRP, while *Gigaspora margarita* and *Scutellospora* sp1 were negatively correlated with Mn and associated with FWP and PPF forest types. The AMF species *Archaeospora trappei*, *Dentiscutata biornata*, *Acaulospora* sp1, and *Scutellospora* sp2 were positively correlated with Ca and associated with FWP and PPF (Figure 3). In the rainy season, the results revealed that Fe, pH, Sand, Mg and Zn (P <0.001) were predictor variables associated by the AMF communities. In this sense, *Gigaspora* sp1 was positively correlated with Zn and associated with PRF. AMF species *Acaulospora spinosa*, *Acaulospora* sp1, *Acaulospora* sp2, *Archaeospora trappei*, *Glomus* sp1, *Glomus* sp2, *Scutellospora* sp1, and *Scutellospora* sp2 were negatively correlated with all soil properties previously mentioned and were associated with forest types FWP and PPF (Figure 4). The PERMANOVA test based on the presence and absence of data indicated that the AMF community composition differed among all sites and seasons (P <0.001).

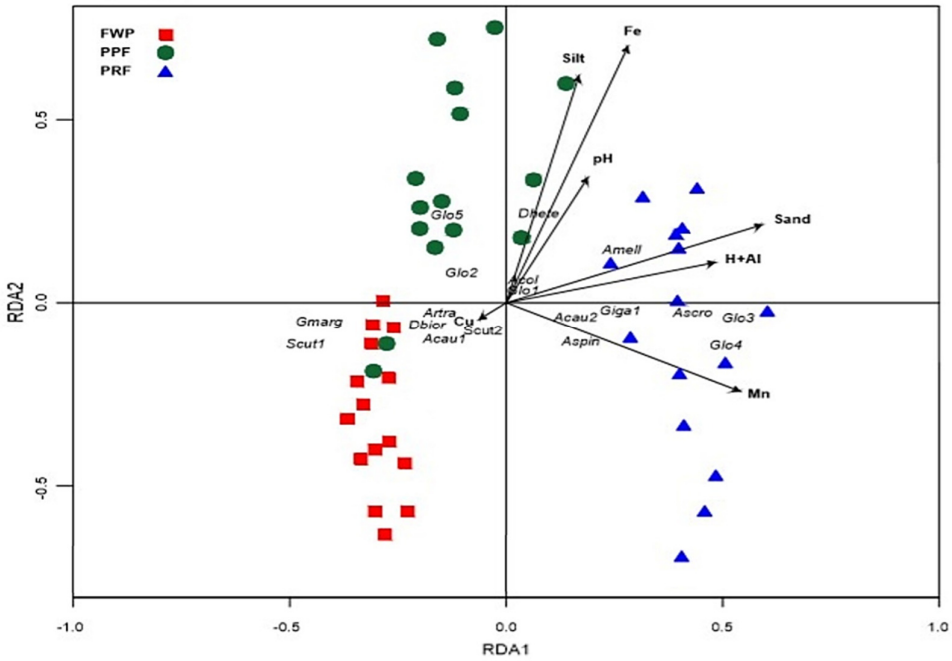

Figure 3. Redundancy Analysis (RDA) of AMF communities with soil parameters and forest types in the dry season at Maracá Ecological Station, Brazil
Abbreviation of species are as shown in Table 2

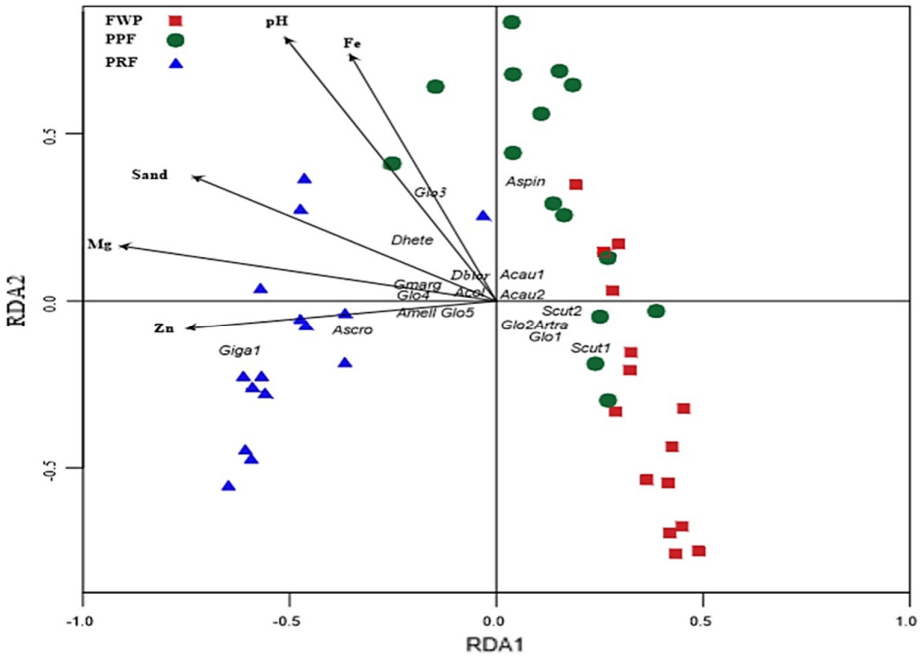

Figure 4. Redundancy Analysis (RDA) of AMF communities with soil parameters and forest types in the rainy season at Maracá Ecological Station, Brazil
Abbreviation of species are as shown in Table 2

Discussion

This study represents the first comprehensive research on the diversity and composition of AMF species communities associated with ecotonal forests in the Maracá ecological station of northern Brazilian Amazonia. The results revealed some associations between the richness of AMF species, spore density and the colonization of *P. gracilipes* roots with the type of vegetation, soil properties and seasonality. We did not find evidence to reject our working hypothesis that AMF community structure is a factor contributing to the monodominance of *P. gracilipes* in the sampling area. In our work, we found higher abundance, diversity, and richness of AMF species, both in the dry and rainy seasons, associated with PRF compared to FWP and PPF forest types, which might be an indicator that the AMF is interacting favourably for the survival of the *P. gracilipes* species. Our work contributes to revealing AMF species diversity in an ecosystem associated with the Brazilian Amazon tropical forest by reporting 18 AMF species associated with the three vegetation types (FWP, PPF and PRF) located on the island of Maracá. AMF species richness and diversity here are within the range detected in five natural areas of savannas (21 species by Stürmer *et al.*, 2018) and different land use systems (16 species by Araújo *et al.*, 2019) from Roraima.

We were able to recover six additional AMF species in trap cultures using *Urochloa brizantha* as a host plant. Despite not using different dilutions with native soil, as recommended by Stutz and Morton (1996), our results were somewhat superior to those recorded by Stürmer *et al.* (2018). These authors established trap cultures with soils from savannas using a dilution methodology (50%, 25%, and 12.5% of field soil mixed with sterilized sand), recovering only two additional species that were not sporulating in the field. Lovera and Cuenca (2007) recorded only three additional species from trap cultures from soils of La Gran Sabana in Venezuela. These results seem to indicate that the inoculum potential of these savannas and forest types are low, and this constrains colonization of the trap host plant and further sporulation.

This study is the first to investigate the relationship between a monodominant species (*P. gracilipes*) and the presence of AMF. Studies related to monodominance by some forest species have previously only associated with ectomycorrhizal fungi, as is the case of work by McGuire *et al.* (2008), who found that ectomycorrhizal fungi are closely linked to the survival and dominance mechanisms of *Dicymbe corymbosa* Spruce ex Benth. and *Dicymbe altsonii* Sandwith, both species of the Caesalpiniaceae family in a Guyana tropical forest. This result is in agreement with that reported by Connell and Lowman (1989), mentioning that the monodominance of a plant species would be related to the occurrence of interactions between ectomycorrhizal fungi and the dominant species. In the case of the forest of *P. gracilipes* located in Maracá, Nascimento (1994), studying the monodominance of this species in this area revealed that the trees of *P. gracilipes* are symbiotic with AMF rather than with ectomycorrhizae. Investigations in monodominant forests, indicate that there is no single ecological mechanism responsible for monodominance (Torti *et al.*, 2001), but rather, a set of important attributes, among which, microorganisms should be considered (Holste and Kobe, 2017). AMF are important components of the soil biota, mainly for plants in natural ecosystems (Moreira and Siqueira, 2006). In symbiosis with plants, AMF develop into typical structures within the root cortex and distribute their hyphae throughout the soil, increasing the area of water and nutrient uptake, especially for low mobility nutrients such as phosphorus. The nutrients are transferred to their host resulting in better growth rates and plant nutrition. In addition, the external mycelium of the fungus acts in the physical aggregation of the soil through the tangling of hyphae in soil particles (Purin and Klauberg Filho, 2010). These functions make AMF important for tropical soils of low fertility, where symbiosis with AMF affects the survival and growth of tropical woody species and also influences plant succession and the recovery of degraded areas. The results found herein that some attributes of the AMF community, both in the dry and rainy seasons, are associated with PRF, which may indicate that the AMF is interacting favourably for the survival of the *P. gracilipes* species.

This study registered strong seasonal variations in spore density and AMF species richness and diversity, with high values of these parameters being registered in the dry season. This result was expected as intense sporulation in the dry season represents a survival strategy during the water stress phase of host plants (da Silva *et al.*, 2014; Deepika and Kothamasi, 2015). Quantification of spores is one of the parameters used to assess the presence of AMF in the soil, and factors such as temperature and humidity, in addition to the phenology of the host, can influence sporulation. Several studies have proven the seasonal variation of spore production, with a pattern that varies according to AMF species (Morton *et al.*, 2004). In degraded and recovering areas of a tropical region, Carneiro et al. (2016) found high seasonal variation in spore numbers, with a higher number of viable spores in the dry season compared to the rainy season. We also observed seasonal variation in the mycorrhizal colonization of *P. gracilipes* with values significantly higher in the dry season than in the rainy season (Table 4). Seasonal changes in the AMF community have received substantial attention in previous studies, where spore density and root colonization were higher in dry season than in rainy season in a seasonal dry forest in Mexico (Guadarrama *et al.*, 2014), an agroforestry ecosystem in Brazil (de Oliveira and de Oliveira, 2005), an Atlantic rain forest in Brazil (Zangaro *et al.*, 2013) and a subtropical secondary forest in China (Maitra *et al.*, 2019). Taken together, these results all emphasize the need to sample during distinct seasons to recover most of the AMF species sporulating in a given system.

AMF communities on Maracá Island, during both seasons, were characterized by codominance among Glomeraceae (5 species), Acaulosporaceae (6 species), and Gigasporaceae (6 species). The dominant families in a *P. gracilipes* forest are typical of Brazilian floristic domains and other tropical regions (Lovelock *et al.*, 2003; Stürmer and Siqueira, 2011; da Silva *et al.*, 2014; Trejo *et al.*, 2016). For other ecosystems in Roraima state, Araújo *et al.* (2019) found dominance by the family Acaulosporaceae (8 species out of 16) in three vegetation types, while Stürmer *et al.* (2018) found dominance by the family Gigasporaceae in savannas. Hart and Reader (2002) mention that AMF species members of the Gigasporaceae family form an extensive extraradicular mycelium and that they colonize the roots with greater intensity along with members of the Glomeraceae and Acaulosporaceae family. The high proportion of soil reached by these fungi can be important for plant

nutrition in soils poor in nutrients, as is the case with the soil on Maracá Island, according to its physical and chemical properties (Table 1).

Another factor that can affect AMF community structure is soil characteristics. The major correlations between the physical and chemical attributes of soil with the abundance and richness of AMF species obtained in the present work were with Mg, Mn, Ca, B, and organic matter in the dry season and with P, K, and pH in the rainy season. In this case, factors such as acidity, concentration of organic matter, phosphorus, potassium, nitrogen, aluminium, copper, zinc, and magnesium in the soil interfere in the establishment and performance of symbiosis (Hernández-Hernández *et al.*, 2017), which is reflected in the ability of the host to colonize and produce fungal spores (Peña-Venegas *et al.*, 2007). According to Bencherif *et al.* (2016), the tolerance of AMF to acidity and high levels of some macro and microelements is still controversial. However, in acid soils of the argisol type, these factors do not seem to affect the performance of native mycorrhiza, including fungi that can accumulate aluminum in their mycelium and vesicles. Stürmer et al. (2013) hypothesized that sandy soils with low organic matter content are associated with the dominance of AMF species belonging to the Gigasporaceae family. Soils on the island of Maracá are high in sand content, especially in the PRF forest type (Villela and Proctor, 2017). The numbers of AMF spores found here were high (60 to 150 in the dry season and between 25 and 70 in the rainy season) compared to a study conducted by Stürmer et al. (2018) in a transition area between savannas - forests, conducted in Roraima, where they recorded between 5 and 25 spores of AMF per 100 g of soil. Some soil properties, such as organic carbon and soil pH, are parameters known to drive AMF diversity on a global scale (Davison *et al.*, 2015), and although AMF species as a group tend to be selective for a particular habitat type (Álvarez-Lopeztello *et al.*, 2019), the RDA analysis showing the relationship between soil properties and the distribution of AMF species on Maracá Island, conducted in both seasons, allowed us to observe that selectivity seems to be common among most of the studied AMF species. We found few species that could be indicative of a certain forest type.

Of the three forest types studied at Maracá, only in the PRF forest type were there unique indicator species (Giga1 and A. Scro) both in the dry and rainy seasons, and these species may positively influence the monodominance of *P. gracilipes* in this area. We were able to detect other AMF species that were characteristic of a combination of the forest types under study, in contrast to a study of AMF spore diversity in neotropical ecosystems in Mexico by Álvarez-Lopeztello *et al.* (2019), which did not detect an exclusive AMF indicator species of a habitat type. However, the presence of indicator species of a particular habitat type, such as species that are colonizing the PRF, provides an additional reason to preserve this type of vegetation and to try to understand its function.

Conclusions

Our results reveal important differences in the diversity of AMF species in contiguous but contrasting vegetation types on Maracá Island. These differences can be explained in large part by the AMF communities with the vegetation types, seasonality and soil properties. Compared to the other types of environments studied in this research, the PRF forest type has a high richness and diversity of AMF species, some of which are exclusive to this forest type, suggesting that they represent another factor explaining the monodominance of *P. gracilipes* in these environments.

Authors' Contributions

Conceptualization, OOPB, KDS, RIB, and SLS; Data curation, OOPB, KDS, RIB, and EDNC; Formal analysis, OOPB, KDS, RIB, and JPUZ; Funding acquisition, KDS, and RIB; Methodology, OOPB, KDS, and RIB; Project administration, OOPB, KDS, and RIB; Resources, OOPB, KDS, and RIB; Supervision, KDS, and

RIB; Validation, KDS, and RIB; Writing – original draft, OOPB, KDS, and RIB; Writing – review & editing, OOPB, KDS, RIB, SLS, and JPUZ. All authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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