

Mycorrhizal Symbioses in South America Grasslands and Pastures

Subjects: Biodiversity Conservation

Contributor: Mónica A. Lugo, Roberto Emanuel Ontivero, Hebe J. Iriarte, Bakhytzhan Yelikbayev, Marcela C. Pagano

The vast majority of natural ecosystems and agroecosystems are made up of high percentages of plants that form mycorrhizal symbioses. Grasslands in a good state of conservation present a high abundance and diversity of Glomeromycota species) 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, are especially influenced by AM fungal associations.

Keywords: pastures ; grasslands ; South America ; mycorrhizal symbioses

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][2][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][8][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][25][26][27][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 scantily 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.

2. 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][42][43][44][45][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, improvement 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.

3. 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][61][62] and in field experiments focused on one or two grass species [63][64][65][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].

References

1. Pagano, M.C.; Lugo, M.A. Mycorrhizal Fungi in South America; Life Science Series, Fungal Biology; Springer: Cham, Switzerland, 2019; p. 365.
2. Smith, S.E.; Read, D.J. Mycorrhizal Symbiosis, 2nd ed.; Academic Press: Cambridge, UK, 2008; p. 787.
3. Brundrett, M.C.; Tedersoo, L. Evolutionary history of mycorrhizal symbioses and global host plant diversity. *New Phytol.* 2018, 220, 1108–1115.
4. Aguilera, P.; Ortiz, N.; Becerra, N.; Turrini, A.; Gainza-Cortes, F.; Silva-Flores, P.; Aguilar-Paredes, A.; Romero, J.K.; Jorquera-Fontena, E.; Mora, M.d.L.; et al. Application of arbuscular mycorrhizal fungi in vineyards: Water and biotic stress under a climate change scenario: New challenge for Chilean grapevine crop. *Front. Microbiol.* 2022, 13, 826571.
5. Velázquez, M.S.; Fabisik, J.C.; Barrera, M.; Allegrucci, N.; Valdez, F.; Abarca, C.L.; Cabello, M. Diversity and abundance of arbuscular mycorrhizal fungi (Glomeromycota) associated with *Ilex paraguarens* in Northeastern Argentina. *Rev. Biol. Trop.* 2020, 68, 1231–1240.
6. Song, X.-P.; Hansen, M.C.; Potapov, P.; Adusei, B.; Pickering, J.; Adami, M.; Lima, A.; Zalles, V.; Stehman, S.V.; Di Bella, C.M.; et al. Massive soybean expansion in South America since 2000 and implications for conservation. *Nat. Sustain.* 2021, 4, 784–792.
7. Salloum, M.S.; Guzzo, M.C.; Velázquez, M.S.; Sagadin, M.B.; Luna, C.M. Variability in colonization of arbuscular mycorrhizal fungi and its effect on mycorrhizal dependency of improved and unimproved soybean cultivars. *Can. J. Microbiol.* 2016, 62, 1034–1040.
8. Molina, A.S.; Lugo, M.A.; Pérez Chaca, M.V.; Vargas-Gil, S.; Zirulnik, F.; Leporati, J.; Ferrol, N.; Azcón-Aguilar, C. Effect of arbuscular mycorrhizal colonization on cadmium-mediated oxidative stress in *Glycine max* (L.) Merr. *Plants* 2020, 9, 108.

9. Díaz, L.; Paz, G.; Ontivero, R.E.; Iriarte, H.J.; Lugo, M.A. Effect of land use change on arbuscular mycorrhizal colonization in the Caldenal (Espinal Ecoregion, San Luis, Argentina). In Proceedings of the III Reunión de la Asociación Micológica Carlos Spegazzini, Córdoba, Argentina, 21 October 2022.
10. Faggioli, V.; Cabello, M.; Grilli, G.; Opik, M. Root colonizing and soil borne communities of arbuscular mycorrhizal fungi differ among soybean fields with contrasting historical land use. *Agric. Ecosys. Environ.* 2019, 269, 174–182.
11. Igiehon, N.O.; Babalola, O.O. Biofertilizers and sustainable agriculture: Exploring arbuscular mycorrhizal fungi. *Appl. Microbiol. Biotechnol.* 2017, 101, 4871–4881.
12. Tyagi, J.; Chaudhary, P.; Bhagwiti, U.; Bhandari, G.; Chaudhary, A. Impact of endophytic fungi in biotic stress management. In *Plant Protection. From Chemicals to Biologicals*; Soni, R., Chandra Suyal, D., Goel, R., Eds.; De Gruyter: Berlin, Germany, 2022; pp. 447–461.
13. Tyagi, J.; Chaudhary, P.; Mishra, A.; Khatwani, M.; Dey, S.; Varma, A. Role of endophytes in abiotic stress tolerance: With special emphasis on *Serendipita indica*. *Int. J. Environ. Res.* 2022, 16, 62.
14. Stevens, C.J. Recent advances in understanding grasslands. *F1000Research* 2018, 7, F1000 Faculty Rev-1363.
15. Gibson, D.J. *Grasses and Grassland Ecology*; Oxford University Press, Biology: New York, NY, USA, 2009; p. 323.
16. O'Mara, F.P. The role of grasslands in food security and climate change. *Ann. Bot.* 2012, 110, 1263–1270.
17. Available online: <https://www.fao.org/agriculture/crops/thematicsitemap/theme/compendium/scpi-practices/management-of-grassland-and-pasture-areas> (accessed on 18 August 2022).
18. Fedele, G.; Locatelli, B.; Djoudi, H.; Colloff, M.J. Reducing risks by transforming landscapes: Cross-scale effects of land-use changes on ecosystem services. *PLoS ONE* 2018, 13, e0195895.
19. Available online: <https://www.fao.org/agriculture/crops/thematic-sitemap/theme/biodiversity/> (accessed on 6 October 2022).
20. Lehman, R.M.; Acosta-Martinez, V.; Buyer, J.S. Soil biology for resilient, healthy soil. *J. Soil Water Conserv.* 2015, 70, 12A–18A.
21. Dodd, I.C.; Ruiz-Lozano, J.M. Microbial enhancement of crop resource use efficiency. *Curr. Opin. Biotech.* 2012, 23, 236–242.
22. De Vries, F.T.; Wallenstein, M.D. Below-ground connections underlying above-ground food production: A framework for optimising ecological connections in the rhizosphere. *J. Ecol.* 2017, 105, 913–920.
23. Gianinazzi, S.; Gollotte, A.; Binet, M.N.; van Tuinen, D.; Redecker, D.; Wipf, D. Agroecology: The key role of arbuscular mycorrhizas in ecosystem services. *Mycorrhiza* 2010, 20, 519–530.
24. Van der Heyde, M.; Bennett, J.A.; Piter, J.; Hart, M.M. Long-term effects of grazing on the arbuscular mycorrhizal symbiosis. *Agric. Ecosys. Environ.* 2017, 243, 27–33.
25. Van der Heyde, M.; Abbott, L.K.; Gehring, C.; Kokkoris, V.; Hart, M.M. Reconciling disparate responses to grazing in the arbuscular mycorrhizal symbiosis. *Rhizosphere* 2019, 11, 100167.
26. Faghihinia, M.; Zou, Y.; Chen, Z.; Bai, Y.; Li, W.; Marrs, R.; Staddon, P.L. Environmental drivers of grazing effects on arbuscular mycorrhizal fungi in grasslands. *Appl. Soil Ecol.* 2020, 153, 103591.
27. Klironomos, J.N.; McCune, J.; Moutoglou, P. Species of arbuscular mycorrhizal fungi affect mycorrhizal responses to simulated herbivory. *Appl. Soil Ecol.* 2004, 26, 133–141.
28. Hart, M.M.; Reader, R.J.; Klironomos, J.N. Plant coexistence mediated by arbuscular mycorrhizal fungi. *Trends Ecol. Evol.* 2003, 18, 418–423.
29. IICA. Informe Anual; Instituto Interamericano de Cooperación para la Agricultura: San José, Costa Rica, 1994; pp. 1–36.
30. Maraschin, G.E. Production potential of South America grasslands. In Proceedings of the XIX International Grassland Congress, São Paulo, Brazil, 11–21 February 2001; Available online: <https://uknowledge.uky.edu/igc> (accessed on 21 November 2022).
31. Toledo, C.S. The Chaco savanna lands of South America with particular reference to the processes of degradation in their pastoral and forestry resources. In Proceedings of the XVII International Grassland Congress, Palmerston North, New Zealand, 8–21 February 1993; pp. 241–246.
32. Modernel, P.; Rossing, W.A.H.; Corbeels, M.; Dogliotti, S.; Picasso, V.; Tittonell, P. Land use change and ecosystem service provision in Pampas and Campos grasslands of southern South America. *Environ. Res. Lett.* 2016, 11, 113002.
33. FAO. *Livestock's Long Shadow: Environmental Issues and Options*; FAO: Rome, Italy, 2006; Available online: <https://www.fao.org/3/a0701e/a0701e.pdf> (accessed on 6 October 2022).

34. Meyer, C.; Kreft, H.; Guralnick, R.; Jetz, W. Global priorities for an effective information basis of biodiversity distributions. *Nat. Commun.* 2015, 6, 8221.
35. Wetzel, F.T.; Bingham, H.C.; Groom, Q.; Haase, P.; Kõljalg, U.; Kuhlmann, M.; Martin, C.S.; Penev, L.; Robertson, T.; Saarenmaa, H.; et al. Unlocking biodiversity data: Prioritization and filling the gaps in biodiversity observation data in Europe. *Biol. Conserv.* 2018, 221, 78–85.
36. Olson, D.M.; Dinerstein, E. The global 200: Priority ecoregions for global conservation. *Ann. Miss. Bot. Garden* 2002, 89, 199–224.
37. Marín, C.; Bueno, C.G. A systematic review on south American and European mycorrhizal research: Is there a need for scientific symbiosis. In *Mycorrhizal Fungi in South America*; Pagano, M.C., Lugo, M.A., Eds.; Life Science Series, Fungal Biology; Springer: Cham, Switzerland, 2019; pp. 97–110.
38. Lugo, M.A.; Pagano, M.C. Overview of the mycorrhizal fungi in South America. In *Mycorrhizal Fungi in South America*; Pagano, M.C., Lugo, M.A., Eds.; Life Science Series, Fungal Biology; Springer: Cham, Switzerland, 2019; pp. 1–27.
39. Cofré, N.; Soterias, F.; Del Rosario Iglesias, M.; Velázquez, S.; Abarca, C.; Risio, L.; Ontivero, E.; Cabello, M.; Domínguez, L.S.; Lugo, M.A. Morphospecies biodiversity of arbuscular mycorrhizal fungi in South America. A review. In *Mycorrhizal Fungi in South America*; Pagano, M.C., Lugo, M.A., Eds.; Life Science Series, Fungal Biology; Springer: Cham, Switzerland, 2019; pp. 49–72.
40. Clark, F.E.; Paul, E.A. The microflora of grasslands. *Adv. Agron.* 1970, 22, 375–435.
41. Schöps, R.; Goldmann, K.; Herz, K.; Lentendu, G.; Schöning, I.; Bruehlheide, H.; Wubet, T.; Buscot, F. Land-use intensity rather than plant functional identity shapes bacterial and fungal rhizosphere communities. *Front. Microbiol.* 2018, 9, 2711.
42. Navrátilová, D.; Tláškalová, P.; Kohout, P.; Dřevojan, P.; Fajmon, K.; Chytrý, M.; Baldrian, P. Diversity of fungi and bacteria in species-rich grasslands increases with plant diversity in shoots but not in roots and soil. *FEMS Microbiol. Ecol.* 2019, 95, fyy208.
43. Chao, L.; Ma, X.; Tsetsegmaa, M.; Zheng, Y.; Qu, H.; Dai, Y.; Li, J.; Bao, Y. Response of soil microbial community composition and diversity at different gradients of grassland degradation in Central Mongolia. *Agriculture* 2022, 12, 1430.
44. Romdhane, S.; Spor, A.; Banerjee, S.; Breuil, M.-C.; Bru, D.; Chabbi, A.; Hallin, S.; van der Heijden, M.G.A.; Saghai, A.; Laurent Philippot, L. Land-use intensification differentially affects bacterial, fungal and protist communities and decreases microbiome network complexity. *Environ. Microbiome* 2022, 17, 1.
45. Stoian, V.; Vidican, R.; Florin, P.; Corcoz, L.; Pop-Moldovan, V.; Vaida, I.; Vătcă, S.-D.; Stoian, V.A.; Pleșa, A. Exploration of soil functional microbiomes—A concept proposal for long-term fertilized grasslands. *Plants* 2022, 11, 1253.
46. Wang, Y.; Dang, N.; Feng, K.; Wang, J.; Jin, X.; Yao, S.; Wang, L.; Gu, S.; Zheng, H.; Lu, G.; et al. Grass-microbial inter-domain ecological networks associated with alpine grassland productivity. *Front. Microbiol.* 2023, 14, 1109128.
47. Busso, M.A.; Busso, M.B. Arbuscular mycorrhizal fungi and common mycorrhizal networks benefit plants through morphological, physiological and productive traits and soil quality. *Lilloa* 2022, 59, 301–317.
48. Bengtsson, J.; Bullock, J.M.; Egoh, B.N.; Everson, C.; Everson, T.; O'Connor, T.; O'Farrell, P.J.; Smith, H.G.; Lindborg, R. Grasslands-more important for ecosystem services than you might think. *Ecosphere* 2019, 10, e02582.
49. Bullock, J.M.; Jefferson, R.G.; Blackstock, T.H.; Pakeman, R.J.; Emmett, B.A.; Pywell, R.J.; Grime, J.P.; Silvertown, J. Semi-natural grasslands. In *The UK National Ecosystem Assessment*; UNEP-WCMC: Cambridge, UK, 2011; pp. 161–196.
50. Zhao, Y.; Zhifeng Liu, Z.; Wu, J. Grassland ecosystem services: A systematic review of research advances and future directions. *Landsc. Ecol.* 2020, 35, 793–814.
51. Franzluebbers, A.J.; Sawchik, J.; Taboada, M.A. Agronomic and environmental impacts of pasture–crop rotations in temperate North and South America. *Agric. Ecosyst. Environ.* 2014, 190, 18–26.
52. Porqueddu, C.; Ates, C.S.; Louhaichi, M.; Kyriazopoulos, A.P.; Moreno, G.; del Pozo, A.; Ovalle, C.; Ewing, M.A.; Nichols, P.G.H. Grasslands in 'Old World' and 'New World' mediterranean climate zones: Past trends, current status, and future research priorities. *Grass Forage Sci.* 2016, 71, 1–35.
53. Cheeke, T.E.; Zheng, C.; Koziol, L.; Gurholt, C.R.; Bever, J.D. Sensitivity to AMF species is greater in late-successional than early-successional native or nonnative grassland plants. *Ecology* 2019, 100, e02855.
54. Melo, C.; Walker, C.; Rodríguez-Echeverría, S.A.V.; Borges, P.; Freitas, H. Species composition of arbuscular mycorrhizal fungi differ in semi-natural and intensively managed pastures in an isolated oceanic island (Terceira,

55. Lopes Leal, P.; Siqueira, J.O.; Stürmer, S.L. Switch of tropical Amazon forest to pasture affects taxonomic composition but not species abundance and diversity of arbuscular mycorrhizal fungal community. *Appl. Soil Ecol.* 2013, 71, 72–80.
56. Joubran, A.M.; Pierce, K.M.; Garvey, N.; Shalloo, L.; O'Callaghan, T.F.A. perspective on pasture-based dairy systems and products. *J. Dairy Sci.* 2021, 104, 7364–7382.
57. Hartnett, D.C.; Wilson, G.W.T. The role of mycorrhizas in plant community structure and dynamics: Lessons from the grasslands. *Plant Soil* 2002, 244, 319–331.
58. Ambrosino, M.L.; Velázquez, M.S.; Ontivero, E.; Cabello, M.N.; Lugo, M.A. Communities of Glomeromycota in the Argentine Arid Diagonal: An Approach from their Ecological Role in Grassland Management and Use. In *Mycorrhizal Fungi in South America—Biodiversity, Conservation, and Sustainable Food Production*; Lugo, M.A., Pagano, M.C., Eds.; Life Science Series, Fungal Biology; Springer: Cham, Switzerland, 2022; pp. 373–392.
59. Powell, J.R.; Rillig, M.C. Biodiversity of arbuscular mycorrhizal fungi and ecosystem function. *New Phytol.* 2018, 220, 1059–1075.
60. Bever, J.D.; Richardson, S.C.; Lawrence, B.M.; Holmes, J.; Watson, M. Preferential allocation to beneficial symbiont with spatial structure maintains mycorrhizal mutualism. *Ecol. Lett.* 2009, 12, 13–21.
61. Jones, S.L.; French, K. Soil nutrients differentially influence root colonisation patterns of AMF and DSE in Australian plant species. *Symbiosis* 2021, 83, 209–223.
62. Williams, A.; Manoharan, L.; Rosenstock, N.P.; Olsson, P.A.; Hedlund, K. Long-term agricultural fertilization alters arbuscular mycorrhizal fungal community composition and barley (*Hordeum vulgare*) mycorrhizal carbon and phosphorus exchange. *New Phytol.* 2017, 213, 874–885.
63. Frater, P.N.; Borer, E.T.; Fay, P.A.; Jin, V.; Knaeble, B.; Seabloom, E.; Sullivan, L.; Wedin, D.A.; Harpole, W.S. Nutrients and environment influence arbuscular mycorrhizal colonization both independently and interactively in *Schizachyrium scoparium*. *Plant Soil* 2018, 425, 493–506.
64. Klichowska, E.; Nobis, M.; Piszczek, P.; Błazkowski, J.; Zubek, S. Soil properties, rather than topography, climatic conditions, and vegetation type, shape AMF–feathergrass relationship in semi-natural European grasslands. *Appl. Soil Ecol.* 2019, 144, 22–30.
65. Pan, S.; Wang, Y.; Qiu, Y.; Chen, D. Nitrogen-induced acidification, not N-nutrient, dominates suppressive N effects on arbuscular mycorrhizal fungi. *Glob. Chang. Biol.* 2020, 26, 6568–6580.
66. Xu, M.; Li, X.L.; Cai, X.B.; Li, X.L.; Christie, P.; Zhang, J.L. Land use alters arbuscular mycorrhizal fungal communities and their potential role in carbon sequestration on the Tibetan Plateau. *Sci. Rep.* 2017, 7, 3067.
67. Sikes, B.A.; Powell, J.R.; Rillig, M.C. Deciphering the relative contributions of multiple functions within plant-microbe symbioses. *Ecology* 2010, 91, 1591–1597.
68. Kasanke, C.P.; Zhao, Q.; Alfaro, T.; Walter, C.A.; Hobbie, S.E.; Cheeke, T.E.; Hofmockel, K.S. Grassland ecosystem type drives AM fungal diversity and functional guild distribution in North American grasslands. *Mol. Ecol.* 2023, 32, 1133–1148.