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Review

The Diversity of Arbuscular Mycorrhizal Fungi and Their Associations in South America: A Case Study of Argentinean and Brazilian Cattle Raising Productive Ecosystems: A Review

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Abstract: Mycorrhizal fungus diversity is an ecosystem health indicator, and thus, the appreciation of the aboveground as well as the belowground biota, such as fungi associated with natural and managed ecosystems, is essential to provide sustainable products and suggestions to farmers. Less is known about the totally arbuscular mycorrhizal fungi (AMF) and fungal endophytes useful to agroecology, which are environment friendly microbial biofertilizers to mitigate the complications of conventional farming. Specific AMF are found in most covers; grassy ecosystems are increasingly investigated through their exclusive fungal species that improve sustainable cultivation. Different grazed pastures, forages, and their diversity are important objects of study either in economic or ecological scope. Based on recent reports, the occurrence of AMF in grasslands and pastures is significant, supporting more diverse AMF than native forests. Therefore, we show current information on these topics. We conducted a Web of Science search of published articles on AMF, pastures, and grasslands and analyzed them. The results confirmed the important role of pH as the driver of AMF diversity distribution between the grassy ecosystems from Argentina and Brazil. In grasslands, the main family represented was Glomeraceae, while pastures maintain predominantly Acaulosporaceae. Brazilian grasslands and pastures presented four times the AMF richness of those from Argentina.

Keywords: arbuscular mycorrhizal fungi; agroecology; pastures; grasslands; cattle raising; Argentina; Brazil

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1. Introduction

Plants and soils are increasingly appreciated along the different terrestrial ecosystems as they support several ecosystem services for high quality human life. However, anthropogenic activities have introduced fertilizers and pesticides in the fields, modifying the biota in the different South American ecosystems [1]. The vast majority of natural ecosystems and agroecosystems are made up of high percentages of plants that form mycorrhizal symbioses. Arbuscular mycorrhizas (AMs) are the ones that predominate in these ecosystems and they are formed by arbuscular mycorrhizal fungi (AMF, Glomeromycota) that colonize the roots and absorption plant's organs, such as rhizoids [1–3]. In South America, plants with great economic importance for Argentina and Chile, wine-producing countries [4], such as vineyards, increasingly cultivated, as well as *Ilex paraguariensis*, "yerba

mate", native to South America, are associated with AMF [5]. Crops such as soybeans are also increasingly cultivated, as near half of the world's soybean production arises from South America [6], and research on soybeans carried out in Argentina showed its colonization by AMF [7–9]. In Argentina, Faggioli et al. [10] also showed the high AMF diversity under soybean fields. As agricultural soils can benefit from microbial inoculants and biofertilizers, plants with AMF associations can obtain sufficient supplies of phosphorus from soils in sustainable crop production [11]. Additionally, other components are the fungal endophytes, which provide nutrients (such as phosphorus, iron, zinc, copper, etc.) from the soil to the plant and also protect the host [12]. These endophytes can be found in various parts of the plant, such as branches, roots, and leaves [13]; however, they are not commonly detected in tropical grasses. For instance, *Brachiaria* spp. from different pastures in Brazil presented 28 taxa of stem-associated endophytic fungi, 18% of isolates belonging to 4 of the most common species [11]. As Tyagi et al. [13] pointed out in their review, these endophytes can be the answer to palliate the conventional farming practices as these are environment friendly microbial biofertilizers that colonize the plant without damage. Endophytes rather help in increasing the growth of plants and also help in abiotic and biotic stress tolerance in host plants. Natural grasslands (hereafter grasslands) are ecosystems where the herbaceous vegetation type prevails, including grasses and other grass-like vegetation instead of pastures, are the grasslands managed by means of cutting or cattle-grazing [14]. Globally, the great terrestrial ecosystem's area is grasslands, covering ca. 40% of the Earth's surface [15]; they are found on all continents except for Antarctica, in a wide range of climates, and on a wide range of soil types. Furthermore, grasslands are overgrazed, and, consequently, soil erosion and weed encroachment are common ecological problems affecting them. Thus, many of the world grasslands are ecosystems functionally impoverished and present degraded conditions [16]. Additionally, pastures are the basic worldwide resources of feed for livestock, and in humid zones, mixed farming systems of managed grasslands supply over 90% of the milk, 70% of the sheep and goat meat, and 35% of the beef. Currently, it is estimated that 26% of the terrestrial surface of the Earth and 70% of the world agricultural lands are covered by grassy ecosystems or grasslands sensu lato (i.e., natural grasslands and pastures), providing support to over 800 million people. Pastures are the principal source for livestock feed, a wildlife habitat, an environmental protection tool, an important in situ conservation of carbon storage, water, and plant genetic resources. Around the world, grasslands and pastures are threatened ecosystems; they are at degradation risk due to the rapid population increase, together with the climate change effects, which have negatively pressured them, affecting more strongly arid and semi-arid environments [17]. Moreover, grasslands and pastures are important to people due to the fact that they are important providers of different ecosystem services (ESs) [14]. Biodiversity is an important factor involved in the ecosystems functioning, and consequently, an essential link in the provision of ESs [18,19]. Health and quality of soil ecosystems are directly involved in agronomical practices, and soil microbial communities play an important role in soil sustainability [20]. Among soil microorganisms, AMF and bacteria [21] are proposed as the key organisms for soil sustainability due to their capability to promote soil biodiversity and functioning [22]. Furthermore, AMF are a key functional group of the soil biota involved in agricultural grassland's management and productivity with potential capabilities for sustainable production by ESs [23]. However, the effects of herbivory on AMF are controversial due to their responses to grazing are context-dependent, directly related to the carbon flux within the plant-AMF-soil system, to the intensity and extent of grazing over time, to the mycorrhizal dependence of the grazed plant's species, and to the adaptation of AMF and their host plants to grazing [24–28].

In general, the natural grasslands of South America have grown on soils with low fertility [29], except for the Pampas of Argentina, southern Chile, and the southern portion of Uruguay. Furthermore, the environmental features of most of the South American regions occupied by grasslands are highly vulnerable to excessive use [30]. As early as 1993, it had been warned that the "extent of the degradation process of these savannas

could be larger than in other savannas of the world. Their fragility would reflect also less resilience due to the weakness of the natural resources and the abusive utilization" [31]. This erosive problem has also been observed by Modernel et al. [32], who emphasized the negative effect that it entails for the provision of ESs of these biomes. Globally, six major areas of livestock concentration were observed, namely the Central and Eastern United States, Central America, Western and Central Europe, India and China, and South America, South Brazil, and Northern Argentina [33]. Moreover, native grasslands in the Pampas and Campos in Argentina, Brazil, and Uruguay in southern South America have produced beef cattle since the 16th century. These grasslands provide feed for 43 million cattle heads and 14 million sheep, with small external input additions. In a meta-analysis conducted using published and secondary data between 1945 and 2015, Modernel et al. [32] have examined the ESs provision and its relationship with land use changes by these grasslands that are considered biodiversity hotspots. In the Pampas and Campos, they have registered 4000 native plant species, 300 bird species, 29 mammal species, 49 reptile species, and 35 amphibian species inhabiting the biome. However, and surprisingly, fungi, and especially AMF, have not been considered in that meta-analysis despite the biodiversity survey being carried out exhaustively.

Data from the Southern Hemisphere are scantly represented among global biodiversity studies; particularly, fungal and mycorrhizal fungi and their symbioses are underrepresented [34,35]. This biodiversity information lacks in contradiction to the high biodiversity of South American hotspots and ecosystems still understudied and which need to be conserved [36]. In addition to the above, when the scientific production of South American mycorrhizal biodiversity was analyzed, Brazil had the higher number of publications on those issues, followed by Argentina [37]. These countries represented the higher number of available data on mycorrhizal associations and their biodiversity to be used as data sources. Argentina and Brazil are the South American countries that present more publications related to plant and mycorrhizal associations [37,38] and the main number of studies also in AMF diversity [39]. However, the relationship between AMF, cattle raising, and grasslands remains unexplored.

1.1. Grasslands and Pastures

The vegetation types with prevalence of Poaceae grasses and other grass-like vegetation are considered natural grasslands or grasslands, and the those managed for cutting or cattle-grazing are named pastures. Grasslands present great ecological, economic, and social values [16] but continue to receive limited scientific attention. The microbiota associated with grassland vegetation was also under-investigated in the past time [40]; however, during the last five years, the interest in studying these plant–microbe interactions has been promoted [41–46]. Among the microbiota associated with the grassland plant species, the AMFs represent important components interconnecting soil and plants through the hyphal networks and secreted substances, such as glomalin, useful to the restoration and sustainability of these for these valuable ecosystems at risk [47].

Earlier, Modernel et al. [32] and recently Bengtsson et al. [48] listed those ESs provided by natural and semi-natural grasslands, from South America, Africa, and Europe such as those related to soil organic carbon stock, climate change mitigation, water provision, nutrient cycling and erosion control, including fodder production, cultural, connected to livestock production, and population-based regulating services (e.g., pollination and biological control) which are connected to biodiversity. They also showed that these grasslands can supply additional non-agricultural services, such as water supply and flow regulation, carbon storage, erosion control, climate mitigation, and cultural ESs.

Three major types of grasslands can be distinguished within agricultural production systems: natural, semi-natural, and improved grasslands [49,50]. Then, Franzluebbers et al. [51] reviewed the agronomic and environmental impacts of pastures and crop rotations in South America, showing the benefits of pastures grown before crops, such as enhancement of soil organic matter in the soil surface with perennial pastures, improve-

ment in water infiltration and water quality, and synergies between crop and livestock systems. Thus, more studies are needed on the management of grasslands for fodder and meat production. Nowadays, pastures have obtained increasing importance worldwide due to the need of sustainable management for increasing their productivity. There is also much interest to improve grassland resilience under environmental alterations [52]. Several reports showed that pasture species were highly mycorrhizal dependent [53]. Moreover, spore density can be low in intensively managed pastures, but fungal richness can be high in semi-natural pastures compared to native grasslands and forests, which are usually used as a reference of pristine ecosystems. In this work, we show significant reports from Argentina and Brazil and explore them.

1.2. Mycorrhizal Symbioses in Temperate Grasslands and Pastures

Higher species richness (42 AMF species) was recovered from seminatural subtropical pastures in Portugal [54]. However, only two species were shared between subtropical and tropical pastures. Notably, *Scutellospora calospora* was a common species in pastures. In general, other species are frequently found preferentially in native forests, such as *Acaulospora lacunosa* [54], *Acaulospora spinosa*, *Ambispora brasiliensis*, *Dentiscutata heterogama* [55]. Under intensively managed pastures, some AMF, such as Claroideoglomeraceae, dominated soils [54]. Pastures grazed by domesticated livestock and products from cows are crucial for milk and cheese production [56].

Grasslands in a good state of conservation present a high abundance and diversity of Glomeromycota species [57,58]) capable of contributing to great ecological and environmental values due to their multiple attributes and functional traits. Grassland ecosystems, where many late successional native plant species are highly dependent on symbiotic interactions with AMF [53], are especially influenced by AM fungal associations. Although AMF have been more extensively studied in temperate grasslands compared to any other biomes [59], "temperate grassland" is a broad classification that encompasses many different ecosystem types, such as tallgrass prairies or shortgrass prairies with distinct plant and fungal communities that may respond differently to perturbations. The C for nutrient exchange dynamics between plant hosts and AMF has been well described in highly controlled systems (e.g., laboratory, greenhouse, agronomic blocs) [60–62] and in field experiments focused on one or two grass species [63–66]. However, monoculture or species-specific responses are not readily scaled to diverse grasslands. Due to their importance in plant-nutrient cycling and the differential nutrient distribution patterns between AMF taxa [67], an ecosystem-scale understanding of the drivers of AMF distribution patterns is needed [68].

This work reviewed the impact of cattle raising on soil propagule multiplication and the diversity of the indigenous AMF species by comparing the AMF diversity in South American grasslands and pastures with special focus in Argentina and Brazil, where only 1% to 10% of these areas are protected [69]. In this review, we focused on the natural and agronomic grassy ecosystems, with economic importance for the different regions of South America, with details for Argentina and Brazil, two South American countries with the highest number of publications in AMF diversity [37,39,70], and their associations in grasslands and pastures [71,72].

2. Materials and Methods

During March to October 2022, a Web of Science search of articles published through these dates was conducted based on selected papers included in the database focusing on AMF diversity, grasslands, and pastures. The search was focused in Argentina and Brazil in South America. Six different sets of keywords were used in order to increase the number of publications obtained: "arbuscular mycorrhizal fungi grassland Brazil OR arbuscular mycorrhizal fungi pasture Brazil OR arbuscular mycorrhizal fungi grassland Argentina OR arbuscular mycorrhizal fungi pasture Argentina OR hongos micorrícicos arbusculares pastizales Argentina OR hongos micorrícicos arbusculares pasturas Argentina".

Each publication was revised, and those that did not conduct a direct analysis of AMF in Argentina and Brazil grasslands and pastures were excluded from the dataset. A database was carried out, including AMF species, grassland ecosystem type (grassland, pasture), citation, country (Argentina, Brazil), coordinates (UTM system), biodiversity variables measured (spore density, spore abundance, richness), and soil-climatic variables (precipitations, Koopen climatic type, pH, phosphorous concentration, and soil type).

The data obtained were analyzed using non-metric multidimensional scaling (NMDS) to visualize and assess patterns of dissimilarity between pastures and grasslands based on their AMF species composition. Then, similarity analyses (ANOSIM) were performed to test the hypothesis of differences in species composition between pastures and grasslands. The ANOSIM analysis applied was based on a Jaccard dissimilarity matrix using species presence/absence data; p values were obtained from 999 permutations. To discriminate the differences by country (Argentina vs. Brazil) and by grassy ecosystem type (grassland vs. pasture), a cluster analysis was carried out. Additionally, a Spearman correlation analysis was performed between species richness and soil-climatic variables. Further, all statistical analyses were performed using the R statistical software (vegan and BiodiversityR inversion 3.3.2 packages).

3. Results and Discussion

3.1. Argentina

Sustainable production is increasing worldwide [73]. Sustainable agroecosystems in Argentina are also increasingly established. Additionally, sustainable wine production is more studied and the sustainability of traditional management in different vineyard systems in Berisso, Buenos Aires province, Argentina was evaluated [74], comparing the conventional management to organic; however, they did not evaluate the mycorrhizal associations in those fields.

In Argentina, AMF diversity in grassy ecosystems (Figure 1) was registered in very different biogeographic areas. Furthermore, grasslands were widespread along a wide range of bioclimatic regions, including megathermic grass communities in Chaco and Mesopotamia, mesothermic in Espinal, Monte, Pampa, and Prepuna, but also microthermic in Patagonia and Puna, whereas most of pastures studied were placed in the Pampa region [75], occupied by mesothermic grasses, and only one pasture was reported in the Espinal (Figure 1). In addition, in these mega-, meso-, and microthermic grass communities, the proportion of grass species changes in their photosynthetic pathways (C_3 or C_4), with the higher number of C_4 grass species inhabiting arid and semiarid and hot areas with a replacement with C_3 species accompanying the temperature decrease and elevation increase in microthermic grass communities [75]. Moreover, these mesothermic and microthermic grasses are included in the temperate grasslands, such as Pampas and southern Campos (Figure 1) [75], with co-dominance of C_3 and C_4 grasses accompanied by scant shrublands and forests; these gassy systems are also considered as temperate subhumid grasslands [76] or the Río de la Plata grasslands because their continuous plain extensions are surrounding the estuary of the "Río de la Plata" along eastern Argentina, Uruguay, and southern Brazil; see [76] and references therein. Although Pampas and southern Campos show similar physiognomic and vegetation uniformity, it is possible to separate these temperate grasslands biogeographically into vegetation units such as Rolling Pampa, Mesopotamic Pampa, Flat Inland Pampa, West Inland Pampa, Flooding Pampa, and Austral Pampa [69,77]) and Northern Campos and Southern Campos [78]. Megathermic grasses in Chaco grasslands are characteristic [75] of the Argentine Dry Chaco that involved the 69% of the total South American Chaco region, together with the dry forest and savannas. In this region with annual rainfall highly variable, natural grasslands are under a strong degradation process, probably due to the main cattle grazing production system in this region based on sedentary cattle managing results in overgrazing; in addition, only 12% of the region's area is protected [79].

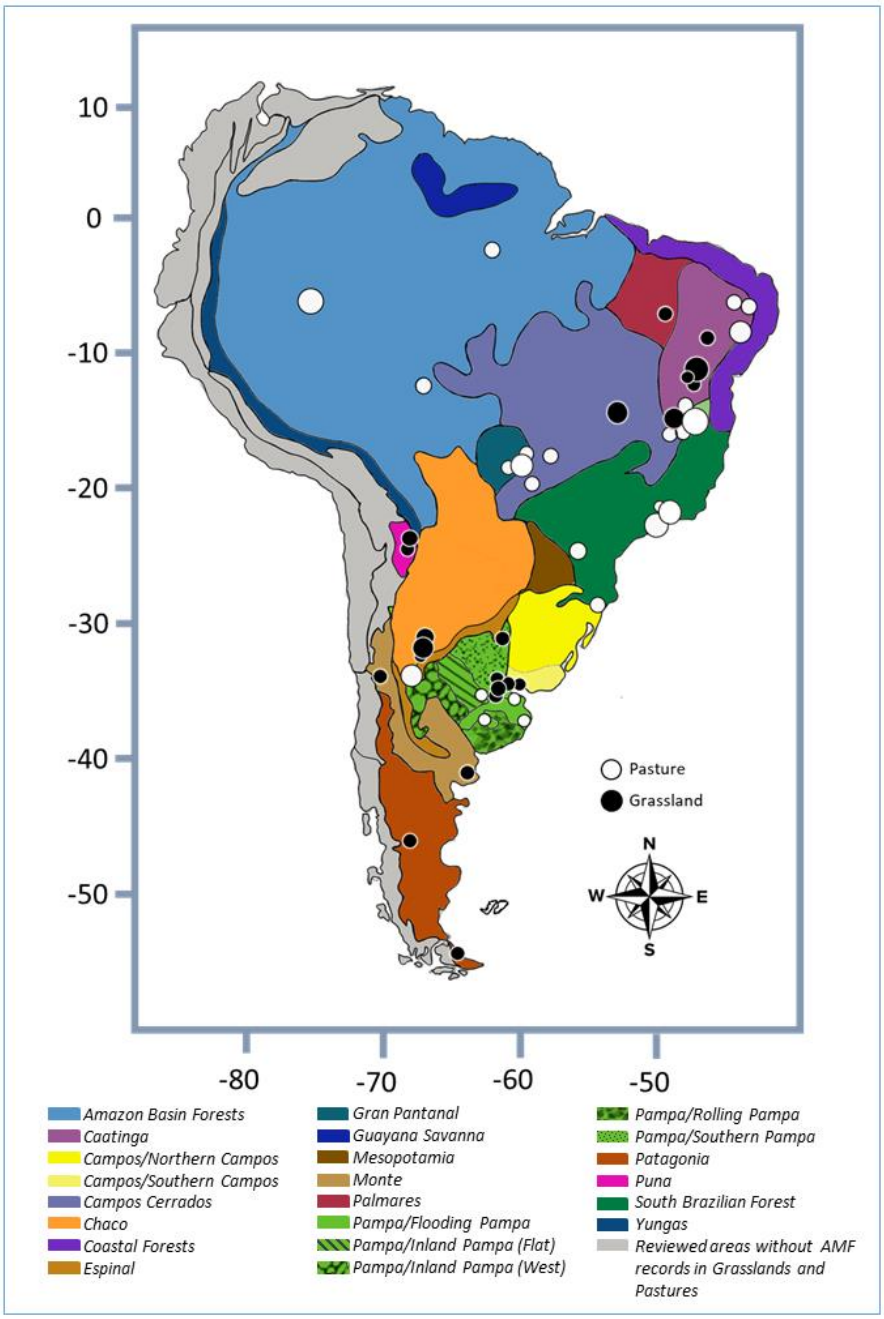


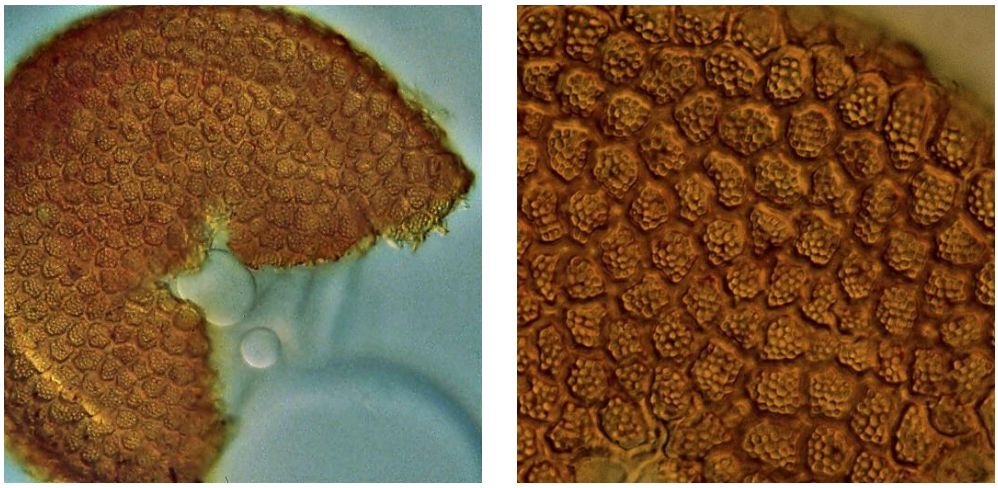
Figure 1. AMF distribution in Argentinean and Brazilian grasslands and pastures among South American grassy environments. Reference: The map's marked points indicate the data obtained from the reviewed bibliographic citations, and the sizes of the points are correlated with the number of citations found for each site.

Moreover, C_3 or C_4 synthetic pathways are correlated to the adaptation to and distribution of grasses at different environmental conditions; thus, megathermic C_4 grasses are able to settled in more hot and dry environments than microthermic C_3, which grow in cold environments and highlands or montane grasslands, and C_3 grasses replace C_4 with elevation increments [75–77,79–81]. Additionally, C_3 or C_4 photosynthetic pathways in Poaceae are correlated to the degree of dependence for the growth of the grass species on their AMF fungal symbiont or mycotrophy; thus, C_3 grasses are in general facultative mycotrophs and C_4 hosts are mainly obligate mycotrophs [82–84]. In Argentinean grasslands, AMF diversity was negatively affected by elevation in Puna grasslands, although

grass AMF colonization was related more to the photosynthetic pathways of grasses than to the elevation increase [71,85–87]. In Chaco highlands, AMF diversity was related to many AMF taxa differentially associated with C_3 or C_4 grasses [71,88]. In microthermic C_3 grasslands of the Patagonia steppe, AMF diversity was affected by cattle racing, thus AMF spore abundance decreased under intense grazing [89]; in the southern microthermic grasses in Tierra del Fuego, sheep grazing further accompanied a low abundance of spores and richness of AMF [90]. Moreover, AMF colonization in C_3 grasses in the southern Monte region was also negatively influenced by experimental defoliation [91] at the field level.

Among Argentinean pastures, they were mainly encompassed in the Pampa region, with few exceptions for Espinal pastures of *Eragrostis curvula* (Schrad.) Nees. (Figure 1). Along communities of mesothermic grasses of the Pampa region, the AMF family's diversity and root colonization have been shown to be good indicators of soil pH and exchangeable Na features and of management conditions such as herbicide use [92]. In these pastures, Glomeraceae was the most abundant family under cattle grazing [72], and similar results have been registered in Tierra del Fuego natural grasslands used as sheep pastures [90] and for C_4 *E. curvula* monospecific pasture in the Espinal region with prevalence of rhizophilic AMF guild followed by ancestral and a few edaphophilic species [93,94].

From 1997 to 2023, AM symbiosis and AMF diversity were studied in Argentinean grasslands and pastures. During the last decade, twenty-five AMF species were registered in eleven publications (Table 1) belonging to genera *Acaulospora*, *Ambispora*, *Dentiscutata*, *Entrophospora*, *Funneliformis*, *Gigaspora*, *Glomus*, *Pacispora*, *Rhizoglomus*, *Rhizophagus*, *Sclerocystis*, *Scutellospora*, and *Septoglomus*. Along the same period and similar scientific publications from these Brazilian ecosystems, the AMF richness registered was four times higher than in Argentinean systems (Table 1). Although in the last ten years, most of the AMF genera were found in ecosystems from both countries ecosystems, some were exclusively reported in Brazil, such as *Archaeospora*, *Cetraspora*, *Diversispora*, *Fuscutata*, *Oehlia*, *Paraglomus*, and *Sieverdingia* (Table 1). Thus, Brazilian grasslands and pastures presented in this decade four times the AMF richness of those from Argentinean ecosystems; some taxa found in these ecosystems are illustrated belonging to the most represented Glomeromycota families, such as Acaulosporaceae (Figure 2), Ambisporaceae (Figure 3), Diversisporaceae (Figure 4), Entrophosporaceae (Figure 5), Gigasporaceae (Figure 6), Glomeraceae (Figure 7), and Scutellosporaceae (Figure 8).



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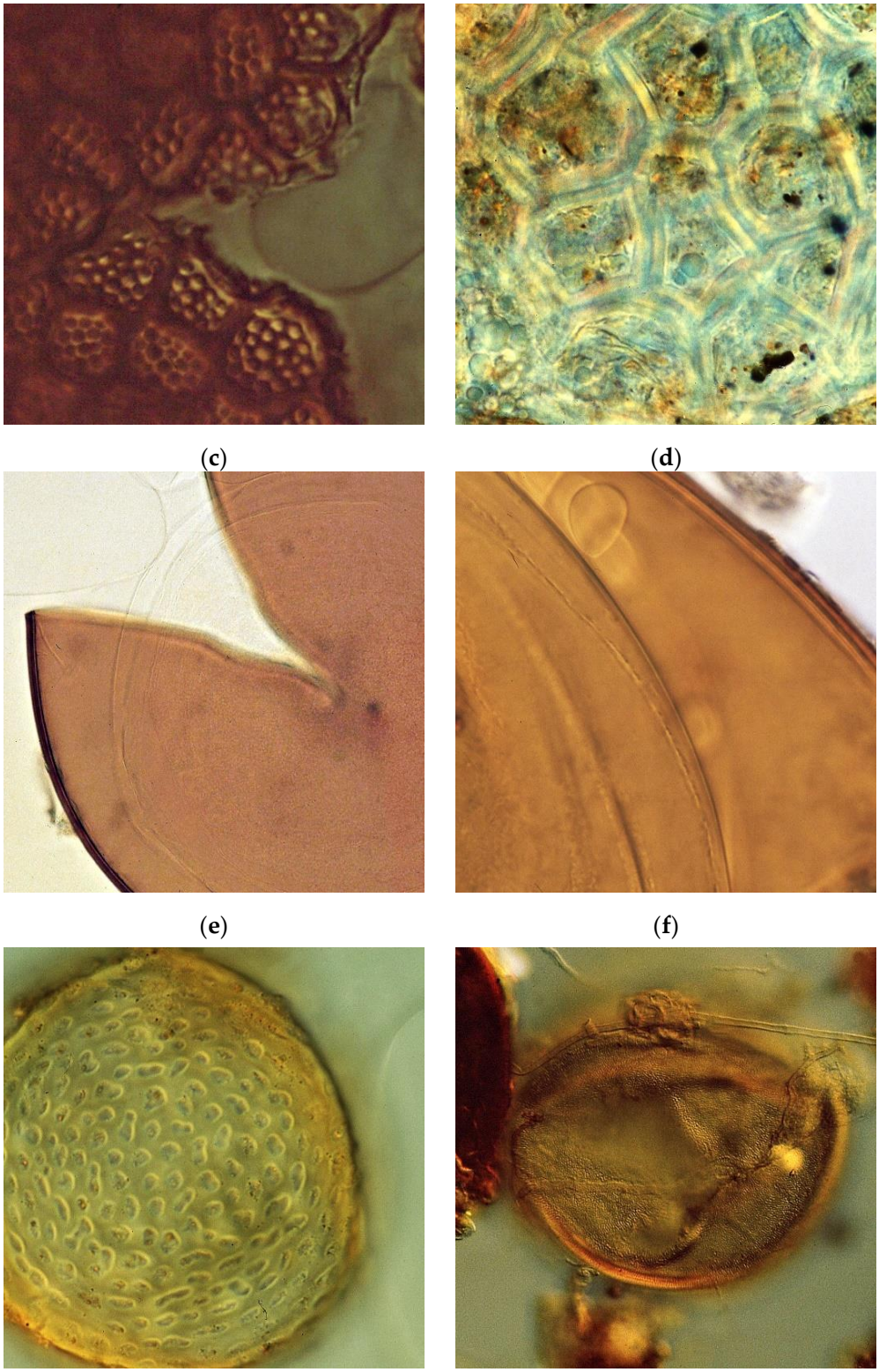

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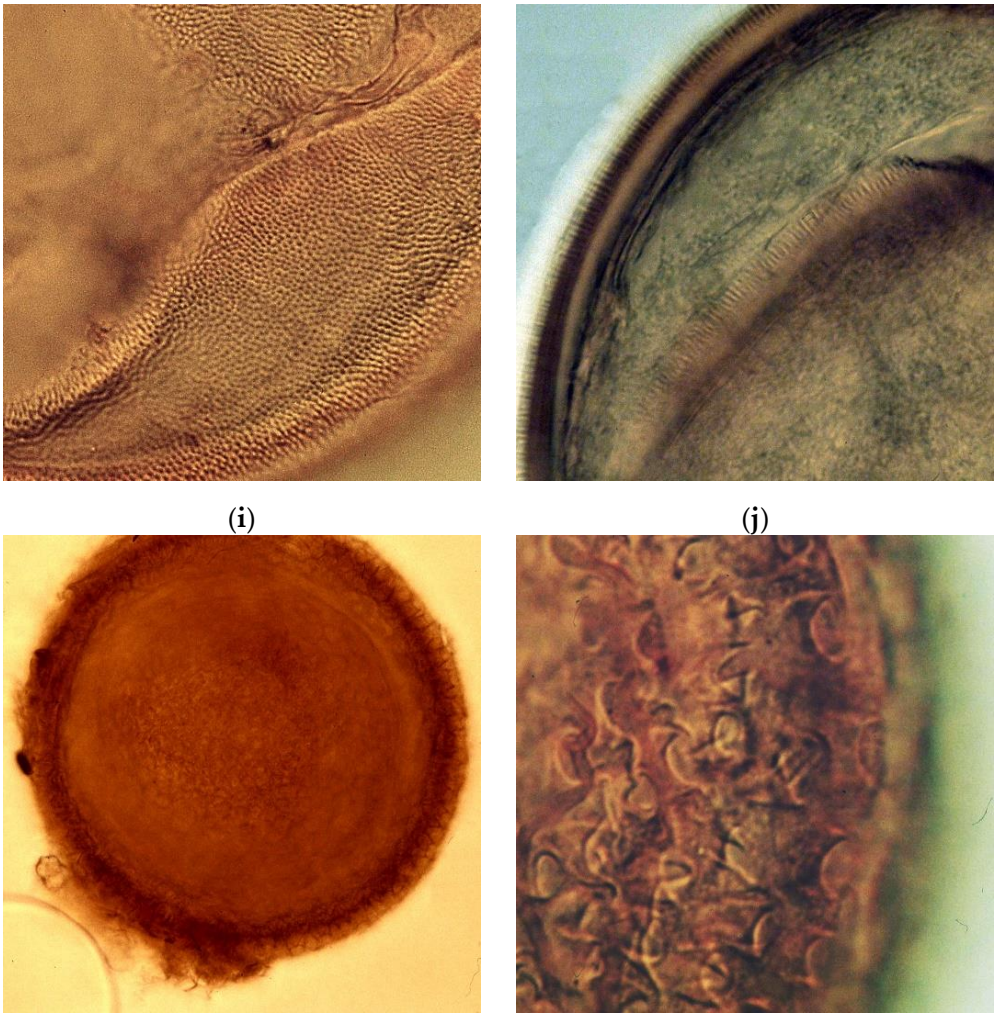
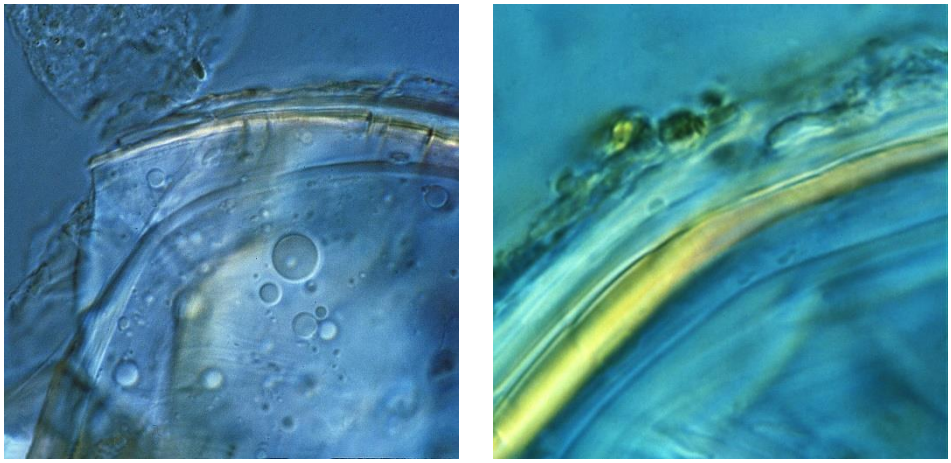


(**i**) (**j**)

(**k**) (**l**)

Figure 2. Acaulosporaceae in grasslands and pastures of Argentina and Brazil. AMF spores of *Acaulospora bireticulata* (**a**–**c**), *A. excavata* (**d**), *A. laevis* (**e**,**f**), *A. scrobiculata* (**g**), *A. spinosa* (**h**–**j**), and *A. tuberculata* (**k**,**l**) recorded in this study.



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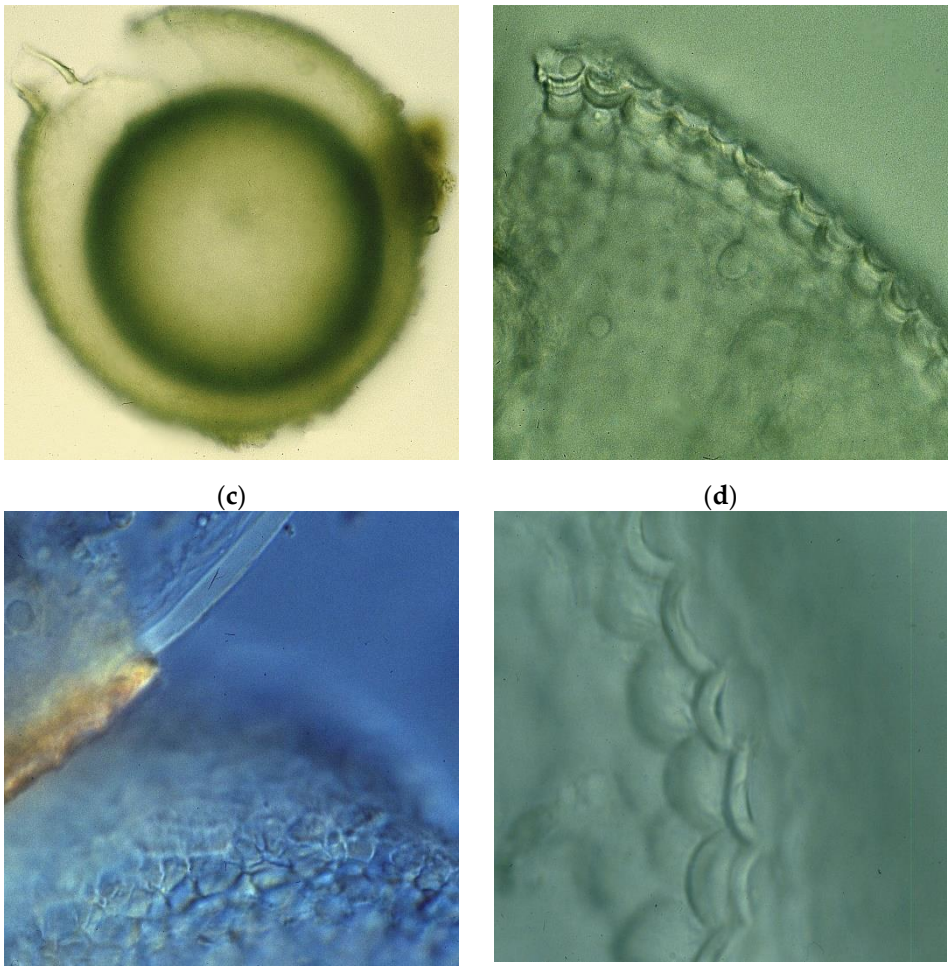
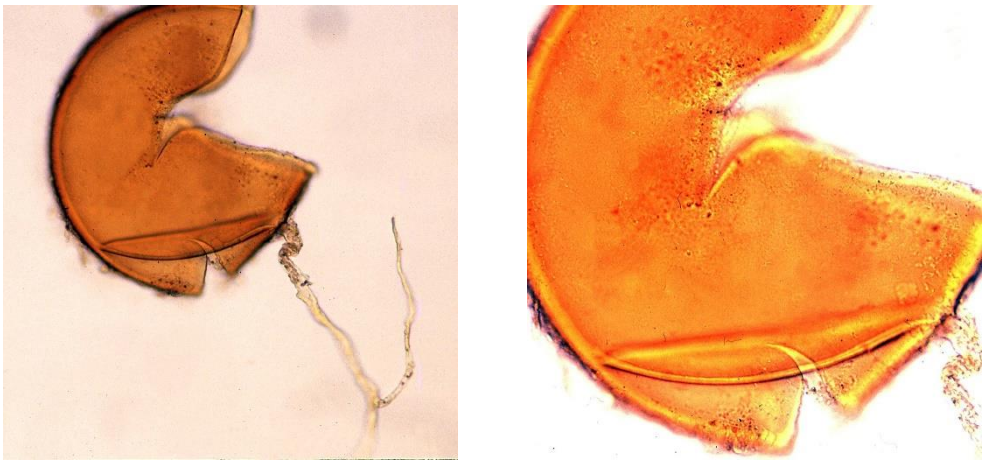


(**c**) (**d**)

(**e**) (**f**)

Figure 3. Ambisporaceae recorded in grasslands and pastures of Argentina and Brazil. AMF spores of *Ambispora gerdemannii* (**a**,**b**), *Am. Leptoticha* (**c**–**f**).



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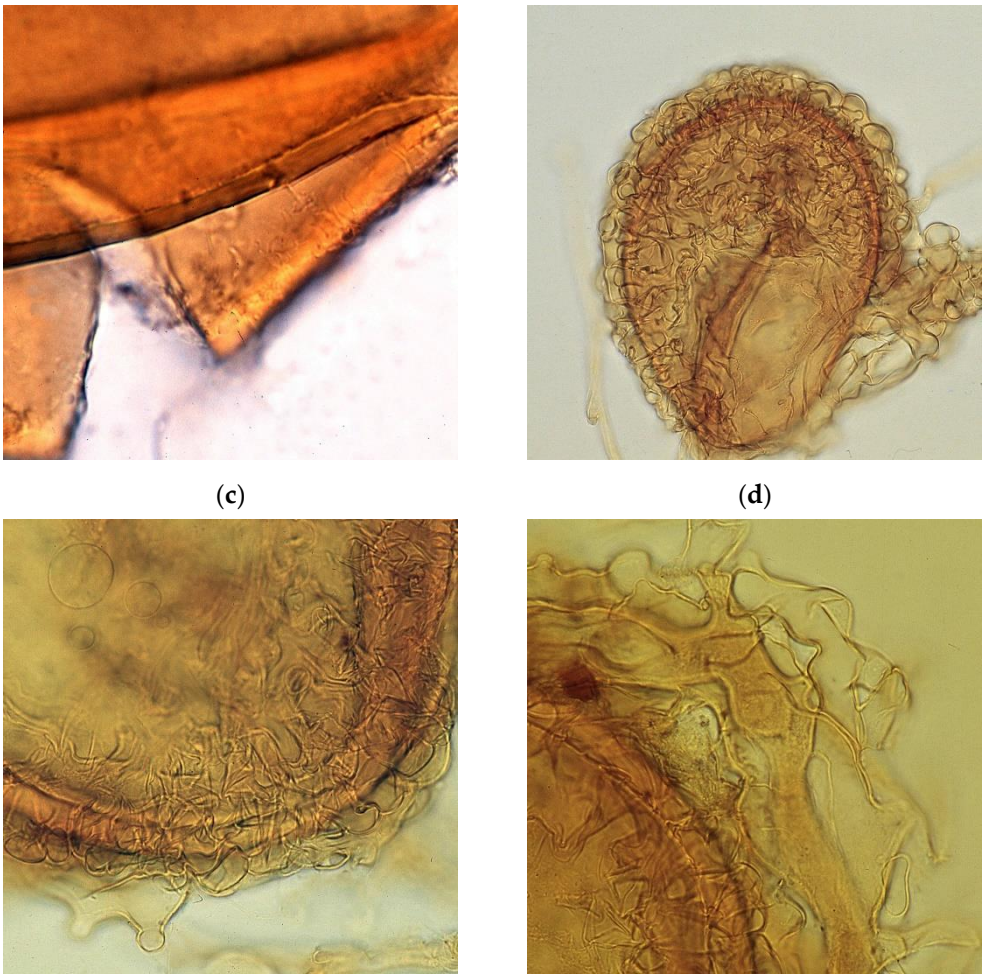
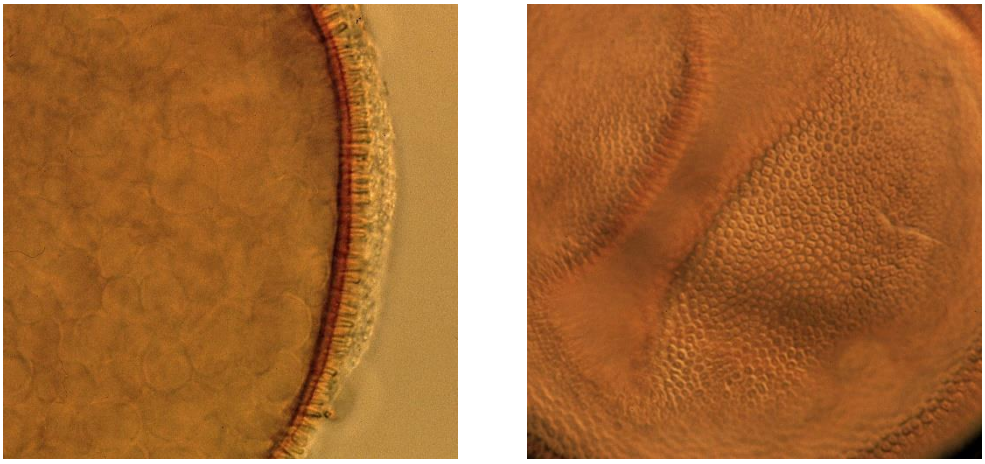


(**c**) (**d**)

(**e**) (**f**)

Figure 4. Diversisporaceae recorded in grasslands and pastures of Argentina and Brazil. AMF spores of *Diversispora* sp. (**a**–**c**); *Sieverdingia tortuosa* (**d**–**f**).



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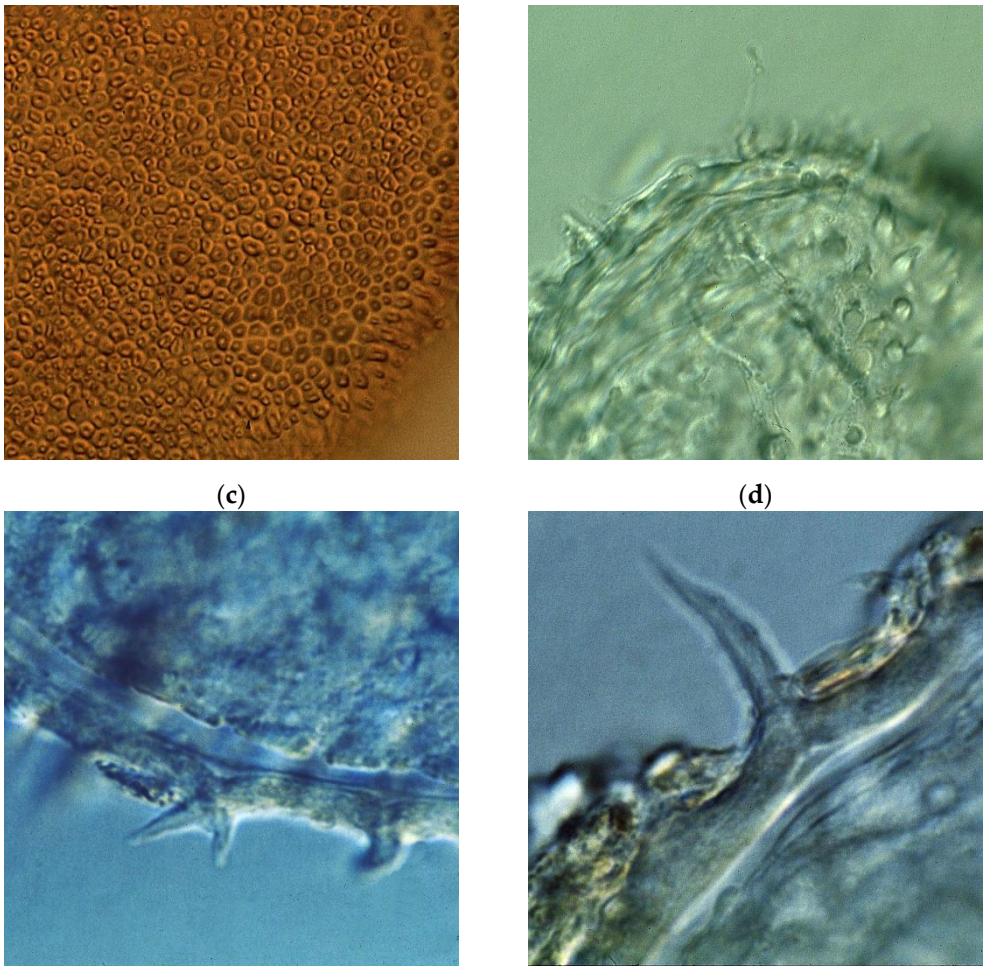
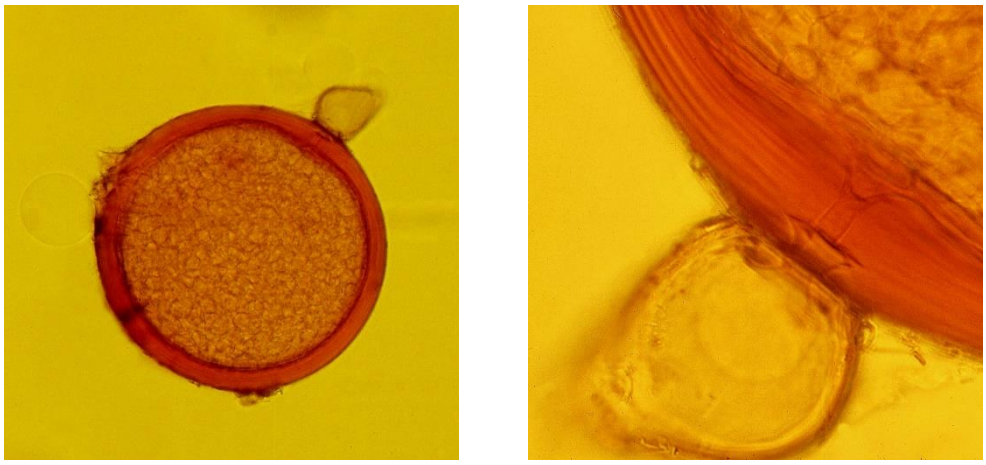


(**c**) (**d**)

(**e**) (**f**)

Figure 5. Entrophosporaceae recorded in grasslands and pastures of Argentina and Brazil. AMF spores of *Entrophospora infrequens* (**a**–**c**), *E. nevadensis* (**d**–**f**).



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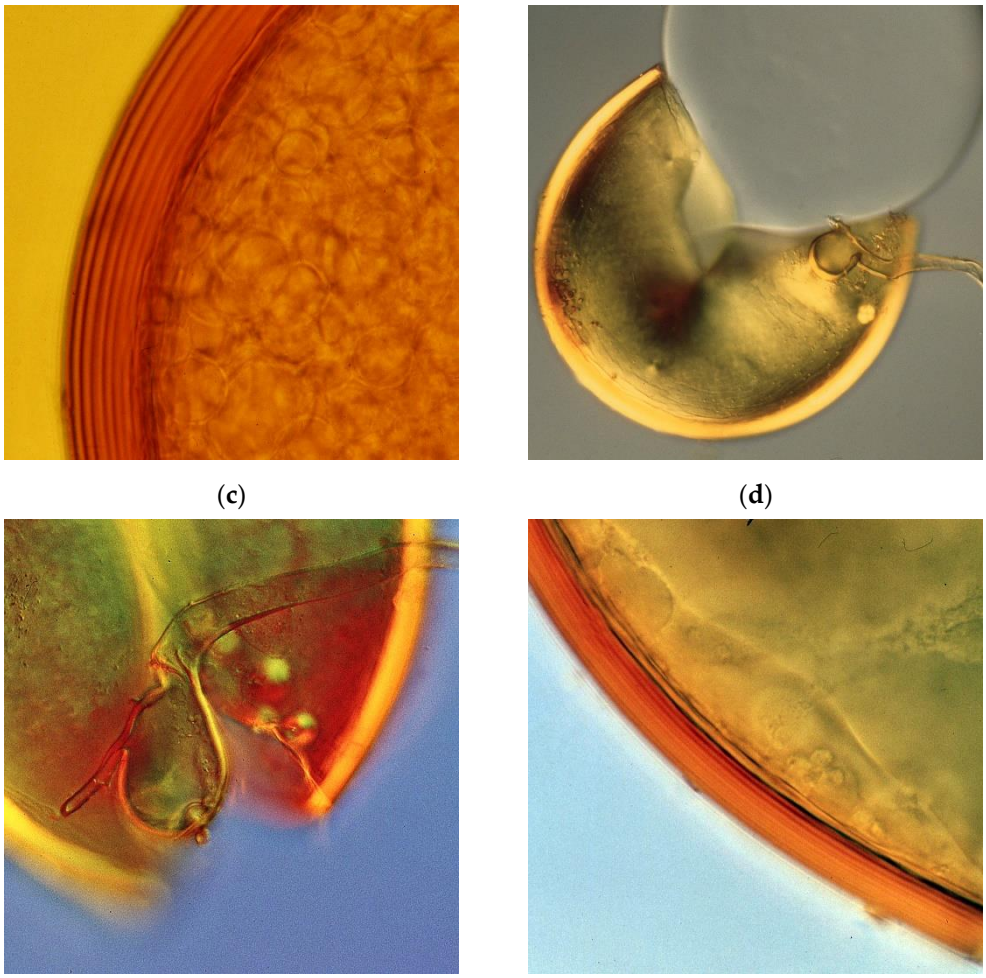

(**c**) (**d**)

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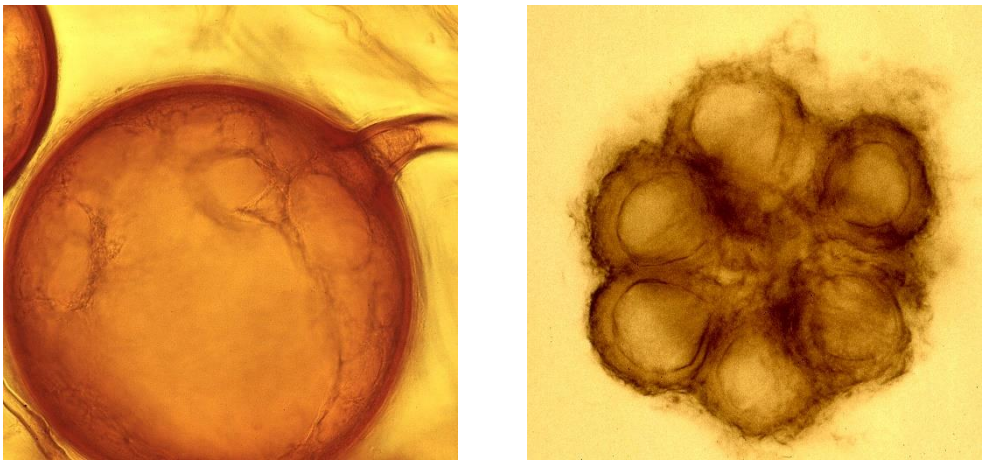
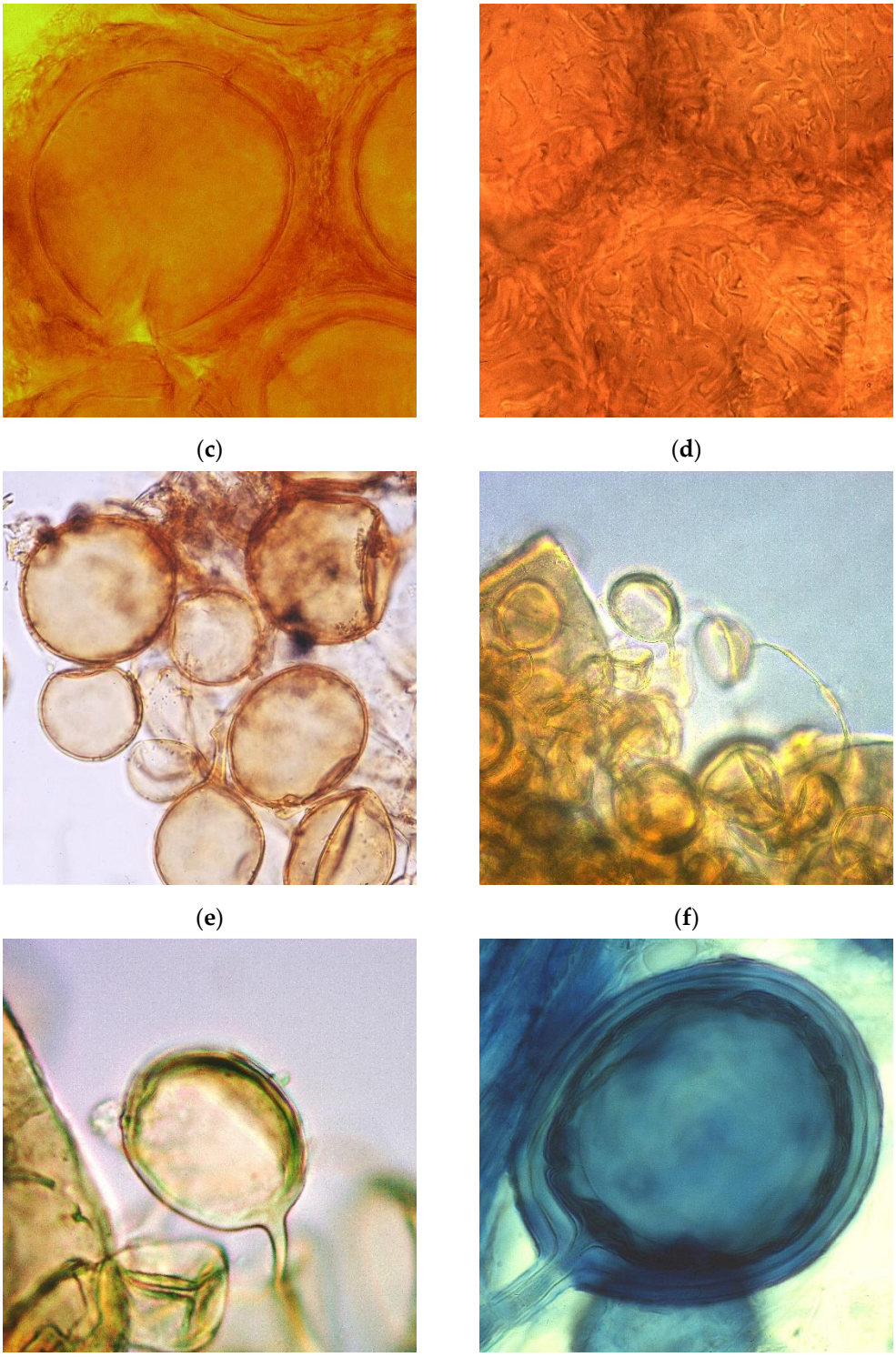
Figure 6. Gigasporaceae recorded in grasslands and pastures of Argentina and Brazil. AMF spores of *Dentiscutata* sp. (**a**–**c**), *Gigaspora* sp. (**d**–**f**).



(**a**) (**b**)

Figure 7. *Cont.*

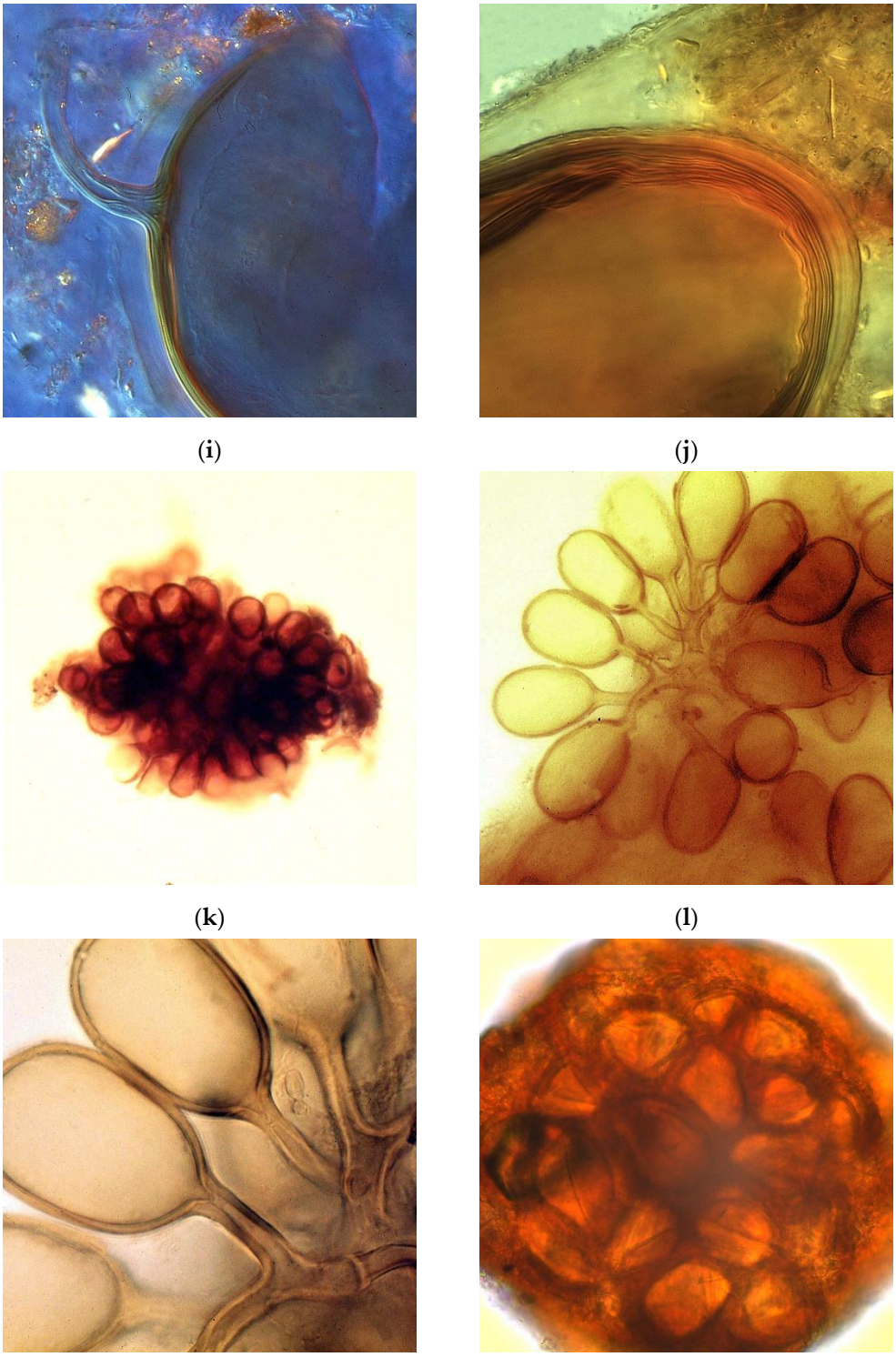


(**c**) (**d**)

(**e**) (**f**)

(**g**) (**h**)

Figure 7. *Cont.*



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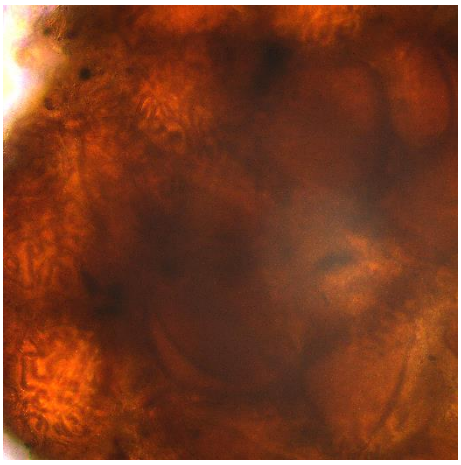
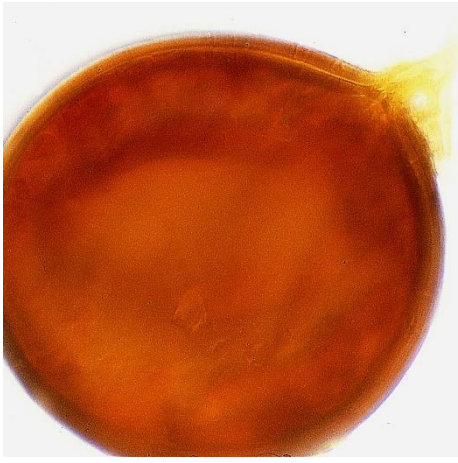
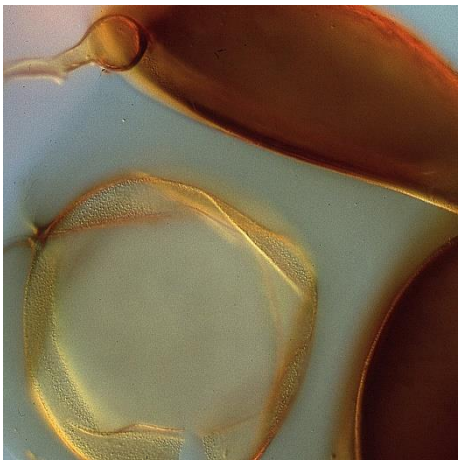


(**o**)

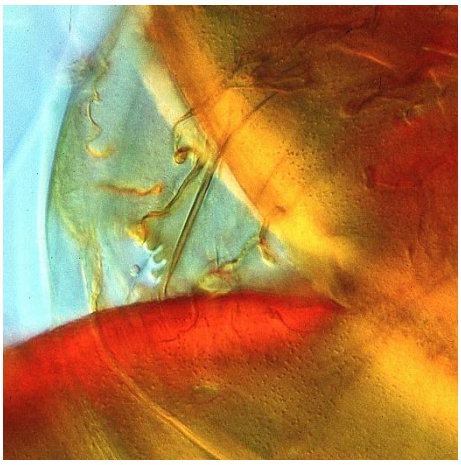


(**p**)

Figure 7. Glomeraceae recorded in grasslands and pastures of Argentina and Brazil. AMF spores of *Funneliformmis mosseae* (**a**), *Glomus fuegianum* (**b**–**d**), *Rhizoglomus microaggregatus* (**e**–**g**), *Rhizophagus intraradices* (**h**–**j**), *Sclerocystis rubiformis* (**k**–**m**), *S. sinuosa* (**n**,**o**), *Septoglomus constrictum* (**p**).



(**a**)



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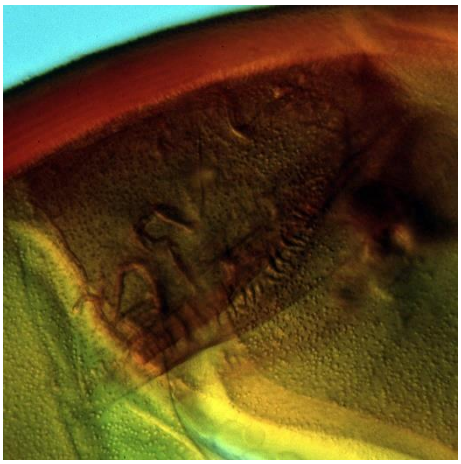
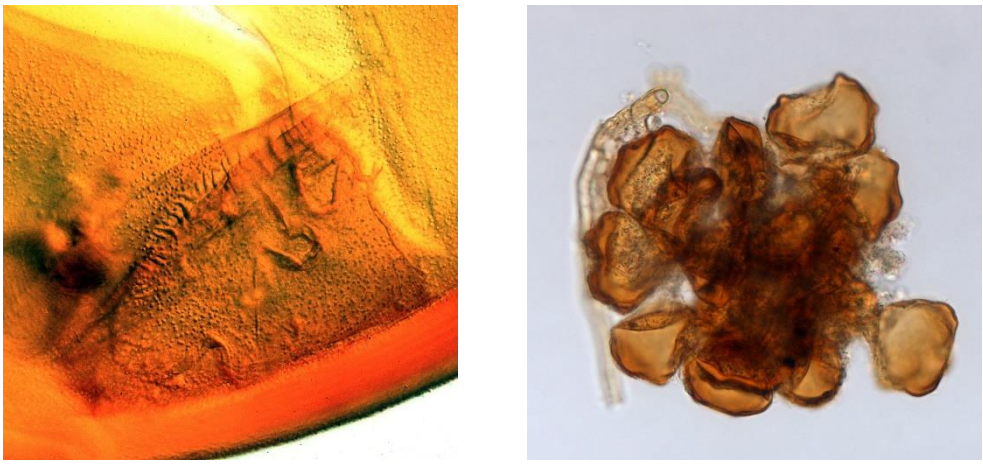


(**d**)

Figure 8. *Cont.*



(**e**) (**f**)

Figure 8. Scutellosporaceae reported in grasslands and pastures of Argentina and Brazil. AMF spores *Scutellospora biornata*, general view (**a**); ornamentations in two spore layers (**b**,**c**); scutellum in the inner spore layers (**d**,**e**); auxiliary cells from Scutellosporaceae (**f**).

3.2. Brazil

In Brazil, AMF diversity was recorded along diverse all-grassy ecosystems (Figure 1); thus, temperate subhumid grasslands covered the southern Brazil in the southern Campos region, and there are also tropical and subtropical grasslands [75,76]. However, these were distributed only along megathermic grass communities and are considered tropical grass ecosystems; thus, C_4 grasses prevail among them [75]. Therefore, throughout these tropical and subtropical grasslands, central savanna and Cerrado grasslands, there is vegetation covering large extensions [69,76], mainly by obligate mycotrophic C_4 grasses [82–84] with a high probability of being associated with AMF. Additionally, permanent tropical pastures also involved C_4 grasses, such as *Brachiaria* sp., that are commonly established in Brazil; those pastures allocate frequent AMF species, like *Acaulospora mellea, Claroideoglomus etunicatum*, *Dentiscutata heterogama, Funneliformis geosporus*, and *Scutellospora calospora* [95].

Exclusive AMF species are generally found in different plant communities such as in the pastures of Amazonia, Brazil, or under forest. Most of the species included Acaulosporaceae (*Acaulospora*) (Figure 2), Diversisporaceae (*Diversispora*), Gigasporaceae (*Gigaspora*, *Scutellospora*) (Figures 4 and 5), Glomeraceae (*Glomus* and *Rhizophagus*) (Figure 7), and *Scutellospora* (Figure 8) (Table 1). The species richness of Acaulosporaceae was higher in pastures compared to forest, while the species of Glomeraceae and Gigasporaceae were in higher numbers in forest [55].

Table 1. Arbuscular mycorrhizal fungi (AMF) species from grassy ecosystems in South America during the last decade.

AMF Species	Vegetation Type	Reference	Country
Acaulospora bireticulata	Grassland; Pasture	[96,97]	Argentina
Acaulospora cavernata	Pasture	[97]	
Acaulospora excavata	Grassland; Pasture	[91,98]	
Acaulospora laevis	Grassland; Pasture	[91,96,99,100]	
Acaulospora scrobiculata	Grassland; Pasture	[92,97–99]	
Acaulospora spinosa	Grassland; Pasture	[92,99–102]	
Ambispora leptoticha	Grassland; Pasture	[91,92]	
Dentiscutata heterogama	Grassland	[96,99]	
Entrophospora claroidea	Grassland; Pasture	[92,97,99,100]	
Entrophospora etunicata	Grassland; Pasture	[91,92,96,97,99,100]	

Table 1. *Cont.*

AMF Species	Vegetation Type	Reference	Country
Entrophospora infrequens	Grassland; Pasture	[92,97,99–102]	
Entrophospora nevadensis	Grassland; Pasture	[92,97,100]	
Funneliformis badium	Grassland	[98,102]	
Funneliformis mosseae	Grassland; Pasture	[89,91,92,97,99–102]	
Gigaspora candida	Grassland	[96,99]	
Gigaspora margarita	Grassland; Pasture	[97,102]	
Glomus fuegianum	Grassland	[98,102]	
Glomus hoi	Grassland	[98,102]	
Pacispora scintillans	Grassland	[98,102]	
Rhizophagus intraradices	Grassland; Pasture	[92,98,102]	
Sclerocystis sinuosa	Grassland	[101]	
Scutellospora biornata	Grassland; Pasture	[92,96,99]	
Scutellospora calospora	Grassland	[89,96,99]	
Scutellospora dipapillosa	Grassland	[89,96,99]	
Septoglomus constrictum	Grassland; Pasture	[92,97,99–101]	
Acaulospora sp. 1 [103]	Pasture	[103]	Brazil
Acaulospora sp. 1 [55]	Pasture	[55]	
Acaulospora sp. 1 [104]	Grassland	[104]	
Acaulospora sp. 2 [103]	Pasture	[103]	
Acaulospora sp. 2 [104]	Grassland	[104]	
Acaulospora sp. 3 [103]	Pasture	[103]	
Acaulospora sp. 3 [104]	Grassland	[104]	
Acaulospora sp. 4	Grassland	[105]	
Acaulospora sp. 5	Grassland	[105]	
Acaulospora bireticulata	Grassland	[104]	
Acaulospora brasiliensis	Grassland	[104]	
Acaulospora colombiana	Pasture	[55]	
Acaulospora colossica	Grassland	[104,105]	
Acaulospora delicata	Grassland	[104,105]	
Acaulospora elegans cf	Pasture	[55]	
Acaulospora excavata	Pasture	[106,107]	
Acaulospora foveata	Pasture	[55,95,105,108]	
Acaulospora foveoreticulata	Pasture	[106]	
Acaulospora gedanensis cf	Pasture	[55,103]	
Acaulospora koskei	Grassland	[104,105]	
Acaulospora laevis	Grassland; Pasture	[55,105]	
Acaulospora longula	Pasture	[106]	
Acaulospora mellea	Grassland; Pasture	[104–106]	
Acaulospora morrowiae	Grassland	[104,105]	
Acaulospora rehmii	Pasture	[55]	
Acaulospora rugosa	Grassland	[104,105]	
Acaulospora spinosa	Grassland; Pasture	[55,104]	
Acaulospora scrobiculata	Grassland; Pasture	[104–106,109]	
Acaulospora tuberculata	Grassland; Pasture	[55,105]	
Ambispora appendicula	Grassland; Pasture	[55,104,107,107]	
Ambispora callosa	Grassland	[104]	
Ambispora leptoticha	Pasture	[103]	
Archaeospora trappei	Pasture	[55]	
Cetraspora pellucida	Pasture	[55,103,105]	
Dentiscutata erythropus	Grassland; Pasture	[104,106]	
Dentiscutata heterogama	Pasture	[103]	
Diversispora sp.	Grassland	[104]	
Diversispora spurca cf	Grassland; Pasture	[55,105]	
Entrophospora claroidea	Grassland; Pasture	[105,106]	
Entrophospora etunicata	Grassland; Pasture	[95,104–106,110]	
Entrophospora infrequens	Grassland	[105]	

Table 1. *Cont.*

AMF Species	Vegetation Type	Reference	Country
Entrophospora lamellosa	Grassland	[104]	
Entrophospora lutea	Grassland	[105]	
Funneliformis sp.	Grassland	[104]	
Funneliformis geosporus	Grassland	[95,104,105]	
Funneliformis mosseae	Grassland	[104,105]	
Fuscutata heterogama	Grassland	[104]	
Gigaspora sp. 1	Pasture	[103]	
Gigaspora decipiens	Grassland	[104,105]	
Gigaspora gigantea	Grassland	[104,105,110]	
Gigaspora margarita	Grassland	[104]	
Glomus sp. 1 [104]	Grassland	[104]	
Glomus sp. 1 [105]	Grassland	[105]	
Glomus sp. 2 [104]	Grassland	[104]	
Glomus sp. 2 [105]	Grassland	[105]	
Glomus sp. 3	Grassland	[104]	
Glomus sp. 4 [55]	Pasture	[55]	
Glomus sp. 4 [104]	Grassland	[104]	
Glomus sp. 5 [104]	Grassland	[104]	
Glomus sp. 5 [105]	Grassland	[105]	
Glomus sp. 6	Grassland	[104]	
Glomus sp. 7	Grassland	[105]	
Glomus sp. 8	Grassland	[105]	
Glomus sp. 9 [55]	Pasture	[55]	
Glomus sp. 9 [105]	Grassland	[105]	
Glomus sp. 10	Grassland	[105]	
Glomus sp. 13	Grassland	[105]	
Glomus sp. 15	Pasture	[55]	
Glomus sp. 16 [55]	Pasture	[55]	
Glomus sp. 16 [105]	Grassland	[105]	
Glomus corymbiforme	Pasture	[55]	
Glomus glomerulatum	Grassland; Pasture	[104,106]	
Glomus hoi	Grassland	[105]	
Glomusmicrocarpum	Grassland	[104,105]	
Oehlia diaphana	Grassland	[104,105]	
Pacispora sp.	Grassland	[104]	
Paraglomus albidum	Grassland	[105]	
Paraglomus occultum	Grassland	[104,105]	
Rhizoglomus microaggregatum	Grassland	[104,105]	
Rhizophagus clarus	Grassland; Pasture	[55,104,105]	
Rhizophagus fasciculatus	Grassland	[104]	
Rhizophagus intraradices	Pasture	[55,106]	
Rhizophagus invermaius	Grassland	[104,105]	
Sclerocystis clavispora	Grassland	[105]	
Sclerocystis sinuosa	Grassland	[105]	
Scutellospora sp.	Grassland	[104]	
Scutellospora auriglobosa	Pasture	[106]	
Scutellospora biornata	Grassland; Pasture	[55,104]	
Scutellospora calospora	Grassland	[104]	
Scutellospora dipurpurescens	Grassland	[104]	
Scutellospora pernambucana	Grassland	[104]	
Scutellospora rubra	Grassland	[104]	
Scutellospora scutata	Pasture	[95,108]	
Septoglomus constrictum	Grassland	[104,105]	
Sieverdingia tortuosa	Pasture	[103]	

References: when the specific names of taxa were unresolved, i.e., *Glomus* sp1, and taxa nomenclature was presented along different publications, the number of the respective citation was added to the taxon name; e.g., *Glomus* sp1 [105] is the new taxon name of *Glomus* sp1 recorded in the citation [105] Zangaro et al. (2013) to avoid duplicated names for different AMF.

3.3. AMF Diversity in Argentinean and Brazilian Grasslands and Pastures

When the whole dataset was analyzed (Figure 9a), the NMDS plots suggested that there are no significant differences in the species composition between pastures and grasslands (Figure 9b), neither between Argentina nor Brazil (Figure 9c), considering that the stress value for NMDS of the pooled data was greater than 0.2, and therefore, its interpretation should proceed with caution. This result was also confirmed by the ANOSIM (R = 0.1379, p = 0.001).

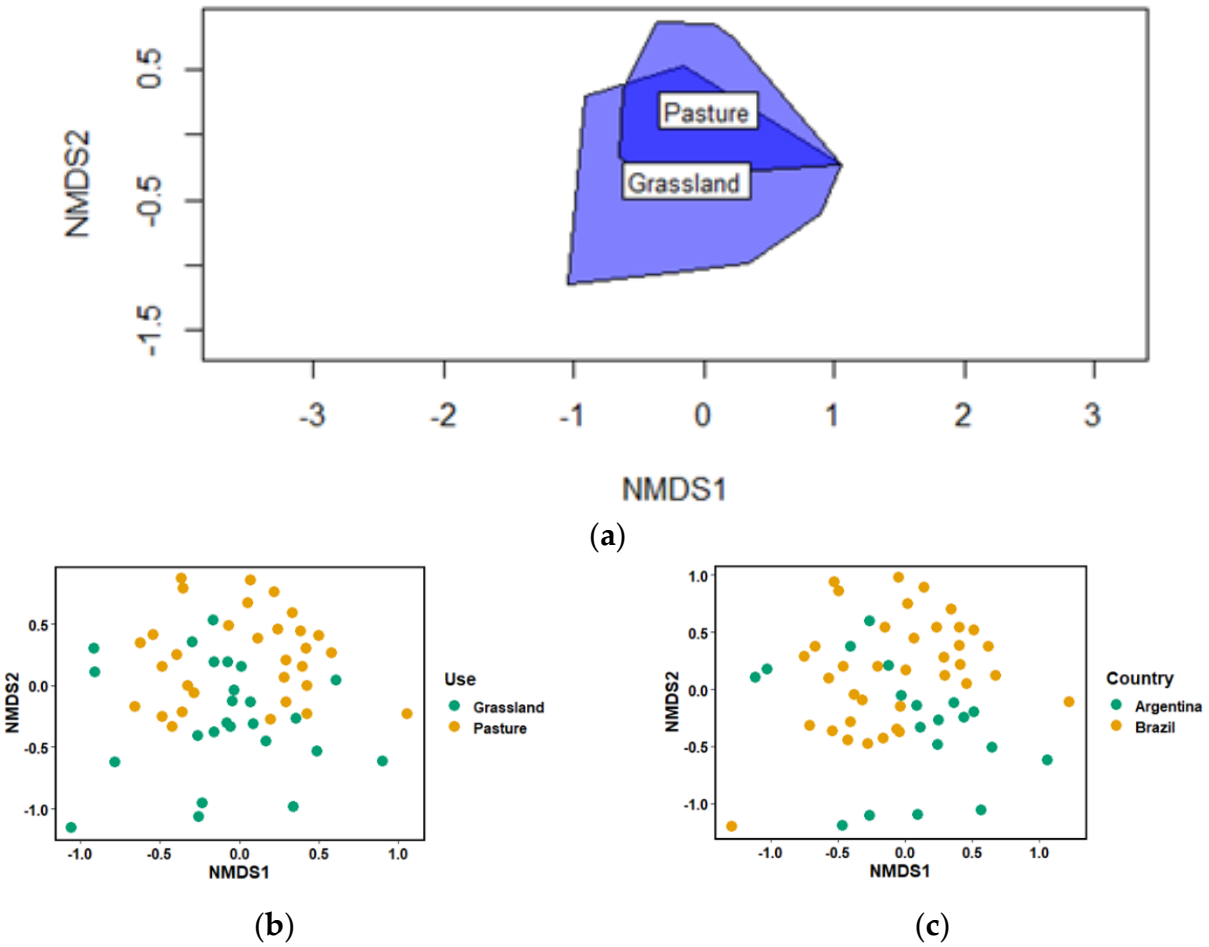


Figure 9. Non-metric multidimensional scaling (NMDS) showing dissimilarity between pastures and grasslands based on their AMF species composition, considering (**a**) whole dataset and (**b**) comparison between grasslands vs. pastures and (**c**) between countries.

The total AMF diversity in pastures and grasslands was analyzed considering the richness or number the species at family level, including also species *Incertae sedis*. The taxonomic location of each species followed the Wijayawardene et al. (2020) [111] proposal. In general (see Figure 10), the main families were Glomeraceae, Acaulosporaceae, and Gigasporaceae, and Ambisporaceae, Entrophosporaceae, Paraglomeraceae, Diversisporaceae, Archaeosporaceae, Pacisporaceae, Perviscutaceae, and Scutellosporaceae, were scantly represented.

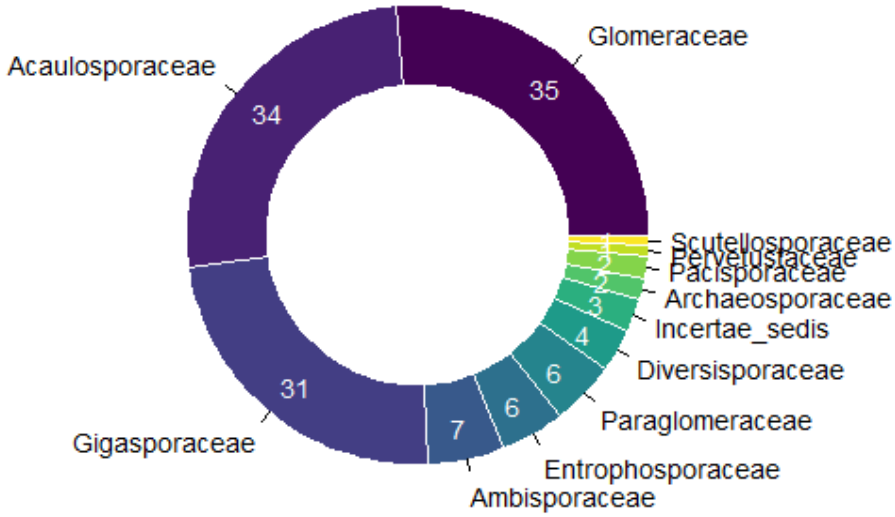
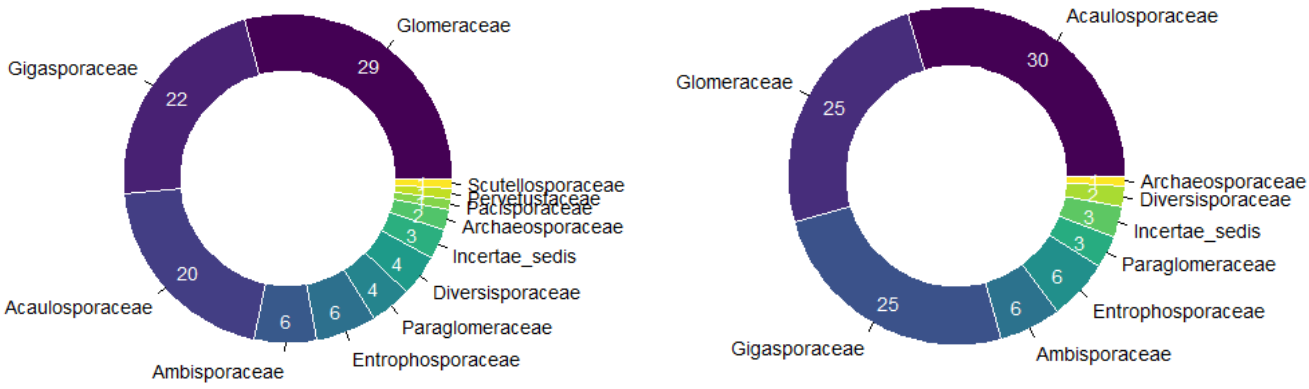


Figure 10. Richness of total AMF species in pastures and grasslands distributed in Glomeromycota families.

In grasslands, the main (Figure 11a) families represented were Glomeraceae (29 species), Gigasporaceae (22), and Acaulosporaceae (20), with a third number of fewer species being Ambisporaceae, Entrophosporaceae, Paraglomeraceae, Diversisporaceae, *Incertae sedis*, Archaeosporaceae, Pacisporaceae, Perviscutaceae, and Scutellosporaceae. Thus, Glomeraceae is one of the families, together with Claroideoglomeraceae and Paraglomeraceae, considered as part of the rhizophilic guild of AMF [94], and they may be capable of protecting their hosts against root pathogen colonization. Furthermore, Glomeraceae is a family that thrives in nutrient-rich environments and survives against major soil disturbances, such as those that occur in agroecosystems [112,113] but also in harsh natural ecosystems such as montane and highland grasslands in the arid ecosystems of Argentina and Brazil in South America [71,85]. Moreover, Glomeraceae has short life cycles with rapid growth and abundant production of spores [101,114,115]; these characteristics are consistent with a ruderal life strategy [116] that allows them a rapid and wide distribution at the ecosystem level but also biogeographically, being found in almost all the biomes of South America, the neotropics, and worldwide [39,117,118]). In the analyzed grasslands, Gigasporaceae plays the role of the edaphophilic guild [94] with the function of increasing the uptake of nutrients in the host plant, mainly benefiting those plants with thick roots, poorly adapted to nutrient absorption, and that depend on AMF for their nutrition, as is the case of C_4 grasses that are obligate mycotrophs [82–84]; also, this is a competitive family [116] with low abundance and species richness in arid environments [94].

In pastures (Figure 11b), the main families were Acaulosporaceae, followed by Glomeraceae and Gigasporaceae, and a few species were found belonging to Ambisporaceae, Entrophosporaceae, Paraglomeraceae, *Incertae sedis*, Diversisporaceae, and Archaeosporaceae. The families Pacisporaceae, Pervestutaceae, and Scutellosporaceae were not reported in pastures. Thus, AMF communities in grasslands were distributed among more families (12) than in pastures (9), bringing to the AMF biodiversity of grassland soil higher functionality than in the studied pastures because a larger number of AMF families could be involved in different ecosystem functions and may provide different and more numerous benefits to plants in grasslands than in pastures [93,94,116].



(**a**) (**b**)

Figure 11. Richness of AMF among Glomeromycota families in Argentina and Brazil, considering (**a**) grasslands, (**b**) pastures.

The greater presence of species belonging to the Acaulosporaceae family in pastures may be related to the constant disturbance that most pastures considered in the study undergo. This disturbance is grazing, which causes a loss of biomass and a reduced allocation of carbon to the roots and, consequently, to the arbuscular mycorrhizal symbionts. It has been demonstrated that ancestral AMF, to which the Acaulosporaceae family belongs, may have the lowest carbon demand from the plant host due to the relatively low amount of both intraradical and extraradical hyphae [68,94]. Therefore, in agroecosystems like pastures, Acaulosporaceae species would be able to thrive due to their ability to use carbon more efficiently [116].

The number of AMF species shared between the grasslands and pastures of Argentina and Brazil is shown in the Venn diagram (Figure 12). The Brazilian pastures are the grassy ecosystems that have the higher number of exclusive species, while Argentinean pastures presented the lowest number of shared species (Figure 12).

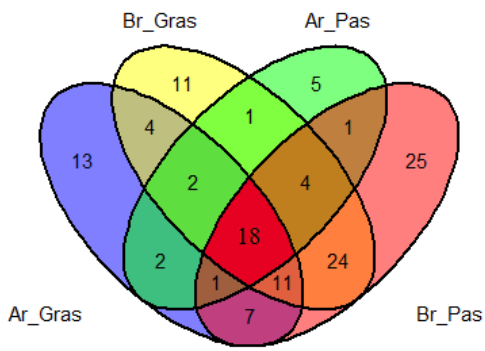


Figure 12. Venn diagram of AMF species shared between grasslands and pastures of Argentina and Brazil with the number of identified species shared in each grassy ecosystem analyzed. References: Ar_Gras, Argentinean grasslands; Ar_Pas, Argentinean pastures; Br_Gras, Brazilian grasslands; Br_Pas, Brazilian pastures. Species exclusive to Argentinean grasslands are shown in blue, while those exclusive to Argentinean pastures are in green. Yellow represents species exclusive to Brazilian grasslands, and pink represents species exclusive to Brazilian pastures. Additionally, there are color tones in overlapping ovals representing the mixture between the basic colors overlapped, and the numbers within these overlaps are the species shared among different biomes; the central red overlapping area represents species shared by all the studied biomes.

The AMF diversity differences between the studied grassy ecosystems were clustered by country rather than by ecosystem type (Figure 13), although the differences were not

significant. These differences could be due to biogeographical reasons. Thus, the AMF diversity in these grassy ecosystems depends on the fact that the Brazilian grasslands and pastures are ecosystems of tropical areas, and the Argentine ecosystems are temperate with variants from humid to semi-arid and arid environmental conditions. Therefore, tropical Brazilian grassy ecosystems may involve more potential host plants for AMF than the temperate Argentinean grasslands and pastures analyzed.

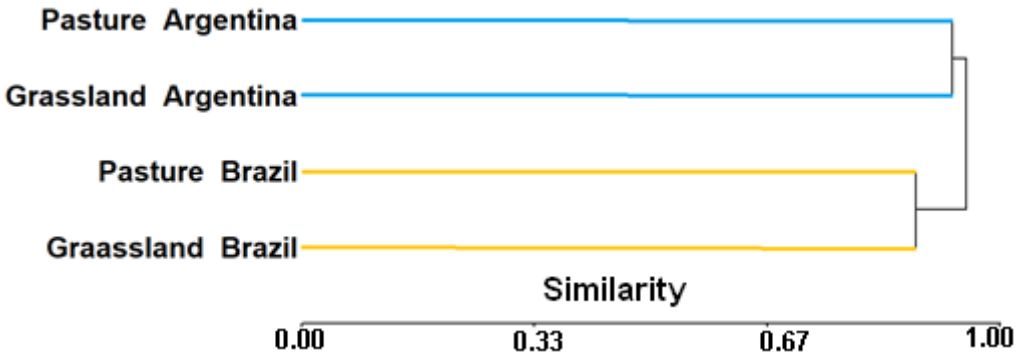


Figure 13. Cluster analysis dendrogram based on the presence/absence of arbuscular mycorrhizal fungi (AMF) species in soils from grasslands and pastures in Argentina and Brazil. References: similarity values are shown in the x-axis.

Local environmental conditions and the spatial distance between sites are also important drivers of AMF community structure [117–119]. In line with this, Hazard et al. [120] demonstrated that landscape-scale distribution of AMF taxa is driven by the local environment, especially by abiotic factors, including pH, rainfall, and soil type [120,121]. In our study, pH was the only edaphic-environmental factor that showed a moderate correlation (p = 0.0235) with species richness. This correlation was negative, meaning that the richness of AMF decreases as pH increases.

Soil fungi tolerate large ranges of soil pH values compared to other microorganisms, such as bacteria. This is attributable to both individual fungal taxa drastically differing in their optimal pH range and many fungal species being capable of withstanding more than five pH units of difference [122]. Soil fungi generally display higher diversity in lower-pH environments [122,123]. This could be attributed to increased competition with soil bacteria in higher-pH soils rather than a direct effect of pH itself [122,124]. Thus, to some degree, the impact of pH on soil fungal assemblages may be regarded as an indirect effect of plant community composition [125,126].

Several case studies have also shown that soil pH importantly influences the community composition of AMF [127–130]) and of fungal communities in general [131]. Experiments showing that liming can strongly modulate AM fungal spore number and root colonization suggest that pH may have an important direct influence on AMF growth and performance [132–134]. Given the limited evidence of dispersal limitation and larger spatial resolution of climatic variables, it seems probable that soil pH is the most important abiotic determinant of relative abundance at the local scale [135].

4. Conclusions

Our results demonstrating the important role of pH as driver of AMF diversity distribution between grassy ecosystems in Argentina and Brazil are consistent with those previously reported for bacteria and other fungi [136] and for protists [137], although both studies identified precipitation as an important additional driver. Moreover, pH has been found as the shaper of AMF diversity worldwide [120,121,131,133–135], in agreement with the AMF community's behavior analyzed in South America for grasslands and pastures in this work. At the same time, it is clear that there remain unmeasured factors that may

be important drivers of AM fungal performance or may underlie associations with other variables, such as those identified here [135,138].

The excessive use of fertilizers and pesticides is a global threat that affects ecosystems worldwide and particularly in South America, decreasing the plant associated biodiversity. Pastures grazed and products from cows (the basis for milk and cheese production) [56] are also affected by agricultural inputs, especially, tropical pastures of *Urochloa* spp., which are commonly established in Brazil. However, these vegetation types can allocate frequent AMF species, such as *Acaulospora mellea*, *Claroideoglomus etunicatum*, *Dentiscutata heterogama*, *Funneliformis geosporus*, *Scutellospora calospora*, among others (Table 1), that counteract those effects benefiting plants and soils. Exclusive AMF species are generally found in pastures or under forest. Most of those species include taxa of Acaulosporaceae (*Acaulospora*) and Glomeraceae (*Glomus* and *Rhizophagus*), *Gigaspora*, *Diversispora* and *Scutellospora*. Thus, the management of AMF by the introduction of AMF inoculum into the soil of interest can diminish the utilization of agrochemicals, which are dangerous to human populations and to the environment. Sales et al. [139] showed that farm inoculation of native AMF species belonging to the genus *Gigaspora* (*Gigaspora margarita* and *Gigaspora* sp.) in the field improved a C_4 grass (sugarcane) cultivation in Brazil. Moreover, possible solutions to the main problems caused by climate change in different grasslands, pastures, crops, and vineyards will be elucidated, especially regarding the symbiosis with AMF.

Traditionally, it is believed that forests are more diverse than grasslands; nevertheless, new findings showed that grasslands present high microbial diversity. Among these microbial communities, AMF diversity is higher in grasslands globally [140]. In general, AMF diversity was not significantly different between South American grasslands and pastures. The native grasslands have been under the effect of grazing for ca. 500 years since the European conquest of the continent, and in Pampa grasslands livestock production had its beginnings in 1536 and 1573, when the first horses and cows were introduced, respectively [51,141,142]. Additionally, in Andean regions, grazing by South American camelids is more ancient since the pastoral systems began earlier than the Spanish conquest of the territory [143]. It has been proposed that grassy ecosystems in Africa and North and South America have become resilient to grazing after being exposed to this disturbance for long periods of time [144], as could be the case for the grasslands and pastures studied. Furthermore, at the landscape scale, grazing has been associated with the spatial heterogeneity loss [145,146]. Thus, grazing effects may be associated with the homogenization of the landscape and increase of the resilience [144–146], which could be reflected in the apparent similarity of the associated microbial communities, such as the AMF, in soils also previously recorded for mountain grasslands and pastures in South America [71,88,147]. Therefore, the AMF communities inhabiting these environments could be adapted to grazing by means of similar AMF diversity to cope with a sustainable functionality and with the prevalence of resilient and tolerant AMF families, such as Glomeraceae and Acaulosporaceae, as in the case of the Argentinean and Brazilian grasslands and pastures.

We demonstrated differential distribution of AMF families between grasslands and pastures; although the main families with the higher numbers of species (20 to 30 species) were recorded in both grassy ecosystems (Acaulosporaceae, Gigasporaceae, and Glomeraceae), the number de AMF species per family showed differences between grasslands and pastures. Among AMF taxa, pastures maintain predominantly Acaulosporaceae as indicator of tolerance to the continuous grazing stress and as an ancestral guild. Surprisingly, in grasslands, Glomeraceae was the main family by its richness, functioning as ruderal and like a rhizophilic guild, and Gigasporaceae, a competitive and edaphophilic family [94,116,148], also maintained fewer species than the pastures. In addition, some families were completely absent among pastures, such as Pacisporaceae, Perviscutaceae and Scutellosporaceae. Surprisingly, up to now, their ecosystem functions, life strategies, or the guild they belong to are unknown. Thus, a new gap comes out in the information on the diversity of AMF at the level of ecosystem functioning that needs to be explored and investigated to contribute to the knowledge of these fungi and their interactions with their

hosts in grasslands and pastures. It is important to highlight that the grassy ecosystems in general are named "grasslands" in sensu lato [140], without discriminating between pastures (grazed ecosystems with anthropogenic intervention, e.g., sowing of exotic species, thinning of shrubs, etc.) or grasslands sensu stricto (natural grasslands) as they were defined in this work. Future research focused on AMF diversity and functional ecology in grasslands and pastures should consider the land use histories of each grassy ecosystem to be analyzed, since these significantly influence the diversity of AMF; see [149] and references therein.

In South America, especially in Argentina, the natural grasslands are under pressure in a harsh process of desertification, and its vulnerability is strongly affected by the reduced areas for conservation [16,76,79,150]. Taking into account the ESs awarded by grasslands [32,48], together with the high productivity in meat and milk provided by these grassy ecosystems [51,146,151,152], involvement of AMF in grasslands and pastures management urgently call for sustainable use of these valuable and unique ecosystems. Recently, the capacity of amendments involving native AMF species in restoring grasslands in North America has been demonstrated [153]; in tall prairies, the invasive weed populations were reduced by means of low densities of native AMF inoculum application, and an AMF restoration effect also persisted over time, establishing a native AMF community in the grassland due to positive feedback from host plants (predominantly native grasses and legumes) and inoculated native AMF [153]. Moreover, North American native grasslands are invaded by an exotic grass, *Setaria faberi*; in greenhouse bioassays Koziol et al. [154] showed that the inoculation with native AMF plus ex-arable soil experimental treatments increase the abundance of native plants, plants in the late successional grassland stage, and total plant diversity also were greatest, together with the increment of native seedlings establishment; furthermore, this native plant's population improvement was concomitant with the reduction in the invasive *S. faberi* [154]. In addition, Gou et al. [155] demonstrated that inoculation with AMF in agroecosystems significantly reduced the nutrient losses induced by soil erosion and proposed the use of AMF inoculation as a sustainability support among these and other environments. This type of inoculation study, with native inoculants applied as amendments in the field and in greenhouses in the short, medium, and long term in grassy ecosystems, with and without grazing, does not exist in South America. Therefore, our results on the differential native AMF diversity between South American grasslands and pastures and the pH effect on native AMF communities in these grassy systems are an important starting point to elaborate microbial amendments with possibilities of being applied to restore these ecosystems from plant invasions, erosion, and degradation to which are exposed and to promote sustainable production in South American grassy ecosystems.

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