Chapter 3
Biodiversity of Arbuscular Mycorrhizal Fungi in South America: A Review

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3.1 Introduction

Identification of species is crucial in understanding how diversity changes affect ecosystemic processes. Particularly, soil microbial are key factors of ecosystemic functioning (Copley 2000). Among soil microbes, arbuscular mycorrhizal fungi (AMF, phylum Glomeromycota) are worldwide distributed (Tedersoo et al. 2018) and form symbiotic associations with almost 80% of the vascular plants of the earth, except for one species, *Geosiphon pyriformis*, which associates with the cyanobacteria *Nostoc* (Smith and Read 2008). AMF comprise around 300 morphologically defined or 350–1000 molecularly defined taxa (Davison et al. 2015 and references therein). Since AMF associate with aboveground community, their occurrence and

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composition can influence ecosystemic processes either through affecting plant community composition and thus its processes rates, or soil microbial communities, which are directly involved in nutrient cycling (Rillig 2004). According to Pärtel et al. (2016), soil microorganisms are considered a potentially suitable target for studying regional and local effects on diversity. The symbiosis with AMF not only increases nutrient uptake by the plant of mainly phosphorus (P) and nitrogen (N) in exchange for plant-assimilated carbon (C), but also improves the tolerance of plants to various biotic and abiotic stresses such as pathogens, salinity, and drought (Smith and Read 2008).

External factors (abiotic and biotic) and intrinsic properties of species (dispersal ability, rates of speciation and extinction) affect the AMF geographical distributions (Chaudhary et al. 2008). For instance, the abiotic factors of temperature and precipitation constrain AMF occurrence (Davison et al. 2015) while biotic ones such as host preferences determine the rhizospheric AMF community (Senés-Guerrero and Schüßler 2016; Soteras et al. 2016). Moreover, anthropogenic activities like agricultural practices that alter soil conditions could influence the occurrence of AM fungal taxa (Cofré et al. 2017). At the same time, either external or internal factors may indirectly influence each other, causing changes in AMF taxa occurrence and distribution (Chaudhary et al. 2008). Currently, an increasing number of studies attempt at unravelling the worldwide geographical patterns of AMF (Öpik et al. 2010, 2013; Kivlin et al. 2011; Tedersoo et al. 2014; Davison et al. 2015). These researches reviewed AMF descriptions based on DNA methods and showed contrasting results of AMF biogeographical patterns. For instance, Öpik et al. (2010) found that two-thirds of AMF taxa showed restricted distribution, but Davison et al. (2015) postulated that most of the AMF taxa show a cosmopolitan distribution and that species richness of AMF virtual taxa decreases with latitude at the global scale. However, in South America (SA), molecular characterization of AMF communities is fairly scarce (Grilli et al. 2015; Senés-Guerrero and Schüßler 2016; Soteras et al. 2016). In a recent review, Stürmer et al. (2018) described large-scale patterns of distribution of taxa within the phylum Glomeromycota reported on 7 continents and in 87 countries, including ultramarine country territories like Canary Islands, Kerguelen Island, the Bermudas, and Guadeloupe Islands. They concluded that this phylum mainly comprises cosmopolitan taxa. So far, AMF communities morphologically described have been analyzed from a biogeographical perspective in few studies (Stürmer et al. 2018), while distributional patterns across South American ecological divisions have never been deeply acknowledged. Therefore, in this Chapter we reviewed studies of SA that morphologically described the AMF community. Despite morphologically described AMF species (hereafter morphospecies) being highly intraspecifically variable, not necessarily representing root colonizing taxa, and not always sporulating during sampling, they could give a first approach of the AMF community of a particular place and moment. However, further DNA-based descriptions should be combined with morphospecies approach in order to deeply characterize AMF distribution in SA.

3.2 Arbuscular Mycorrhizal Morphospecies

AMF spores are asexual multinucleate single cells which originate from the differentiation of vegetative hyphae (Smith and Read 2008). Sporulation in the soil depends on several factors such as the fungal and host plant identity, soil fertility, and temperature among others (Smith and Read 2008). Spores represent the genetic unit of fungal species, being responsible for the colonization of new habitats and initiation of new individuals (Morton et al. 1993; Błaszkowski 2012). Since many components of the subcellular structure of the spores such as wall layers are stable under different environmental conditions, they are considered as diagnostic traits for the morphological identification of AMF. Although the identification of species is crucial to understanding geographical patterns of biodiversity (Zak et al. 2003), the taxonomic classification of AMF is under continuous debate due to the high variation of morphological traits, difficulties in spore extraction from soil and their pure culture under controlled conditions (Błaszkowski 2012). Since the definition of species in Glomeromycota is controversial (Rosendahl 2008), the term "morphospecies" has been chosen to refer to AMF species (Robinson-Boyer et al. 2009) when their identification is based on the morphological traits and ontogeny of spores.

In this Chapter we used the AMF morphospecies classification proposed by Redecker et al. (2013) and Schüßler and Walker (2010). We followed the AMF species list that was updated in September 2018 in http://www.amf-phylogeny.com/amphylotaxonomy.html. That last classification recognizes within the phylum Glomeromycota a single class (Glomeromycetes) which includes 4 orders (Glomerales, Diversisporales, Paraglomerales and Archaeosporales), 12 families (Acaulosporaceae, Ambisporaceae, Archaeosporaceae, Claroideoglomeraceae, Diversisporaceae, Geosiphonaecae, Gigasporaceae, Glomeraceae, Pacisporaceae, Paraglomeraceae, Pervetustaceae and Sacculosporaceae), 34 genera and approximately 316 AMF morphospecies validly described. *Glomus tenue* was considered in the species list but it is important to clarify that it was moved to *Planticonsortium* in the subphylum Mucoromycotina (Walker et al. 2018).

3.3 Arbuscular Mycorrhizal Fungi in South America

South America is globally recognized for its vast and incredible biodiversity linked to its unique geology, climate and biogeographic history. The great plant diversity in SA is the result of its complex evolutionary history over the last 250 million years (Fittkau 1969; Lavina and Fauth 2011). The floristic composition of SA (particularly in Chile, Argentina and "Cordillera de los Andes" or Andean Range) turns this area into a vegetation relict (Villagrán and Hinojosa 1997). Moreover, the region presents a great diversity of mycorrhizas that varies from angiosperm and gymnosperm forests dominated by arbuscular mycorrhizal (AM) to ectomycorrhizal

(ECM) *Nothofagus* spp. ones (Fontenla et al. 1998; Palfner 2001; Bueno et al. 2017). In accordance with the particular characteristics of the region, research on mycorrhizal patterns has provided interesting findings, such as the occurrence of new mycorrhizal associations (Bidartondo et al. 2002) and regional differences in the distribution of mycorrhizal fungi (Tedersoo et al. 2014; Davison et al. 2015). Alarming advances in deforestation, desertification and loss of biodiversity mainly due to soybeanization (the expansion of the agricultural frontier due to the planting of soybean) and with consequent processes of marginalization and social persecution, constitute a worrying reality that is increasingly widespread within the South American region (Viglizzo et al. 2011). Therefore, knowing the biotic diversity of the region is of great importance to protect it, so that diversity studies in the different types of ecological divisions of South America are essential for the expansion of knowledge about this ecosystemically diverse and threatened region.

In this Chapter, the available published studies on AMF morphospecies diversity have been compiled. To this end, we searched for Google Scholar articles from 1955 to 2018 containing the term combination "arbuscular mycorrhizal" AND "country name" and grouped them into ecological divisions. Studies on AMF morphological diversity from Paraguay, Guyana, Surinam, French Guiana could not be found. This research process included the review of a total of 110 articles dealing with AMF morphospecies diversity of the following nine countries: Argentina (27), Bolivia (8), Brazil (40), Chile (13), Colombia (6), Ecuador (1), Perú (2), Uruguay (2) and Venezuela (9), see Table 3.1. Particularly, the works of Uruguay only showed species richness number without any other details about the species identified.

3.4 South American Arbuscular Mycorrhizal Morphospecies Diversity

3.4.1 Arbuscular Mycorrhizal Fungi Morphospecies Richness in South America

Considering the 110 articles above mentioned, 186 AMF morphospecies were identified at the species level (Table 3.1) while a large number of taxa were identified at the genus level (608) but were not considered for geographical descriptions. Ordered according to the increasing number of the morphospecies identified: in Brazil, there were recorded 158 morphospecies to species level and 258 to genus level; in Argentina, 83 and 133; Chile, 59 and 36; Venezuela, 38 and 144; Perú, 31 and 21; Colombia, 20 and 6; Bolivia, 15 and 5; and Ecuador, 4 and 4.

In a recent review, Stürmer et al. (2018) described large-scale patterns of taxa distribution within the phylum Glomeromycota. Their results showed 131 identified morphospecies among the 1280 registered until 2012 in South America. In contrast, in our study we found 2187 records until June of 2018 in SA, representing 186

Table 3.1 List of the AMF morphospecies described or cited in the literature of South America analyzed in this Chapter. The total citations of each one and of all the morphospecies, the total of species and the total of research articles are shown for each region[a]

Families	Genus	Species	Biogeographic region														
			Amazonia	Atlantic Forest	Caatinga	Cerrado	Chaco	Dry South central Andes	Guianan Uplands and Highlands	Llanos	Mediterranean Chile	Moist north central Andes	Moist Pacific Mesoamerican	Moist Pacific temperate	Pampas	Patagonia	Total records
Acaulosporaceae	*Acaulospora*	*alpina*					5							4	2	4	15
Acaulosporaceae	*Acaulospora*	*bireticulata*	1	2	3	8	15			1					4	1	35
Acaulosporaceae	*Acaulospora*	*brasiliensis*	1	1		8		1									11
Acaulosporaceae	*Acaulospora*	*cavernata*				1	1							1		3	6
Acaulosporaceae	*Acaulospora*	*colombiana*	3	7	5	4			3	1		1	3				27
Acaulosporaceae	*Acaulospora*	*colossica*		5		4			1	2	1			1			14
Acaulosporaceae	*Acaulospora*	*delicata*	2	1	4	4	2								4	4	21
Acaulosporaceae	*Acaulospora*	*denticulata*		1	3	7	3	1				5			2	1	23
Acaulosporaceae	*Acaulospora*	*dilatata*			1		2				1			1		4	9
Acaulosporaceae	*Acaulospora*	*elegans*	1	2			1										4
Acaulosporaceae	*Acaulospora*	*endographis*		1													1
Acaulosporaceae	*Acaulospora*	*entreriana*					1										1
Acaulosporaceae	*Acaulospora*	*excavata*	1	1	13	2	10					4			4		35
Acaulosporaceae	*Acaulospora*	*foveata*	3	10	8		4		1			1				1	28
Acaulosporaceae	*Acaulospora*	*foveoreticulata*			1												1
Acaulosporaceae	*Acaulospora*	*herrerae*			7												7
Acaulosporaceae	*Acaulospora*	*ignota*		1													1
Acaulosporaceae	*Acaulospora*	*kentinensis*	1	1													2
Acaulosporaceae	*Acaulospora*	*koskei*		2	2	7					1			1			13
Acaulosporaceae	*Acaulospora*	*lacunosa*		4	2		5				1						12
Acaulosporaceae	*Acaulospora*	*laevis*	1	7	5		8		1	1	3	4		5	4	4	43
Acaulosporaceae	*Acaulospora*	*longula*	1	5	4	1				1		2	1	4			19

Table 3.1 (continued)

Families	Genus	Species	Biogeographic region														
			Amazonia	Atlantic Forest	Caatinga	Cerrado	Chaco	Dry South central Andes	Guianan Uplands and Highlands	Llanos	Mediterranean Chile	Moist north central Andes	Moist Pacific Mesoamerican	Moist Pacific temperate	Pampas	Patagonia	Total records
Acaulosporaceae	*Acaulospora*	*mellea*	4	18	9	8	12			2		5		2	4	3	67
Acaulosporaceae	*Acaulospora*	*morrowiae*	3	10	9	7				3		1					33
Acaulosporaceae	*Acaulospora*	*myriocarpa*		2								1		2			5
Acaulosporaceae	*Acaulospora*	*papillosa*		1													1
Acaulosporaceae	*Acaulospora*	*paulinae*	1			3					2			5			11
Acaulosporaceae	*Acaulospora*	*polonica*	1														1
Acaulosporaceae	*Acaulospora*	*punctata*	1								1			2			4
Acaulosporaceae	*Acaulospora*	*reducta*			1												1
Acaulosporaceae	*Acaulospora*	*rehmii*	4	4	9		7			1		5			2	1	33
Acaulosporaceae	*Acaulospora*	*rugosa*		2		2	4								1		9
Acaulosporaceae	*Acaulospora*	*scrobiculata*	5	21	19	6	16			1	1	5		3	3	4	84
Acaulosporaceae	*Acaulospora*	*sieverdingii*		1	3						2			1			7
Acaulosporaceae	*Acaulospora*	*spinosa*	4	11	8	7	11		1			5	1	5	3	3	59
Acaulosporaceae	*Acaulospora*	*spinulifera*		1													1
Acaulosporaceae	*Acaulospora*	*splendida*			1												1
Acaulosporaceae	*Acaulospora*	*thomii*												3			3
Acaulosporaceae	*Acaulospora*	*tuberculata*	3	7	6	1	2		1								20
Acaulosporaceae	*Acaulospora*	*undulata*	1				8							2			11
Ambisporaceae	*Ambispora*	*appendicula*	1	11	8	8	4		1	1		2	2				38
Ambisporaceae	*Ambispora*	*callosa*			1	7											8
Ambisporaceae	*Ambispora*	*fecundispora*		1													1
Ambisporaceae	*Ambispora*	*gerdemannii*	1	3	1		2							1		3	11
Ambisporaceae	*Ambispora*	*jimgerdemannii*		1	1												2
Ambisporaceae	*Ambispora*	*leptoticha*	3	3	7		8			2		4		2	3	1	33

Ambisporaceae	*Ambispora*	*leptoticha*					1										1
Archaeosporaceae	*Archaeospora*	*schenckii*									1			1			2
Archaeosporaceae	*Archaeospora*	*trappei*	5	6	1		3			3		1		9	2		30
Gigasporaceae (unclear)	*Bulbospora*	*minima*		1													1
Gigasporaceae	*Cetraspora*	*auronigra*		1		1											2
Gigasporaceae	*Cetraspora*	*gilmorei*		4	1	1	2				2			1	1	3	15
Gigasporaceae	*Cetraspora*	*pellucida*	2	10	10	3	2								6		33
Gigasporaceae	*Cetraspora*	*striata*							1								1
Claroideoglomeraceae	*Claroideoglomus*	*claroideum*	3	5	2	1					3	4		8	4	2	32
Claroideoglomeraceae	*Claroideoglomus*	*drummondii*	1														1
Claroideoglomeraceae	*Claroideoglomus*	*etunicatum*	2	11	19	8	12			1	3	1		9	5	4	75
Claroideoglomeraceae	*Claroideoglomus*	*lamellosum*		1		3								1			5
Claroideoglomeraceae	*Claroideoglomus*	*luteum*	2	1	1		10								2		16
Claroideoglomeraceae	*Claroideoglomus*	*maculosum simil C. claroideum*		1													1
Claroideoglomeraceae	*Claroideoglomus*	*walkeri*	1														1
Diversisporaceae	*Corymbiglomus*	*corymbiforme*	1														1
Diversisporaceae	*Corymbiglomus*	*globiferum*		1													1
Diversisporaceae	*Corymbiglomus*	*pacificum*												2			2
Diversisporaceae	*Corymbiglomus*	*tortuosum*	1	4	4		1		1	2					1	2	16
Gigasporaceae	*Dentiscutata*	*cerradensis*	2	4	2												8
Gigasporaceae	*Dentiscutata*	*colliculosa*			2												2
Gigasporaceae	*Dentiscutata*	*erythropus*			2												2
Gigasporaceae	*Dentiscutata*	*heterogama*	2	16	3	5	5					1	2		4	1	39
Gigasporaceae	*Dentiscutata*	*nigra*						1									1
Gigasporaceae	*Dentiscutata*	*reticulata*		1										1			2
Gigasporaceae	*Dentiscutata*	*savannicola*		1	2							2					5
Diversisporaceae	*Diversispora*	*eburnea*	1		1		2								1		5

Table 3.1 (continued)

Families	Genus	Species	Biogeographic region														
			Amazonia	Atlantic Forest	Caatinga	Cerrado	Chaco	Dry South central Andes	Guianan Uplands and Highlands	Llanos	Mediterranean Chile	Moist north central Andes	Moist Pacific Mesoamerican	Moist Pacific temperate	Pampas	Patagonia	Total records
Diversisporaceae	*Diversispora*	*insculpta*				1											1
Diversisporaceae	*Diversispora*	*spurca*	4	3	1		5				1			6			20
Diversisporaceae	*Diversispora*	*trimurales*	1														1
Glomeraceae	*Dominikia*	*aurea*		1							1			2	1		5
Glomeraceae	*Dominikia*	*minutum*	1	1	2	1									1		6
	Entrophospora	*baltica*	1											1			2
	Entrophospora	*infrequens*	2	4	12		15	1		3	1	4	1	1	4	1	49
Glomeraceae	*Funneliformis*	*badium*	1				4				1			2			8
Glomeraceae	*Funneliformis*	*caledonium*													1		1
Glomeraceae	*Funneliformis*	*coronatum*					4				1			3	3		11
Glomeraceae	*Funneliformis*	*dimorphicus*					2										2
Glomeraceae	*Funneliformis*	*geosporum*	3	7	3	8	11	1	1					2	3		39
Glomeraceae	*Funneliformis*	*halonatus*		1	3												4
Glomeraceae	*Funneliformis*	*monosporum*		1										1			2
Glomeraceae	*Funneliformis*	*mosseae*		7	7	8	13			2	1			5	9	2	54
Glomeraceae	*Funneliformis*	*verruculosum*				1											1
Gigasporaceae	*Fuscutata*	*heterogama*		1		1											2
Gigasporaceae	*Gigaspora*	*albida*		6	6						1						13
Gigasporaceae	*Gigaspora*	*candida*					1										1
Gigasporaceae	*Gigaspora*	*decipiens*		14	11	7	1								3		36
Gigasporaceae	*Gigaspora*	*gigantea*		6	8	1	4								3		22
Gigasporaceae	*Gigaspora*	*margarita*	1	8	10	7	7								5		38
Gigasporaceae	*Gigaspora*	*ramisporophora*			3				1								4
Gigasporaceae	*Gigaspora*	*rosea*	1	4			7								1		13

Glomeraceae	*Glomus*	*ambisporum*	1	2	3		2							1	1		10
Glomeraceae	*Glomus*	*arborense*		1	1												2
Glomeraceae	*Glomus*	*atrouva*	1														1
Glomeraceae	*Glomus*	*australe*	2														2
Glomeraceae	*Glomus*	*botryoides*		1													1
Glomeraceae	*Glomus*	*brohultii*	2	2	3		10		1					1	2		21
Glomeraceae	*Glomus*	*deserticola*		1											2		3
Glomeraceae	*Glomus*	*formosanum*		1													1
Glomeraceae	*Glomus*	*fuegianum*	1	1			8								2		12
Glomeraceae	*Glomus*	*glomerulatum*	1	4	7	8	1			1		1	1				24
Glomeraceae	*Glomus*	*heterosporum*	1	1													2
Glomeraceae	*Glomus*	*hoi*		2			1				2			3			8
Glomeraceae	*Glomus*	*macrocarpum/F. geosporum*	3	8	15	8					1			4			39
Glomeraceae	*Glomus*	*magnicaule*	1				4										5
Glomeraceae	*Glomus*	*microcarpum*	2	5	7	7	1						1				23
Glomeraceae	*Glomus*	*multicaule*			1												1
Glomeraceae	*Glomus*	*multiforum*				1											1
Glomeraceae	*Glomus*	*nanolumen*	1														1
Glomeraceae	*Glomus*	*pallidum*			1									4			5
Glomeraceae	*Glomus*	*pansihalos*		1													1
Glomeraceae	*Glomus*	*pustulatum*	1														1
Glomeraceae	*Glomus*	*reticulatum*		1													1
Glomeraceae	*Glomus*	*spinuliferum*		1													1
Glomeraceae	*Glomus*	*tenebrosum*	1						1								2
Glomeraceae	*Glomus*	*tenue*								1							1
Glomeraceae	*Glomus*	*trufemii*		1	1												2
Glomeraceae	*Glomus*	*versiforme*	2	1	1									5			9
Pacisporaceae	*Pacispora*	*chimonobambusae*										4					4

Table 3.1 (continued)

Families	Genus	Species	Biogeographic region														
			Amazonia	Atlantic Forest	Caatinga	Cerrado	Chaco	Dry South central Andes	Guianan Uplands and Highlands	Llanos	Mediterranean Chile	Moist north central Andes	Moist Pacific Mesoamerican	Moist Pacific temperate	Pampas	Patagonia	Total records
Pacisporaceae	*Pacispora*	*dominikii*	1			1	4				2			5			13
Pacisporaceae	*Pacispora*	*franciscana*			3												3
Pacisporaceae	*Pacispora*	*patagonica*					4									2	6
Pacisporaceae	*Pacispora*	*robigina*	1			1	3										5
Pacisporaceae	*Pacispora*	*scintillans*				1											1
Gigasporaceae	*Paradentiscutata*	*bahiana*		1		1											2
Gigasporaceae	*Paradentiscutata*	*maritima*		2													2
Pacisporaceae	*Paraglomus*	*bolivianum*		2	2										2		6
Paraglomeraceae	*Paraglomus*	*brasilianum*			1	1											2
Paraglomeraceae	*Paraglomus*	*laccatum*					1							1			2
Glomeraceae	*Paraglomus*	*lacteum*	1									4					5
Paraglomeraceae	*Paraglomus*	*occultum*	2	6	9	10			1		1	2	3	6			40
Paraglomeraceae	*Paraglomus*	*pernambucanum*				1											1
Gigasporaceae	*Racocetra*	*alborosea*		1													1
Gigasporaceae	*Racocetra*	*castanea*	1	1		3											5
Gigasporaceae	*Racocetra*	*coralloidea*		4	2		1										7
Gigasporaceae	*Racocetra*	*fulgida*		4	7	7	1								3		22
Gigasporaceae	*Racocetra*	*gregaria*		1	9		1										11
Gigasporaceae	*Racocetra*	*intraornata*		2	4												6
Gigasporaceae	*Racocetra*	*novaum*			1												1
Gigasporaceae	*Racocetra*	*persica*	1	1	1	2											5
Gigasporaceae	*Racocetra*	*tropicana*		2													2
Gigasporaceae	*Racocetra*	*verrucosa*		4	3												7
Gigasporaceae	*Racocetra*	*weresubiae*		3	2									1			6

Diversisporaceae	*Redeckera*	*fulvum*		1													1
Glomeraceae	*Rhizophagus*	*aggregatus*	1	3	2		5	1		1	1			1	6		21
Glomeraceae	*Rhizophagus*	*antarcticus*															1
Glomeraceae	*Rhizophagus*	*arabicus*			1												1
Glomeraceae	*Rhizophagus*	*clarus*	2	5	3	10			1			4			4	2	31
Glomeraceae	*Rhizophagus*	*diaphanus*	2	5	1	6	2		1		3			5	1		26
Glomeraceae	*Rhizophagus*	*fasciculatus*	2	4	2	6	4					2	2	5	4	1	32
Glomeraceae	*Rhizophagus*	*intraradices*	1	2	5	2	14				3	4		5	4		40
Glomeraceae	*Rhizophagus*	*invermaius*	1	4	1	8								3			17
Glomeraceae	*Rhizophagus*	*irregularis*			1										1		2
Glomeraceae	*Rhizophagus*	*manihotis*		1					1	1		1	2				6
Glomeraceae	*Rhizophagus*	*microaggregatus*	1	3	2	4	5			1					7	2	25
Glomeraceae	*Rhizophagus*	*natalensis*		1													1
Glomeraceae	*Rhizophagus*	*vesiculifer*										1		1			2
Glomeraceae	*Sclerocystis*	*coremioides*	3	3	4		1								2		13
Glomeraceae	*Sclerocystis*	*clavispora*	1	2	5									1			9
Glomeraceae	*Sclerocystis*	*liquidambaris*					1										1
Glomeraceae	*Sclerocystis*	*pachycaulis*								1			1				2
Glomeraceae	*Sclerocystis*	*rubiformis*	4	2	2		3				1			1			13
Glomeraceae	*Sclerocystis*	*sinuosa*		6	7		3			2					3		21
Glomeraceae	*Sclerocystis*	*taiwanensis*	1	2	2												5
Gigasporaceae	*Scutellospora*	*arenicola*	1						1						1		3
Gigasporaceae	*Scutellospora*	*auriglоba*		3	5									1			9
Gigasporaceae	*Scutellospora*	*biornata*	1	1	5	8	12		1			4			2	1	35
Gigasporaceae	*Scutellospora*	*calospora*	1	3	7	6	3				3	1		4	2		30
Gigasporaceae	*Scutellospora*	*crenulata*							2								2
Gigasporaceae	*Scutellospora*	*dipapillosa*		2			3					4			3		12
Gigasporaceae	*Scutellospora*	*dipurpurescens*	1	1	3	3								3			11
Gigasporaceae	*Scutellospora*	*hawaiiensis*		1													1

Table 3.1 (continued)

Families	Genus	Species	Biogeographic region														
			Amazonia	Atlantic Forest	Caatinga	Cerrado	Chaco	Dry South central Andes	Guianan Uplands and Highlands	Llanos	Mediterranean Chile	Moist north central Andes	Moist Pacific Mesoamerican	Moist Pacific temperate	Pampas	Patagonia	Total records
Gigasporaceae	*Scutellospora*	*pernambucana*		5	3	3											11
Gigasporaceae	*Scutellospora*	*rubra*			1	5	3								1		10
Gigasporaceae	*Scutellospora*	*scutata*	1	2	2												5
Gigasporaceae	*Scutellospora*	*spinosissima*	1	1					2								4
Gigasporaceae	*Scutellospora*	*tricalypta*		1													1
Glomeraceae	*Septoglomus*	*constrictum*		3	2	4	11			1	1			2	3		27
Glomeraceae	*Septoglomus*	*titan*			2												2
Glomeraceae	*Septoglomus*	*viscosum*		1											1		2
		Total records/ecoregion	137	416	409	269	355	6	25	36	47	90	20	163	153	60	2187
		Total species/ecoregion	81	120	96	61	71	6	21	24	30	32	12	57	54	26	
		Research articles/ecoregion (110)	5	18	19	4	20	1	6	3	4	7	1	7	9	2	

[a]Research articles' sources: Aguilera et al. (2014, 2017); Aidar et al. (2004); Albuquerque (2008); Angulo-Veizaga and García-Apaza (2014); Becerra and Cabello M (2008); Becerra et al. (2011, 2014); Bonfim et al. (2013); Cabello (1994, 1997); Carrenho et al. (2001); Casanova-Katny et al. (2011); Castillo et al. (2005, 2006, 2010, 2016); Cofré et al. (2017); Colombo et al. (2014); Cordoba et al. (2001); Coutinho et al. (2015); Covacevich et al. (2006); Cuenca et al. (1998); Cuenca and Herrera-Peraza (2008); Cuenca and Lovera (1992); Cuenca and Meneses (1996); da Silva et al. (2005, 2008, 2012, 2014); de Carvalho et al. (2012); de Mello (2011); de Mello et al. (2013); de Oliveira Freitas et al. (2014); Dhillion et al. (1995); Dodd et al. (1990); Escudero and Mendoza (2005); Fernandes and Siqueira (1989); França et al. (2007); de Oliveira Freitas (2006); Frioni et al. (1999); Furrazola et al. (2013); García et al. (2017); Gómez-Carabalí et al. (2011); Goto and Costa Maia (2005); Goto et al. (2009, 2010a, b); Grilli et al. (2012); Herrera-Peraza et al. (2001, 2016); Janos et al. (1995); Jobim et al. (2016, 2018); Krüger (2013); Leal et al. (2009); Lemos (2008); Longo et al. (2014); Lugo and Cabello (1999, 2002); Lugo et al. (2005, 2008); Marín et al. (2016, 2017); Medina et al. (2014, 2015); Meier et al. (2012); Mendoza et al. (2002); Menéndez et al. (2001); Menoyo et al. (2009); Mergulhão (2007); Moreira et al. (2009); Janos et al. (1995); Oehl and Sieverding (2004); Oehl et al. (2010);Oehl et al. (2011a, b); Pagano et al. (2013); Pereira et al. (2014); Pontes et al. (2017); Purin et al. (2006); Rabatin et al. (1993); Rivero-Mega et al. (2014); Rojas-Mego et al. (2014); Schalamuk et al. (2006); Schenck et al. (1984); Schneider et al. (2013); Sieverding and Howeler (1985); Sieverding and Toro (1987); Silva et al. (2007); Siqueira et al. (1987, 1989); Soteras et al. (2012, 2014, 2015); Sousa et al. (2013); Souza et al. (2013); Spain et al. (2006); Stürmer and Bellei (1994); Stürmer and Siqueira (2011); Urcelay et al. (2009); Vasconcellos et al. (2016); Velázquez and Cabello (2011); Velázquez et al. (2013, 2016); Vestberg et al. (1999); Vilcatoma-Medina et al. (2018); Walker et al. (1998); Zangaro et al. (2013)

different AMF morphospecies and evidencing an increasing interest in the study of these fungi in the region in recent years.

All the taxa were included in 9 families: Acaulosporaceae (40 morphospecies), Ambisporaceae (7), Archaeosporaceae (2), Claroideoglomeraceae (7), Diversisporaceae (9), Glomeraceae (62), Gigasporaceae (46), Pacisporaceae (7), Paraglomeraceae (4), and within 24 genera: *Acaulospora* (40 morphospecies), *Ambispora* (7), *Archaeospora* (2), *Bulbospora* (1), *Cetraspora* (4), *Clareoideoglomus* (7), *Corymbiglomus* (4), *Dentiscutata* (7), *Diversispora* (4), *Dominikia* (1), *Entrophospora* (2), *Funneliformis* (8), *Fuscutata* (1), *Gigaspora* (7), *Glomus* (29), *Pacispora* (6), *Paradensticutata* (2), *Paraglomus* (6), *Racocetra* (11), *Redeckera* (1), *Rhizophagus* (13), *Sclerocystis* (7), *Scutellospora* (13), *Septoglomus* (3). In consistency with Stürmer et al. (2018), Glomeraceae was the dominant family in South America according to the number of species per family. The next most dominant family was Acaulosporaceae in SA as well as in other parts of the world like North America, Europe and Antarctica, together with the Gigasporaceae family in Africa, Asia, and Oceania.

3.4.2 Arbuscular Mycorrhizal Fungi in South America: Ecological Divisions

We used the primary eighteen ecological divisions of SA described by Kelt and Meserve (2014) and modified by Young et al. (2007) and Josse et al. (2003) (Fig. 3.1). The Amazonia, Atlantic Forest, Caatinga and Chaco were the ecodivisions with the highest species records thus being the main research focus of SA (Table 3.1). Meanwhile, the Cerrado, Moist Pacific Temperate and Pampas showed an intermediate number of species records, while the lowest was observed in the Dry-South Central Andes, Guianan Uplands and Highlands, Llanos, Mediterranean Chile, Moist North-Central Andes, Moist Pacific Mesoamerica and Patagonia.

Morphospecies richness varied from 3 to 68 considering the taxa identified up to genus level. Most of the richest points were located in Brazil, which is considered one of the most biodiverse countries in the world, comprising six biomes with two hotspots: the Cerrado (Brazilian Savanna) and the Atlantic Forest. We observed a general pattern of high AMF richness along the diagonal comprised of the Caatinga, Atlantic Forest, Cerrado (Brazil), Pampas, Chaco (Argentina) and Moist Pacific Temperate (Chile) (Fig. 3.1). Other points of high species richness were located in the Amazonia, Llanos and Moist North Central Andes.

Many authors have discussed evidence about whether the current vegetation of the "savannah corridor" or "diagonal of open formations", which extends across South America from north-northeastern Brazil to the Chaco region of northern Argentina, represents the remnants of a once continuous forests (Prado and Gibbs 1993).

We visualized the similarities of AMF composition among the Atlantic Forest, Caatinga and Chaco in a Venn diagram (Fig. 3.2) using BioVenn (Hulsen et al. 2008).

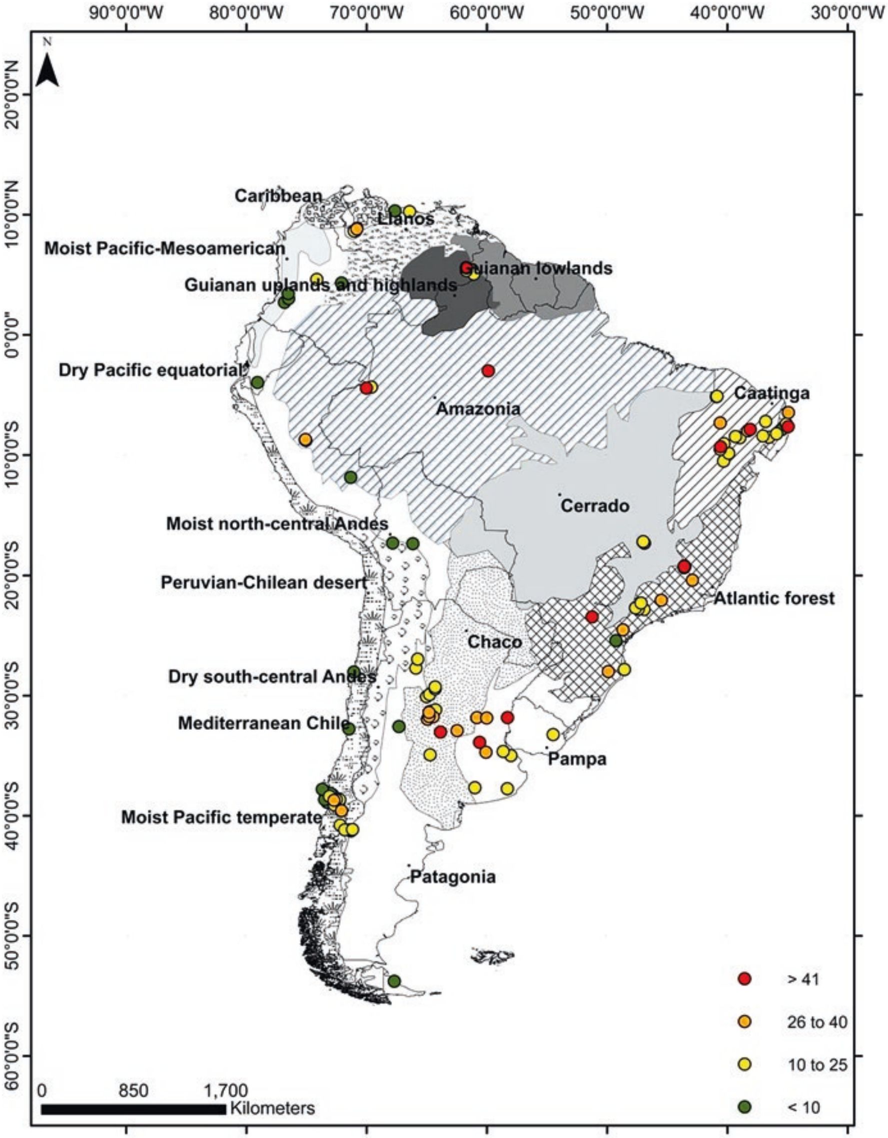

Fig. 3.1 Map with the primary ecological divisions of South America (Kelt and Meserve 2014, modified from Young et al. 2007 and Josse et al. 2003), showing the species richness distribution of AMF cited in the 110 reviewed research articles

The three ecodivisions shared 47 morphospecies of the 154 identified. The Atlantic Forest and Caatinga showed the highest species composition similarities (30), followed by the Atlantic Forest and Chaco (6), and finally by the Caatinga and Chaco (3) which were the most dissimilar ecodivisions. The Atlantic Forest showed 37 unique morphospecies, the Caatinga 16, and Chaco 15.

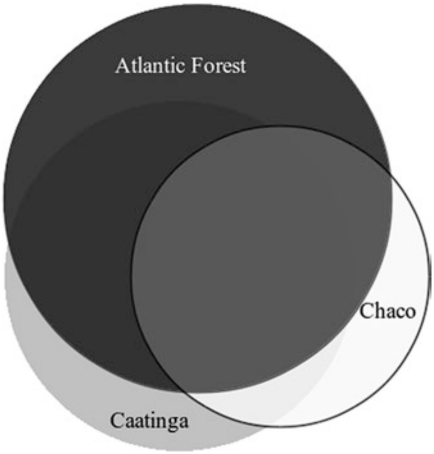

Fig. 3.2 Venn diagram comparing AMF morphospecies occurrence across the diagonal comprised of the Atlantic Forest, Caatinga and Chaco ecodivisions

Acaulospora scrobiculata (84 times recorded), *Claroideoglomus etunicatum* (75), *A. mellea* (67), *A. spinosa* (59), *Funneliformis mosseae* (54), and *Entrophospora infrequens* (49) were the morphospecies more frequently recorded in the studies reviewed. All these morphospecies except for *F. mosseae* occurred in most of the SA ecodivisions (between 11 to 13 of the 15 ecological divisions). Several morphospecies (106) occurred in no more than 3 ecodivisions and were recorded from 1 to 13 times (Table 3.1). These morphospecies could be defined as generalists (e.g. *A. scrobiculata, C. etunicatum* and *A. spinosa*) and specialists (e.g. *A. ignota, A. nicolsonii, A. fecundispora, Bulbospora minima* and *Septoglomus titan*) sensu Oehl et al. (2010). These authors differentiate specialist from generalists considering the number of times a species is found. Specialist morphospecies probably evidence an association with particular niche conditions. In contrast, the generalist species *Acaulospora scrobiculata* was detected in all seven continents (Stürmer et al. 2018) and other generalists such as *A. trappei*, *C. etunicatum* and *R. intraradices* have been commonly found in previous studies carried out in Central Europe (Wetzel et al. 2014; Säle et al. 2015), hence evidencing the worldwide distribution of some AMF taxa.

To evaluate the strength of the association of ecodivisions with AMF morphospecies, an indicator of species analysis was applied using the *indval()* function of the R package labdsv (Dufrene and Legendre 1997; R Core Team 2018; Roberts 2013). The analyses revealed 28 significant AMF morphospecies associated with 12 of the 14 ecodivisions. *G. australe* and *A. scrobiculata* were significantly associated with the Amazonia ecodivision (indicator value = 0.4, P = 0.025; and indicator value = 0.13, P = 0.001 respectively). *C. etunicatum* (indicator value = 0.13, P = 0.002) predominated in the Caatinga ecodivision. *Ambispora callosa* (indicator value = 0.6510; P = 0.005), *A. brasiliensis* (indicator value = 0.5765; P = 0.003), *R. invermaius* (indicator value = 0.4060, P = 0.028), and *R. clarus* (indicator value = 0.2581, P = 0.036) were significantly associated with the Cerrado, and *A. bireticulata* with the Chaco ecodivision. *Dentiscutata nigra* (indicator value = 1.0000; P = 0.013), *Cetraspora striata* (indicator value: 1.0000; P = 0.013), and *Funneliformis geosporum* (indicator value: 0.2238; P = 0.009) prevailed in the Dry South Central Andes; and both *S. crenulata* (indicator value = 0.6667; P = 0.021) and *S. spinosissima* (indicator value = 0.4861; P = 0.047) in the Guianan Uplands and Highlands. *A. morrowiae* (indicator value = 0.2899, P = 0.002) was indicative of the Llanos, and *S. calospora* (indicator value = 0.2971, P = 0.005), *R. diaphanus* (indicator value = 0.2928, P = 0.046), *A. laevis* (indicator value = 0.2842, P = 0.007), and *R. intraradices* (indicator value = 0.2256, P = 0.008) prevailed in the Mediterranean Chile. *Pac. chimonobambusae* (indicator value = 0.8000, P = 0.012), *Par. lacteum* (indicator value = 0.6400, P = 0.041), *S. dipapillosa* (indicator value = 0.4520, P = 0.050), and *A. rehmii* (indicator value = 0.2697, P = 0.008) were significantly associated with Moist north central Andes. Both *A. thomii* (indicator value = 0.3333, P = 0.043) and *G. pallidum* (indicator value = 0.2879, P = 0.050) were preferentially present in the Moist Pacific Temperate, and *F. mosseae* (indicator value = 0.1862, P = 0.002) in Pampas. *A. dilatata* (indicator value = 0.6165, P = 0.008), *A. alpina* (indicator value = 0.5053, P = 0.003) and *A. delicata* (indicator value = 0.3806, P = 0.006) were indicator of Patagonia.

This chapter revealed, that most taxa of Glomeromycota are present in SA, including 62% of the worldwide currently known AMF (~300). The vast majority of the territory is still poorly studied (Fig. 3.1). As a matter of fact, AMF communities in the ecodivisions of the Guianan Uplands and Highlands, Guianan Lowlands, Peruvian-Chilean desert, and the Caribbean are still unstudied. In addition, the Patagonia has been poorly sampled, which validates the idea that AMF diversity of SA will increase in relation to worldwide diversity (Veblen et al. 2015).

The high richness of AMF observed in the diagonal of Caatinga-Chaco is in concordance with other groups of fungi and plants that were located preferentially along these highly biodiverse ecosystems (Greer 2014). Moreover, the diagonal also matches the most studied ecodivisions thus suggesting that biased research may be overestimating AMF diversity. Studies focused on unstudied ecodivisions of this large area should be carried out in order to have a complete picture of the AMF diversity in SA.

3.5 Conclusion

Research on AMF diversity is still scarce in South America. Given the importance of these soil microorganisms for the functioning of ecosystems, it is essential to know their diversity. South America has a great potential to be explored in terms of AMF diversity due to the great diversity of biomes and its geographical extension. Its diversity of AMF represents 62% of the currently worldwide known diversity, and this information coming from studies concentrated only in few regions. It is crucial to generate inventories of species from all the ecosystems of this great region, to isolate fungi obtained and deposit them in germplasm banks. Soybeanization accompanied by monoculture, clearing, fumigation and displacement of peasants increasingly extends the agricultural frontier in this region, thus promoting the loss of biodiversity of the fauna and flora in South America. Therefore, most of the ecoregions that are affected by soybeanization surely have AMF species not yet described for science, which are undoubtedly of great importance for the maintenance of these systems.

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