Acta Botanica Brasilica, 2023, 37: e20230015
doi: https://doi.org/10.1590/1677-941X-ABB-2023-0015

Original article

Succession stages and soil attributes influence the structure of arbuscular mycorrhizal fungi communities in the Atlantic Forest

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Received: March 9, 2023
Accepted: July 04, 2023

ABSTRACT

The objective of this study was to determine the structure, diversity, composition and drivers of AMF communities in succession areas of Atlantic Forest. Soil and root samples were collected in three natural ecosystems (mature rainforests, early and late secondary forests) with three areas on each ecosystem. In total, 38 AMF taxa were identified in field samples and three more in trap cultures with a greater richness of *Acaulospora* and *Glomus*. Based on a richness estimator, 70% of the AMF species were identified. Highest rates of root colonization and number of glomerospores were recorded in the early secondary forest. AMF species diversity differed between early and late forests. The main drivers of AMF distribution were coarse and fine sand, silt, Al, P, Na, pH and base saturation. The greatest number of exclusive species was recorded in the mature rainforests. The distribution of AMF communities was influenced by different successional stages and some soil attributes.

Keywords: Community assembly, Glomeromycota, glomerospores, mycorrhiza, tropical rainforest

Introduction

The Atlantic Forest in Brazil consists of native forest formations [Dense, Mixed (=Araucaria Forest) and Open Ombrophylous Forest; Semideciduous Seasonal Forest; and Seasonal Deciduous Forest and associated ecosystems, such as mangroves, *restingas*, highland fields, inland marshes and forest enclaves in the Northeast (MMA 2022), extending over 112 Mha (Rezende *et al*. 2018). It provides countless environmental services available to the people, such as climate balance, soil stability and water supply (MMA 2010) and constitutes a natural habitat for numerous species of fauna and flora, presenting great biological richness with a high degree of endemism (Myers *et al.* 2000). Fungi are also well represented in this biome with approximately 3,291 species recorded (Flora e Funga do Brasil 2023) performing important ecosystem services. However, much of this biological diversity has been lost, even before its ecological or economic importance was known (Almeida

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2016). The Atlantic Forest is constantly affected by human practices, especially deforestation, which have reduced the forest to small patches of vegetation (MMA 2010). These fragments have become most vulnerable due to the loss of biodiversity highlighting the need for studies to identify and protect all species essential for the maintenance of these environments.

As observed in the Atlantic Forest, secondary forest landscapes are prevailing in tropical forests worldwide (Lugo 2009). Secondary vegetation appears after a certain area has suffered a disturbance, natural or human, such as an area abandoned after its use in agriculture. As a response to human actions or natural events there is a progressive replacement of plant species in nature over time and place, characterizing an ecological succession (Gandolfi *et al*. 2007). This succession of species can be classified as an initial stage [with herbaceous/shrubby physiognomy of small size, variable diversity with few arboreal species, absence of understory and presence of many pioneer species] followed by an intermediate stage [with arboreal and/or shrub physiognomy predominating over herbaceous and greater diversity of woody species in relation to the primary stage] and finally a late stage [with arboreal physiognomy dominating the others, forming a closed canopy] (CONAMA 2007) and species that develop in conditions of light or intense shade, remaining throughout their lives or until reaching the forest canopy (Gandolfi *et al*. 1995).

Arbuscular mycorrhizal fungi (AMF) are important agents for the advancement of plant succession in ecosystems as they provide greater nutritional support for plant species, especially pioneers (Zangaro *et al*. 2007). As essential representatives of the soil micro biota, AMF form a mutualistic symbiotic association with most plant species and, as obligate biotrophs, require the plant to complete their life cycle (Smith & Read 2008).

Classified in the phylum Glomeromycota (Wijayawardene *et al*. 2022), AMF allow an increase in the area of nutrient assimilation by plants, especially mineral nutrients with little mobility in the soil and of extreme importance, such as P, Cu and Zn (Smith & Read 2008). In addition to nutritional benefits, these microorganisms provide greater tolerance to abiotic and biotic stresses (Gianinazzi *et al*. 2010), such as water (Frosi *et al*. 2016) and saline (Yano-Melo *et al*. 2003) stress, also assisting in nutrient cycling (van der Heijden *et al*. 2015).

In order to adapt to different environmental conditions, AMF have evolved different survival strategies, being classified by Chagnon *et al*. (2013) as: competitors, stress tolerant or ruderal (C-S-R). Competitors, such as members of Gigasporales, invest in greater mycelial growth for soil exploration, have lower glomerospore production and require higher carbon content from their plant hosts. The stress-tolerant species have a low growth rate, mycelium with high resistance to abiotic stressors, such as acidity and low temperature, and are represented by members of Acaulosporaceae. Ruderals have a high growth rate, ability to regenerate fragmented hyphae, investing early in the production of glomerospores, such as Glomerales species (Chagnon *et al*. 2013). de León *et al*. (2016) observed that in the early stages of plant succession AMF with ruderal characteristics predominate, colonizing more efficiently such hostile environments. In addition to the different life strategies, these fungal families have different ways of quickly colonizing roots, having highly infective mycelia, while Gigasporales has better structured mycelia and colonize their plant hosts more slowly (Hart & Reader 2002).

In areas of different stages of succession in the Atlantic Forest, vegetation modification can alter the richness and diversity of AMF species (da Silva *et al*. 2015a; b; da Silva *et al*. 2016), as well as glomerospore density (Zangaro *et al*. 2013) and mycorrhizal colonization (Zangaro *et al*. 2000; Aidar *et al*. 2004). As indicated by Pereira *et al*. (2018), vegetation and soil characteristics are important drivers of AMF communities in this biome.

Considering the profound influence of AMF on the stability of successional environments, the following hypotheses were tested: (1) areas of mature forest have greater diversity of AMF species than areas of initial succession; and (2) in areas of initial succession there is a greater abundance of AMF propagules that have a ruderal life strategy, characterized by high production of glomerospores, compared to areas at a more advanced stage of succession. In this context, the objectives of this study were to determine the structure, diversity, composition and structuring factors (drivers) of AMF communities in successional areas of the tropical Atlantic Rainforest in Brazil. This information will support efficient restoration strategies in Atlantic Forest areas.

Material and methods

Study areas

This study was carried out in the Dois Irmãos State Park (PEDI), located in the northwest of the city of Recife, PE, at coordinates 7°59'30" and 8°01'00"S and 34°56'30" and 34°57'30"W (Mesquita *et al*. 2020). The climate of the region is classified as tropical humid coastal type As', according to Koppen, with average monthly temperatures above 25.5 °C (Lima *et al*. 2018), and the predominant soils are ferralsols, acrisols, and arenosols, as mentioned by da Cunha *et al*. (2021). The site is characterized as an environmental protection area. However, it is constantly threatened by human pressures and is vulnerable to predatory actions by the surrounding population, in addition to being surrounded by highways (Rodrigues & Silva 2014).

The PEDI has an area of approximately 1,158 ha and is formed from remnants of the Atlantic Rainforest, characterized as Lowland Dense Ombrophilous Forest (Lima *et al*. 2018), in a stage of secondary succession, resulting from

logging and natural tree death (Rodrigues & Silva 2014). The most common tree families are Fabaceae, Lecythidaceae, Anacardiaceae, Melastomataceae and Moraceae (Braga *et al*. 2021).

Sampling

Soil and root samples were collected during the dry season (February 2021), in three ecosystems of PEDI, with three areas for each stage of succession: early secondary forest (<38 years), late secondary forest (38-50 years) and mature forest (at least 60 years old). The average annual precipitation at the sampling areas is 2.263 mm, with a rainy period concentrated from April to August (Falcão & Silva 2022). The mature forest fragment covers 384.42 ha, while the younger secondary forest, with two successional stages (early and late) comprises 774.09 ha (da Cunha *et al*. 2021). The history of these areas was determined from aerial photos and satellite images, delimiting a chronosequence, according to da Cunha *et al*. (2021). The predominant species in each successional forest stage are listed in Tab. 1. In each area a geographically demarcated 30x30 m grid was established, from which five simple samples of rhizospheric soil (0-15 cm depth) were collected, totalling 45 sampling units.

Trap cultures

Trap cultures were established to stimulate the production of spores, especially from species that had not sporulated in the field before soil sampling, and to obtain new glomerospores in good condition to facilitate identification. The cultures were mounted in plastic pots with 500 g of sterilized sand + 500 g of soil from field samples. In each pot, three seeds of bean (*Phaseolus vulgaris* L.), three of forage sorghum (*Sorghum bicolor* L.) and three of corn (*Zea mays* L.) were placed. The pots were kept in a greenhouse of the Mycology Department / Federal University of Pernambuco for a period of four months and watered every other day, without adding nutrient solution. After this period, the plants were subjected to water stress for two weeks. Then aliquots of 100 g of soil were taken from each sample for extraction of glomerospores and subsequent taxonomic identification.

Quantification of glomerospores and AMF identification

Glomerospores from field samples and trap cultures were extracted from 100 g^{-1} of homogenized dry soil by wet sieving (Gerdemann & Nicolson 1963) and sucrose

Table 1. Dominant plant species in the early secondary forest, late secondary forest and mature forest in Dois Irmãos State Park, PE.

Family/species	Forests		
	Early secondary	Late secondary	Mature
Anacardiaceae			
Anacardium occidentale L.	X		
Tapirira guianensis Aubl.			X
Araliaceae			
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin			X
Arecaceae			
Bactris ferruginea Burret		X	
Burseraceae			
Protium heptaphyllum (Aubl.) Marchand			X
Fabaceae			
Albizia pedicellaris (DC.) L. Rico			X
Chamaecrista ensiformis (Vell.) H.S.Irwin & Barneby		X	
Parkia pendula (Willd.) Benth. ex Walp.*			X
Lecythidaceae			
Eschweilera ovata (Cambess.) Mart. ex Miers		X	
Lecythis pisonis Cambess.		X	
Malvaceae			
Luehea ochrophylla Mart.		X	
Melastomataceae			
Miconia amacurensis Wurdack DC.*			X
Miconia prasina (Sw.) DC.	X		
Moraceae			
Helicostylis tomentosa (Poepp. & Endl.) Rusby *			X
Myrtaceae			
Myrcia splendens (Sw.) DC.	X		
Nyctaginaceae			
Guapira laxa (Netto) Furlan		X	

* Exclusive to mature areas. (Source: Rodrigues, 2019).

centrifugation (Jenkins 1964). The isolates from the field samples were quantified in a channelled plate, with the aid of a stereomicroscope (40x). After that, all glomerospores (from field and trap cultures) were separated by morphotypes and mounted in glass slides with PVLG (polyvinyl alcohol and lactoglycerol) and PVLG + Melzer's reagent for further identification of AMF species, using specific literature including the most recent descriptions of AMF species.

Analysis of mycorrhizal colonization

The collected roots were separated from each soil sample, washed, diaphanized with KOH (10%) and the fungal structures inside the roots were stained with Trypan blue (0.05%) following the methodology of Phillips and Hayman (1970). The percentage of colonization was established by the intersection method proposed by McGonigle *et al.* (1990), considering the following structures in the roots: hyphae, arbuscules, vesicles and glomerospores.

Data analysis

The following parameters were determined for all samples: number of glomerospores, mycorrhizal colonization, AMF species richness and Shannon and Weaver (1949) diversity index. Glomerospore number data were transformed into log (x+1) and colonization data transformed into log 10, before analysis of variance (ANOVA). To determine whether the richness and diversity of AMF species vary between the successional stages, analyses of variance (ANOVA) were used and, when significant differences were detected, the Tukey test was applied.

In order to estimate the richness of AMF species we used a method based on the extrapolation of the accumulation curve to represent the entire AMF richness (Chao *et al.* 2013; Hsieh *et al.* 2016). The relative abundance of glomerospores of each species per area was calculated from the ratio between the numbers of spores of a given species by the total number of spores per area. The frequency of occurrence (FO) of the species in each successional stage was determined according to the equation: FO = Ji/k where, FO = frequency of occurrence of the species, Ji=number of samples from the area (15) in which the species occurred, k = total number of soil samples. The relative frequency of occurrence is expressed as a percentage and the AMF species were classified as: dominant (FO>50%), very common (FO between 31% and 50%), common (FO between 10% and 30%) and rare (FO<10%) (Zhang *et al.* 2004). To test the relationship of AMF species with the different successional stages, an indicator species analysis was used (Dufrêne & Legendre 1997). The indication values (IV) were calculated for each species and the significance determined by the Monte Carlo test using 999 permutations.

Multivariate permutation analysis (PERMANOVA), based on Bray-Curtis distance, was applied to test whether AMF communities differed between environments in succession. PERMANOVA was also applied, based on Euclidean distance, to test whether the physicochemical properties differed between the study areas, using the "adonis" function in the "'vegan" package (Oksanen *et al.* 2022). For the physical and chemical soil attributes one-way ANOVA was also applied among areas.

Redundancy analysis (RDA) was used to explore whether there was a significant relationship between the composition of AMF communities and soil variables (phosphorus (P), pH, potassium (K), sodium (Na), aluminum (Al), calcium (Ca), magnesium (Mg), hydrogen (H), cation exchange capacity (CEC), base saturation (V), coarse sand, fine sand, silt and clay. Venn diagrams were built to demonstrate the number of unique and shared species between areas, using a web tool available at (http://www.interactivenn.net//).

The significance of all statistical tests was assessed based on $p < 0.05$, except in cases of multiple comparisons where the p value was corrected based on the Bonferroni test. All statistical and ecological analyses were carried out using the R program (R Core Team 2022).

Results

Mycorrhizal colonization

Total mycorrhizal colonization differed statistically ($p < 0.05$) among the areas and was higher in roots collected in the early secondary forest compared to late secondary forest and mature forest (Table 2). Colonization by hyphae, vesicles, arbuscules and spores was also higher in the initial secondary forest area (Table 2).

Table 2. Mycorrhizal colonization by hyphae, arbuscules, vesicles, spores and total, in root fragments in early secondary forest (ESF), late secondary forest (LSF) and mature (MF) forest in Dois Irmãos State Park, PE.

Areas	Colonization (%)				
	hypha	arbuscules	vesicles	spores	total
MF	14.3b	0.05b	3.98b	0.13b	18.4b
LSF	21.5b	0.08b	21.5b	0.18b	30.5b
ESF	0.46a	47.3a	47.3a	6.49a	70.2a

Means followed by the same letter in the row do not differ by the Tukey test (p<0,05).

AMF spore density

There was a greater abundance of glomerospores per 100 g of soil in the initial secondary forest (249) than in the mature forest (175) and in the late secondary forest (159; p=0.01; Fig. 1).

Species richness and diversity

Thirty-eight AMF species were recorded in field samples (Table 3) and three additional species in the trap

cultures (*Acaulospora scrobiculata, Dominikia* sp. 2 and *Glomus* sp. 4), distributed in 10 families (Acaulosporaceae, Archaeosporaceae, Ambisporaceae, Entrophosporaceae, Glomeraceae, Dentiscutataceae, Gigasporaceae, Scutellosporaceae, Paraglomeraceae and Racocetraceae) and 15 genera: *Acaulospora*, *Archaeospora*, *Ambispora*, *Claroideoglomus*, *Cetraspora*, *Dominikia*, *Dentiscutata*, *Funneliformis*, *Gigaspora*, *Glomus*, *Fuscutata*, *Oehlia*, *Orbispora*, *Paraglomus* and *Racocetra*. The most representative genera were *Acaulospora* and *Glomus*, with nine species each, equivalent to 48% of the number of AMF species recorded in this study (Fig. 2). *Dominikia* was represented by four taxa, *Racocetra, Cetraspora, Funneliformis* and *Gigaspora* by two species, and the others (*Archaeospora, Ambispora, Claroideoglomus, Dentiscutata, Fuscutata, Oehlia, Orbispora, Paraglomus*) represented by only one specific taxon.

Five species (13.1%) were recorded in two of the areas (*Cetraspora sp. 1, Glomus microcarpum, Orbispora pernambucana, Paraglomus sp. 1* and *Racocetra fulgida*) and 24 (63.2%) occurred in only one of the areas (Table 3).

Glomus brohultii and *G. macrocarpum* were the most abundant species and dominated in all three forest ecosystems. *Acaulospora longula, A. mellea* and *Dominikia aurea* were also recorded in the three ecosystems, with greater abundance, either in the mature forests, in the early secondary and mature forests, or in the early secondary forest respectively. Regarding rare species, 16 were recorded in the mature forest, whereas 6 and 3 were identified in the late and early secondary forest areas, respectively (Table 3).

The identified taxa represent almost 10% of all known for the phylum Glomeromycota. Of the 38 taxa recorded in field samples, nine were shared across all areas: *Acaulospora mellea, A. morrowiae, A. foveata, A. longula, Glomus australe, G. glomerulatum G. macrocarpum, G. brohultii* and *Dominikia aurea* (Fig. 3). Of the 26 species recorded in mature forest areas, 14 occurred only in these locations and of the 18 species found in the late secondary forest, five were exclusive to these areas.

No significant difference was observed on richness of AMF species between the successional stages. However, the

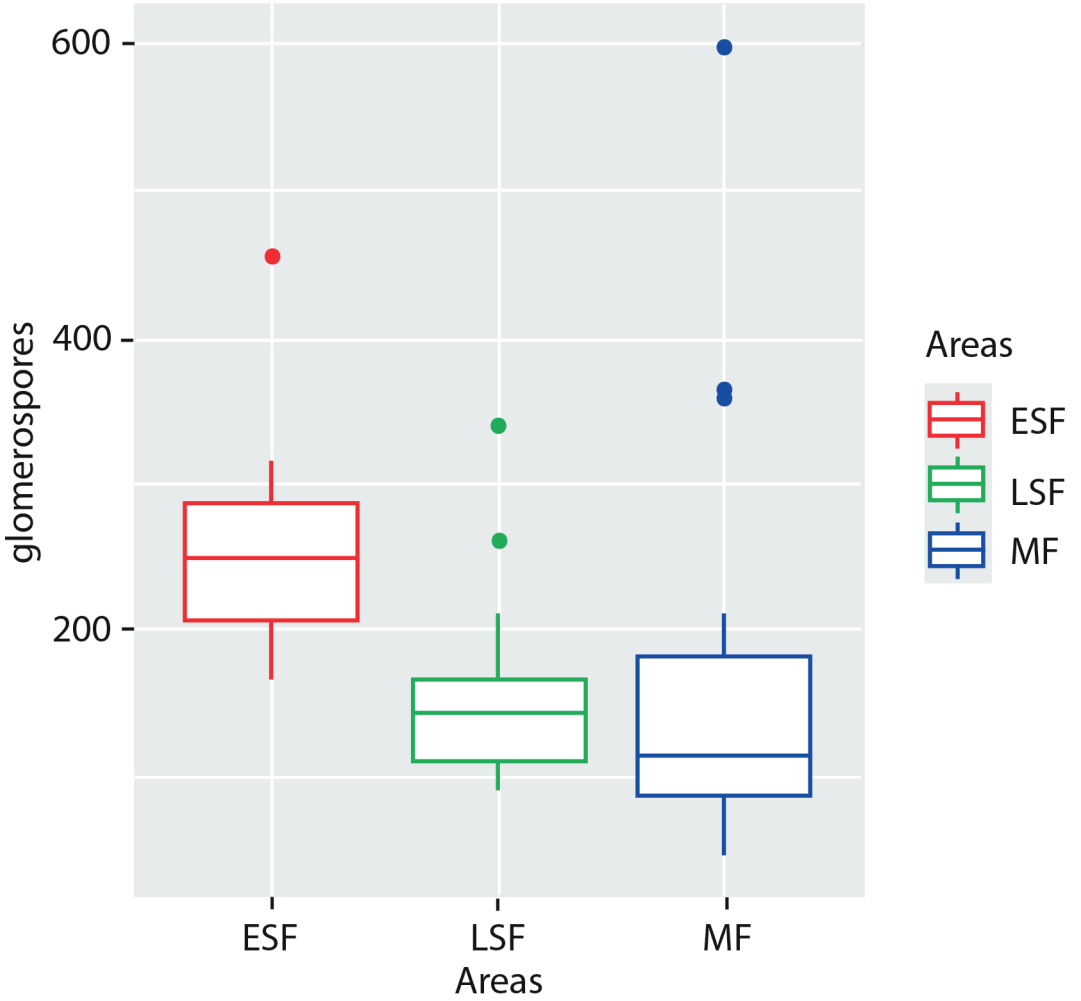

Figure 1. Number of glomerospores in soil samples collected in early secondary forest (ESF), late secondary forest (LSF) and mature forest (MF) in Dois Irmãos State Park, PE.

Table 3. Relative abundance (RA) and frequency of occurrence (FO)[a] of arbuscular mycorrhizal fungi in areas of early secondary forest (ESF), late secondary forest (LSF) and mature forest (MF) in Dois Irmãos State Park, PE.

AMF taxa	Areas					
	ESF		LSF		MF	
	RA	FO	RA	FO	RA	FO
Archaeosporales						
Archaeosporaceae						
Archaeospora sp. 1	-	-	-	-	0.09	R
Ambispora appendicula (Spain, Sieverd. & N.C. Schenck) C. Walker	-	-	-	-	0.19	R
Diversisporales						
Acaulosporaceae						
Acaulospora aspera Corazon-Guivin, Oehl & G.A. Silva	0.07	VC	-	-	-	-
A. foveata Trappe & Janos	0.26	VC	0.10	C	0.19	C
A. herrerae Furrazola, B.T. Goto, G.A. Silva, Sieverd. & Oehl	0.34	C	-	-	-	-
A. ignota Błaszk., Góralska, Chwat & Goto	-	-	-	-	2.47	C
A. longula Spain & N.C. Schenck	0.45	VC	0.27	C	8.42	R
A. mellea Spain & N.C. Schenck	3.06	D	0.43	C	2.77	D
A. morrowiae Spain & N.C. Schenck	0.07	C	0.05	R	0.04	R
Acaulospora sp. 1	-	-	-	-	0.09	C
A. spinosa Walker & Trappe	-	-	-	-	0.04	R
Gigasporales						
Dentiscutataceae						
Dentiscutata cerradensis (Spain & J. Miranda) Sieverd., F.A. Souza & Oehl	0.11	C	-	-	-	-
Fuscutata aurea Oehl, C.M. Mello & G.A. Silva	-	-	-	-	0.04	R
Gigasporaceae						
Gigaspora gigantea (T.H. Nicolson & Gerd.) Gerd. & Trappe	-	-	0.10	R	-	-
G. margarita W.N. Becker & I.R. Hall	-	-	-	-	0.09	R
Racocetraceae						
Cetraspora gilmorei (Trappe & Br Gerd.) Oehl, F.A. Souza & Sieverd.	0.22	C	-	-	-	-
C. pellucida (T.H. Nicolson & N.C. Schenck) Oehl, F.A. Souza & Sieverd.	-	-	-	-	0.04	R
Cetraspora sp. 1	0.03	R	0.71	C	-	-
Racocetra fulgida (Koske & C. Walker) Oehl, F.A. Souza & Sieverd.	0.11	R	-	-	0.04	R
Racocetra verrucosa (Koske & C. Walker) Oehl, F.A. Souza & Sieverd.	-	-	-	-	0.04	R
Scutellosporaceae						
Orbispora pernambucana (Oehl, D.K. Silva, N. Freitas, L.C. Maia) Oehl, G.A.Silva & D.K. Silva	0.68	VC	0.10	C	-	-
Glomerales						
Entrophosporaceae						
Claroideoglomus etunicatum (W.N. Becker & Gerd.) C. Walker & A. Schüßler	-	-	-	-	0.04	R
Glomeraceae						
Dominikia aurea (Oehl & Sieverd.) Błaszk., Chwat, G.A. Silva & Oehl	4.44	D	0.98	VC	0.49	C
D. bernensis Oehl, Palenz., Sánchez-Castro, N.M.F. Sousa & G.A.Silva	-	-	0.05	R	-	-
Dominikia sp. 1	-	-	0.05	R	-	-
Funneliformis halonatus (S.L. Rose & Trappe) Oehl, G.A. Silva & Sieverd.	-	-	-	-	0.09	R
Funneliformis sp. 1	0.07	R	-	-	-	-
Glomus australe (Berk.) S.M. Berch	0.15	C	0.76	VC	0.04	R
G. brohultii Sieverd. & R.A. Herrera	45.82	D	27.55	D	45.31	D

Table 3. Cont.

AMF taxa	Areas					
	ESF		LSF		MF	
	RA	FO	RA	FO	RA	FO
G. glomerulatum Sieverd.	0.34	VC	0.21	C	0.69	C
G. macrocarpum Tul. & C. Tul	43.67	D	65.77	D	36.84	D
G. magnicaule I.R. Hall	-	-	0.27	R	-	-
G. microcarpum Tul. & C. Tul	-	-	0.05	C	0.49	VC
Glomus sp. 1	-	-	-	-	0.69	VC
Glomus sp. 2	-	-	2.40	C	-	-
Glomus sp. 3	-	-	-	-	0.04	R
Oehlia sp. 1	-	-	-	-	0.04	R
Paraglomerales						
Paraglomeraceae						
Paraglomus sp. 1	-	-	0.05	R	0.49	R
AMF species richness	**17**		**18**		**26**	

[a] Categories according to frequency of occurrence (D- dominant; VC-very common; C- commom; R- rare).

Shannon species diversity differed between the areas of late and early secondary forests (F= 3.99, df= 2, p= 0.02) (Fig. 4).

Based on the first order Jackknife richness estimator, the estimated number of AMF species was 54 for all areas, with 38 species recovered in the field samples, equivalent to 70% (Fig. 5). For the areas of initial secondary forest, 19 species were estimated and 17 (89%) recovered; in the late forest, 24 species were estimated and 18 (75%) recovered, and of the 41 species estimated for the mature forest, 26 (63 %) were identified.

AMF indicator species

Of the recorded AMF species, three were revealed as indicators of mature forest areas (*Glomus* sp.1, *G. microcarpum*, and *Acaulospora mellea*), three for early secondary forest areas (*Dominikia aurea, Orbispora pernambucana* and *Acaulospora mellea*) and only one species (*Glomus australe*) was an indicator of late secondary forest (Table 4).

Considering the species by the type of spore formation (acaulosporoid, gigasporoid and glomoid), the acaulosporoid type was an indicator of areas of mature forest and early secondary forest, with indication values of 87% and $p < 0.01$.

Soil attributes and arbuscular mycorrhizal fungal communities

The soils of the study areas were considered acidic, with a lower pH in the mature forest areas (pH = 3.82b), in comparison with the other ESF (pH= 4.52a) and LSF (pH= 4.31a) areas. Phosphorus and aluminum contents differed significantly between areas and were higher in mature forest areas. P concentration in mature forest soils was 5.60 mg/dm^3, while in ESF areas it was 3.87 mg/dm^3 and in LSF 3.40 mg/dm^3, without differing between them. Al content ranged from 1.23 cmolc/dm^3 in soils of mature forest to 0.63 cmolc/dm^3 in LSF and 0.59 cmolc/dm^3 in ESF, with no significant difference between soils of these two successional stages.

Regarding the physical characteristics, in all areas predominated coarse sand (percentages of 60,86b in the MSF; 55,06b and 71,33a respectively in the LSF and ESF). Proportions of silt varied from 10.2a (MSF), 8.26a (LSF) and 3.80b (ESF), and those of fine sand were from 14-20%.

Table 4. Indicator AMF species in areas of mature forest, late secondary forest, early secondary forest in Dois Irmãos State Park, PE.

Areas	IV	p
Mature Forest		
Glomus microcarpum	60	0.01
Glomus sp.1	57	0.007
Acaulospora mellea	77	0.01
Late Secondary Forest		
Glomus australe	58	0.04
Early Secondary Forest		
Dominikia aurea	86	0.001
Orbispora pernambucana	54	0.02
Acaulospora mellea	77	0.01
Spore formation type		
Mature Forest and Early Secondary Forest		
Acaulosporoid	87	0.01

IV = indication value (>25%); p = significance level.

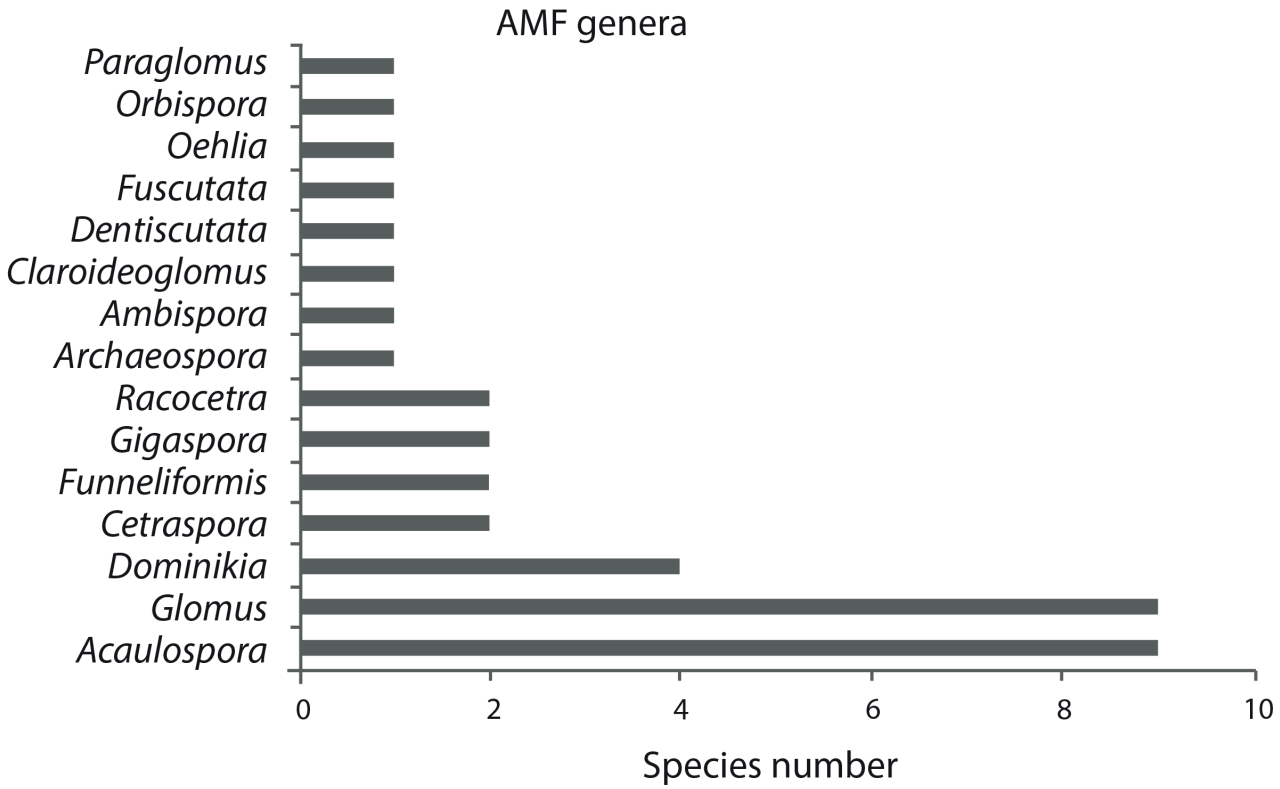

Figure 2. Representativeness of AMF genera in areas of early secondary forest (ESF), late secondary forest (LSF) and mature forest (MF) in Dois Irmãos State Park, PE.

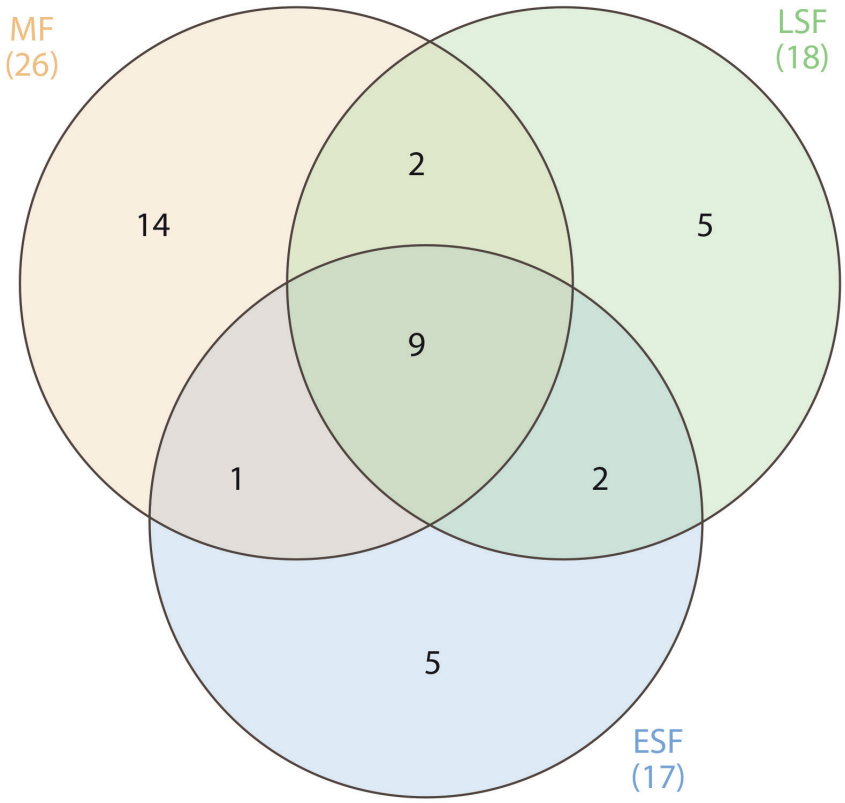

Figure 3. Richness of exclusive and shared AMF taxa in areas at different successional stages: mature forest (MF), late secondary forest (LSF) and early secondary forest (ESF) in Dois Irmãos State Park, PE.

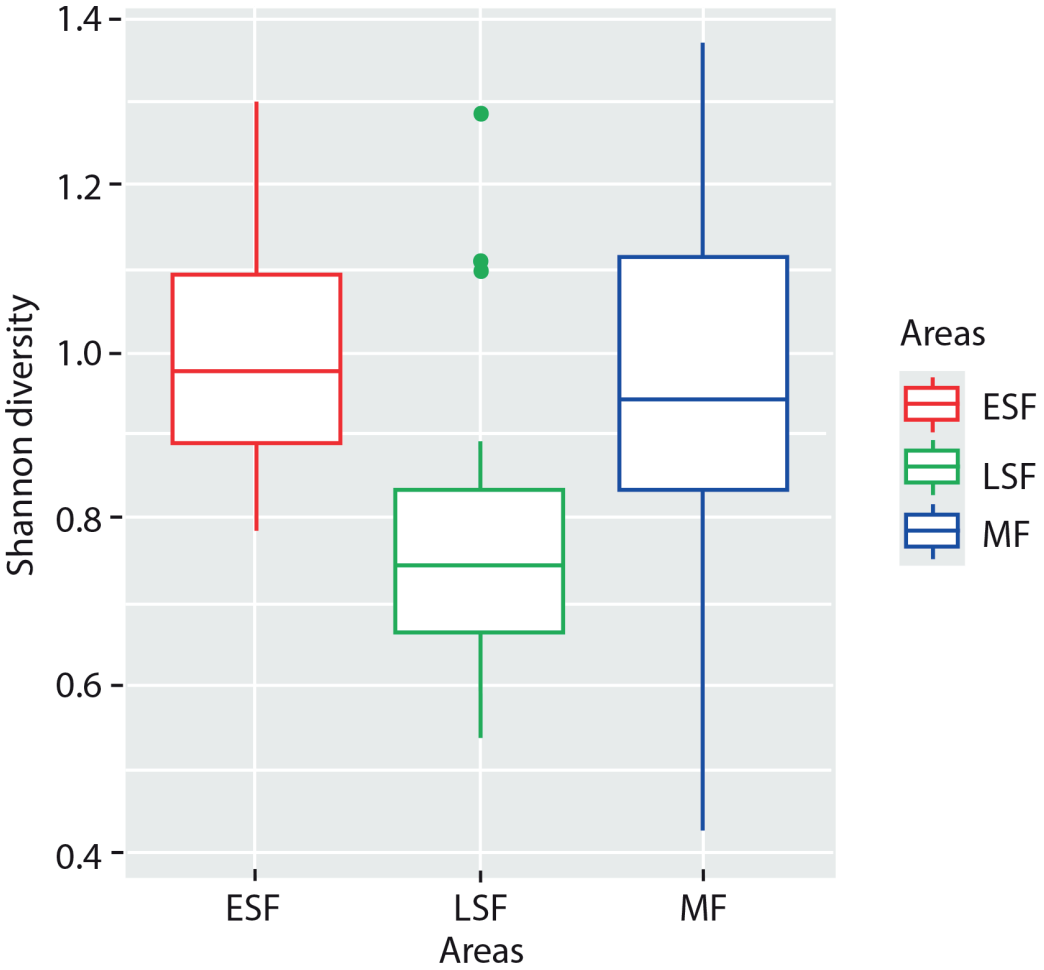

Figure 4. Diversity of arbuscular mycorrhizal fungi (AMF) in soil samples collected in early secondary forest (ESF), late secondary forest (LSF) and mature forest (MF) in Dois Irmãos State Park, PE.

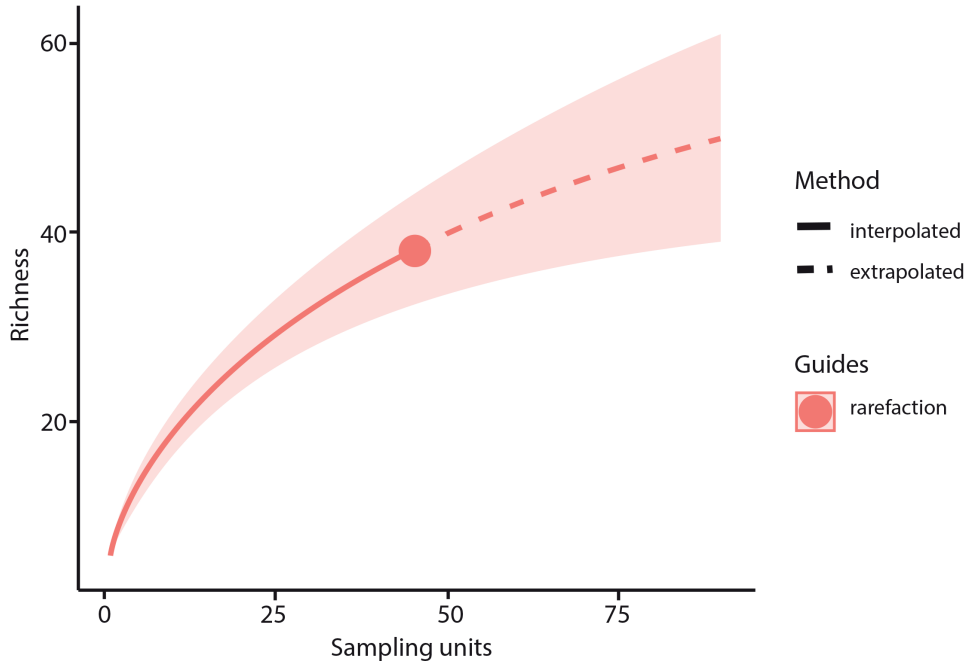

Figure 5. Accumulation curve of AMF species in areas of Atlantic rainforest in Dois Irmãos State Park, PE.

The multivariate permutation analysis (PERMANOVA), based on the physical and chemical components of the soil, showed differences between forest types/ecosystems (early secondary forest, late secondary forest, and mature forest) ($F=10.773$; $p < 0.0001$). The composition of AMF communities also differed between late secondary and mature ($F=11.055$; $p < 0.003$) and late secondary and early ($F=22.014$; $p < 0.003$) forest areas.

Redundancy analysis (RDA) explained 16% of the total variation, with the largest part for axis 1 (8.8%) and the smallest for axis 2 (7.8%) of the RDA. The following main factors influenced the AMF communities in the forests: coarse sand, silt, fine sand, aluminum, cation exchange capacity, phosphorus, sodium, potassium, hydrogen, magnesium, pH and base saturation (Fig. 6).

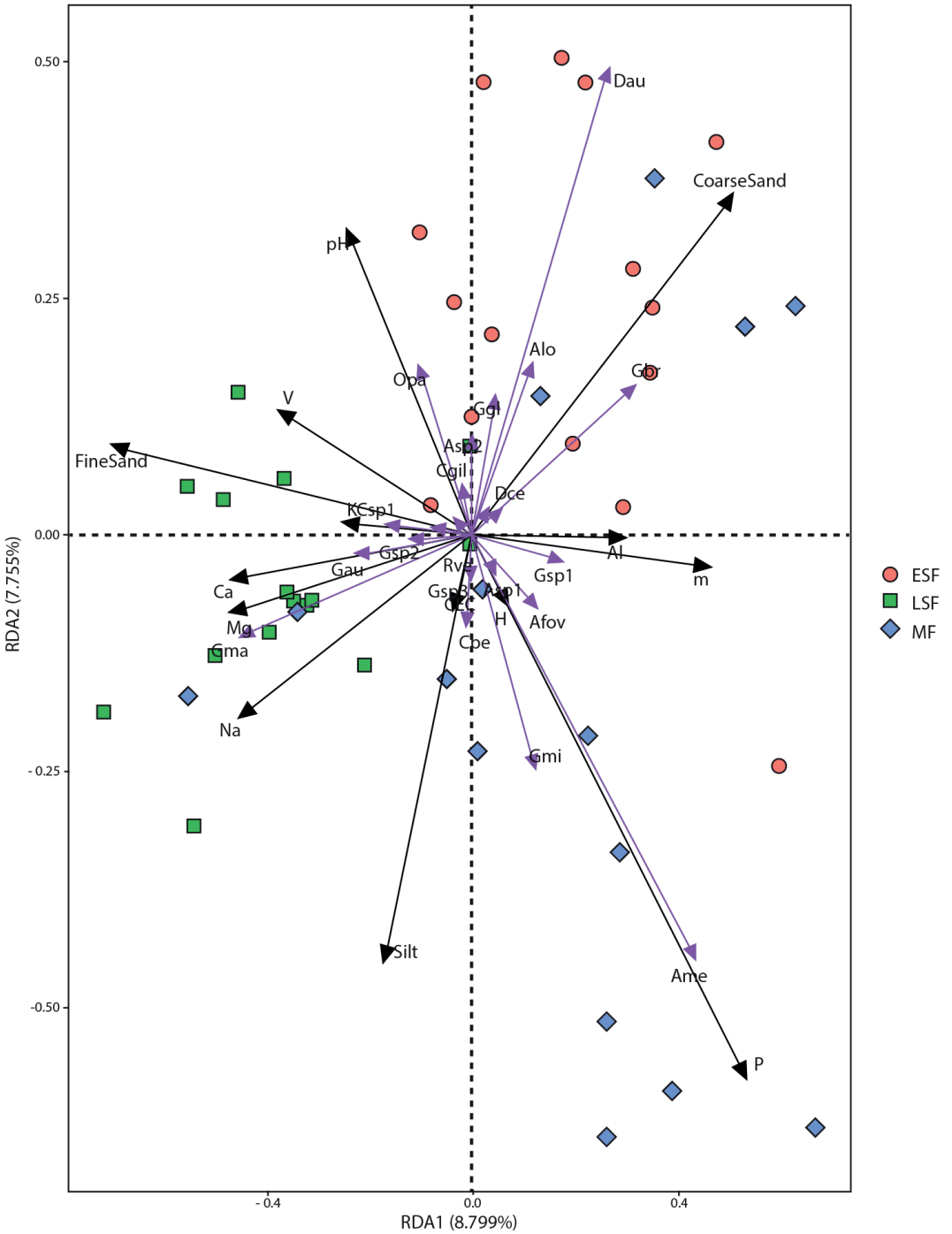

Figure 6. Redundancy analysis (RDA) based on AMF communities' composition in areas of mature forest, late secondary forest and early secondary forest in Dois Irmãos State Park, PE. Abbreviations: P (phosphorus), K (potassium), Na (sodium), Al (aluminum), Ca (calcium), Mg (magnesium), m (aluminum saturation), H (hydrogen), CEC (cation exchange capacity) and V (base saturation).

Discussion

In this study, the structure of AMF communities was investigated in areas of Atlantic Forest characterized as mature forest, early secondary forest and late secondary forest, using ecological data on richness, diversity and species composition of this fungal group.

The analysis of root fragments collected in each of the areas showed that mycorrhizal colonization was higher in the initial secondary forest. In other studies, a higher percentage of colonization was also recorded in areas undergoing initial regeneration, compared to more advanced stages of succession (Zangaro *et al.* 2007; 2013). Greater mycorrhizal colonization in plant species in the first stages of succession indicates greater dependence on the benefits promoted by fungi in more hostile environments, as they help in the establishment, growth and survival of the plants (Zangaro *et al.* 2000). In contrast, plants in more advanced stages of succession which by definition are in more balanced environments exert less nutritional demand making the association with AMF less necessary (Zangaro *et al.* 2002). On the other hand, if individual observations are made it is possible to find a higher proportion of colonization in late-successional plants than in early successional plants when inoculated with some AM fungal species, indicating that the response depends also on the associated AMF (Koziol & Bever 2016).

Plant species characteristic of environments in initial succession have a high growth rate and photosynthetic activity, increasing the carbon available to AMF (Gamage *et al.* 2004). Therefore, the greater number of arbuscules recorded in plants at this stage demonstrates that the association is in its initial period, with a large bilateral transfer of resources between the symbionts (Bonfante & Genre 2010; Gutjahr & Parniske 2013).

The presence of certain fungal structures, such as hypha, is essential for the regeneration of forests (Guadarrama *et al.* 2008), because the plants provide photosynthates to fungi, favouring the growth of hyphae inside and outside the roots, and resulting in high transfer of nutrients from the soil to the hosts (Lebrón *et al.* 2012). The largest amount of hypha recorded in the initial stages of forest regeneration may also indicate greater transfer of essential nutrients for plant growth in this initial stage of succession.

As lipid storage structures, vesicles may be important in regenerating environments as they are useful as energy sources for glomerospore germination under suitable conditions (Roth & Paszkowski 2017). Glomerospores are effective structures for the persistence, colonization and propagation of AMF communities, especially for communities in succession (Wu *et al.* 2007). Therefore, the greater amount of these structures found in the areas of initial secondary forest compared to more mature areas may be related to the survival and reproduction of fungi.

AMF communities are sensitive to the chemical and physical attributes of the soil (de Assis *et al.* 2018; Ezeokoli *et al.* 2020; Bi *et al.* 2021; Zhang *et al.* 2021), which act as environmental filters for the presence of species in different environments (Rodríguez-Echeverría *et al.* 2017). The value of some of these attributes, such as pH, differed between the studied areas.

The AMF community of the areas in initial regeneration was influenced by the pH and coarse sand contents of the soil. This physical attribute was recorded as influencing the distribution of AMF communities in a chronosequence of tropical humid forest in Colombia (Rodríguez-León *et al.* 2021). In rupestrian fields, the coarse sand content also affected the occurrence of AMF species (Carvalho *et al.* 2012).

The soil factors most related to AMF communities in areas undergoing late regeneration were fine sand, sodium, magnesium, calcium, potassium and base saturation contents. Sodium is considered a stressor for AMF, and may induce greater sporulation in environments with a high value of this element (Kumar *et al.* 2014).

For mature forest areas, phosphorus, silt and cation exchange capacity (CEC) were the factors most related to AMF communities. Álvarez-Lopeztello *et al.* (2019) reported that in a tropical forest in Mexico a higher CEC induced an increase in glomerospore density. This soil attribute is directly linked to soil fertility, as it represents the amount of exchangeable cations that the soil can fix to be later absorbed by plants (Teixeira *et al.* 2017).

Phosphorus is essential in plant metabolism and is often found in an inaccessible form in soil (Wright *et al.* 2018); in general, the levels of this element decrease with the successional advance of forests (Li *et al.* 2013; Ullah *et al.* 2020). The role of AMF in regenerating environments is crucial, as they accelerate the process of phosphorus solubilization for plants, especially when it is bound to other nutrients such as aluminum and iron (Liu *et al.* 2021). Changes in the composition of AMF communities were observed when the species were submitted to different degrees of fertilization by phosphorus, suggesting greater competition of fungi for plant carbohydrates, since with the nutritional increase of the soil, the mycorrhizal association is less favoured (Liu *et al.* 2015). In areas with different successional stages, due to mining practices, phosphorus was also one of the soil factors responsible for changes in the composition of AMF communities. Therefore, the status of this element is important in the process of recovering degraded areas, interfering in the relationship of benefits between AMF and plants (Bi *et al.* 2021).

The highest aluminum levels were found in mature forest areas. Aluminum is a limiting factor for plant growth (Alotaibi *et al.* 2021), since it can inhibit phosphorus absorption, making it unavailable to plants (Liu *et al.* 2021). AMF can be affected by aluminum as they receive lower amounts of photosynthates when plants are subjected to

stress by this element, decreasing mycorrhizal colonization (Alotaibi *et al.* 2021). Showing that the association with AMF can decrease aluminum levels in plants, these authors also noted that "the impact of aluminum levels on mycorrhizal development appears to be plant species dependent". Thus, AMF colonization in mature forest areas may also have been affected by the greater amount of aluminum present in the soil in these areas.

Although soils in all areas were considered acidic, those in the mature forests had the lowest pH values, what explains the highest aluminum recorded in these locations. Aluminum becomes soluble when pH decrease and, as a consequence, its amount in the soil solution increases and can become toxic to plants; mycorrhization can aleviate this problem (Alotaibi *et al*. 2021). Soil pH plays an important role, influencing plant growth, mobilization and nutrient availability (Neina 2019). In relation to AMF, different species adapt to a specific range of pH to develop (Kawahara *et al.* 2016) and it has been suggested that pH is the main driver of AMF communities (Oehl *et al.* 2010; Hazard *et al.* 2013; Sun *et al.* 2016). The presence of one *Acaulospora* species (*A. mellea*) among the most abundant in the mature forest can be explained by the higher acidity of the soil in this area, as species of this genus are constantly associated with low pH environments (Liu *et al.* 2021). Kawahara *et al.* (2016) mentioned that fungi from acidic soils occur in a wide range of pH and called them pH generalists; moreover, acid-tolerant fungi may predominate and have an important role in the establishment of vegetation in early primary succession.

The total average of glomerospores in the present study reached approximately 2 g^{-1} of soil, which can be considered low. However, other works in succession areas in the Atlantic Forest, recorded an average of 1 to 10 glomerospores g^{-1} of soil (Aidar *et al.* 2004) and 2 to 8 glomerospores g^{-1} of soil (Stürmer *et al.* 2006). In a review paper, Pagano *et al.* (2019) mention that the density of glomerospores in the Atlantic Forest is variable and can reach 20 glomerospores g^{-1} of soil. In others tropical humid forest, in China, the density has ranged from less than one to 25 glomerospores g^{-1} of soil (Zhao *et al.* 2003). This variability can be attributed to different types of soil and diversity of plant species (Pagano *et al.* 2019). Moreover, AMF have different sporulation rates and periods (Oehl *et al.* 2009).

Glomerospore density can be affected by soil attributes (da Silva *et al.* 2017; Vieira *et al.* 2020) and vegetation (Turrini *et al.* 2018). In the present study, soils in areas undergoing initial regeneration were classified as sandy (dos Santos *et al.* 2018), which are generally characterized by low nutrient availability, low water retention capacity and low levels of organic matter (Rocha *et al.* 2021). This type of soil favours sporulation and dissemination of AMF (Aker *et al.* 2022), since it has larger porous spaces, also facilitating soil-root exchange through AMF (Vieira *et al.* 2020). Conversely, soils in areas of late secondary and mature forest may contain higher clay contents, which can negatively affect the propagation of AMF in the environment (Lekberg *et al.* 2007), considering that they are made up of heavier and less porous particles, which makes sporulation difficult (Moebius-Clune *et al.* 2013).

Higher AMF sporulation was recorded in areas of early secondary forest compared to other forest areas. Similar results were recorded in areas of the Atlantic Forest under environmental pressures, such as areas with little restoration time (Bonfim *et al.* 2013), in natural regeneration (Rodrigues 2019) and under different land uses (Oehl *et al.* 2010; Pereira *et al.* 2014). In stressed environments, AMF seek survival, which is reflected in high sporulation rates, as glomerospores are the resistance structures of these fungi (da Silva *et al.* 2006). This demonstrates a greater action of AMF in soils that are in the recovery process (Piotrowski *et al.* 2008), unlike what is observed in conserved areas, with fungi investing more energy in mycelial growth than in glomerospore production, as observed for areas of late and mature secondary forest in the Amazon Forest (Stürmer & Siqueira 2011).

The 29 AMF taxa identified at the species level in field samples and trap cultures correspond to 18% of the recorded taxa (153) in the Atlantic Forest (Maia *et al.* 2020) and to 8% of all species described (343) in the phylum Glomeromycota (Wijayawardene *et al.* 2022). A similar number of taxa was also recorded in successional areas in the Amazon (Reyes *et al.* 2019) and in Chile (Castillo *et al.* 2006), but differed from that observed in other studies in natural areas and in succession in the Atlantic Forest, where in some cases it was higher (Aidar *et al.* 2004; Bonfim *et al.* 2013) and in others it was lower (Rodrigues *et al.* 2021).

Glomus and *Acaulospora* were the most representative genera in the studied places, together representing 48% of the registered taxa. The dominance of these genera has also been observed in other successional environments in the Atlantic Forest (Aidar *et al.* 2004; Stürmer *et al.* 2006), in the Brazilian Amazon (Reyes *et al.* 2019) and in a tropical forest in Chile (Castillo *et al.* 2006). These AMF genera are commonly found in tropical forests around the world (Marinho *et al.* 2018) and are prevalent in natural and modified environments (Oehl *et al.* 2003; Aidar *et al.* 2004; Stürmer *et al.* 2006; Zangaro & Moreira 2010; Pereira *et al.* 2014). The greater number of described species (Wijayawardene *et al.* 2022) and the characteristics of these two genera, such as high sporulation, adaptation to environmental stresses and use of different propagules to colonize the hosts, allow the occurrence of *Acaulospora* and *Glomus* species in several environments (Hart & Reader 2002; Chagnon *et al.* 2013).

Among the most frequent species found in the studied areas, *Glomus macrocarpum* has cosmopolitan distribution (Stürmer *et al.* 2018), occurring in successional environments, under different land uses and agrosystems (Pereira *et al.* 2014; Sousa *et al.* 2014; Pontes *et al.* 2017; Reyes *et al.* 2019). *Glomus brohultii* has been commonly

found in natural and regenerating areas in the Atlantic Forest (Pereira *et al.* 2018; Rodrigues *et al.* 2021), as well as *Glomus glomerulatum,* recorded also in successional areas in the Amazon (Santos *et al.* 2018; Reyes *et al.* 2019). *Glomus australe* was found in natural areas in the Atlantic Forest and in areas under different uses in the Amazon (Stürmer & Siqueira 2011; Jobim *et al.* 2018). *Dominikia aurea,* other member of Glomeraceae, has been recorded in areas with different uses in the Atlantic Forest and the Brazilian Cerrado (Jobim *et al.* 2018; Vieira *et al.* 2019).

The species of *Acaulospora* identified in all three forest types have a worldwide distribution (da Silva *et al.* 2022). In Brazil, *Acaulospora foveata* has been registered in several ecosystems (de Souza *et al.* 2010; Bonfim *et al.* 2016; Maia *et al.* 2020); *A. longula* is found in tropical forests in South America and also in regenerating environments in the Atlantic Forest (Castillo *et al.* 2006; Zangaro *et al.* 2013); *A. mellea* occurs both in natural and pasture areas, in the Atlantic Forest (da Silva *et al.* 2016; de Cristo *et al.* 2018) and in revegetated areas in the Amazon (Caproni *et al.* 2003); *A. morrowiae* is frequently found in successional environments in the Atlantic Forest and other humid tropical forests (Lovelock *et al.* 2003; Stürmer *et al.* 2006; Zangaro *et al.* 2013).

A large number of species (14) was classified as exclusive to the mature secondary forest in the present study. According to the moderate microbial endemicity model, not all microorganisms have a cosmopolitan distribution, with a fraction having a more restricted distribution, even in suitable environments (Foissner 2008). As pointed out by Foissner (2006), information on the distribution patterns of microorganism species is limited by the scarcity of taxonomists, failures in species identification and insufficient sampling, with many areas not yet studied. In the case of the AMF, Stürmer *et al.* (2018) observed evidence of endemism for some species when describing large-scale distribution patterns. This observation supports the hypothesis of moderate endemicity, with some taxa being recorded on only one continent. Reyes *et al.* (2019) attributed the differences in AMF taxa composition alongside plant succession in Amazonia to this more restricted distribution of certain species.

The presence of exclusive species also suggests a great affinity of these fungi for specific habitats (Carvalho *et al.* 2012). Mature forests are known to have greater stability and less competition of AMF for specific niches (Scoriza *et al.* 2016), representing important reservoirs of AMF species adapted to local environmental conditions (Belay *et al.* 2020). Therefore, it is essential to conserve natural environments such as the Atlantic Forest which are constantly threatened by human activities.

Although there were no significant differences in AMF richness in the studied forests, the highest absolute number of species was recorded in mature forest areas (26 species), with 18 and 17 species respectively in areas of late and early secondary forests. Similar data were recorded by Bonfim *et al.* (2013), with greater AMF richness in native areas of Atlantic Forest than in areas in restoration gradients. On the other hand, in another study, greater AMF richness was recorded in areas under regeneration than in natural ecosystems; areas subjected to stress, with a history of environmental degradation (crop and fire) may favour the sporulation of a greater number of AMF species (Rodrigues *et al.* 2021).

The hypothesis that greater AMF diversity would be found in mature areas than in initial succession was refuted, once that there was no significant difference for this ecological measure between these two stages. It was observed, however, that among the three areas the diversity was lower in the areas of late succession. Zhang *et al.* (2021) recorded greater AMF diversity in mature forests, associating the phenomenon with greater plant diversity in these forests. Taking into account that the Shannon-Weaver index uses the richness and abundance of individuals per species, the diversity was certainly influenced by the greater abundance of AMF species in the areas of early secondary forest. The same was observed in other studies, where areas under environmental stress showed greater AMF diversity (Pereira *et al.* 2014; Yang *et al.* 2021). Santos *et al.* (2018) reported that in tropical dry forest with different successional stages, the area in initial regeneration showed higher production of propagules, which also reflected in greater diversity of AMF species. Sporulation is a survival strategy of AMF which is more intense in stress situations.

The AMF species accumulation curve did not reach the maximum stabilization point, but it did recover 70% of the predicted species for the study areas. As the morphological identification counts only the glomerospores to estimate the richness, the species that were in the non-sporulating phase are underestimated (Bartz *et al.* 2008). Other studies based on morphological identification were able to access similar or higher percentages of estimated AMF species richness, between 70% and 77% in natural and cultivated areas (Pereira *et al.* 2014), However, there are also reports of higher percentages: 80% of the estimated species in tropical coastal dunes (da Silva *et al.* 2015b), 82% in natural and regenerating areas (Rodrigues *et al.* 2021), between 85% and 93% in protected areas of the Atlantic Forest (Pereira *et al.* 2018), and 98% in sandy coastal plain ecosystems of the Atlantic forest (da Silva *et al.* 2017). This variation in the number of taxa is directly linked to the sampling effort. Therefore, accumulation curves are useful to assess how much samples were sufficient to characterize AMF communities in the studied areas (Hart *et al.* 2015).

With the trap cultures it was possible to add three more taxa, which constitute species distinct from those observed directly in the field samples: one at a specific level (*Acaulospora scrobiculata*) and two at a genus level: *Dominikia* sp. 2 and *Glomus* sp. 4, recorded in the areas of early, mature and late secondary forest. *Acaulospora*

scrobiculata is one of the most widely distributed (da Silva *et al*. 2022), being recorded in natural environments, pastures and plant succession, as well as in degraded environments (Bonfim *et al*. 2016; Reyes *et al*. 2019; de Jesus *et al*. 2020; Maia *et al*. 2020). Trap cultures provide complementary information on the richness of AMF communities, and viable fungal structures for taxonomic identification (Leal *et al*. 2018). Ecological studies using this bioassay have been successful in identifying species that were not sporulating during field collections (Säle *et al*. 2015; de Assis *et al*. 2016; dos Passos *et al*. 2021).

The analysis of indicator species selected taxa for all areas, demonstrating that the characteristics of each location favored the distribution of AMF in different successional stages. This type of analysis considers the relative abundance and relative frequency of species. Of the indicator species, most belong to the genus *Glomus*, characterized as ruderal, with a high growth rate and early production of glomerospores (Chagnon *et al*. 2013). In addition, their representatives are fast colonizers in successive environments (de León *et al*. 2016), being well represented in disturbed environments (Jefwa *et al*. 2012; Soka & Ritchie 2018). Two *Glomus* species were indicators of mature forest areas: *Glomus microcarpum* and *Glomus sp. 1*. Species of *Glomus* have been reported in natural and disturbed areas (Pereira *et al*. 2018; Maia *et al*. 2020; Rodrigues *et al*. 2021). *Glomus microcarpum*, recorded as an indicator for mature forest areas, is commonly found in natural areas in the Atlantic Forest (Zangaro *et al*. 2013; da Silva *et al*. 2015a) and was also selected as an indicator in maritime dunes, in the Atlantic Forest (de Assis *et al*. 2016).

Acaulospora mellea, the only one of the genus *Acaulospora* indicated for areas of early and mature secondary forest was also an indicator for other regenerating areas in the Atlantic Forest (Rodrigues *et al*. 2021). Species of *Acaulospora* are prevalent in early stages of revegetation (Caproni *et al*. 2018) and also in tropical rainforest (Lovelock *et al*. 2003). Species of this genus support acidic soils, as in tropical forests, and show resilience to environmental disturbances (Hart & Reader 2002; Winagraski *et al*. 2019). As recorded for *A. mellea*, an acaulosporoid species, this type of spore formation was found to be an indicator for areas of early secondary forest and mature forest. Acaulosporoid AMF species require lower nutritional demands from their hosts, which may be useful in more stabilized environments (Gehring & Whitham 2002) and are also prevalent in disturbed environments, with mycelium resistant to soil mechanical disturbances (Chagnon *et al*. 2013; van der Heyde *et al*. 2017). Therefore, they are well adapted to the regenerating areas of the present study, where soils are acidic, and this characteristic may have been decisive for the selection, as an indicator, of species with this type of glomerospore formation, since they are well adapted to pH ranging between 4 and 6 (Oehl *et al*. 2011).

Orbispora pernambucana, an indicator of areas of early secondary forest, was also indicator of succession areas in the Amazon (Reyes *et al*. 2019) and in natural areas of the Atlantic Forest (Pereira *et al*. 2014). The presence of this species in areas of early secondary forest may reflect greater availability of nutrients for plants at this stage, due to the investment in extraradical mycelium characteristic of the Gigasporales group, to which it belongs (Chagnon *et al*. 2013). The presence of indicator species reinforces the importance of preserving natural environments (Álvarez-Lopeztello *et al*. 2019) and supports the use of AMF species adapted to different ecosystems as bioinoculants in the production of seedlings for the restoration of degraded areas (Robinson-Boyer *et al*. 2009; Pedone-Bonfim *et al*. 2018).

The composition of AMF communities did not differ between the initial and mature areas, as also recorded in other areas in initial (20 years) and advanced (50 years) regeneration of the Atlantic Forest (Morales-Londoño *et al*. 2019). Likewise, Bi *et al*. (2021) did not find differences between areas with five and 15 years of recovery in a tropical forest in China. Teixeira *et al*. (2020) reported that in 25-50 years areas in recovery can reach the characteristics found in primary forests. This might explain why the initial and mature secondary forests did not differ in relation to the composition of AMF communities in the studied forests, but it is not clear why those of late secondary forests differed from the other two forests.

Vegetation can influence the composition of AMF communities over time as the nutrient requirements of plants at each successional stage may vary, with plant species at the beginning of regeneration needing rapid nutrient acquisition to supply the high growth rate and metabolic demand, unlike plants in more advanced stages (Zangaro *et al*. 2003). This would justify the greater need for mycorrhizal association in this initial period of regeneration. On the other hand, the species composition of AMF can vary depending on the group of associated plants, as in the case of woody or grassy plants (Davison *et al*. 2020).

The vegetation in the studied areas differs in terms of the most frequent species, characterizing a succession process. Thus, in the areas of early secondary forest, the most frequent tree species are members of Anacardiaceae, Araliaceae, Chrysobalanaceae and Myrtaceae; in late secondary forest are more commonly found species of Melastomataceae and Fabaceae, while in the mature forest also predominate species of Fabaceae and Melastomataceae, together with species of Lecythidaceae, Anacardiaceae, and Moraceae (Braga *et al*. 2021). AMF are successful inoculants of species of the Myrtaceae family (Lattuada *et al*. 2019), and there are also reports of benefits promoted by AMF in species of Moraceae (Mazzoni-Viveiros & Trufem 2004), in addition to species of Fabaceae, family known to be highly mycotrophic (Ghosh & Dutta 2016). Probably the differences in vegetation composition are influencing the AMF communities in the studied areas, as reported by other authors (Zangaro *et al*. 2003; Davison *et al*. 2020).

Conclusions

From this study it was possible to expand our knowledge about the diversity and composition of AMF species in secondary forests of the Atlantic Rainforest.

The plants in the initial secondary forest are more susceptible and probably more benefited by AM symbiosis compared to those in the other areas.

A high number of exclusive AMF species in the mature forest indicate that it harbours a unique set of species well adapted to the stable condition of this type of forest.

The composition of AMF communities is influenced by different successional stages and by physical and chemical properties of the soil, notably coarse sand, silt, fine sand, phosphorus, pH and base saturation.

The detection of some species of AMF as indicators of regenerating forests shows that they are more adapted to these environments and may be promising for use in future environmental restoration projects in the studied areas.

The first hypothesis raised, that mature forest areas have a greater diversity of AMF species than the initial secondary forest was refuted because the diversity index did not differ between the two areas. The second hypothesis that in areas of early secondary forest there is a greater abundance of AMF propagules that have a ruderal life strategy, characterized by high production of glomerospores was confirmed. The three most abundant species (*Glomus brohultii, G. macrocarpum* and *Dominikia aurea*) are characterized by glomoid formation.

This study reinforces the potential of the Atlantic Forest to harbour a great diversity of AMF, mainly exclusive species and the need for *in situ* preservation of this group of fungi to guarantee the stability of forest ecosystems.

Acknowledgments

Thanks are due to: Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for providing a Post-Doctorate fellowship (Proc.88887.337977/2019-00) to DMA, the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for grant support and a fellowship (Proc. 306.880/2020-2, 420.129/2018-9, and 441.578/2020-9) provided to LCM, Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco (FACEPE) that provided a Master scholarship to JAS (IBPG-0075-2.03/20), a research grant to LCM (APQ-0392-2.03/21) and a Visiting Professor grant to FO (APV-0014-2.03/19). We also thank the Dois Irmãos State Park (PEDI) administration for research permission and the PPBio Mata Atlântica Program (PPBio-MA) for allowing the use of data related with characterization of the studied area. Special thanks are due to Dr. Ana Carolina Borges Lins e Silva (UFRPE) for her support.

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