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Species diversity of Glomeromycota in Brazilian biomes

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Brazil is a megadiverse country, with around 20 % of all known biodiversity in the world. This diversity is distributed in six major biomes that present different floristic characteristics. These environments suffer constant threats, and the knowledge about their communities is essential for conservation. Among the soil organisms, the arbuscular mycorrhizal fungi (AMF – Glomeromycota) play a fundamental role in maintaining plant communities and are distributed in manifold environments, symbiotically associated to most terrestrial plants. The present synthesis brings the Brazilian records of 192 AMF species, belonging to 38 genera and 15 families, which represents circa 60 % of all diversity known in Glomeromycota. Most of the records of AMF species are in the Atlantic rainforest (153 species), Cerrado savanna (140), Caatinga dry forest (120) and the Amazon rainforest (97 species). Pantanal and Pampa so far have 19 and five AMF species, respectively. In general, Brazilian biomes harbor high AMF species richness, constituting an important repository of Glomeromycota taxa. The conservation of these areas is necessary to ensure the permanence of the native plant communities and associated fungi. Likewise, the importance of AMF diversity studies has to be emphasized, considering that these microorganisms are essential elements for the conservation of terrestrial environments and the survival of many threatened plant species.

Kew words: Amazon rainforest, Atlantic rainforest, biodiversity, Caatinga, Cerrado.

Brazil, with an area of 8.5 million of km^2, contains six biomes, namely the Amazon rainforest, Atlantic rainforest, Cerrado, Caatinga, Pampa and Pantanal (Tab. 1, Fig. 1). Two of them, the Atlantic rainforest and the Cerrado, are considered as biodiversity hotspots (Myers et al. 2000, MMA 2019) and the Amazon rainforest harbors 10 to 15 % of all land biodiversity (Lewinsohn & Prado 2002).

The Amazonian is the largest rainforest in the world and the largest Brazilian biome, covering approximately 4.2 million km^2, almost 50 % of the country (IBGE 2004, MMA 2010). As described by Pires & Prance (1985) "the Amazon region is a physiographic and biological entity, which is well defined and distinct from most of the South America by its dense forest and large biomass". Although physiognomically uniform, this forest presents local variations of vegetation and floristic composition. The ecological importance of the Amazon is indisputable (Lewinsohn & Prado 2002). According to Gibbs et al. (2007) it stores 150 to 200 billion tons of carbon. However, the forest has been explored for wood extraction and intensification of agriculture. According to the Brazilian National Institute of Spatial Research, 700,000 km^2 of the Brazilian Amazon were already deforested (INPE, 2019).

The Atlantic rainforest extends along the coast of Brazil (3° S to 30° S), covering more than 1.1 million km^2. It shows longitudinal (35°W to 60°W) and altitudinal (0–2,900 m a.s.l.) variation, and it is established in various climatic zones, which guarantee intense changes in the average air temperature and soil types, providing the biome with great biological diversity, with many rare and endemic species (MMA 2010, Ribeiro et al. 2011). It comprises a variety of forest formations and associated ecosystems, such as mangle, restingas, altitude forests, inland swamps, northeastern forest enclaves, and oceanic islands (IBGE 2004, MMA 2007). Recent research estimates that the Atlantic rainforest has a vegetation cover of about 0.32 million km^2, which corresponds to 28 % of the remaining vegetation (Rezende et al. 2018). Despite the intense devastation and indiscriminate deforestation caused mainly by urbanization, industrialization, and agricultural expansion, this biome presents high species

Tab. 1: Characterization of areas of occurrence of Arbuscular Mycorrhizal Fungi in Brazilian biomes.

Biomes*/area size (km^2)	Areas	
	Undisturbed	Disturbed
Amazon rainforest 4.196.943	Dense Ombrophilous Forest	Experimental field, agroforest, agrosystem, regenerating area, mined areas, pasture
Atlantic rainforest 1.110.182	Dense Ombrophilous Forest, Semidecidual Seasonal Forest, Restingas, Araucária Forest, Montana Forest, Brejos de altitude, Oceanic Islands and Mangrove.	Agrosystems, experimental field, recovering area, mined area
Cerrado 2.036.448	Rupestrian fields, Murundu fields, Decidual Seasonal Forest, Cerrado sensu stricto, Gallery Forest, Altitude Cerrado	Experimental field, agrosystem, mined area, revegetated area, pasture and livestock areas
Caatinga 844.453	Dense Arboreal Caatinga, Deciduous Forest, Carrasco, Inselbergs and River dunes	Agrosystem, recovering area, mined area
Pantanal 150.355	Semideciduous Forest, Cerradão, Campo Limpo, Campo Cerrado, Edge of bays, and Lowlands	–
Pampa 176.496	Grassland	Agrosystem

Source: IBGE 2004

Fig. 1. Map of distribution of Brazilian biomes. Source: IBGE 2004 (adapted)

richness due to its extremely heterogeneous composition, generating the right conditions for the development of highly rich plant and animal biotic clusters (Rezende et al. 2018). Myers et al. (2000) ranked the Atlantic rainforest among the top five biodiversity hotspots due to its species richness and high levels of endemism that are continually in danger.

Characterized as the largest savanna in the Americas and the most species-rich in the world, the Cerrado constitutes the second largest tropical biome in South America, extending from North Eastern and South Eastern Brazil up to Paraguay and Bolivia, and covering about 2.0 million km^2. It borders the Amazonian rainforest in the North and Atlantic Rainforest fragments in the East, with large transition areas also with the Caatinga in the Northeastern and the Pantanal in the Southwestern of Brazil (IBGE 2004, MMA 2010). The Cerrado contains 5 % of the world's and 30 % of the Brazilian flora and fauna (Myers et al. 2000, Françoso et al. 2015), but data on fungi are scarce (de Pontes et al. 2017a). The vegetation is characteristic and, as described by Eiten (1972): "the trees and shrubs almost always have thick bark (especially as contrasted with the thin bark of the mesophytic forests) and also twisted limbs and trunks, especially where fires are frequent". Due to its high species richness and elevated degree of endemism, this biome has been considered as a world centre of biodiversity (Myers et al. 2000). However, the Cerrado is highly endangered by the deforestation produced by expansion of modern agriculture and livestock (Carranza et al. 2014). More than 65 % of the biome is already lost in favour of high agricultural (especially soybean and eucalyptus), and cattle production (WWF 2019a).

The Caatinga is a unique dry forest savanna in Northeastern Brazil. It is the largest seasonally dry

tropical forest (ca. 0.85 million km^2), presents the richest biota among the dry forests of South America and appears in several biogeographic analyses as an important area of endemism for various groups of organisms (Pennington et al. 2000, WWF 2019b). The xeromorphic vegetation is typical of this Brazilian savanna forest, with diverse physiognomies and habitat heterogeneity going from dense grassland to almost closed woodland of 12–15 m height, to rocky outcrops with sparse low shrubs (Sampaio 1995). The Caatinga flora exhibit adaptive mechanisms, such as thorns, small leaves, and some xerophytic features to alleviate water stress that are related to environmental conditions reflecting particular characteristics of the biome. These include a warm (24–26 °C), semi-arid climate with low (250–1000 mm per year) and irregular rainfall, with absence of rain during a few years in some areas, low relative humidity, high evaporation, solar radiation and average temperature (Nimer 1979, Tabarelli & Silva 2003).

The Pampa biome is located in the extreme south of Brazil towards Argentina and Uruguay, and extends over an area of ca. 0.18 million km^2 (Tab. 1). It is characterized by a humid subtropical to temperate climate, with extensive plains covered by grassy vegetation, and presence of tree strata, riparian forests, slope forests, shrub formations and rocky outcrops (IBGE 2004, MMA 2010). Analysis of 2009 showed that 64.2 % of its native vegetation has been lost, mainly due to the intensification of agricultural activity and pasture uses (IBAMA 2011).

Pantanal is a particular biome that occurs as an open forest in the Brazilian Midwest, between the Amazon rainforest and the Cerrado. This Brazilian wetland is located in the hydrographical basin of the Upper Paraguay River (80–190 m above sea level), and presents elements from the Amazon rainforest in its Northwest, the tropical Cerrado savanna in the East, the steppic Chaco savanna in the Southwest and, patchy, even elements from the Atlantic rainforest (Pott & Pott 2004). Besides its unique characteristics and biodiversity, as one of the largest freshwater wetlands on Earth, covering 0.15 million km^2 of the Brazilian territory (MMA 2010), the Pantanal is also subject to anthropic impact. Several changes of its vegetation cover have been registered (Miranda et al. 2018). These affect the climatic-hydrologic dynamics of the Pantanal and, as a consequence, its biological diversity.

Due to the high species richness in the Brazilian biomes, the country is considered mega-biodiverse, concentrating about 20 % of the total number of species found in the planet, with 118,000 species of animals and 47,000 species of algae, fungi and plants (ICMBIO 2019). Although the importance of these biomes is recognized for the conservation of biological diversity on the planet, these areas suffer intense environmental devastation and are subject to multiple pressures, such as forest fragmentation, conversion to agriculture, climate change and consequent loss of biodiversity (MMA 2019). Therefore, it is essential to know the biological communities that occur in these places, especially of the organisms that help in the maintenance of ecological processes indispensable for the stabilization of terrestrial ecosystems.

One of these groups are the arbuscular mycorrhizal fungi (AMF, Glomeromycota), obligate biotrophic organisms that form a mutualistic symbiosis with plant roots, transferring nutrients from the soil to the host plant and receiving carbohydrates and lipids from the plant (Smith & Read 2008, Luginbuehl et al. 2017). These fungi play a key role in ecosystems and plant diversity, as they have the ability to induce multiple responses in the development of plant species, affecting the diversity and productivity of multiple terrestrial ecosystems (van der Heidjen et al. 2008). As important components of the edaphic microbiota, the AMF provide a number of nutritional and non-nutritional benefits to plant communities, including increase in plant growth (Gianinazzi et al. 2010), disease tolerance (Jacott et al. 2017), drought tolerance (Frosi et al. 2016), salinity tolerance (Porcel et al. 2012), water absorption ability (Smith & Read 2008), and protection against root pathogens (Sikes 2010). In addition, they contribute to soil quality by maintaining soil structure and stabilizing aggregates through glomalin production (Rillig 2004).

Present in the most diverse terrestrial ecosystems, the AMF are considered cosmopolitan, with occurrences recorded in tropical and temperate forests, deserts and grasslands up to high alpine, nivale and arctic climates (Oehl & Körner 2014, Davison et al. 2015). These fungi apparently have an efficient dispersal range on a global scale, considering the numbers presented by Davison et al. (2015): "93 % of them occur on multiple continents and 34 % on all six continents". The AMF are classified in the phylum Glomeromycota within the subkingdom Mucoromyceta, and distributed in three classes (Archaeosporomycetes, Glomeromycetes and Paraglomeromycetes), five orders (Archaeosporales, Diversisporales, Gigasporales, Glomerales and Paraglomerales; Tedersoo et al. 2018), 16 families and 50 genera, with 326 described species and steadily increasing species numbers (Wijayawardene et al. 2020).

Given the relevant role played by AMF in ecosystem processes and plant communities, this study aimed to inventory the Glomeromycota species in the Brazilian biomes, thus contributing to the knowledge of the distribution of these fungi.

Material and methods

The data are the result of literature review, consulting the databases Scielo, Scopus and Google Academics, and the list of publications is available in the appendix. Most of the research mentions that the identification was based on morphological studies. Only a few studies used molecular analysis for AMF identification. These were not included in the list, but were discussed separately.

In order to characterize the study areas, we considered the forest formations and associated ecosystems that make up each biome (Tab. 1). The areas were classified as 'undisturbed' (U, natural, and without visible human intervention), 'disturbed' (D, under human pressure, including scientific experimental fields, agrosystems, mined areas, and areas subjected to pasture and livestock) and 'lacking information' (L, when information regarding human activity in the area was not provided). The similarity of AMF species among the biomes was determ4ined by the Sorensen' index: S = (2c/a + b) x 100 where, c = number of species common to two biomes (1 and 2), a = number of species in biome 1; b = number of species in biome 2 (Sorensen 1948).

The classification used for Glomeromycota was based on Oehl et al. (2011), including recent updates (e.g. Błaszkowski et al. 2017, Corazon-Guivin et al. 2019) and for the taxonomic organization of classes, order, families and genera we followed Baltruschat et al. (2019) and Wijayawardene et al. (2020).

Results

Based on the literature, we found 192 Glomeromycotean species reported for the Brazilian biomes, considering disturbed and undisturbed areas (Tab. 2). These are distributed in 38 genera: *Acaulospora, Albahypha, Ambispora, Archaeospora, Bulbospora, Cetraspora, Claroideoglomus, Corymbiglomus, Dentiscutata, Diversispora, Dominikia, Entrophospora, Funneliformis, Fuscutata, Gigaspora, Glomus, Halonatospora, Intraornatospora, Kuklospora, Oehlia, Orbispora, Pacispora, Paradentiscutata, Paraglomus, Pervetustus, Quatunica, Racocetra, Redeckera, Rhizoglomus, Sacculospora, Sclerocarpum, Sclerocystis, Scutellospora, Septoglomus, Sieverdingia, Simiglomus, Tricispora* and *Viscospora*. These taxa belong to all three Glomeromycota classes (Archaeosporomycetes, Paraglomeromycetes and Glomeromycetes) and included also all five orders of the phylum (Archaeosporales, Paraglomerales, Diversisporales, Glomerales, and Gigasporales). They are classified in 15 of the 16 known families (Fig. 2), in decreasing order on number of species: Glomeraceae (60), Acaulosporaceae (43), Racocetraceae (14), Dentiscutataceae (13), Diversisporaceae (12), Scutellosporaceae (11). Ambisporaceae (=Appendicisporaceae) (7), Archaeosporaceae (3), Entrophosporaceae (7), Gigasporaceae (6), Paraglomeraceae (6), Pacisporaceae (5), Intraornatosporaceae (3), Pervetustaceae (1), and Sacculosporaceae (1).

The representativeness of families varied among the biomes (Fig. 3), with only five recorded in all of them (Acaulosporaceae, Dentiscutataceae, Entrophosporaceae, Gigasporaceae, and Glomeraceae). Three families (Ambisporaceae, Paraglomeraceae, and Racocetraceae) were recorded in five biomes; four (Archaeosporaceae, Diversisporaceae, Pacisporaceae, and Scutellosporaceae) in four biomes; one family (Intraornatosporaceae) was found in three biomes, one (Sacculosporaceae) in two biomes, and only one family (Pervetustaceae) was represented exclusively in one of the Brazilian biomes.

The representativeness of the AMF genera was considered by comparing the number of species in a genus recorded in this study with the total number of species within a genus (Fig. 4). Thirteen genera were 100 % represented considering that all their known species were recorded in the studied biomes. These comprised especially mono- to oligo-specific genera, i.e. *Albahypha, Bulbospora, Halonatospora, Intraornatospora, Oehlia, Paradentiscutata, Pervetustus, Quatunica, Sclerocarpum, Sieverdingia, Simiglomus, Tricispora* and *Viscospora*. Additional seven genera (*Archaeospora, Dentiscutata, Fuscutata, Paraglomus, Racocetra, Scutellospora* and *Sclerocystis*) had 75 % or more of the total species recorded in Brazil. *Acaulospora* (72 %), *Claroideoglomus* and *Gigaspora* (67 %, each), *Ambispora* (64 %), *Funneliformis* (58 %), *Rhizoglomus* (52 %), *Cetraspora* and *Kuklospora* (50%, each) had 50–72% representativeness. On the other hand, *Glomus* (47 %), *Diversispora* (33 %), and *Septoglomus* (33 %) had less than 50 %, and *Dominikia* (23 %), and *Redeckera* (17 %) < 25 % representativeness.

Of the 192 species recorded, 153 species were identified in the Atlantic Rainforest, 140 in Cerrado, 120 in Caatinga, 97 in the Amazon Rainforest, 19 in the Pantanal and only five in the Pampa. Sixty-one species were recorded in four biomes, while 34 were

Tab. 2. Arbuscular Mycorrhizal Fungi reported in Brazilian biomes (U = undisturbed; D = disturbed; L = lacking information). *AMF species described from Brazilian soils.

AMF	Amazon rainforest	Cerrado	Atlantic rainforest	Caatinga	Pampa	Pantanal
Archeosporomycetes						
Archaeosporales						
Ambisporaceae						
Ambispora						
A. appendicula	U[26,47], D[47], L[44,51]	U[9,29,63,64], D[21,29,63]	U[5,6,10,14,15,17,18,30,45,52,58], D[10,13,14,45,52,53]	U[17,18,20,28,34,43,50], D[28,34,36], L[44]	–	–
*A. brasiliensis**	L[44]	U[9,29]	U[46]	–	–	–
A. callosa	–	U[9,29], D[29]	–	L[44]	–	–
A. fecundispora	–	U[29]	U[30]	–	–	–
A. gerdemannii	L[44,51]	U[29]	U[6,30]	U[50], D[19], L[44]	–	–
A. jimgerdemanni	–	–	U[30,40], D[40,45]	D[28], L[44]	–	–
A. leptoticha	U[57], D[3,32,57], L[44,51]	U[1,2,7,29,60], D[1,2,7,8,60,62]	U[16,30,42,48], D[42,48]	U[28], D[28], L[44]	–	U[27]
Archaeosporaceae						
Archaeospora						
A. myriocarpa	–	U[21,29], D[29]	U[30], L[44]	–	–	–
A. trappei	U[26,57], D[32,57], L[44,51,56]	U[21,59,60,62,64], D[21,29,62]	U[30,45], D[65]	D[19,20,28], L[44]	–	–
A. undulata	L[44,56]	D[2,21]	U[49]	–	–	–
Glomeromycetes						
Diversisporales						
Acaulosporaceae						
Acaulospora						
A. alpina	–	D[60]	–	–	–	–
A. baetica	–	U[62], D[62]	–	–	–	–
A. bireticulata	D[32], L[44,56]	U[9], L[44]	U[30,40], D[40],L[44]	U[11,43], D[28], L[44]	–	–
A. capsicula	–	U[24]	–	–	–	–
A. cavernata	–	U[2,7,8,29], D[8,24], L[44]	U[30,58]	U[18,33]	–	–
A. colossica	–	U[9,29], L[44]	U[5,30,65], D[65], L[44]	–	–	–
A. delicate	U[32,57], D[32, 47,57], L[44,56]	U[9,29,64], L[44]	U[65], D[65], L[30,44]	U[11,28,34,43], D[28], L[44]	–	–
A. denticulata	D[41]	U[2,9,29], D[2,7,21,24], L[44]	U[30], L[44]	U[28,50], D[19,34], L[44,54]	–	–
A. dilatata	–	D[29]	–	L[44]	–	–
A. elegans	D[47,57], L[44]	–	U[30], D[45], L[44]	D[28,36]	–	–
*A. endographis**	–	–	U[30], D[45], L[44]	–	–	–

AMF	Amazon rainforest	Cerrado	Atlantic rainforest	Caatinga	Pampa	Pantanal
A. entreriana	–	D[8]	–	–	–	–
A. excavata	D[41,57], L[44,51]	U[64], D[1,24,30], L[44]	U[6,30], D[45,53], L[44]	U[18,28,43,50], D[19,20,28, 34,36], L[44]	-	-
A. foveata	U[26,38,57], D[3,32,38,41,47,57], L[44]	U[1,2,7,21,24,29,59,62,63,64], D[2,7,24,29,62]	U[6,10,13,14,16,17,18,30, 40,45,46,48,49,58,65], D[5,10,13,40,42,45,52,53,65], L[44]	U[17,28,34,43,50], D[20,28, 35], L[44]	–	–
A. gedanensis	U[57], D[57]	–	–	U[34]	–	–
*A. herrerae**	–	U[29,60], D[8,29,60]	U[15,30], D[13]	U[33], D[19], L[44]	–	–
*A. ignota**	–	–	U[30]	–	–	–
A. kentinensis	L[44]	–	L[44]	U[28]	–	–
A. koskei	–	U[9,24,29], D[24,62], L[44]	U[30,65], D[65]	U[28], L[44]	–	–
A. lacunosa	–	U[60,62], D[24,60,62]	U[5,6,17,30], D[5]	U[17,28,33, 34,43,50], D[61], L[44]	–	–
A. laevis	U[57], D[3,38,57], L[44,51,56]	U[7,64], D[21,29,63]	U[6,15,18,30,40,42,48], D[42,48,65], L[44]	U[20,34,43,50], D[28], L[44]	–	–
A. longula	L[44]	U[21,29,63], D[21,29,63], L[44]	U[6,17,30,65], D[45]	U[18,20,28,34,50,61], D[19, 20,28,61], L[44]	–	U[27]
A. mellea	U[26,32,38,47,57], D[3,38,47,57], L[44]	U[1,2,7,9,21,24,29,59,60,62,63,64], D[1,7,8,21,24,29,39,60,62,63] L[44]	U [5,6,13,14,15,17,18,30,40,45,49 ,65], D[5,10,13,14,45,48,65]	U[11,17,18,20,28,34,43,50, 61], D[20,28,36,34,61], L[44]	–	U[27]
A. minuta	–	–	U[18]	U[11,20], D[20]	–	–
A. morrowiae	U[26,47], D[32, 41,47,57], L[44,51]	U[9,21,29,60,62,63,64], D[8,21,24,29,39,60,62,63]	U[6,13,14,17,18,30,52,58,65], D[10,13,45,52,53,65]	U[11,17,18,28,33,34,50,61], D[28,36,34], L[44]	–	U[27]
A. nivalis	–	D[60]	–	–	–	–
*A. papillosa**	–	–	U[30]	–	–	–
A. paulinae	D[57], L[44]	U[24], L[44]	–	–	–	–
A. polonica	D[57], L[44]	–	–	–	–	–
A. punctata	L[44]	U[62], D[62]	–	–	–	–
*A. reducta**	D[47]	U[29], D[21]	U[15,30,46]	U[18], D[20], L[44]	–	–
A. rehmii	U[26], D[3,32,41,47,57], L[44,51]	U[2,24,29], D[2,7,24,29]	U[10,18,30,46,49,58], D[65]	U[28,43,50], D[19,28,36], L[44]	–	–
A. rugosa	–	U[9,29], D[24]	U[30,65], D[65], L[44]	U[33]	–	–
A. scrobiculata	U[38,57], D[3,32,38,41,47,57], L[44,51,56]	U[1,2,7,9,21,24,29,59,62], D[1,2,7,8,21,24,37,39,59,60,62], L[44]	U[5,6,10,13,15,16,17,18,30,40, 45,48,49,58,65], D[5,10,13,14, 40,42,45,48,52,53,55,65]	U[11,17,18,20,28,34,43], D[20,28,34,36,61], L[44]	D[35]	U[27]
A. sieverdingii	–	D[21]	U[10,18,30], D[10,13]	U[11,34,50], D[19,20,34], L[44]	–	–
A. spinosa	U[57], D[32,47,57], L[44,51,56]	U[9,21,24,29,60], D[21,24,29,60]	U[6,13,15,16,17,18,30,40,46,65], D[5,10,13,40,45,48,53,65]	U[11,18,28,33,43,50], D[20, 28], L[44]	–	U[27]
A. spinosissima	–	D[21,62]	U[6,15,17,18,30]	U[6,15,17,18,30]	–	–
*A. spinulifera**	–	U[22], D[22]	U[30]	–	–	–

AMF	Amazon rainforest	Cerrado	Atlantic rainforest	Caatinga	Pampa	Pantanal
A. splendida	–	–	L[30]	U[11]	–	–
A. sporocarpia	D[3]	–	–	–	–	–
A. tuberculata	U[56], D[3,32,38,57], L[44,51,56]	U[2,24,29,62,63], D[2,7,21,24,60,62,63]	U[6,10,13,16,18,30,49,65], D[10,13,45,48,52,53,65]	U[28,33,34,43,50], D[28,34], L[44,54]	-	U[27]
A. walkeri	U[57], D[57]	U[59,60,62], D[60,62]	-	-	–	–
Kuklospora						
K. colombiana	U[26,38], D[3,32,38,57], L[44,51]	U[29,59,60,62], D[2,21,29,37,60,62,63]	U[16,30,40,49,65], D[40,52,55,65]	U[11,20,34], D[34],L[44]	–	U[27]
Diversisporaceae						
Corymbiglomus						
C. corymbiforme	U[57], D[57]	–	–	–	–	–
C. globiferum	–	–	U[15,30,58], L[44]	–	–	–
Diversispora						
D. aurantia	–	–	U[18]	–	–	–
D. eburnea	L[44]	U[64], D[21,63]	U[6,15,30]	U[50], D[20],L[44]	–	–
D. insculpta	–	L[44]	L[44]	–	–	–
D. pustulata	L[44]	–	–	–	–	–
D. spurca	D[57]	U[64], D[62]	U[58], D[65], L[30,44]	U[11,28], D[28], L[44]	–	–
D. trimurales	D[57]	–	U[30,58]	–	–	–
D. versiformis	U[26]	–	U[30]	U[20], L[44]	–	–
Redeckera						
R. fulva	–	U[29,60]	U[30], D[65]	–	–	–
Sieverdingia						
S. tortuosa	U[57], D[3,38], L[44,51,56]	U[1,7,64], D[1,2,7,29]	U[18,30,42,48,49], D[42,45,52,53,65]	U[11,28], D[19,20,28], L[44]	–	–
Tricispora						
T. nevadensis	–	D[63]	–	–	–	–
Pacisporaceae						
Pacispora						
P. chimonobambusae	L[56]	–	–	–	–	–
P. dominikii	L[44]	U[29]	–	–	–	–
P. franciscana	–	–	–	U[43], L[44]	–	–
P. robiginia	U[26]	U[62], D[62]	–	–	–	–
P. scintillans	–	U[29], L[44]	L[30]	–	–	–
Sacculosporaceae						
Sacculospora						

AMF	Amazon rainforest	Cerrado	Atlantic rainforest	Caatinga	Pampa	Pantanal
S. baltica	L[44]	–	U[30]	–	–	–
Gigasporales						
Dentiscutataceae						
Dentiscutata						
D. biornata	D[57]	U[9,29,59,62], D[8,29,59,62]	U[30,52], D[52]	U[28,34,50], D[28,43], L[43]	-	U[27]
*D. cerradensis**	U[26]	U[21,24,29,63,64], D[21,24,37,39]	U[10,15,18,30,46,49,58], D[10,13,45,52,53]	U[20,33,34,50], D[20,28,36], L[44,54]	-	-
*D. colliculosa**	–	–	U[30]	U[18,28], L[44]	-	-
D. hawaiiensis	–	–	U[30,58]	-	-	-
D. heterogama	D[3, 38]	U[1,2,7,29,59,60], D[1,2,7,8,29,39,59], L[44]	U[5,30,40,49], D[5,55]	U[18], L[44,54]	U[35], D[35]	U[27]
D. nigra	–	U[2], D[2,21,29]	U[30]	–	–	–
D. reticulata	–	U[1,2,7,29], D[8]	U[46]	–	–	–
*D. scutata**	U[38,47,57], D[3,38,47], L[44,56]	U[2,7,21,24,59], D[1,2,7,24]	U[16,30,42,46,48,49], D[10,42]	U[28,34,43], D[34,36], L[44]	–	–
Fuscutata						
*F. aurea**	–	D[21]	U[30], D[45]	–	–	–
*F. heterogama**	–	U[9,29], D[21]	U[6,17,30,48,52], D[45,48,52,65]	U[17,18,28,50], D[19,28,33,35]	–	–
*F. rubra**	–	U[9,29], D[21,24]	U[15,17,30], D[53]	U[17,34], D[34], L[44]	–	U[27]
F. savannicola	–	U[62], D[62]	U[30], D[10]	U[34,50], D[34], L[44]	–	–
Quatunica						
Q. erythropa	-	-	U[30]	U[43], D[28], L[44,54]	-	-
Gigasporaceae						
Gigaspora						
G. albida	–	U[24,29,64], D[8,24,62]	U[30,46,58], D[5]	U[20,28,33,34], D[20,28,34], L[44,54]	–	–
G. decipiens	L[56]	U[9,24,29,62,64], D[8,21,24,29,62,63], L[44]	U[5,10,17,18,30,40,46,52,58], D[5,10,45,52,65]	U[11,17,20,28,33,34,43,50], D[28,34,36], L[44,54]	–	–
G. gigantea	–	U[9,21,29,62,63,64], D[2,21,24,29,37,39,62], L[44]	U[10,13,15,17,30,40,45,46,49], D[10,13,14,40,45,65]	U[11,17,18,20,28,33,43,50], D[20,28,34,36], L[44,54]	–	–
G. margarita	U[32], D[47]	U[9,21,24,29,59,63,64], D[21,24,29,37,59,62,63], L[44]	U[6,10,13,14,15,17,18,30,65], D[10,13,14,40,45,65]	U[11,17,18,20,28,34,43,50], D[20,28,34,36], L[44]	U[35], D[35]	U[27]
*G.ramisporophora**	–	D[29]	U[17,30]	U[17,28], D[28], L[44]	–	–
G. rosea	U[26]	U[24,29], D[26]	U[15,17,30], D[5]	U[17], L[28]	–	–
Intraornatosporaceae						
Intraornatospora						
*I. intraornata**	–	U[62,64]	U[5,6,15,17,30,46], D[53]	U[11,34], D[34,36], L[44]	–	–

AMF	Amazon rainforest	Cerrado	Atlantic rainforest	Caatinga	Pampa	Pantanal
Paradentiscutata						
*P. bahiana**	–	U[64], D[29,63]	U[30,46]	U[18,34], D[34]	–	–
*P. maritima**	–	U[64]	U[10,14,15,17,30,46], D[10,13,14,45,53]	U[17,18,50], D[34]	–	–
Racocetraceae						
Cetraspora						
*C. auronigra**	–	U[29], D[63]	L[44]	–	–	–
C. gilmorei	–	U[21,29,63,64], D[29,63], L[44]	U[15,18,30,45,46], D[14]	U[28,34,50], D[34], L[44]	–	–
C. pellucida	U[57], D[3,41,57], L[44,56]	U[2,21,24,29,59,60,62,64], D[2,21,24,29,60,62], L[44]	U[10,30,40,49,58], D[5,14,45,52,53,65]	U[11,18,28,34,50], D[20,28, 34,36,43], L[44]	–	U[27]
Racocetra						
R. alborosea	–	D[21]	D[45]	–	–	–
R. castanea	U[26]	U[64], D[24]	U[10,30], D[10]	D[28]	–	–
R. coralloidea	–	U[29,64], D[21,62]	U[10,15,16,17,30,58], D[10,14,45]	U[11,17,20,34], D[19,28,34], L[44,54]	–	–
*R. crispa**	–	D[23]	–	–	–	–
R. fulgida	–	U[9,29,59,62,64], D[8,21,59,62]	U[6,10,15,16,17,30,45,58], D[10,13,45]	U[17,18,34,43,61], D[19,28,61], L[44]	–	–
R. gregaria	–	D[1,24,37]	U[15,30,58], D[52,53]	U[28,34,43], D[28,36], L[44]	–	U[27]
R. persica	D[57]	U[29], D[29]	U[16,30,58], D[55]	D[28], L[44]	–	–
*R. tropicana**	–	U[21,63,64], D[21,29]	U[6,10,14,30,46], D[10,13,45,52,53]	U[50], D[19]	–	–
R. undulata	–	U[21]	–	U[34]	–	–
*R. verrucosa**	–	U[29,62], D[8,24,29,62]	U[6,10,30,49,65], D[10]	U[28,43,61], D[28,61], L[44]	–	–
R. weresubiae	L[51]	U[59]	U[30,46,58], D[45]	U[28], D[34], L[44]	–	–
Scutellosporaceae						
Bulbospora						
*B. minima**	–	U[21,63,64], D[63]	U[17,30,46]	U[34]	–	–
Orbispora						
*O. pernambucana**	U[47], D[41,47]	U[9,21,29,59,62,63,64], D[8,59,63]	U[6,10,13,17,18,30,45,46], D[13]	U[28,33,34,43], D[34], L[44]	–	–
Scutellospora						
*S. alterata**	–	–	–	U[34,50]	–	–
S. arenicola	U[26], L[44]	–	–	–	–	–
S. aurigloba	–	U[21,29,63,64]	U[6,10,15,17,30,45], D[10,45,52,53]	U[17,28], D[28], L[44]	–	–

AMF	Amazon rainforest	Cerrado	Atlantic rainforest	Caatinga	Pampa	Pantanal
S. calospora	U[26], D[41], L[44,51]	U[9,21,29,63,64], D[8,21,29,63], L[44]	U[6,17,30,40,58,65], D[40]	U[17,18, 28,34,43,50], D[28, 34,36], L[44,54]	–	–
S. dipapillosa	–	U[29], D[29]	L[30,44]	–	–	–
S. dipurpurescens	U[26], L[44]	U[9,29]	U[30], D[52], L[44]	U[28], L[44]	–	–
S. spinosissima	L[44]	U[29,62,63,64], D[62,63]	U[6,46]	U[18]	–	–
S. striata	–	D[62]	–	–	–	–
S. tricalypta	–	U[29]	L[44]	–	–	–
Glomerales						
Entrophosporaceae						
Albahypha						
A. drummondii	U[26], L[44]	–	–	–	–	–
A. walkeri	L[44]	–	–	–	–	–
Claroideoglomus						
C. claroideum	U[26], D[32]	U[21,29], D[21]	U[30,65], D[65]	U[20,34,50], D[20,28], L[44]	–	–
C. etunicatum	U[26], D[38,47], L[44,51]	U[2,7,9,21,24,29,63,64] D[2,7,21,29,37,62,63], L[44]	U[6,10,15,17,30,40,45,46,52,65], D[10,40,52,65]	U[11,17,20,28,33,34,43,50,61], D[19,20,28,61], L[44,54]	U[35], D[35]	U[27]
C. lamellosum	–	U[9,29], D[2]	U[42,48,49,] D[42,48,65]	–	–	–
C. luteum	U[26]	–	U[65,] D[65]	U[20,34,] D[20,] L[44]	–	–
Entrophospora						
E. infrequens	D[32,41,57,] L[44,51]	U[62,] D[29,62]	U[6,15,30,65,] D[65]	U[11,28,43,50,61,] D[19,28,61,] L[44,57]	-	-
Glomeraceae						
Dominikia						
D. aurea	–	U[64]	U[17,18,30]	U[17]	–	–
D. bernensis	–	U[63]	U[18]	-	–	–
D. minuta	U[26]	L[44]	L[44]	L[44]	–	–
Funneliformis						
F. caledonius	–	–	–	L[54]	–	–
F. geosporus	U[26,47], D[47,57], L[44,51]	U[9,21,29], D[2,29], L[44]	U[5,6,10,15,30,65], D[5,65]	U[28,33], D[28], L[44,54]	–	–
F. halonatus	U[47], D[41,47]	U[21]	U[10,13,14,17,18,30,46,52], D[10,13,52]	U[18,28], L[44]	–	–
F. monosporus	–	U[29]	U[30]	D[28]	–	–
F. mosseae	–	U[9,21,29,63,64], D[21,24,29,62], L[44]	U[6,15,17,18,30,45,65], D[45,52,65]	U[11,17,18,20,28,50,61], D[19,20,28,61], L[44,54]	–	–
F. multiforus	–	U[29], D[62]	–	–	–	–

AMF	Amazon rainforest	Cerrado	Atlantic rainforest	Caatinga	Pampa	Pantanal
F. verruculosus	–	L[44]	U[16,48,49]	–	–	–
Glomus						
G. ambisporum	U[47,] D[3,47,57]	U[21,62,] D[21,62]	U[10,15,16,17,18,30,] D[13,14,45]	U[11,28,34,] D[34,] L[44]	–	–
G. arborense	–	–	L[30,44]	D[28,] L[44]	–	–
G. atrouva	L[44]	–	–	–	–	–
G. australe	U[57,] D[57], L[44,56]	–	L[30]	–	–	–
G. badium	L[44]	D[7]	–	–	–	–
G. botryoides	–	–	L[30]	–	–	–
G. brohultii	L[44]	U[21,63,64], D[21,63]	U[10,14,15,17,18,30,45,46], D[10,14]	U[20,34,50], D[20,34,61], L[44]	–	–
G. formosanum	–	U[1], D[1]	U[30]	–	–	–
G. fuegianum	U[26], L[44,56]	U[29,62]	L[44]	–	–	–
G. glomerulatum	U[47,57], D[47,57]	U[9,21,29,63,64], D[21,29,63]	U[13,15,17,18,30,45,46,49,52], D[10,13,14,45,52,53,65]	U[11,17,20,28,35,43,50], D[20,28,34], L[44]	–	–
G. heterosporum	U[26]	U[59], D[39]	U[30]	D[28]	-	-
G. macrocarpum	U[26,38,47,57], D[3,37,47,57], L [44,51,56]	U[1,2,7,9,21,29,63,64], D[1,2,7,21,29,63], L[44]	U[6,13,14,15,16,17,18,40,42,45,48,49,65], D[13,14,40,42,45,48,55,65]	U[11,17,18,20,28,34,43,50,61,] D[20,28,35,61], L[44]	–	–
G. maculosum	–	–	U[30]	–	–	–
G. magnicaule	U[57], L[44,56]	U[60], D[60]	–	–	–	–
G. microcarpum	U[26], D[38], L [44,51]	U[9,21,29,62,63,64], D [21,29,39,63], L[44]	U[13,14,15,17,18,30,40,48,65], D[13,40,48,65]	U[11,17,20,28,34,50,61], D[20,28,34], L[44]	–	–
G. multicaule	–	–	L[30]	U[43], L[44,54]	–	–
G. nanolumen	D[57]	–	U[18]	–	–	–
G. pallidum	–	–	U[30]	D[28], L[44]	–	–
G. reticulatum	–	–	U[30]	–	–	–
G. spinuliferum	–	U[62], D[62]	U[17,30]	–	–	–
G. tenebrosum	U[44]	–	U[30,48], D[48]	–	–	–
G. ¨tenue¨	–	–	U[30]	–	–	–
*G. trufemii**	U[47], D[47]	–	U[6,17,18,30], D[45]	U[20,33,34], D[20], L[44]	–	–
Halonatospora						
H. pansihalos	–	–	U[30]	–	–	–
Oehlia						
O. diaphana	U[26], L[44,51]	U[2,9,21,29,60], D[29], L[44]	U[16,30,65], D[40,65]	U[28], D[28], L[44]	–	U[27]
Rhizoglomus						
R. aggregatum	L[44]	D[39]	U[30,58], D[45]	U[11,20], D[20,28], L[44,54]	–	–

AMF	Amazon rainforest	Cerrado	Atlantic rainforest	Caatinga	Pampa	Pantanal
R. arabicum	–	–	–	D[20], L[44]	–	–
R. clarum	U[32,57], D [32,57], L[44,51]	U[2,7,9,21,29,60,63,64], D[1,2,8,21,29,39,60,62,63], L[44]	U[6,15,16,30,46], D[45,52,65]	U[20,35,50], D[20,28,35], L[44,54]	U[35]D[35]	U[27]
R. fasciculatum	D[3], L[44,51,56]	U[9,29,60], D[29,60], L[44]	U[18,30]	U[28,35,50], D[34], L[44]	–	–
R. intraradices	U[57], D[57], L [44, 56]	U[21,64], D[21,29,63], L[44]	U[15,17,18,30]	U[11, 17,20,28,34,50], D[19,20, 28,34], L[44]	–	U[27]
R. invermaium	D[57], L[44,51]	U[9,29]	U[30,65], D[52,55,65]	U[28], D[28], L[44]	–	–
R. irregulare	–	U[64], D[21]	U[17,30]	U[20,50], D[20], L[44]	–	–
*R. maiae**	–	–	U[4]	–	–	–
R. manihotis	–	U[29], D[37]	L[30,44]	–	–	–
R. microaggregatum	U[57], D[57], L[44,51]	U[9,21,29,60], D[1,8,24,29,39,60,62	U[6,16,30,65], D[65]	U[28,34], D[28,34], L[44]	–	–
*R. natalense**	–	D[21]	U[15,17,30]	U[50]	–	–
R. vesiculiferum	–	–	U[12]	–	–	–
Sclerocystis						
S. coremioides	U[57], D[57]	U[21,29,62], D[21,39]	U[30,45,46], D[45,52,65]	U[11,20,28,35], D[20,28,35], L[44]	–	–
S. clavispora	U[57], D[38,57], L[44,56]	U[2,7,29], D[2,7,29]	U[16,18,30,49,65], D[42,65]	U[28], L[44]	–	–
S. pachycaulis		–	U[30,46]	–	–	–
S. rubiformis	U[26], D[38,57], L[44,56]	–	U[10,30,52]	U[11], L[44]	–	–
S. sinuosa	U[57], D[41,57]	U[21,29]	U[10,14,15,17, 18,30,46,58,65], D[10,13,45,52,65]	U [11,17,18,20,28,34], D[19,20, 28,34,36], L[44]	–	–
S. taiwanensis	U[26], L[44,56]	–	U[30,45,46], D[10,45,52,53]	U[43], D[36], L[44]	–	–
Sclerocarpum						
*S. amazonicum**	U[31]	–	–	–	–	–
Septoglomus						
S. constrictum	–	U[29,63]	U[6,15,30,58,65], D[13,55,65]	U[11,20], D[19,20,28], L[44]	–	–
S. deserticola	–	D[29]	U[16,30]	D[28]	–	–
S. furcatum	–	–	–	U[50]	–	–
*S. titan**	–	D[29]	U[6,30]	U[50], L[44]	–	–
Simiglomus						
S. hoi	–	–	U[65], D[45,65], L[30,44]	–	–	–
Viscospora						
V. viscosa	L[51]	D[60,62]	U[6,30,] D[5]	–	–	–
Paraglomeromycetes						
Paraglomerales						

AMF	Amazon rainforest	Cerrado	Atlantic rainforest	Caatinga	Pampa	Pantanal
Paraglomeraceae						
Paraglomus						
P. albidum	–	U[29], D[29]	U[65], D[65]	U[28]	–	–
P. bolivianum	L[51]	D[39]	U[10,30,45], D[45]	U[61], D[19,61],L[44]	–	–
*P. brasilianum**	L[51]	D[24,29,37]	–	D[28], L[44]	–	–
P. lacteum	U[57], D[57], L[44,56]	–	–	–	–	–
P. occultum	D[32], L[44,51,56]	U[9,21,29,60,64], D[21,29,39], L[44]	U[6,30,65], D[52,55,65]	U[20,28,61], D[28,61], L[44]	–	U[27]
*P. pernambucanum**	–	U[29,64], D[29,63]	U[46]	U[11,20], D[19,20]	–	–
Pervetustaceae						
Pervetustus						
P. simplex	–	U[64]	–	–	–	–

	Amazon rainforest			Cerrado			Atlantic rainforest			Caatinga			Pampa		Pantanal
Research studies	**10**			**16**			**23**			**14**			**1**		**1**
Status+	**U**	**D**	**L**	**U**	**D**	**L**	**U**	**D**	**L**	**U**	**D**	**L**	**U**	**D**	**U**
Total records/area	77	117	113	338	298	32	512	247	34	321	189	112	5	5	19
Exclusive species	**11**			**11**			**15**			**5**			**0**		**0**
Total species/biome	**97**			**140**			**153**			**120**			**5**		**19**
Total species recorded in Brazil	**192**														

Areas were classified as U ('Undisturbed', natural, and without visible human intervention), D ('Disturbed', under human pressure, including scientific experimental fields, agrosystems, mined areas, and areas subjected to pasture and livestock), and L ('Lacking information', when information regarding human activity in the area was not provided). * species described firstly from Brasil.

Appendix

List of consulted references with record of AMF in Brazilian biomes.

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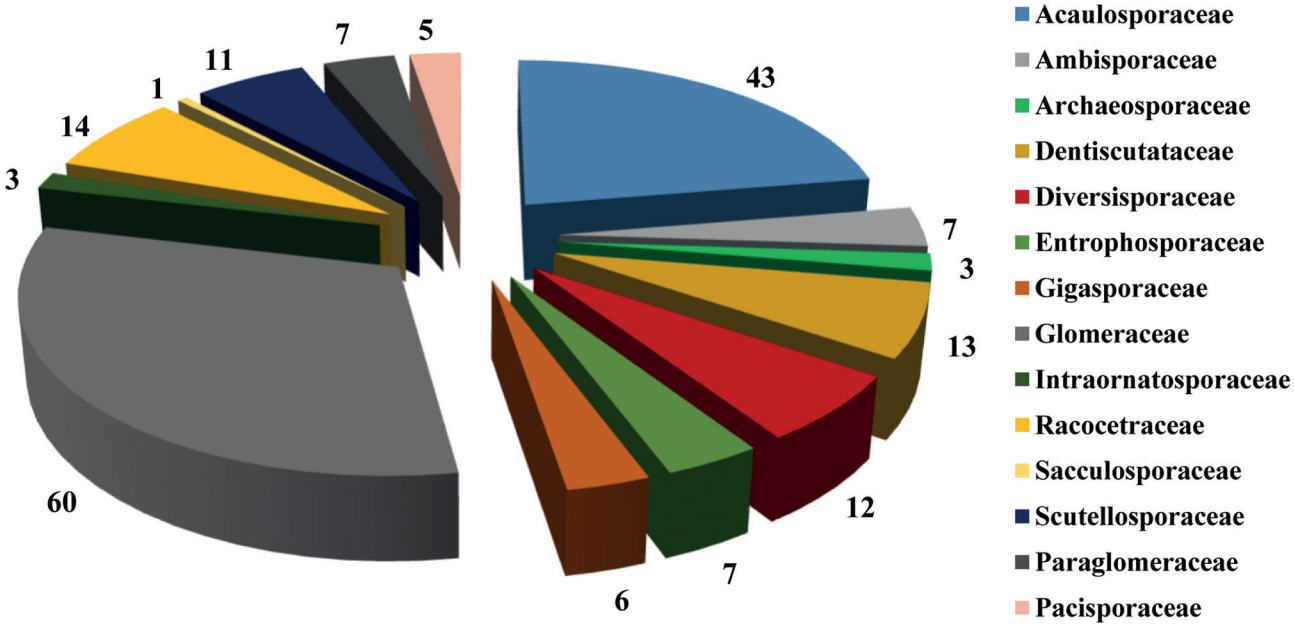

Fig. 2. Representativeness of Glomeromycotean species (AM fungi) by family in all six Brazilian biomes.

only recorded in three of them: Caatinga, Cerrado and Atlantic rainforest (Fig. 5). *Acaulospora* and *Glomus* were the most common genera in number of species (41 and 23 species recorded, respectively) in all biomes, except for the Pantanal and Pampa, where no records of *Glomus* species were found.

The AMF species were distributed irregularly among the biomes, but five of them (*Acaulospora scrobiculata, Claroideoglomus etunicatum, Dentiscutata heterogama, Gigaspora margarita*, and *Rhizoglomus clarum*) were found in all of them showing wide distribution and ability to grow in diverse environmental conditions. Twelve species (*Acaulospora longula, A. mellea, A. morrowiae, A. spinosa, A. tuberculata, Ambispora leptoticha, Cetraspora pellucida, Dentiscutata biornata, Kuklospora colombiana, Oehlia diaphana, Paraglomus occultum*, and *Rhizoglomus intraradices*) are also widely dispersed in Brazil, considering their presence in five of the six biomes.

The following species were recorded only in soils of the Amazon rainforest: *Acaulospora polonica, A. sporocarpia, Albahypha drumondii, A. walkeri, Corymbiglomus corymbiforme, Diversispora pustu-*

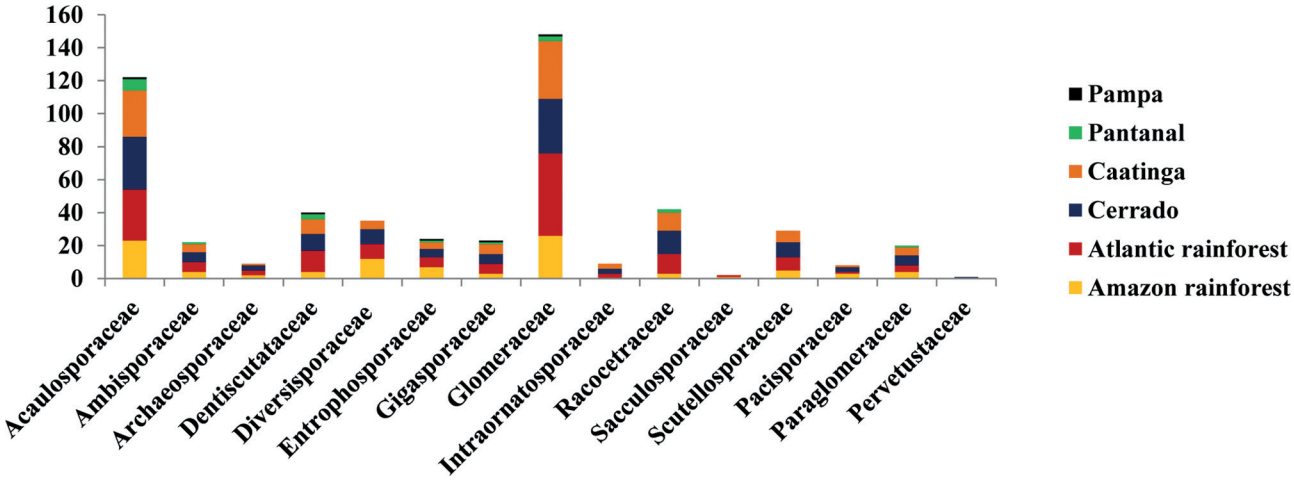

Fig. 3. Number of Glomeromycotean species (AM fungi) per family found in each Brazilian biome.

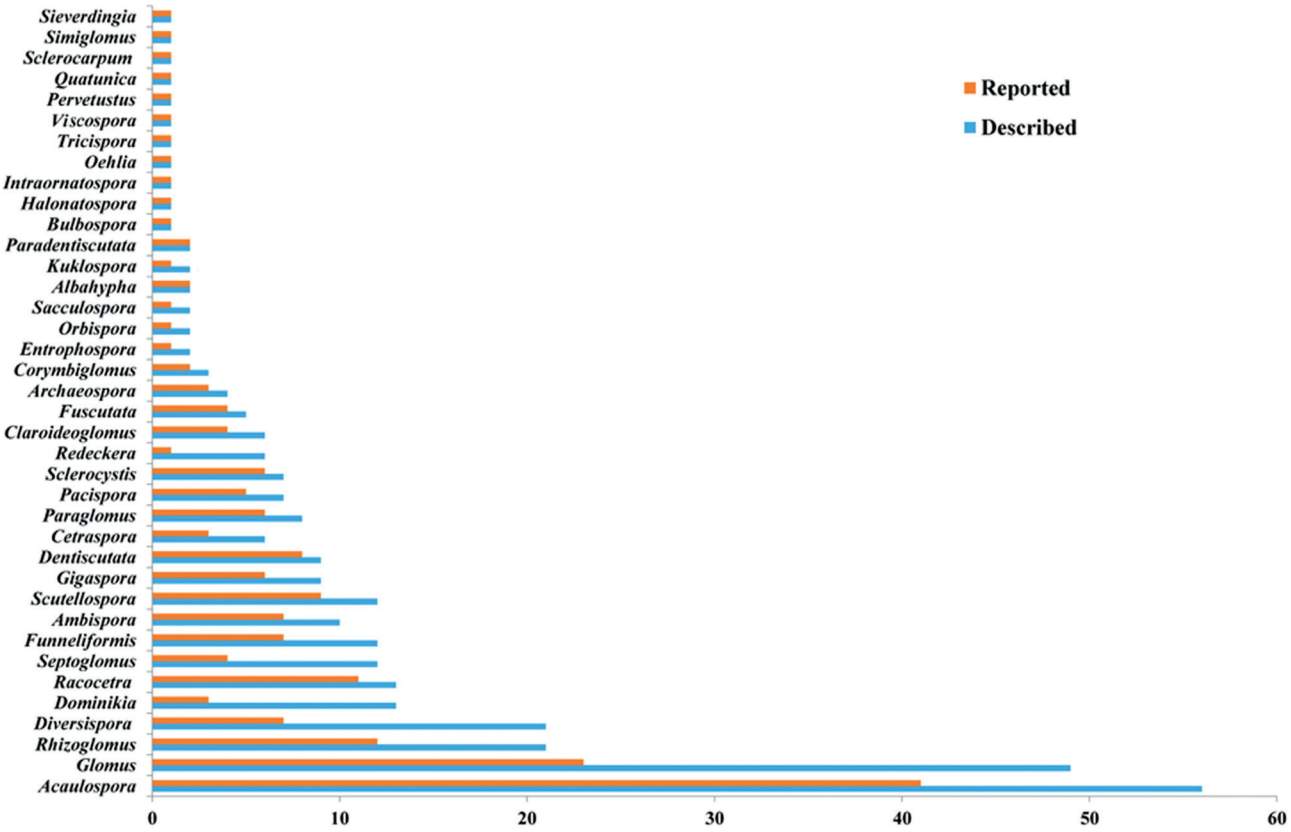

Fig. 4. Number of Glomeromycotean species (AM fungi) per genus worldwide described, and registered in all six Brazilian biomes.

lata, Glomus atrouva, Pacispora chimonobambusae, Paraglomus lacteum, Sclerocarpum amazonicum and *Scutellospora arenicola*. The genera *Albahypha* and *Sclerocarpum* were recorded as exclusive to this biome.

Species of *Halonatospora, Simiglomus* and *Sacculospora* were recorded only in the Atlantic Rainforest. The largest number of exclusive species (15) was also recorded in this biome: *Acaulospora endographis, A. ignota, A. papillosa, Corymbiglomus globiferum, Diversispora aurantia, Dentiscutata hawaiiensis, Glomus botryoides, G. maculosum, G. reticulatum, G. 'tenue', Halonatospora pansihalos, Rhizoglomus vesiculiferum, R. maiae, Sclerocystis pachycaulis* and *Simiglomus hoi*.

The genera *Pervetustus* and *Tricispora* were recorded only in the Cerrado, where *Acaulospora alpina, A. baetica, A. capsicula, A. enteriana, A. nivalis, Funneliformis multiforus, Diversispora insculpta, Pervetustus simplex, Racocetra crispa, Scutellospora striata* and *Tricispora nevadensis* were also exclusive.

Funneliformis caledonius, Pacispora franciscana, Rhizoglomus arabicum, Scutellospora alterata and *Septoglomus furcatum* occurred only in the Caatinga, and no species was exclusive for Pampa and Pantanal.

In the literature, we found 1270 records of 173 AMF species in undisturbed areas, and 851 records of 148 AMF species in disturbed areas. More 292 records of 109 species where from areas without information on conservation status. Although more species are reported for natural, undisturbed areas, those antropized also maintained a high diversity of Glomeromycotean species (Tab. 2). Twenty species, belonging to 14 genera, were exclusively reported in natural areas, three species belonging to *Acaulospora* and *Glomus* (each), two of *Dominikia* and *Rhizoglomus* (each), and only one species of *Ambispora, Dentiscutata, Diversispora, Halonatospora, Pervetustus, Racocetra, Sclerocarpum, Sclerocystis, Septoglomus*, and *Scutellospora*. Only eight species (*Acaulospora alpina, A. entreriana, A. nivalis, A. sporocarpia, Racocetra alborosea, R. crispa, Scutellospora striata* and *Tricispora nevadensis*) were exclusively found in disturbed areas in Brazil.

The similarity of Glomeromycotean species separated the biomes in two groups: one cluster with

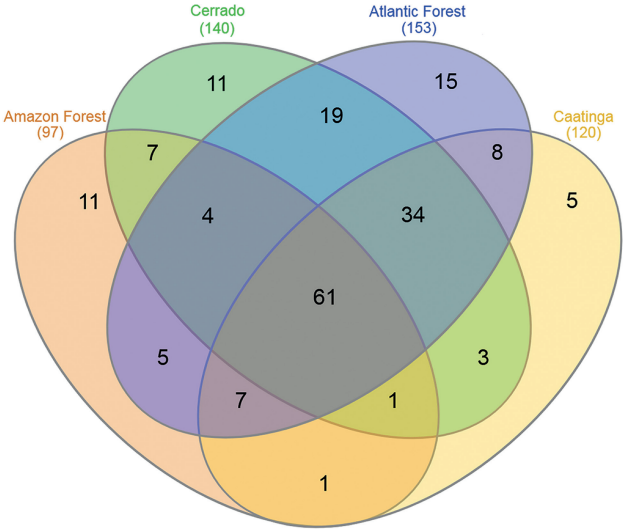

Fig. 5. Venn's diagram showing the number of Glomeromycotean species (AM fungi), exclusive and in common among four Brazilian biomes (there were no exclusive AMF species related to Pampa and Pantanal).

the four more studied biomes and other cluster with Pampa and Pantanal, considering the low number of collections in these biomes, what might have biased the result (data not shown). Glomeromycotean communities in Atlantic rainforest and Caatinga were the most similar (81 %), presenting also 80 % of similarity with the Cerrado's species, while the Amazon rainforest presented lower similarity index with all of them (<70 %).

Discussion

In this study, data taken from published diversity studies on Glomeromycotean species were carefully analysed. Some problems certainly impaired a better picture of the Glomeromycota species richness recorded in Brazil. Most of the studies were based only on morphological identification. This approach has increasingly been used all over the world (Solís-Rodríguez, 2020, De Pontes et al. 2017b, Oehl et al. 2009, Songachan & Kayang, 2013) and sometimes it was even more efficient than modern molecular approaches (Wetzel et al. 2014). However, it might be not enough to disclose the complete diversity, considering the difficulties for identification such as: low spore numbers, spores lacking enough taxonomic information, or specimens not sporulating in the weeks or days before collection. We should also consider that the number of experts in morphological taxonomy of Glomeromycota has never been high, and although increasing recently, even in our days the chance of missing some species in the process of identification is still considerable. Morphological knowledge is important, also for those researchers using molecular analysis, who should always try to know, how the spores of those species look like, which they are working with. The best practice would be to associate both, morphological and molecular analyses of soil and roots, and using more tools to register the presence of Glomeromycotean species, as also discussed by Colombo et al. (2014).

Another consideration regarding the data are the number, replicates and size of study areas in each biome, as collection conditions and number of samples differ among surveys, as well as the examination techniques. With a simplified collection or multiplication scheme, there is always a risk for losing some spore types that might represent additional species in a study area. In some studies, authors use trap cultures or micro- to mesocosms, to increasing the chance of getting more spores and species, in better conditions for examination. Others do not include this strategy, but might sample more intensively per area or throughout the year. In trap cultures, sometimes Glomeromycotean species are favoured that sporulate faster than others or are more easily adapted to culture (Hart & Reader 2002). Other species sporulate regularly in the field, but might be unable to sporulate under specific trap culture conditions (Leal et al. 2018). Although trap cultures might always be somehow selective, they can always be an important additional tool for gaining knowledge on the species composition of a specific place. It should also be considered that colonization and the sporulation strategy differ among groups of AMF, as some direct more energy to reproduction, thus forming high number os glomerospores, while others spend more effort in mycelial growth, according to their life strategy (Hart et al. 2001, Hart & Reader 2002). Thus, when looking at species diversity data for Glomeromycota, we should take all these difficulties in account.

This review shows that Brazilian biomes host approximately 60 % of all known Glomeromycota species richness. In an earlier survey on the occurrence of AMF species in Brazil, Maia et al. (2015) recorded 157 species. Thus, the knowledge on the richness of these fungi was increased for the country by 22 % within five years of intensified research.

Considering the surveys in all areas, 171 Glomeromycotean species were recorded in 169 undisturbed, not anthropized locations, while 148 species were identified in 138 disturbed areas. Most of the species were recorded in undisturbed areas, as also

referred by Bonfim et al. (2013), Leal et al. (2013), De Pontes et al. (2017b), and Marinho et al. (2019). However, this result must be analysed carefully, because the number of studies carried out in undisturbed areas is higher than that for disturbed areas. Unfortunately, in some studies a description of the conditions (undisturbed vs. disturbed) of the collection area was not provided, preventing the inclusion of this aspect in a general discussion. In natural habitats, species associations play an important role in structuring the Glomeromycotean communities, as well as management practices and environmental variables such as vegetation, climate, sites and soil properties influence the distribution of these microorganisms (Pereira et al. 2018, 2019).

The Atlantic rainforest and the Cerrado, known as hotspots of biological diversity, have the greatest richness of AMF species and a large number of exclusive species, showing that these two biomes are important sources for conservation of soil microorganisms. In a recent inventory, Jobim et al. (2018) recorded 128 Glomeromycotean species in the Atlantic rainforest. An even higher number of species (153) was registered in the present study, representing approximately 47 % of the worldwide known AMF richness. This confirms that this biome, with its various forest formations and associated ecosystems, is an important habitat for a diverse AMF mycobiota.

For Cerrado soils, 92 Glomeromycotean species were known (Jobim et al. 2016), and an increase in the number of studies in recent years led to 140 taxa in these soils (De Pontes et al. 2017a; Teixeira et al. 2017; Vieira et al. 2017, 2019a, b; Fernandes et al. 2019; Moraes et al. 2019). The recent description of a new species (*Racocetra crispa*; De Souza et al. 2018) and all recent reports suggest that unexpected high diversity of AMF can still be found in this biome despite of the progressing conversion of natural habitats into agricultural crop- and grasslands.

About 50 % of all Glomeromycota diversity recorded for Brazil was found in the Amazon rainforest (97 species). The lower species richness found in the Amazon rainforest than in the Atlantic rainforest and in the Cerrado might be explained by the lower number of surveys in the Amazon (10) in comparison with those in the other two biomes (23 and 16, respectively). Besides, there are also differences on degree of seasonality within the Amazon forest, especially in untouched areas, where still daily rainfalls occur, comparing to the more seasonal Atlantic rainforest and Cerrado, where dry seasons of 3–7 months are common in some areas (MMA 2010; Bustamante et al. 2012). This could account for more sporulation of Glomeromycotean fungi during the dry seasons, allowing the collection of spores and species identification.

For the Caatinga, in the last inventory of Glomeromycotean diversity, 75 species were recorded (Maia et al. 2010). Due to our research, another 45 species were now included in the list. In this biome, the dry seasons generally last at least 7–9 months, and in some areas the absence of rain may occur even for a few years (Nimer 1979), which might be already a major constraint for several AMF species with longer life cycles than 2–3 months.

The Pantanal has 19 species recorded, a result directly linked to the low number of studies carried out in this region (Gomide et al. 2014). Considering the great diversity of plants and animals reported for this biome (MMA 2019), one can assume that the Glomeromycota, as well as other fungal groups, should also be important ecosystem components in this biome.

The Pampa had the lowest Glomeromycotean richness recorded (5 species), which is certainly linked to the lack of studies from this biome in Brazil. This is supported by data from the Pampa Ondulata region, in Argentina, where using morphological analysis or a pyrosequencing approach, Colombo et al. (2014) found 188 OTUs (molecular operational taxonomic units) and identified through morphology only 29 Glomeromycotean species, in natural and agronomic areas. Besides this richness, the authors observed a negative effect of soil cultivation on diversity of Glomeromycotean fungi in these areas.

It is worth mentioning that the number of studies differs among biomes and this has also affected the number of records. More surveys were done in the Atlantic rainforest (23), Cerrado (16), and Caatinga (14), and less in the Amazon rainforest (10), which probably is also extremely diverse in Glomeromycotean fungi. Pampa and Pantanal are still less studied (one study each), deserving much more attention, especially as they are also known as highly diverse in plants and animals.

The Atlantic rainforest and the Caatinga have 110 species in common, forming a group of high similarity (81 %); the same percentage of similarity was recorded between Atlantic rainforest and Cerrado. The geographical proximity between Atlantic rainforest and Cerrado and between Atlantic rainforest and Caatinga allowed the dispersion of taxa and probably contributed to the high number of shared species between these biomes. The Amazon rainforest and Caatinga had more Glomeromycotean species in common than Amazon rainforest versus Atlantic rainforest and Amazon rainforest ver-

sus Cerrado. These results were not expected considering the differences in environmental conditions: the Caatinga has the longest period of drought, with no rain at all in some places, while the others (Atlantic rainforest and Cerrado) have fewer periods without rain – on the opposite, in the undisturbed larger subregions of Amazonia, it still rains almost daily (MMA 2019). Higher similarity between the Amazon rainforest and Atlantic rainforest was expected considering that during periods of its evolution, the Atlantic rainforest was directly connected, among others, with the Amazon rainforest (Ribeiro et al. 2011). This was observed especially for the Atlantic rainforest in the north of the San Francisco River, which share many species of wood plants with the Amazon Forest (Tabarelli et al. 2006).

The low similarity of Glomeromycotean communities separating Pantanal and Pampa from the other biomes may be explained by the lower number of studies and records of taxa in these two biomes. The similarity index is sensible to variation in richness between the communities, and this measurement was diverse among Pantanal and Pampa and the other four biomes. It reinforces the need for more studies in these poorly collected areas in order to uncover the richness of AMF that probably also exist in their soils. We assume that also the Brazilian Pampa should have interesting Glomeromycotean communities associated with the characteristic grassy vegetation, but also in the acompanying riparian and manifold slope forests, and also in the shrub formations towards Uruguay, Argentina and Paraguay (IBGE 2004, Colombo et al. 2014).

Taxa of Glomeromycota are present in all continents, with generally greatest diversity in tropical regions (Davison et al. 2015). Glomeromycotean species distribution can be affected by several factors, including soil characteristics (Oehl et al. 2010, 2017; Rodriguez-Echeverria et al. 2017), size of the area and connectivity between areas (Vannette et al. 2016), vegetation type (Engelmoer & Kiers 2015, Martínez-García et al. 2015), and land use practices (van der Gast et al. 2011, Moora et al. 2014). Da Silva et al. (2017b) observed that in coastal Atlantic rainforest areas, spatial, climatic and edaphic factors shape the structure of AMF communities.

Gigasporales species are more common in warmer than colder climates (Oehl et al. 2017), as also observed by Stürmer et al. (2018a, b) who reported greater richness of species of some genera (e.g. *Cetraspora, Dentiscutata, Racocetra* and *Scutellospora*) in tropical regions, compared with temperate regions. Moreover, other genera, such as *Bulbospora, Intraornatospora, Orbispora* and *Paradentiscutata*, were so far detected exclusively in tropical regions (Marinho et al. 2018). Low occurrence of Gigasporales was reported in agricultural soils in Switzerland (Oehl et al. 2017), with higher abundance in acidic than in calcaric soils (Oehl et al. 2010). Within a region or landscape, soil texture might also be among the factors related with occurrence of species of Gigasporales, which seems to be favoured in sandy soils (Lekberg et al. 2007). Remarkably, species of this order corresponded to approximately 25 % of all reported species in the present inventory.

Glomeraceae was recorded in all biomes, and this family, having the highest genus and species richness within the Glomeromycota, is frequently reported as dominant family in genus and species richness in global inventories of Glomeromycotean diversity (Öpik et al. 2013), e.g. in biomes similar to those found in Brazil, such as humid forests, tropical pastures and savannas (Tchabi et al. 2008, De Pontes et al. 2017b), but also in other climates, especially, when soil pH is > 7.0, or in cultivated soils (Oehl et al. 2017, Baltruschat et al. 2019). Among the 20 species reported only in undisturbed areas of the six Brazilian biomes, 11 belong to this family, that was observed as indicator of undisturbed areas also in a temperate forest (Moora et al. 2014) or in semi-natural grasslands (Oehl et al. 2017). Some taxa of Glomeraceae, above all sporocarpic genera like *Sclerocystis* and *Sclerocarpum*, may have a reduced capability of dispersion and recolonization after disturbance, as they may depend mainly on hypha fragments to recolonize their hosts or have longer life cycles than other Glomeromycotean taxa (Hart & Reader 2002, Oehl et al. 2009, Bowles et al. 2017). This might explain the predominance of these taxa in undisturbed areas.

In several studies, Acaulosporaceae is the second best represented family, in number of species, both in temperate (Öpik et al. 2010) and tropical forests (Marinho et al. 2018). This family is also very common in all studied Brazilian biomes. This suggests that taxa of this family have a wide tolerance range to diverse environmental conditions, corresponding to their often seasonal life strategy, characterized as stress tolerant, e.g. against several months of drought or cold temperatures below 0 °C (e.g. Chagnon et al. 2013).

Acaulospora and *Glomus* have the largest species number described and were frequently most numerous genera in several studies on Glomeromycotean diversity in Tropical rainforests, dry forests and savannas (Marinho et al. 2018, Pagano & Lugo

2019, Tchabi et al. 2008). This survey confirms the prevalence of these genera, corresponding to 33 % of the Glomeromycota species richness recorded in Brazil. However, with respect to representativeness for the different genera both, *Acaulospora* (74 %) and *Glomus* (47 %), showed only average values. Of all genera with higher species numbers in this survey, seven (especially *Dentiscutata, Fuscutata, Racocetra*, and *Sclerocystis*) had > 75 % of the total species number known for each genus, while *Diversispora* and *Septoglomus* (each 33 %), and especially *Dominikia* and *Redeckera* (<25 %) had much lower values.

Among the species reported in the Brazilian biomes, four (*Acaulospora mellea, A. morrowiae, A. scrobiculata* and *Claroideoglomus etunicatum*) are present in more than 70 % of the consulted references, which shows their wide distribution. Taxa of *Acaulospora* are geographically widespread and some (*A. mellea, A. morrowiae* and *A. scrobiculata*) have been reported as the most abundant and frequent in several tropical forests of the American and African continent, both in natural and anthropized areas. Apparently they are not strongly affected by soil disturbance, at least in warmer climates (Picone et al. 2000, Lovelock et al. 2003, Tchabi et al. 2008, Souza et al. 2010), while they clearly are affected in cultivated soils of colder climates (e.g. Oehl et al. 2010, 2017).

Several species were reported in the majority of the biomes, such as: *Acaulospora longula, Ambispora leptoticha, Cetraspora pellucida, Dentiscutata heterogama, Gigaspora margarita, Kuklospora colombiana, Oehlia diaphana, Paraglomus occultum, Rhizoglomus clarum* and *R. intraradices*. These species are commonly found in many ecosystems, indicating their ability and resilience to grow in different environmental conditions. Among them, *C. pellucida, C. etunicatum, G. margarita, K. colombiana, O. diaphana, P. occultum* and *R. clarum* have a wide amplitude of occurrence, and presence in humid and semiarid (Chaudhary et al. 2014, Guadarrama et al. 2014), as well as in temperate (Soteras et al. 2015, Chaudhary et al. 2017) and tropical warm environments (Leal et al. 2013, da Silva et al. 2014).

The number of species exclusively found in only one of the biomes was relatively high. The Atlantic rainforest had the greatest number (15), followed by Cerrado and Amazon rainforest (11 species each), and in the Caatinga five species were exclusive, while none was reported only in the Pantanal and Pampa. Among other factors, the composition and diversity of Glomeromycotean species may vary with habitat area (Grilli et al. 2012), and their occurrence in a particular bioregion suggests that environmental (e.g. climatic and edaphic) characteristics influence the distribution of these species (Da Silva et al. 2017b).

Vegetation is one of the main drivers of Glomeromycotean communities (Martínez-García et al. 2015), with clear differentiation between those found in forests and in open areas (grass savannas and Pampa pastures; Rodríguez-Echeverría et al. 2017). In rainforests, the abiotic environment plays a key role in abundance and distribution of the Glomeromycotean fungi, but other drivers should also be taken in account (Pereira et al. 2019). The extremely diverse vegetation of the Brazilian biomes is probably an important structuring factor of the Glomeromycotean communities, affecting not only the identity but also the abundance of species in each environment. Remarkably, the AMF richness may even vary significantly among individuals of the same plant species (Lekberg & Waller 2016).

Some of the recorded species were cited as indicator of some particular ecosystems, e.g. *Glomus macrocarpum*, in areas of Cerrado sensu stricto, but this species was found in all Brazilian biomes, except Pantanal and Pampa. *Gigaspora margarita* and *Racocetra coralloidea* were indicators of agricultural areas of Cerrado under tillage, while *Sclerocystis coremioides* was appointed as indicator of agricultural areas of Cerrado under no-tillage (De Pontes et al. 2017a). These authors mentioned that AMF richness decreased, while the overall diversity of Glomeromycotean species was maintained, although several species disappeared after conversion of the Cerrado savannas to soybean croplands. This reinforces the observation that agricultural practices contribute to changes in soil microbiota, affecting not only the richness, but also the composition of the AMF communities (Oehl et al. 2009, 2010). Soil disturbance and decrease of plant diversity lead by cultivation of crops may select AMF species more capable to support the changes and promote loss of those rare and more susceptible (Trejo et al. 2016).

Fragmentation and progressive loss of habitat may result in dispersion barriers for Glomeromycotean species due to disturbances generated by anthropic action, such as the establishment of agricultural systems (Davison et al. 2015). However, eight species occurred exclusively in disturbed areas, suggesting their 'affinity' to such specific conditions, more or less stressful for all other Glomeromycotean species.

Based on molecular studies it is possible to obtain an extensive list of Glomeromycotean sequenc-

es that not always corresponds to species morphologically described, and this may have led to an over-estimation of the taxa richness in a specific area (Colombo et al. 2014). Nevertheless, the morphological identification may often reveal higher richness of Glomeromycotean species in a community than the molecular analyses (Wetzel et al. 2014), but this may depend of the sporulant fraction present in that community (Hart et al. 2015). Both methods may still have some limitations. Considering that the Glomeromycotean fungi live in the soil and in the roots, the use of morphological and molecular identification is important and complementary, in order to identify the fungi in both niches and to obtain a more complete vision of a specific community, as shown by Vieira et al. (2017) in a study of AMF in a Brazilian savanna and by Pereira et al. (2018, 2019) in the Atlantic Rainforest. Such complementary studies amplify the knowledge on Glomeromycotean diversity of an area. Data on the natural history of most arbuscular mycorrhizal fungi are still scarce. More efforts should be employed connecting molecular and biological data to promote advances in the knowledge and better understanding of the ecology of this important group of fungi, as suggested in general also for all fungi (Peay 2014).

This study provided information regarding the rich Glomeromycotean species diversity in the Brazilian biomes and highlights the great contribution of the Brazilian biomes to the global diversity of these fungi. It is worth to mention that both environments, disturbed and undisturbed account for the high amount of Glomeromycotean species detected and that conservation of the different vegetation types is a key factor to assure maintenance of these important plant symbionts in the ecosystems. New surveys, even in already well studied areas, probably will uncover again new taxa of Glomeromycota. Inventories of this nature are relevant for the definition of biodiversity conservation policies especially for this "invisible" portion of soil biodiversity, responsible for the balance of ecosystems and the maintainance of plant communities, subjected to habitat fragmentation and strong threats such as extinction of species.

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