Chapter 5
A Systematic Review of South American and European Mycorrhizal Research: Is there a Need for Scientific Symbiosis?

César Marín and C. Guillermo Bueno

5.1 Introduction

The study of global biodiversity presents spatially biased data distribution with large differences in the sampling efforts and data resolution between the Northern and Southern hemispheres (Meyer et al. 2015; Wetzel et al. 2018). These differences are exacerbated by monetary, linguistic, geographic, and political barriers, more prevalent in the Southern hemisphere (Amano and Sutherland 2013). Besides regional differences, our knowledge regarding biodiversity information differs among different organisms, being belowground organisms relatively unknown, even though they are fundamental to terrestrial ecosystem functioning and aboveground biodiversity dynamics (Bardgett and van der Putten 2014; Carey 2016). Despite the appearance of new and more efficient molecular and macroecological biodiversity approaches in the last decades (Wiens 2007), which have boosted regional and global biodiversity studies, geographical data gaps are still large on general soil biodiversity (Cameron et al. 2018), and on soil and mycorrhizal fungi in particular (Tedersoo et al. 2014; Davison et al. 2015; Bueno et al. 2017a). This has led to a biodiversity-knowledge paradox: while areas in the Southern hemisphere, such as South America (SA), host the most diverse biodiversity hotspots, they have been largely understudied, particularly on belowground fundamental organisms and associations such as the mycorrhizal symbiosis.

Research efforts via specific scientific networks are efficient strategies to overcome local limitations in resources and to extent the research aims in ecological time or space, which is ideal for answering largely unknown exploratory or

C. Marín (✉)
Universidad de O'Higgins, Rancagua, Chile
e-mail: cesar.marin@uoh.cl

C. G. Bueno
University of Tartu, Tartu, Estonia

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mechanistic questions (Richter et al. 2018). There are increasing networking efforts to monitor changes in global aboveground biodiversity, functions, and ecosystem services (Scholes et al. 2008, 2012; Pereira et al. 2010, 2013; Tallis et al. 2012), while belowground and fungal biodiversity, including mycorrhizal fungi, have barely been covered by any scientific network (Wetzel et al. 2015, 2018). In this context, the integration of Southern needs and perspectives of mycorrhizal research into operative networking efforts in collaboration with Northern researchers, can strengthen local and global research, creating successful and mutualistic collaborative efforts. One recent example of these collaborative efforts is the South American Mycorrhizal Research Network (SAMRN) (Bueno et al. 2017a; Godoy et al. 2017), which is an horizontal scientific community directed towards the progress of mycorrhizal research and knowledge, along with applications and public outreach in SA. The SAMRN is constructed on the basis of collaborative efforts, to overcome the lack of funding or collaboration between South American and European or North American funding agencies (Amano and Sutherland 2013). Despite these local constraints, collaborative networking initiatives are effective and promising tools. For instance, in over two years, this network has strengthened scientific collaboration between and within local and foreign researchers and students through the organization of conferences, symposia, and technical specific workshops (https://southmycorrhizas.org/). These activities have in turn led to several scientific outreach activities and publications, providing a solid ground for the announcement and development of the present book.

Overall, in a context of unbalanced geographical resources and needs, it is important to understand the research efforts done in different regions to ultimately enhance future strategies that will focus on the research needs and knowledge gaps of local and global biodiversity. In this context, the following review focuses on the mycorrhizal symbiosis as a key player of the main terrestrial processes and ecosystem functions (Bardgett and van der Putten 2014), present in most terrestrial plant species (Brundrett and Tedersoo 2018). The objective of this systematic review was to compile, characterize, classify, and compare the scientific literature on mycorrhizal research in South America and Europe from 1975 to 2018. This study represents the first effort to understand South American and European differences in aims and perspectives, which can enable the integration of South American mycorrhizal information and research initiatives into global initiatives and models.

5.2 Systematic Review of Mycorrhizal Literature

In order to develop our review, we followed the PRISMA protocol ("Preferred Reporting Items for Systematic Reviews and Meta-Analyses"; Liberati et al. 2009) which consisted of several steps. First, we conducted a literature search (on 27th of November 2018) using Web of Science with the terms "mycorrhiza*" AND terms for the geographical region. We used the term "mycorrhiza*" to include all the variants of the word mycorrhiza (i.e. "mycorrhizae", "mycorrhizal", etc.). For the geographical terms we used “South America” and “Europe”, in adition to all countries within South America (i.e. “Argentina”, “Bolivia”, “Brazil”, “Chile”, “Colombia”, “Ecuador”, “French Guiana”, “Guyana”, “Paraguay”, “Peru”, “South Georgia”, “Uruguay”, and “Venezuela”) and Europe (i.e. “Armenia”, “Austria”, “Azerbaijan”, “Belarus”, “Belgium”, “Bulgaria”, “Czech Republic”, “Denmark”, “Estonia”, “Finland”, “France”, “Georgia”, “Germany”, “Greece”, “Hungary”, “Iceland”, “Ireland”, “Italy”, “Kazakhstan”, “Latvia”, “Lithuania”, “Luxembourg”, “Macedonia”, “Malta”, “Moldova”, “Montenegro”, “Netherlands”, “Norway”, “Poland”, “Portugal”, “Romania”, “Russia”, “Serbia”, “Slovakia”, “Slovenia”, “Spain”, “Sweden”, “Switzerland”, “Turkey”, “Ukraine”, and “United Kingdom”). Second, we compiled the list of articles for each continent after removing duplicates, using the EndNote Web software for all the European and South American mycorrhizal published scientific articles between 1975 and 2018 in any language (>99% of articles were in English). All research articles as well as reviews and meta-analyses were included. Third, the articles not directly related to the mycorrhizal symbiosis (less than 5% of all articles) were manually excluded. Then, an article dataset was compiled for each continent with information about the country or countries where the studies were conducted, year of publication, and number of citations (2724 articles in total). Fourth, we selected the most influential articles (the ones cited 70 or more times until the 27th of November, 2018) and carefully checked and assigned them to one of the following nine general mycorrhizal topics: “rhizosphere interactions”, “plant invasions”, “phylo/biogeography”, “morphology”, “molecular methods”, “ecosystem remediation”, “community structure”, “biogeochemistry”, and “anthropogenic effects”. These topics referred to the role of the mycorrhizal symbiosis or mycorrhizal fungi in relation to each specific topic. For instance, “rhizosphere interactions” comprised those articles regarding the interaction of mycorrhizal plant roots and their immediate surroundings with other organisms in the soil. When an article included more than one topic, the assigned topic was the most prevailing in the article.

5.3 South American and European Mycorrhizal Research Trends

The literature search yielded a total of 1927 scientific articles for Europe and 797 for SA (Fig. 5.1), showing that even though Europe has a territory roughly four times smaller than SA, its mycorrhizal research was more than double. From the beginnings of the 1990’s, there has been a steady increase in the yearly production of scientific articles in both continents, with an outstanding research increase over the last 10 years (Fig. 5.1). At the end of the 1980’s and up to the 1990’s, several factors could have boosted mycorrhizal research, i.e. the availability of molecular methods that allowed for more efficient and detailed taxonomic and biochemical studies of the mycorrhizal symbiosis (White et al. 1990; Gardes and Bruns 1993;

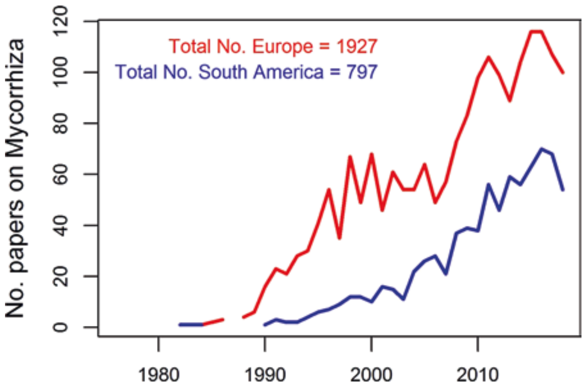

Fig. 5.1 Number of scientific articles on mycorrhizal research yearly published for South America (blue lines) and Europe (red lines) for the period 1975–2018

Harrison and van Buuren 1995; Bianciotto et al. 1996). As a consequence of the new information available, new conceptual developments on mycorrhizal networks (Toju et al. 2014; van der Heijden et al. 2015) and biogeography (Read 1991) were extended. A second research wave on mycorrhiza occurred at the end of the 2000's (Fig. 5.1), which could be explained by the arrival of the 'omics' era (Bonfante 2018). This technological revolution boosted the identification of mycorrhizal genes and their expression in relation to plant physiological processes in fungal colonization and subsequent mycorrhizal activities. Derived from the arrival of this technology, one specific topic that attracted great attention was the identification and classification of fungal mycorrhizal species (Schüßler et al. 2001; Öpik et al. 2010; Nilsson et al. 2018; Tedersoo et al. 2018; Wijayawardene et al. 2018).

Regarding the mycorrhizal scientific production of SA, Brazil was the country with the highest number of scientific articles published, followed by Argentina, Chile, Venezuela, and Ecuador (Fig. 5.2). Brazil is by far the most populated of these countries, and hosts the largest number of scientists in SA. Together with Brazil, Argentina and Chile have a long historical tradition in natural history studies, including mycological studies, which goes back to Darwin (Berkeley 1841). It is worth mentioning the studies carried out in the Patagonian region, which were developed by important European naturalists and mycologists such as Claudio Gay (Montagne 1850) and Rodolfo and Federico Philippi (Philippi 1893; Castro et al. 2006). The interest of European mycologists in Argentinian and Chilean fungi continued over the Twentieth century, resulting in detailed descriptions of fungi and fungal communities (Spegazzini 1921; Singer and Morello 1960; Singer et al. 1965; Singer 1969, 1970).

In Europe, Norway, Spain, Sweden, Germany, and Poland were respectively the five top countries with the highest number of published scientific articles on mycorrhizal research (Fig. 5.3). These five countries are historically well known in the mycorrhizal research field. For instance, the ectomycorrhizal associations in the Swedish and Norwegian coniferous forests have been studied for almost 200 years (Bonfante 2018). These two Nordic countries have also increasingly focused their

Fig. 5.2 Country relevance regarding mycorrhizal scientific production in South America (indicated by blue circle size). The number of articles is only indicated for the top five most productive countries from 1975 to 2018; 59 of the articles were developed in more than one country

research on mycorrhizal signaling and metabolic pathways, and more recently, on soil microbiome interactions with the plant rhizosphere (Bonfante 2018; Sterkenburg et al. 2018). In contrast, the mycorrhizal research in Spain and Poland has been more focused on arbuscular mycorrhizal fungi, particularly on either the anthropogenic effects on fungi or its role in ecosystem remediation (in Spain), and on morphology and taxonomy (in Poland). On the other hand, German mycorrhizal research comprises a wider range of topics that vary from taxonomy and morphology to phylogeography and biogeography of mycorrhizal fungi.

We found that the mycorrhizal topics covered in the most cited articles (70 or more citations) were notably different in SA and Europe. In South America, studies describing the mycorrhizal fungi community structure predominated (7 out of 20 most influential articles; Fig. 5.4), while in Europe the articles were more devoted to the study of the anthropogenic impact on the mycorrhizal symbiosis (41 out of

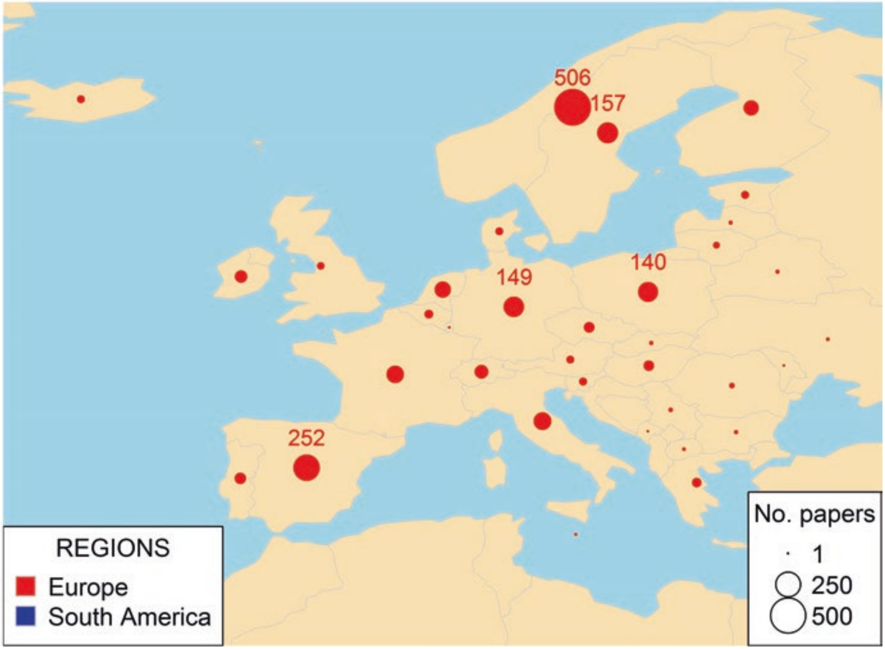

Fig. 5.3 Relative relevance per country following the mycorrhizal scientific production in Europe (indicated by different circle sizes in red). The number of articles is only indicated for the top five most productive countries from 1975 to 2018; 258 mycorrhizal European articles were developed in more than one country

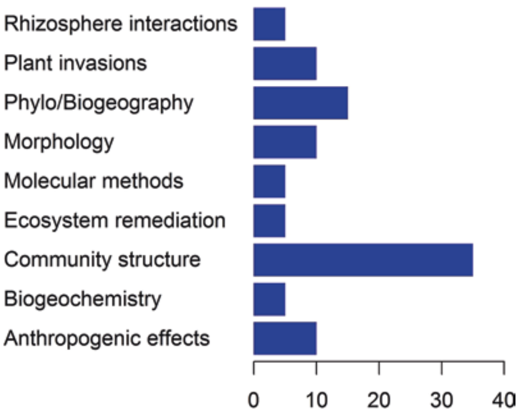

Fig. 5.4 Percentages of the most influential articles for each mycorrhizal topic (20 articles) from 1975 to 2018 in South America

141 most influential articles; Fig. 5.5). This difference indicates that more 'basic science' research was needed in South America, whereas a more applied and specific research was developed in Europe, such as the study of mycorrhizal roles on rhizosphere interactions and on biogeochemistry (Figs. 5.4, 5.5). In any case, this

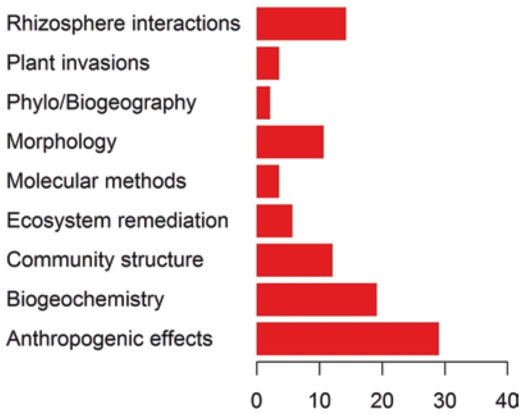

Fig. 5.5 Percentages of the most influential articles for each mycorrhizal topic (140 articles) from 1975 to 2018 in Europe

can also indicate that both territories may have different mycorrhizal research needs. In Europe, the smaller geographical extent and diversity, as well as the higher population densities and larger historical research (Bonfante 2018), could have contributed to be better explored and known in terms of mycorrhizal ecology, where the main concerns are the mycorrhizal roles for nature conservation under the current scenarios of global changes. In contrast, South American highest research interest was on its relatively unknown biodiversity and local mycorrhizal knowledge, which may have enhanced research on more descriptive and fundamental questions (Figs. 5.4, 5.5). It seems logical that the knowledge development has followed some clear steps: after studying the biodiversity patterns of mycorrhizal fungi communities, their effects on the rhizosphere and on biogeochemical cycles will follow.

Regarding the historical impact (number of citations) of each mycorrhizal research topic per continent, SA showed a very different pattern from Europe (Fig. 5.6). South American studies focused on the use and description of molecular methods, highly cited from the middle 1980’s to the late 1990’s (Fig. 5.6). This was followed by a very influential paper on ecosystem remediation issued during the late 1990’s (Franco and de Faria 1997). These trends were temporally replaced by a more diverse group of topics related to mycorrhizal fungal morphology, phylogeography/biogeography (or phylo/biogeography), and mycorrhizal-related plant invasion research (Fig. 5.6). In addition, four influential papers set rhizosphere interactions (Rubiales et al. 2009), biogeochemistry (Ryan et al. 2010), and anthropogenic effects (Cornejo et al. 2008; Stürmer and Siqueira 2011) as very popular topics of the South American literature in the late 2000’s and early 2010’s (Fig. 5.6). Europe had seven times more influential papers and thus the impact of single papers was less pronounced. Overall, the main influential topics during this period were phylo/biogeography from the middle 1980’s to the early 1990’s, ecosystem remediation during the 2000’s, and plant invasions and molecular methods afterwhile (Fig. 5.6).

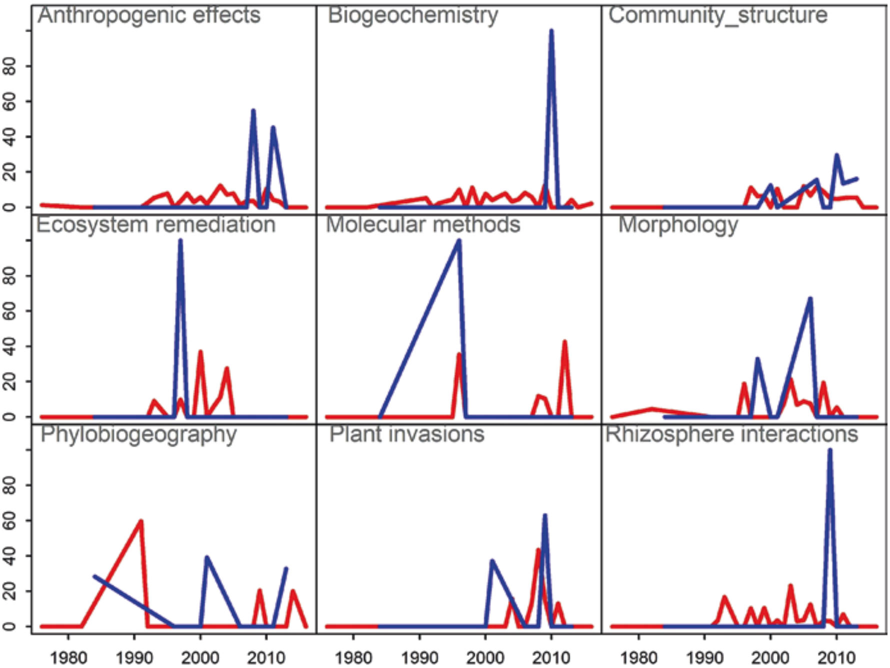

Fig. 5.6 Percentage of citations of highly cited (70 or more citations) scientific articles in South America (blue lines) and Europe (red lines) from 1975 to 2018

5.4 Geographical and Thematic Gaps on South American Mycorrhizal Research

Global studies on soil fungal and mycorrhizal diversity (Tedersoo et al. 2014; Davison et al. 2015) have so far excluded large portions of South American ecosystems and even some countries (Bueno et al. 2017a). These global studies have focused on the southern or northern regions of SA, leaving out much of the most important biodiversity hotspots, such as large areas of the Amazon basin, continental savannas, most of the Andes, and the Chocó biogeographic region, which hosts one of the rainiest and most diverse forests in the world (Galeano et al. 1998). This has already been shown in a review on hypogeous sequestrate fungi (Sulzbacher et al. 2017), indicating potential limitation for research in those areas. This pattern also is more or less consistent with our own findings (Fig. 5.2) since countries as Perú, Bolivia, Paraguay, and Uruguay have been barely studied. The main exception to this pattern among those global studies (Tedersoo et al. 2014; Davison et al. 2015) and our findings (Fig. 5.2) is Brazil, which is the most productive South American country regarding mycorrhizal literature (Fig. 5.2). But even though there is much Brazilian mycorrhizal research conducted on its southern part, closer to their most important universities, it is still scarce in the northern ecosystems, including the Amazon basin or the savanna.

Our review suggests that there are still large and relevant South American areas and ecosystems with a lack of basic mycorrhizal knowledge (Figs. 5.2–5.5), being urgent the development of descriptive science such as the analysis of these areas' fungal mycorrhizal biodiversity and community composition, to ultimately enhance our local and global understanding of biodiversity. Contrarily, in better known areas such as the south of Brazil or the Patagonian region (Fig. 5.2; Bueno et al. 2017a), we suggest to develop more specific and applied research, such as the study of the role of the mycorrhizal symbiosis in relation to rhizosphere interactions, biogeochemistry, or in relation to anthropogenic impacts on ecosystems. This mycorrhizal research would enhance the development of more applied science in terms of sustainable development, environmental conservation, or functional and mechanistic aspects. Needless to say, all these research topics are not mutually exclusive and the research aims need to be aligned with social and environmental local needs, as such is the case of some understudied areas being strongly affected by poverty, anthropogenic pressure, and ecosystem degradation.

Overall, and accounting for the current mycorrhizal research trends presented here and promising lines of mycorrhizal research (Bonfante 2018; Waller et al. 2018), we strongly believe that two main data types might need to be urgently collected in SA: (1) molecular data on mycorrhizal fungi, especially data obtained from environmental samples and which leads to DNA-based classification systems ('species hypothesis', Nilsson et al. 2018; 'virtual taxa', Öpik et al. 2010), and (2) plant roots to define plant mycorrhizal traits (Moora 2014; Bueno et al. 2018). There is a large gap of fungal mycorrhizal molecular data missing on databases, as it was illustrated by a quick search (on 19th of December, 2018) on the database MaarjAM (Öpik et al. 2010), which contains arbuscular mycorrhizal fungi DNA sequences from environmental or cultured samples. In MaarjAM, 373 sampling locations were situated in Europe, while only 97 were in SA. Moreover, in terms of plant mycorrhizal traits (Moora 2014) there are still many areas and entire countries in SA where the distribution of plant species and plant communities is not completely known, in contrast with a relatively well documented distribution of the European flora and vegetation (Kalwij et al. 2014; Soudzilovskaia et al. 2015, 2017). In fact, the plant mycorrhizal traits of most of the South American flora remain unknown. For instance, a recent study conducted in Chile dealing with the latitudinal distribution of plant mycorrhizal traits obtained after a systematic and thorough literature search, showed a coverage of about 13% of continental Chile plant species with geographical information (Silva-Flores pers. com.). Thus, considering Chile as one of the countries where mycorrhizal research has been further developed (Fig. 5.2), this percentage is relatively low in relation to a recent European study which covered around 45% of the European species with available geographic information (Bueno et al. 2017b). Thus, plant mycorrhizal trait collection is clearly needed in SA to estimate the prevalence of the mycorrhizal symbiosis in plant communities and ecosystems, and assign their response to biotic and abiotic conditions. This will ultimately lead to the understanding of the ecological roles of the mycorrhizal symbiosis in SA's unique ecosystems and its future responses to current global changes and local anthropogenic activities.

5.5 Suggested Directions

We believe that there are three steps that can be followed in order to boost South American mycorrhizal research and facilitate its global integration. First, it is necessary to strengthen the communication among South American mycorrhizal researchers and to channel and optimize research efforts through collaborative networking initiatives, such as the South American Mycorrhizal Research Network (SAMRN) (https://southmycorrhizas.org/; Bueno et al. 2017a). This aim could be efficiently achieved through the coordination of international funding public agencies, coordination which has not yet been implemented in SA. For instance, an ideal funding possibility in SA will be a call for large consortiums of international researchers with shared aims. This, in turn, will lead to homogenize discrepancies among methodological and study designs, ultimately enhancing the consolidation of strong international scientific groups in SA. For example, the European Union and their scientific funding agencies provide large international funding calls, which has led to large and significant studies on mycorrhizal diversity (Davison et al. 2015; van der Linde et al. 2018). Second, we suggest to facilitate the integration of intercontinental and global projects. European and North American global projects have not systematically integrated South American researchers, which could enlarge and optimize their sampling schemes as well as our scientific global knowledge. Furthermore, South American research network initiatives such as the SAMRN could enhance the communication among researchers from different continents and the optimization of potential collaborations. For instance, in terms of effective information and resources exchange, South American researchers could contribute with local knowledge, reduce local bureaucracy, offer access to unknown localities, and provide southern research perspectives, research needs and conceptual gaps. In turn, northern researchers could provide a more theoretical approach to global research questions, linked to a higher availability of technological and funding resources. Some integrating initiatives have been started, such as the analysis of worldwide leaf microbiomes (FunLeaf project; https://sisu.ut.ee/funleaf); however, as regards of the mycorrhizal symbiosis, further integration between descriptive and applied research on mycorrhizal diversity, ecosystem functions, and the effects of global changes still need to be promoted. Finally, the scientific interaction between the two continents could be considerably improved by the exchange of graduate students and postdocs. This exchange will facilitate the flow of ideas and research opportunities, and a starting point of the much needed scientific symbiosis between SA and Europe.

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