Chapter 13
Arbuscular Mycorrhizal Fungal Communities of High Mountain Ecosystems of South America: Relationship with Microscale and Macroscale Factors

Florencia Soteras, Eugenia Menoyo, Gabriel Grilli, and Alejandra G. Becerra

13.1 Introduction

South America harbors one of the main hotspots of diversity, the high mountain ecosystems, despite only accounting for a quarter of the Earth's land surface (Myers et al. 2000; Barry 2008; La Sorte and Jetz 2010; Hoorn et al. 2013). Several plants, birds, and macrofungal species show endemism in the high mountain of many regions of South America (Fjeldså and Kessler 1996; Myers et al. 2000; Robledo et al. 2006). These ecosystems comprise natural watersheds, providing several ecosystem services such as hydrological regime regulation, soil protection, and conservation of biodiversity (Grêt-Regamey et al. 2012). Mountain habitats show distinctive abiotic conditions that differentiate them from lowlands (Barry 2008). For instance, temperature decrease in average 6 °C per each km in elevation also influenced by latitude (Barry 2008). Generally, the studies in mountain ecosystems have been focused on aboveground diversity (plants, animals and macrofungi) (Robledo and Renison 2010; Castillo et al. 2017; Nouhra et al. 2018; Quintero and Jetz 2018), but little is known about soil communities (Lugo and Cabello 2002;

F. Soteras (✉)
Laboratorio de Ecología Evolutiva y Biología Floral, IMBIV, CONICET, Universidad Nacional de Córdoba, Córdoba, Argentina
e-mail: fsoteras@conicet.gov.ar

E. Menoyo
Grupo de Estudios Ambientales, IMASL, CONICET, Universidad Nacional de San Luis, San Luis, Argentina

G. Grilli · A. G. Becerra
Laboratorio de Micología, IMBIV, CONICET, and Cátedra de Diversidad Biológica I, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina

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Becerra et al. 2009; Menoyo et al. 2009; Geml et al. 2014; Soteras et al. 2016). Among them, arbuscular mycorrhizal fungi (AMF) are ubiquitous root symbionts in the Glomeromycota that form an obligate root symbiosis with great part of land plants (Schüßler et al. 2001; Spatafora et al. 2006). Despite the large diversity of host plants (ca. 200,000 species), there has just been identified in average 250 AMF morphological taxa (hereafter "morphospecies"), and no correlation between plant species and AMF richness has been globally found (Bever et al. 2001; Tedersoo et al. 2014).

The vast majority of the AMF taxa occur in nearly every climatic zones and continents (Davison et al. 2015). Last studies have postulated that a recent dispersion is the main factor shaping the cosmopolitan distribution of the most of the AMF taxa (Davison et al. 2015). However, these fungi are differentially affected by soil characteristics (Smith and Read 2008). In addition, different host species are colonized by particular AMF present in their rhizosphere (Senés-Guerrero and Schüßler 2016; Soteras et al. 2016), although there is a lack of a global positive correlation with plant richness. As plants and terrestrial animals, AMF taxa richness has been evidenced to correlate negatively with latitude (Hillebrand 2004; Davison et al. 2015), but different from ectomycorrhizal fungi (Tedersoo et al. 2014) and other soil microorganisms (Bardgett and Van Der Putten 2014). In addition, variables such as precipitation and temperature through the alteration of soil moisture, locally affect AMF richness (Davison et al. 2015). South America comprises diverse high mountain ecosystems, from low latitude tropical to high latitude temperate, where different local conditions also influence AMF communities (Matus et al. 2014).

Taxa of AMF could be grouped by their functional characteristics that are phylogenetically constrained (Hart and Reader 2002; Maherali and Klironomos 2007). Thereby, members of Gigasporaceae produce extensive extra-radical mycelia, sporulate lately in the growing season, and provide high nutritional benefits to hosts. On the other hand, Glomeraceae mainly colonize intraradically, produce spores early, and provide less nutritional benefits to hosts. Finally, Acaulosporaceae represents an intermediate colonization strategy, producing low biomass inside and outside the roots, and being highly resistant to soil acidity and low temperatures (Hart et al. 2001; Hart and Reader 2002). Accordingly, and based on the competitor-stress tolerant-ruderal framework of Grime (1979), Gigasporaceae are considered as "competitor", Glomeraceae as "ruderal" and Acaulosporaceae as "stress tolerant" (Chagnon et al. 2013).

In this chapter we reviewed and re-analyzed the data of the studies performed at high mountain ecosystems of South America to evaluate the variation of AMF morphospecies richness and composition of AMF communities in relation to micro- and macro-scale factors. Particularly, we hypothesized that high mountain forests harbor different richness and composition of AMF communities due to changes in microscale (host species, pH, N, P) and macroscale factors (latitude, temperature, and precipitation) rather than similar AMF communities as expected from its cosmopolitan distribution.

13.2 Arbuscular Mycorrhizal Fungi in the High Mountain Ecosystems of South America

Traditionally, the studies of AMF diversity were based on the morphological characteristics and ontogeny of the asexual spores (Smith and Read 2008). The advance of DNA-based methods improved the taxonomic identification of non-sporulating and AMF species. This kind of studies are very scarce in South America even more in mountain ecosystems (Soteras et al. 2016; Senés-Guerrero and Schüßler 2016). Therefore, we only considered the morphological diversity of AMF in high mountain ecosystems of South America. We compiled published studies searching in Google Scholar articles containing the following combination of terms: "arbuscular mycorrhizal" AND "high mountain" OR "Andean". We reviewed all the studies performed at mountain sites at around 1200 meters above sea level focusing on "highlands" *sensu* Barry (2008) that identified AMF spores morphologically. Following this procedure, we obtained in total 12 studies: 6 from Brazil, 5 from Argentina and 1 from Chile (Fig. 13.1, Table 13.1). Considering all of them, 168 AMF morphospecies were identified.

13.3 Arbuscular Mycorrhizal Fungi Richness Versus Macroscale and Microscale Factors

To disentangle the relationship of AMF richness with microscale and macroscale factors we fitted generalized linear models (GLM) with the *glm()* function as implemented in the R environment with Poisson error distribution and identity logarithmic link function (R Core Team 2018). When overdispersion was detected the standard errors were corrected using a quasi-GLM model (Zuur et al. 2009). Microscale factors included: host species or vegetation type and soil characteristics as pH, N and P content, obtained from the studies when available. Macroscale factors included: latitude, mean annual temperature (in degree Celsius multiplied by 10) and mean annual precipitation from MERRAclim (Vega et al. 2017a), available in the DRYAD database (Vega et al. 2017b).

Vegetation type or host species showed significant differences in AMF rhizospheric richness (Fig. 13.2). Mountain ecosystems in Brazil (savanna forest, quartz gravel field dominated by *Vellozia* sp., and rocky outcrops of Cerrado and Atlantic Forest) showed the highest AMF richness. This result is probably due to the dominance of AMF in hot and seasonal environments (van der Heijden et al. 2008). For the contrary, the lowest AMF richness was observed in successional temperate forests of *N. pumilio* (Fig. 13.2). Generally, in temperate forests, where nutrient availability is low and the organic form is present in litter and humus, predominate the colonization by ectomycorrhizal decomposer fungi (Matus et al. 2014). In consequence, ectomycorrhizal fungi are responsible for almost the 80% of the N acquired by plants of temperate and boreal ecosystems (van der Heijden et al. 2008). As in *N.*

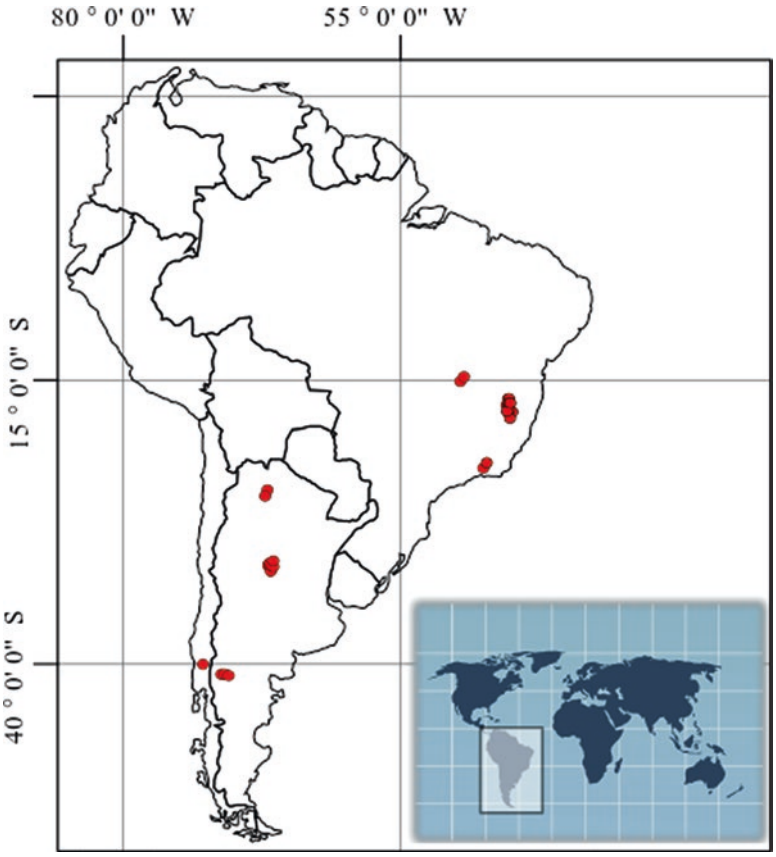

Fig. 13.1 Map showing the location of the high mountain ecosystems included in this study

pumilio forests, we found that reforested *Araucaria* forests of Brazil also showed a very low AMF diversity. In this study, rhizosphere soil samples were taken from reforested areas with *A. angustifolia* (8–12 years old) and *Pinus elliotti* plants (Moreira-Souza et al. 2003). Several studies have described changes in AMF communities associated with exotic plant invasion (Mummey and Rillig 2006). The very low AMF richness in this ecosystem compared with 19 other mountain hosts and ecosystems support the evidence that exotic plant species might negatively influence on soil AMF communities.

Arbuscular mycorrhizal fungi richness related to microscale (pH, N and P content) and macroscale (latitude, mean annual temperature and mean annual precipitation) factors are shown in Fig. 13.3. AMF richness was negatively related to pH ($t = 2.049$, $P = 0.046$, Fig. 13.3a), positively to N ($t = 3.003$, $P = 0.006$, Fig. 13.3b), but not significant relationship was observed with P ($t = 0.236$, $P = 0.81$, Fig. 13.3c). In addition, a negative relationship was observed of AMF richness with latitude in absolute numbers ($t = -4.015$, $P < 0.001$, Fig. 13.3d), and a positive relationship

Table 13.1 Summary of the studies performed in high mountain ecosystems of different sites of South America. Sites are ordered by increasing latitude, and information about treatment of the study, vegetation type or rhizosphere host or dominant plant, altitude, soil texture, P and N is provided

Site	Latitude	Longitude	Treatment	Vegetation type/Rhizosphere host / dominant plant species	Altitude (m)	Soil texture	P (ppm)	N (%)
Brazil[a1]	15°36′6.36″S	47°43′3.92″W	Cerrado CS-I	Savanna forest	1100	Sandy clay loam	2.4	–
	15°35′34.04″S	47°44′12.09″W	Cerrado CS-II	Savanna forest	1100	Sandy clay loam	1.7	–
	15°35′53.74″S	47°42′24.93″W	Cerrado CS-III	Savanna forest	1100	Sandy clay loam	1.4	–
Brazil[a2]	18°12′21.1″S	43°33′47.6″W	Soberbo stream	Rupestrian grassland: *Syngonanthus elegans*, *Loudetiopsis chryssothrix*, *Xyris* sp.	1368	–	5.8	–
	17°55′02.9″S	43°35′53.74″S	National Park "sempre-vivas"		1310	–	2.4	–
Brazil[a3]	19°16′ 50.2″S	43°35′ 27.7″W	Sandy bogs	*Lagenocarpus rigidus*	1158	Sandy loam	2	0.7
	19°16′ 54.4″S	43° 35′ 29″W	Peat bogs	*Axonopus siccus*	1146	Sandy loam	3	1.5
	19°17′ 15.2″S	43°35′ 39.2″W	Rocky outcrops	*Trachupogon spicatus*	1163	Sandy loam	2	0.9
	19°17′ 04.1″S	43°35′ 37.7″W	Quartz gravel field	*Vellozia* sp.	1192	Sandy loam	3	0.8
	19°16′ 57.7″S	43°35′ 40.0″W	Cerrado	*Schizachyrium tenerum* Nees.	1173	Clay loam	2	1.7

(continued)

Table 13.1 (continued)

Site	Latitude	Longitude	Treatment	Vegetation type/Rhizosphere host / dominant plant species	Altitude (m)	Soil texture	P (ppm)	N (%)
Brazil[a4]	19°15′50.6″S	43°35′10.3″W	Cerrado	Rocky outcrop and Cerrado *sensu stricto*	1000	Sandy	1.16	–
	19°13′56.5″S	43°34′34.8″W		Rocky outcrop and Cerrado *sensu stricto*	1100	Sandy	1.15	–
	19°17′43.0″S	43°33′17.4″W		Rocky outcrop	1200	Sandy	2.71	–
	19°17′49.6″S	43°35′28.2″W		Rupestrian grassland	1300	Sandy	1.08	–
	19°16′59.3″S	43°32′08.9″W		Rupestrian grassland	1400	Sandy	2.38	–
Brazil[a5]	22°44′ S	45°30′W	Native *Araucaria* forests	*Podocarpus lambertii*, *Ilex paraguariensis*, *Clethra scabra*, *Weinmannia piannata*, *Cryptocarya aschersoniana*, *Prunus myrtifolia*, *Symplocus aegrota*, *Drymys winterii*	1674	–	10	–
			Reforested *Araucaria* forests	*Araucaria agustifolia* and *Pinus eliotii*	1674	–	4.5	–
Brazil[a6]	23°19′31″S	45°05′02″W	Atlantic forest	*Euterpe edulis* Mart., *Cecropia glaziovii* Snethl., *Guapira opposita* (Vell.) Reitz, *Bathysa australis* (A.St.-Hil.) Benth. & Hook., *Mollinedia schottiana* (Spreng.) Perkins, *Coussarea* sp., *Myrcia spectabilis* DC.	1000	Sandy clay loam	4.8	–
Yungas of Argentina[a7]	26°58′S	65°45′W	Quebrada del Portugués	*Alnus acuminata* Kunth.	2187	Sandy loam	13.75	2.22
	27°43′S	65°54′W	Narváez range	*Alnus acuminata* Kunth.	1820	Loam	9.73	3.65

Site	Latitude	Longitude	Treatment	Vegetation type/Rhizosphere host / dominant plant species	Altitude (m)	Soil texture	P (ppm)	N (%)
Central Argentina[a8,9,10]	31°58′S	64°56′W	Los Molles	*Polylepis australis* Bitt.	1800–2000	Sandy loam	56.86	0.94
	31°23′S	64°48′W	Los Gigantes	*Polylepis australis* Bitt.	1800–1900	Sandy loam	33.23	0.59
	31°44′S	64°47′W	Santa Clara	*Polylepis australis* Bitt.	2000–2200	Sandy loam	34.73	0.72
	31° 25′S	64° 47′W	Los Gigantes	*Polylepis australis* Bitt.	2140	Sandy loam	10.17	0.12
	31° 37′S	64° 49′W	Quebrada del Condorito national park	*Polylepis australis* Bitt.	2190	Sandy loam	16.3	0.11
	31° 20′S	64° 45′W	Mountain grassland	*Briza subaristata* Lam., *Deyeuxia hieronymi* (Hack.) Türpe, *Poa stuckertii* (Hack.) Parodi, *Eragrostis lugens* Nees., *Sorghastrum pellitum* (Hack.) Parodi, *Alchemilla pinnata*	2250	Loam to clay loam	–	–

(continued)

Table 13.1 (continued)

Site	Latitude	Longitude	Treatment	Vegetation type/Rhizosphere host / dominant plant species	Altitude (m)	Soil texture	P (ppm)	N (%)
Chile[a11]	40°47′S	72°12′W	Forest (site 1)	*Nothofagus pumilio*	1150	Silt loam	18.28	24
			Forest (site 2)				17.49	22
			Forest (site 3)				16.70	21
			Crater (site 4)	Successional forest: *Bacharis nivalis* Schultz Bip., *Senecio bipontinii* Wedd., *Pernettya pumila* (L.F.) Hook., *Quianchamalium chilense* Lam.	1273	Silt loam	16.16	47
			Crater (site 5)				14.06	40
			Crater (site 6)				11.97	34
			Disturbed (site 7)	*N. Pumilio*	1050	Silt loam	8.32	13
			Disturbed (site 8)				8.12	12
			Disturbed (site 9)				7.92	12
Patagonia Argentina [a12]	41°16′12″S	71°18′16″W	Chalhuaco Hill	*Chiliotrichum rosmarinifolium* Less.	1629	Sandy loam	26.40	0.33
	41°10′20″S	71°18′56″W	Catedral Hill	*Armenia maritima* (Mill.) Wild.	1886	Sandy loam	1.1	0.07
	41°10′33″S	71°49′04″W	Tronador Hill	*A. maritima, Baccharis magellanica* (Lam.) Pers., *B. empetrifolia* Lam., *C. rosmarinifolium, Nassauvia revoluta* Don., *Quinchamalium chilense, Senecio bipontinii* Wedd.	1904	Sandy loam	1.9	0.08

[a]References: [1]Souza de Pontes et al. (2017), [2]Orlandi Costa et al. (2016), [3]de Carvalho et al. (2012), [4]Coutinho et al. (2015), [5]Moreira-Souza et al. (2003), [6]Bonfim et al. (2016), [7]Becerra et al. (2011), [8]Soteras et al. (2015), [9]Menoyo et al. (2009), [10]Lugo and Cabello (2002), [11]Marín et al. (2016), [12] Velázquez et al. (2016)

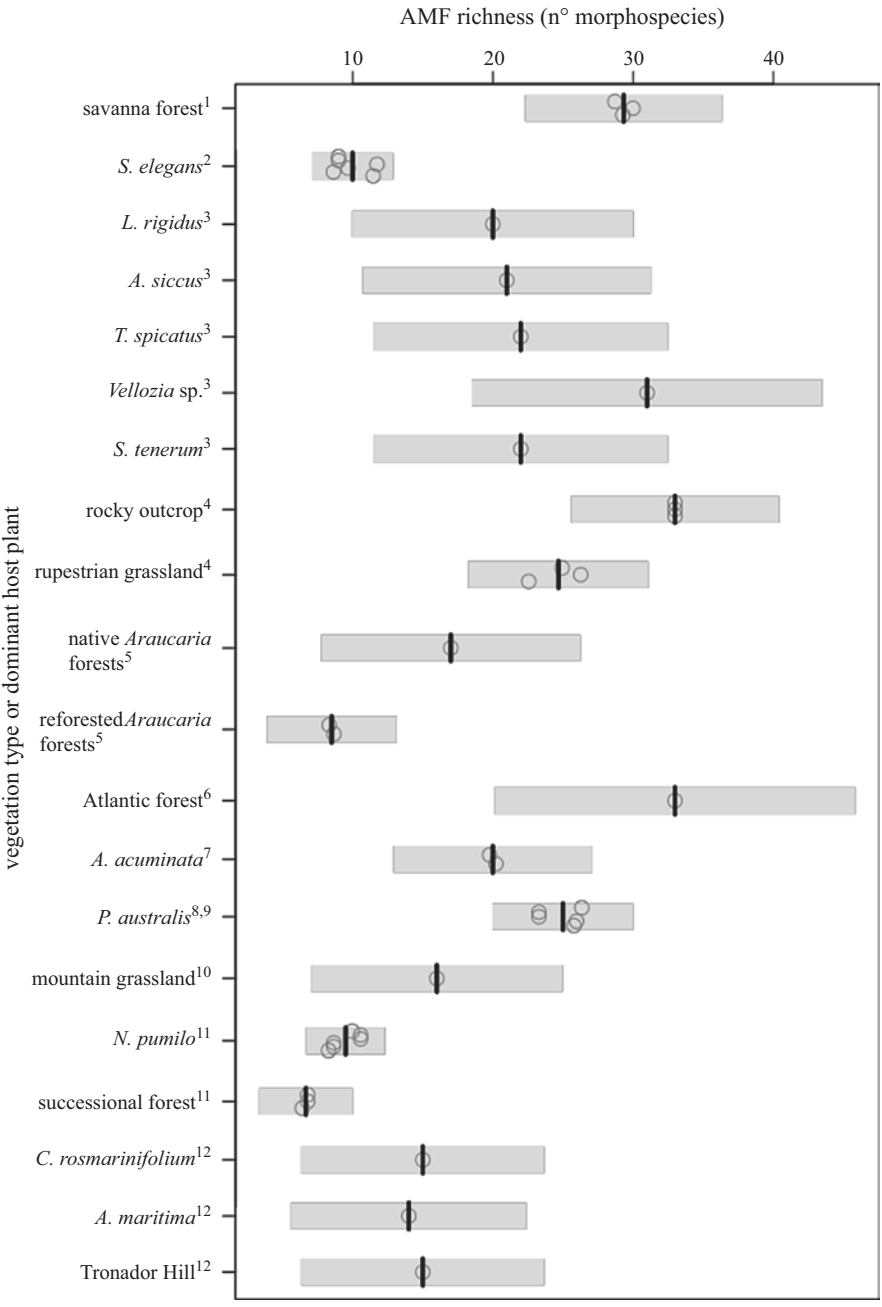

Fig. 13.2 AMF richness related to vegetation type or dominant host plant (ordered by increasing latitude)

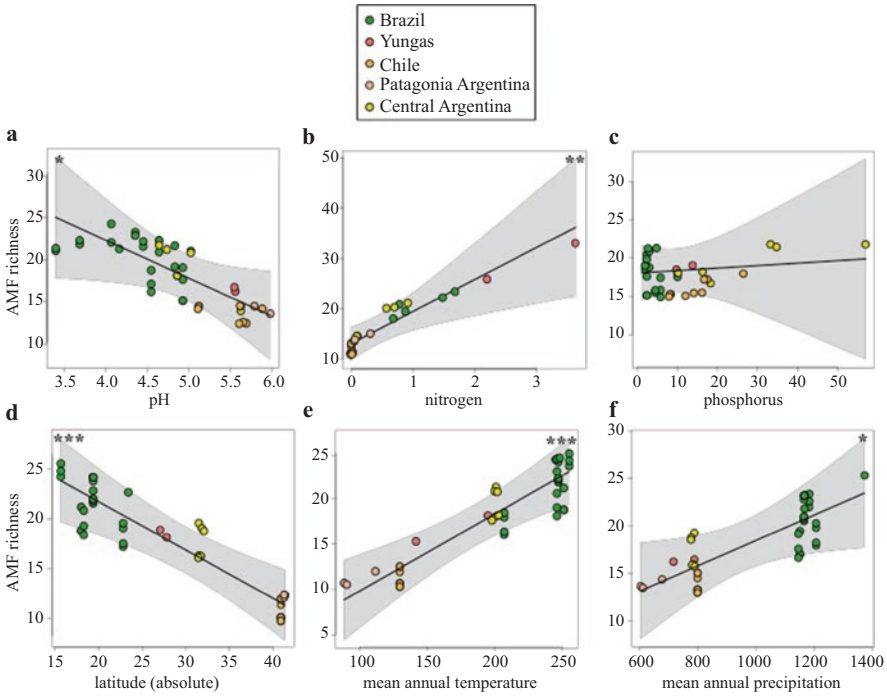

Fig. 13.3 AMF richness related to microscale (pH, N and P content) and macroscale (latitude, mean annual temperature and mean annual precipitation) factors. Asterisks indicate significant relationship according to the GLM (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$). Points color represents sampling sites

with both mean annual temperature ($t = 4.191$, $P < 0.001$, Fig. 13.3e) and precipitation ($t = 2.137$, $P = 0.039$, Fig. 13.3f). AMF communities of high mountain showed high richness at lower latitudinal tropical ecosystems, where seasonal changes of solar radiation, day length and temperature are small (Barry 2008). These ecosystems showed the lowest pH and intermediate N values. The same latitudinal pattern was observed for global AMF richness studies (Davison et al. 2015), plants and animals (Hillebrand 2004), but not for ectomycorrhizal fungi which are associated with specific forest types (Tedersoo et al. 2014).

13.4 Arbuscular Mycorrhizal Fungi Communities' Composition: Geographical Structure and Relationship with Macroscale Factors

In order to evaluate the variation on AMF community composition in relation to different geographical scales and macroscale factors, we first constructed principal coordinates of neighbor matrices (PCNM). The PCNM variables allow to detect if

the biological response (i.e. AMF community composition) is associated with different spatial structures along the study area. We obtained six geographical variables able to detect the spatial structure of the data at all scales encompassed by the sampling design (Borcard and Legendre 2002; Borcard et al. 2004). The order of the PCNM variables follows a progression from larger to smaller spatial scales (Borcard et al. 2004). For each response data model, the most significant PCNM variables were chosen by permutational forward model selection and ensuring that the adjusted R^2 of the reduced models did not exceeded the adjusted R^2 of the global models. The AMF community composition (presence-absence) was partitioned among the selected geographical variables and macroscale factors (latitude, mean annual temperature and mean annual precipitation) using distance-based redundancy analysis (db-RDA), with *capscale()* function from R package vegan (Legendre and Andersson 1999; Oksanen et al. 2018). The dissimilarity distance between pairs of AMF morphospecies was estimated using the Sorensen index. The variation explained by geographical variables and macroscale factors was determined by the automatic selection of variables using forward model choice on adjusted R^2 with 999 permutations using the *ordiR2step()* function. In this procedure, the variables that best fit the data are sequentially selected and added to the final model. The analyses were performed using the vegan package in R. The significance among centroids of sites was assessed with the *envfit()* function of the vegan package after 999 permutations. To determine whether the significant effects were attributed to either differences of multivariate site (between group variability) or to dispersion (within group variability) we used the *betadisper()* function of vegan. Microscale factors were not included in this analysis due to missing data in some sites. The Yungas, Cerrado and Soberbo stream from Brazil (Orlandi Costa et al. 2016; Souza de Pontes et al. 2017) were discarded from the db-RDA analysis due to significant effect of within heterogeneity, which avoids the possibility to differentiate the effects of multivariate dispersion from the compositional change among sites.

Four geographical variables were significantly structuring AMF communities (ordered in increasing importance for final model fit: PCNM1: $F = 17.737$, $P = 0.002$; PCNM3: $F = 11.047$, $P = 0.002$; PCNM4: $F = 4.779$, $P = 0.002$; and PCNM2: $F = 2.697$, $P = 0.018$). The three macroscale variables significantly structured AMF community composition of each site (latitude: $F = 19.899$, $P = 0.002$; mean annual precipitation: $F = 92.853$, $P = 0.002$; and mean annual temperature: $F = 5.532$, $P = 0.002$) being kept in the final model. Site differences in relation to their AMF community was associated 25% with both geographical and macroscale factors ($R^2 = 0.72$, pseudo-F = 12.32, $P = 0.001$, Fig. 13.4a), 21% with only geographical factors ($R^2 = 0.59$, pseudo-F = 12.35, $P = 0.001$, Fig. 13.4b), and 19% with only macroscale factors ($R^2 = 0.55$, pseudo-F = 13.63, $P = 0.001$, Fig. 13.4c).

According to the analysis derived from the db-RDA, the AMF community differed significantly among sites ($r^2 = 0.94$, $P < 0.001$, Fig. 13.4a). At a wider scale (represented by PCNM1; associated with db-RDA1: $r^2 = 0.95$, $P = 0.001$), latitude, precipitation and temperature were highly related to differences between Brazil and Chile in their AMF community composition. This is in concordance with global studies of AMF biogeography that showed influences of temperature and precipitation on AMF root colonizing composition (Öpik et al. 2013; Davison et al. 2015).

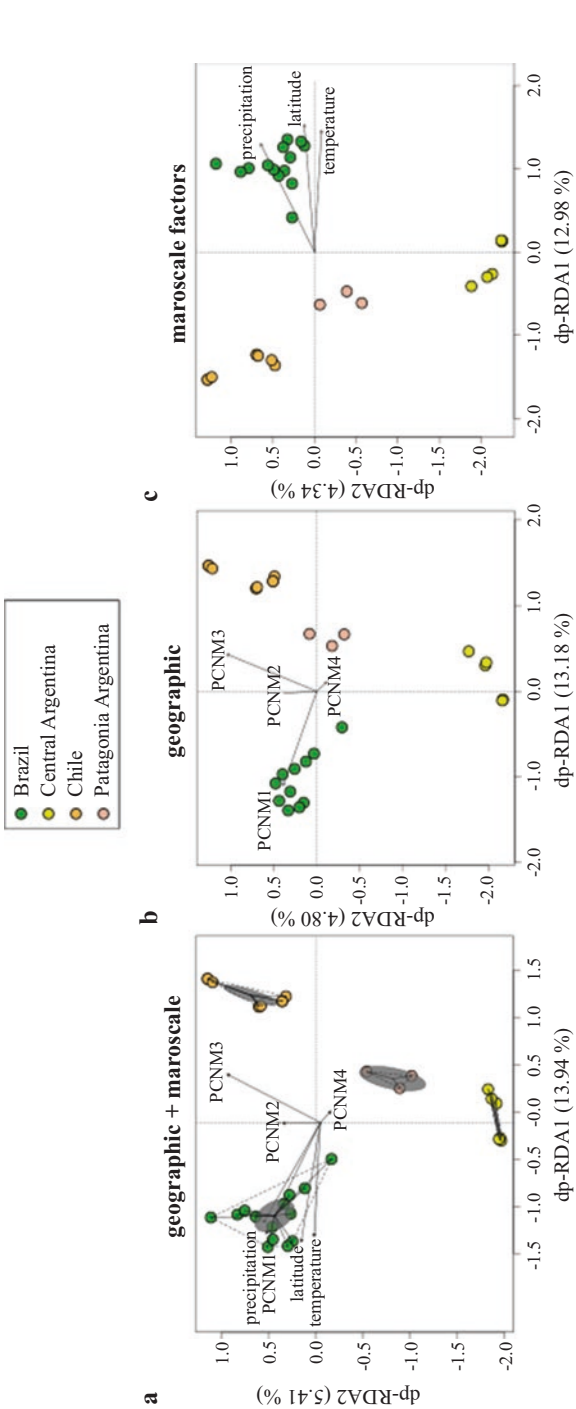

Fig. 13.4 Distance-based redundancy analysis (db-RDA) of localities-based of AMF presence-absence community composition. Arrows indicate the direction of the maximum change in geographical (PCNMs) and macroscale factors (latitude, mean annual temperature and precipitation); **a** complete model: ellipses represent the 95% confidence dispersion around localities centroids, lines connect replicates within localities to their centroids; **b** geographical model, and **c** climatic model

At coarse scales (mainly represented by PCNM3; associated with db-RDA2: $r^2 = 0.66$, $P = 0.001$) Central Argentina and Patagonia Argentina differentiated in their AMF community composition mainly due to the differences in host species (PERMANOVA: $F = 12.54$, $r^2 = 0.77$, $P = 0.001$), soil pH (PERMANOVA: $F = 10.53$, $r^2 = 0.47$, $P = 0.001$) and N content (PERMANOVA: $F = 7.678$, $r^2 = 0.39$, $P = 0.001$). Several studies provide evidence that the distribution of AMF can be affected by host species, pH and total N (Koske 1987; Johnson et al. 1992; Egerton-Warburton et al. 2004).

To evaluate the strength of association of sampling sites, and vegetation type or dominant host with AMF morphospecies, an indicator species analysis was applied using the *indval()* function of the R package labdsv (Dufrene and Legendre 1997; Roberts 2013). Two species were significantly associated with Brazil, nine with Yungas, eleven with Central Argentina, three with Chile, and six with Patagonia. Of the 20 vegetation types and dominant hosts, six AMF morphospecies were significantly associated with savanna forest, one with *A. siccus*, one with *T. spicatus*, four with rocky outcrop, one with rupestrian grassland, one with *A. acuminata*, four with *P. australis*, three with *N. pumilio*, and one with successional forest. A meta-analysis of global distribution patterns of root-colonizing AMF also demonstrated different type of ecosystems hosting different assemblages of AMF morphospecies (Öpik et al. 2006).

13.5 Relationship Between AMF Functional Richness and Abiotic Characteristics

Arbuscular mycorrhizal fungi were grouped into three functional groups according to their traits (*sensu* Chagnon et al. 2013): "ruderal-Glomeraceae" (Claroideoglomeraceae + Glomeraceae + Pacisporaceae + Diversisporaceae), "stress-tolerant-Acaulosporaceae" (Acaulosporaceae + Ambisporaceae + Entrophosporaceae + Archaeosporaceae), and "competitor-Gigasporaceae". To determine the relationship among AMF functional groups with microscale and macroscale factors we fitted generalized linear models (GLM) with the *glm()* function as implemented in the R environment with Poisson error distribution and identity or logarithmic, in the case of Gigasporaceae, link function. When overdispersion was detected, the standard errors were corrected using a quasi-GLM model.

Glomeraceae and Gigasporaceae families were negatively associated with pH ($t = 3.685$, $P < 0.001$; $t = 2.785$, $P = 0.009$; respectively). Meanwhile, and contrary to previous evidence (Veresoglou et al. 2012), Acaulosporaceae did not show a significant relationship with pH ($t = 0.747$, $P = 0.460$). Glomeraceae and Gigasporaceae showed higher morphospecies richness in soils with pH between 3.5 and 5.0, and Acaulosporaceae from 5.0 to 6.0. Contrary to Glomeraceae, sporulation of Acaulosporaceae is promoted in acidic soils, but its members also occur on higher pH soils (Clark 1997). Only Gigasporaceae showed a significant and positive asso-

ciation with N ($t = 5.106$, $P < 0.001$), and a negative association with P ($t = 2.038$, $P = 0.048$). Meanwhile, Glomeraceae and Acaulosporaceae did not show a significant relationship with any of these variables (Fig. 13.5). In P- limited ecosystems with high N availability, host plants may select AMF taxa with extensive hyphal networks that forage P effectively, such as Gigasporaceae (Egerton-Warburton et al. 2007). This is because excess in N availability is expected to improve plant photosynthesis thus making the availability of C for transfer to AMF symbionts less costly for the plant (Johnson 2010). Nonetheless, evidence that increase N availability reduce the occurrence of AMF taxa with greater P benefit (i.e. Gigasporaceae) has been also documented (Treseder et al. 2018).

Among macroscale factors, Glomeraceae and Gigasporaceae showed a negative significant relationship with latitude ($t = 4.450$, $P < 0.001$; $t = 5.180$, $P < 0.001$; respectively), and a positive association with mean annual temperature ($t = 5.302$, $P < 0.001$; $t = 3.902$, $P < 0.001$; respectively) and precipitation ($t = 2.779$, $P = 0.008$; $t = 3.815$, $P < 0.001$; respectively). However, Acaulosporaceae did not show significant association with any of these variables (Fig. 13.5). Gigasporaceae members are adapted to live in stable ecosystems (de Souza et al. 2005), and highly dependent on precipitation (Veresoglou et al. 2012) as observed here.

13.6 Conclusions

High mountain ecosystems of South America differed in their AMF communities due to macroscale and microscale factors, revealing indicator AMF morphospecies associated with either sampling site or vegetation type or host identity. This is in line with global molecular studies of AMF, which evidenced patchily distributed AMF communities (Öpik et al. 2010, 2013), although contrary to an AMF taxa cosmopolitan distribution (Davison et al. 2015). As stated by Davison et al. (2015), several high mountain ecosystems of South America remain unexplored thus making our results probably related to low sampling effort. However, it is important to take into account that these authors presented global patterns of molecularly identified AMF species considering only four records among grassland and successional forests at South America thus probably losing the patchily structure of AMF communities of high mountain ecosystems. The AMF richness relationships with micro and macroscale factors were mainly due to Glomeraceae and Gigasporaceae responses to these variables. At higher scales, tropical and temperate ecosystems differentiated in their AMF community composition due to macroscale factors as latitude, precipitation and temperature. At lower scales, soil characteristics and host species became the most relevant factors in differentiating AMF community composition of sites. High mountain ecosystems of South America comprise a particular environment in which AMF communities could not be framed in a cosmopolitan pattern but rather they adjust to their own pattern associated with specific conditions of the highlands.

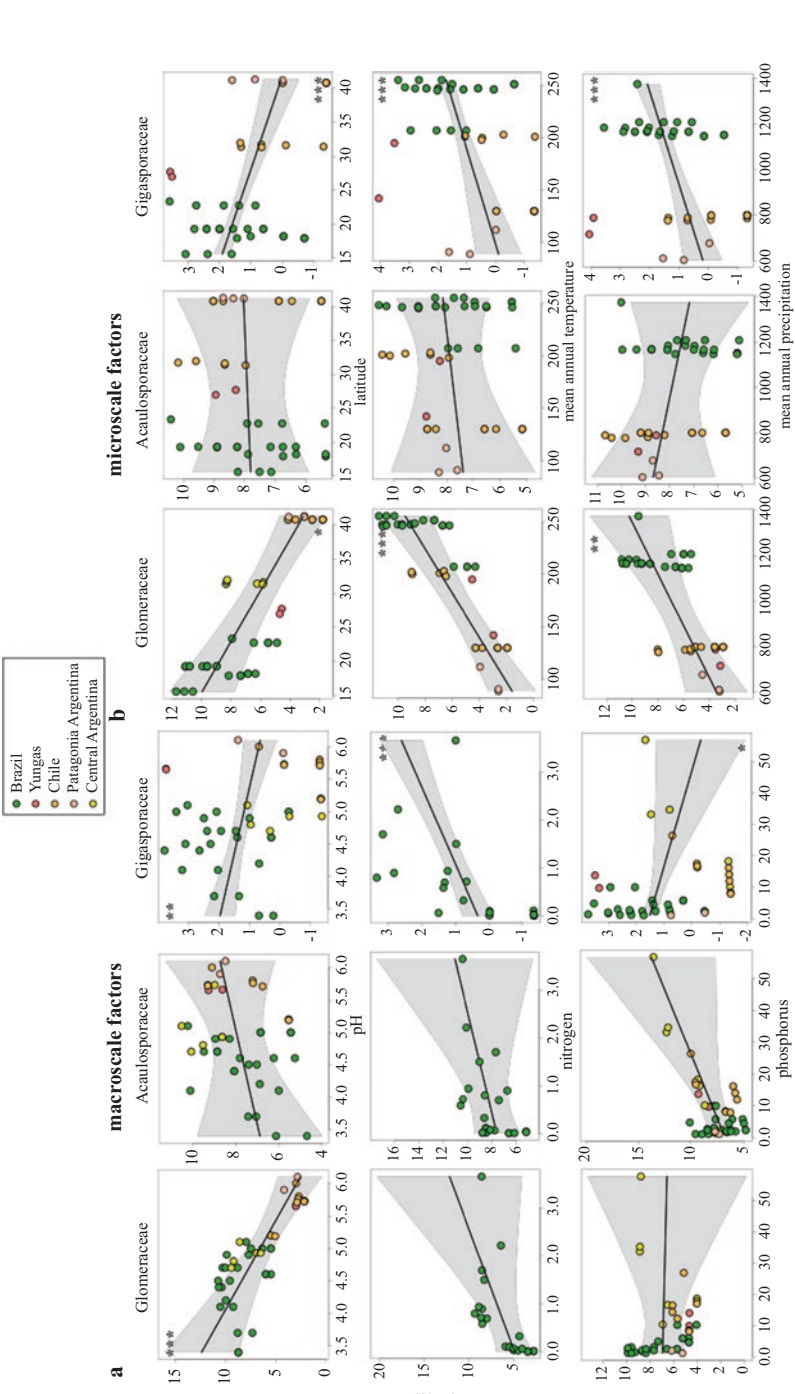

Fig. 13.5 AMF families richness in relation with (**a**) microscale and (**b**) macroscale factors. Asterisks indicate significant relationship according to the GLM (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$). Points color represents sampling sites

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