

Chapter 2

Latitudinal Distribution of Mycorrhizal Types in Native and Alien Trees in Montane Ecosystems from Southern South America



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2.1 Introduction

Biological invasions constitute a global environmental threat that rapidly alters natural communities and ecosystem functioning (Mack et al. 2000; MA 2005). The changes caused by alien plant invasions into novel ecosystems are accompanied by economic losses and environmental and social problems (Pimentel et al. 2000, 2005; Charles and Dukes 2007; Pejchar and Mooney 2009). For these reasons, it is extremely important to know the mechanisms that make an exotic plant to expand into new ecosystems, particularly tree species that are known to profoundly alter biological communities and ecosystem processes (Richardson et al. 2014).

One way to understand the success of alien trees in novel ecosystems is by comparing their ecological strategies with those of natives (Pyšek and Richardson 2007; Van Kleunen et al. 2010). In the case of plants, contrasting strategies to successfully invade novel ecosystems can be expected: (a) those that share attributes with natives and (b) those that differ from native communities (converging and diverging functional strategies, respectively) (e.g. Cleland 2011; Leishman et al. 2007, 2010; Pyšek and Richardson 2007). Whether alien strategies tend to converge or diverge from those of natives depend on geographical scale, climatic conditions, land uses, plant life form, and suite of biological attributes selected (e.g. Tecco et al. 2010, 2013; Zeballos et al. 2014; Funk et al. 2017). However, the comparisons between native and alien species rarely include symbiotic interactions (but see Tecco et al. 2013).

Biological interactions such as belowground symbiosis between plant and fungi, known as mycorrhizas, have also shown to influence the success of alien species in novel ecosystems (Richardson et al. 2000). Mycorrhizas are associations between

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plant and fungi at the root level and are one of the most widespread symbioses. In exchange for carbon, mycorrhizal fungi provide plants the access to limiting nutrients, among other benefits (Smith and Read 2008). According to the anatomy, morphology, and functional attributes of the symbiosis (including the phylogenetic identity of the plant and fungal symbionts), three basic and widespread types of mycorrhizas can be recognized dominating terrestrial ecosystems (Smith and Read 2008; Brundrett 2009): Arbuscular mycorrhizas (AM), Ectomycorrhizas (ECM), and Ericoid mycorrhizas (ERM). There also exist other types of mycorrhizas but they do not dominate in any ecosystem.

Despite the phylogenetic imprints that often characterize mycorrhizal distribution among plants (Brundrett 2009), models on mycorrhizal distribution across environmental gradients, vegetation types (Read 1991; Read 1993) and plant life forms (Brundrett 1991, 2009) have been proposed. At the global scale, the one proposed by Read (1991) is still the best proxy to distribution of mycorrhizal types among biomes. Recent results at the continental scale (Europe), support Read's model and found that distribution of mycorrhizal types is mainly driven by mean annual temperature, soil pH and net primary productivity (Bueno et al. 2017).

Arbuscular mycorrhizas are formed by more than 80% of the terrestrial plants and dominate soils with high mineral N but low P availability such as temperate grasslands, savannahs and subtropical deciduous forests. Ectomycorrhizas are formed by several plant lineages, mainly trees growing in acidic soils with litter accumulation and seasonal N and P availability. They typically dominate in temperate forests and taiga. Instead, Ericoid mycorrhizas are restricted to Ericales and dominate in acidic soils with low N and P contents such as heathlands and the arctic tundra. These mycorrhizal types are associated with different patterns of carbon and nutrient cycling, thus have pivotal role in ecosystem functioning (Cornelissen et al. 2001; Read and Perez-Moreno 2003). For example, Cornelissen et al. (2001) observed that among British plant species, those with ERM mycorrhizas show low growth rates, low foliar N and P concentration, and poor decomposition rates. In contrast, AM plants show comparatively higher growth rates, N and P foliar concentrations, and decomposition rates. While ECM plants show intermediate levels of these attributes. It is worth mentioning that nearly 20% of plant species are Non-mycorrhizal (Brundrett 2009) but they are rarely considered in models of mycorrhizal distribution (but see Brundrett 2017; Bueno et al. 2017).

Some studies aimed to answer whether patterns of mycorrhizal distribution in alien plant species tend to converge or diverge with those in natives. For example, the majority of naturalized plants in Great Britain belong to AM families (Fitter 2005). Menzel et al. (2017) found that mycorrhizal aliens inhabit a wider geographical range when compared with non-mycorrhizal ones in Germany. This trend was more marked when only woody species were compared. Conversely, invasive aliens from non-mycorrhizal plant families are higher in number than those from mycorrhizal ones in California (Pringle et al. 2009). These differences suggest that mycorrhizal types may play different roles in plant invasions in different ecosystems. Moreover, they show that woody species behave differently than non-woody.

In this chapter we examine the patterns of distribution of mycorrhizal types among the most abundant native and alien trees in montane forest ecosystems along a latitudinal gradient in Argentina (Fig. 2.1). We aim to answer two general questions: (1) Do patterns of mycorrhizal distribution in contrasting montane ecosystems behave as is predicted by models on mycorrhizal distribution across biomes, and (2) Do patterns of mycorrhizal distribution in alien species tend to converge or diverge with those in observed in natives?

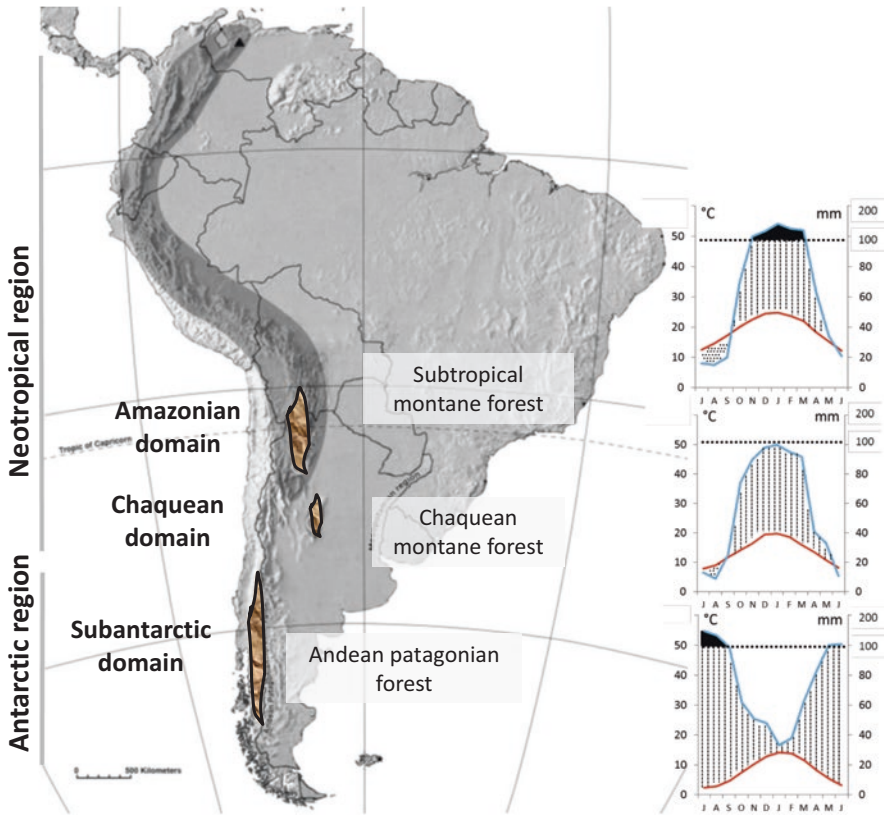


Fig. 2.1 Distribution of montane forests in Argentina. In brown the areas that were subjected to analyses in this chapter. In the right margin representative climate diagrams of these forest ecosystems (26°51'S/65°21'W, 31°6'S/64°27'W and 41°0'S/71°23'W, respectively; WorldClim – Global Climate Data)

2.2 Data Sources

Argentina includes an extensive land area that corresponds to two main regions: Neotropical and Antarctic. These regions are crossed by important montane ranges in north-south direction. The montane ranges correspond to the amazonian, chaquean, and sub-antarctic domains and are mostly covered by forests (Cabrera 1971) (Fig. 2.1). These forests are known as: Subtropical montane forests (also known as Yungas), Chaquean montane forests (also known as Chaco Serrano), and Andean-Patagonian forests (Morello et al. 2012; Oyarzabal et al. 2018). Data from soils were extracted from Rubio et al. (2019).

The **subtropical montane forests** occupy the east slopes in subandean and pampean mountains in northwest Argentina (Catamarca, Tucumán, Salta and Jujuy provinces), between 400 and 3000 m asl. The climate is warm and humid to subhumid with variable mean annual precipitation ranging between 800–3000 mm, 80% concentrated in summer (Fig. 2.1). There is a strong seasonal variation. The mean annual temperature is 22 °C at lower altitudes decreasing to 13 °C at higher altitudes. Three main vegetation types can be identified: premontane rain forests (400–700 m asl), montane rain forests (700–1500 m asl), and upper montane forests (1500–3000 m asl). Soils belong to the Mollisols, Alfisols, Entisols and Inceptisols orders with a pH 5–7.

The **chaquean montane forests** are seasonally dry forest ecosystems located at central Argentina mountain ranges, mainly in Córdoba Province, between 500 and 2790 m asl. The climate is subxerophytic and the mean annual precipitation range between 500 and 900 mm, concentrated in warm months (Fig. 2.1). Mean annual temperature range from 15 °C in lower altitudes and 7.4 °C at the highest points. Soils belong mainly to Entisols, pH 6–7.

The **Andean-patagonian forests** are located in southwest Argentina and Chile. The climate is cool temperate and humid. Mean annual precipitations range from 750 mm in the eastern areas while reach 4000 mm in some western areas known as Valdivian rain forests, albeit most areas average 1800 mm concentrated in winter as rain and/or snow (Fig. 2.1). The mean annual temperature is 8 °C decreasing with increasing latitude and altitude. Andisols, Molisols, Inceptisols and Entisols are the main soil orders represented in the area, pH 4.5–6.

Each of these montane forests consists in different subunits of vegetation. Due to the scale of analysis, each of them is considered as one ecological unit here.

The basic sources of literature for selecting the most abundant native tree species in each region were: Morello et al. (2012) and Oyarzabal et al. (2018), but also Cabido et al. (2018) for the Chaquean region.

Naturalized alien species are those foreign species that have successfully invaded any ecosystem: they have self-sustaining populations that do not require repeated reintroduction (Fitter 2005). For selecting naturalized alien tree species we used: Grau and Aragón (2000) and Sirombra and Meza (2010) for Subtropical montane forests, Giorgis and Tecco (2014) for Chaquean montane forests, and Simberloff et al. (2002, 2003), Kutschker et al. (2015), Datri et al. (2015), and Calviño et al. (2018) for Andean-Patagonian forests.

For assessing the mycorrhizal types in native and alien trees we gathered data from own field surveys and data available from literature such as Wang and Qiu (2006), Brundrett (2009), Fracchia et al. (2009), Tecco et al. (2013), Godoy et al. (1994), Castillo et al. (2006), among other specific resources. Some species form both ECM and AM. They were considered as ECM (except for *Juniperus communis*, see below) because this type has been shown to be more important in terms of mycorrhizal colonization rates (e.g. Van der Heijden 2001) and their nutrient and carbon cycling traits are more similar to those of ECM trees.

A total of 169 cases were analyzed. In the 41 cases of species for which information on mycorrhizal type was not available, we assigned the mycorrhizal type corresponding to congeneric species because there is a strong phylogenetic conservatism in mycorrhizal symbiosis (Brundrett and Tedersoo 2018, but also see Brundrett 2017). In some few cases (4) for which information from congeneric species was also unavailable, we assigned the mycorrhizal type corresponding to the majority of the species in that family. We did not consider mycorrhizal status (i.e. facultative-sometimes colonized by mycorrhizal fungi, others not- or obligate mycorrhizal-always colonized-) because in our experience mycorrhizal plants from these regions are consistently colonized by mycorrhizal fungi in the field. Moreover, such status categories are subjected to a high probability of erroneous assignment (Bueno et al. 2019).

2.3 Mycorrhizal Distribution in Native Trees of Montane Forests from Argentina

In South America, the first approach to mycorrhizal distribution was made by Singer and Morello (1960). They postulated that “a completely (ecto)-mycorrhizal community is characteristic of strongly contrasted thermoperiodical climates” (p. 549), excluding those with excessive dryness or humidity. In other words, in terms of richness and abundance, the importance of ECM trees increases with increasing altitude and latitude but excluding arid or highly humid ecosystems.

More recently, Read (1991) postulated that montane forests from Southern South America would shift from those dominated by AM trees in the subtropics to those dominated by ECM trees in temperate regions. Accordingly, we found that the proportion of ECM native species is greater in temperate Andean-patagonian forests in comparison to subtropical and subxerophytic chaquean montane forests types ($\chi^2 = 17.7, p = 0.0014$) (Fig. 2.2).

For seasonal tropical and subtropical forests from South America, Read (1991) postulated that they are dominated by AM species with some ECM. Accordingly, among the 48 native trees species in subtropical montane forests in northwest Argentina surveyed here, 46 are AM while two are ECM (Fig. 2.2). These two belong to the genus *Alnus* (Betulaceae) and *Salix* (Salicaceae). *Alnus* is a holartic genus that migrated southward through the Andes from North America. *Alnus acu-*

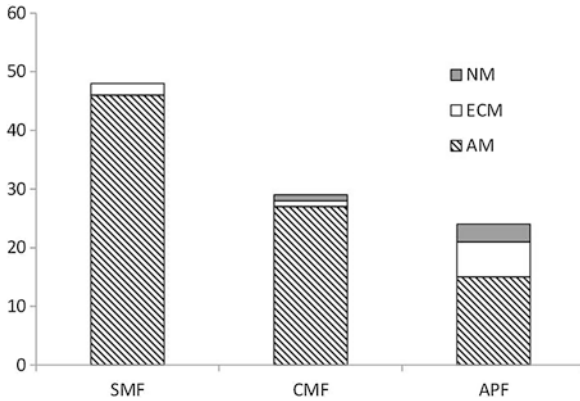


Fig. 2.2 Frequency of mycorrhizal types in native tree species from Subtropical (SMF), Chaquean (CMF), and Andean Patagonian (APF) montane forests. NM, non-mycorrhizal; ECM, ectomycorrhizal; AM, arbuscular mycorrhizal. Surveyed species in SMF: **AM**, *Allophylus edulis*, *Anadenanthera colubrina*, *Blepharocalyx salicifolius*, *Bocconia integrifolia*, *Calycophyllum multiflorum*, *Cedrela angustifolia*, *Chloroleucon tenuiflorum*, *Cordia americana*, *Cordia trichotoma*, *Enterolobium contortisiliquum*, *Eugenia uniflora*, *Ficus maroma*, *Handroanthus impetiginosus*, *Heliocarpus popayanensis*, *Ilex argentina*, *Inga edulis*, *Inga marginata*, *Inga saltensis*, *Jacaranda mimosifolia*, *Juglans australis*, *Myracrodruon urundeuva*, *Myrcianthes callicoma*, *Myrcianthes pseudomato*, *Myrcianthes pungens*, *Myroxylon peruiferum*, *Nectandra cuspidata*, *Ocotea porphyria*, *Ocotea puberula*, *Parapiptadenia excelsa*, *Phyllostylon rhamnoides*, *Podocarpus parlatoresi*, *Podocarpus australis*, *Prunus tucumanensis*, *Pterogyne nitens*, *Sambucus nigra* (var. *Peruviana*), *Schinus areira*, *Senna spectabilis*, *Solanum riparium*, *Tecoma stans*, *Tessaria integrifolia*, *Tipuana tipu*, *Trema micrantha*, *Urera baccifera*, *Urera caracasana*, *Vachellia albicorticata*, *Zanthoxylum coco* – **ECM**, *Alnus acuminata*, *Salix humboldtiana*; in CMF: **AM**, *Acacia aroma*, *Acacia caven*, *Acacia gilliesii*, *Acacia praecox*, *Aspidosperma quebracho-blanco*, *Celtis ehrenbergiana*, *Condalia buxifolia*, *Condalia montana*, *Geoffroea decorticans*, *Jodina rhombifolia*, *Kageneckia lanceolata*, *Lithrea molleoides*, *Maytenus boaria*, *Myrcianthes cisplatensis*, *Parkinsonia aculeata*, *Polylepis australis*, *Porlieria microphylla*, *Prosopis alba*, *Prosopis caldenia*, *Prosopis nigra*, *Prosopis torquata*, *Ruprechtia apétala*, *Schinopsis marginata*, *Schinus fasciculatus*, *Sebastiania commersoniana*, *Zanthoxylum coco*, *Ziziphus mistol* – **ECM**, *Salix humboldtiana* – **NM**, *Bougainvillea stipitata*; and in APF: **AM**, *Aextoxicon punctatus*, *Araucaria araucana*, *Austrocedrus chilensis*, *Dasyphyllum diacanthoides*, *Drimys winteri*, *Fitzroya cupressoides*, *Laureliopsis philippiana*, *Luma apiculata*, *Maytenus boaria*, *Persea lingue*, *Pilgerodendron uviferum*, *Podocarpus nubigenus*, *Saxegothea conspicua*, *Schinus patagonicus*, *Weinmannia trichosperma*, – **ECM**, *Nothofagus alpina*, *Nothofagus Antarctica*, *Nothofagus betuloides*, *Nothofagus dombeyi*, *Nothofagus obliqua*, *Nothofagus pumilio* – **NM**, *Embothrium coccineum*, *Lomatia hirsuta*, *Gevuina avellana*

minata forms monospecific stands in the upper montane forest (1700–2500 m asl) but also occupies riparian areas at lower altitudes. The other ECM species is *Salix humboldtiana* that occurs at riparian areas in the lower altitudinal belts. It has been suggested that this species also migrated from the northern hemisphere to the south through riparian corridors (see Tedersoo 2017). Both species also form AM (Becerra et al. 2005a, b, 2009). Metagenomic analyses of soils show the presence of several ECM fungal lineages in *A. acuminata* forests (Geml et al. 2014; Wicaksono et al. 2017). It was also observed different ECM lineages in soils from the lower altitudi-

nal belts, although the diversity was lower than in *Alnus* forests (Geml et al. 2014). This lower diversity of ECM fungal lineages could be attributed to the fact that there is no dominant ECM tree species in these forests. The only species surveyed is *S. humboldtiana* that is restricted to certain riparian ecosystems. It is also possible that these fungi are associated with ECM tree species not listed in our survey because they are represented in low abundance.

Besides those two exceptions, the other native tree species in these forests (95.8%) form AM and belong to different plant families among which Fabaceae and Myrtaceae are the most numerous (Table 2.1). It is worth mentioning that this region is characterized for the scarcity of mycorrhizal studies.

For subxerophytic Chaquean montane forests, the dominance of AM trees is also predicted (Read 1991). In line, we found that among 29 native tree species, 27 were AM while one was ECM and the other one was Non-mycorrhizal (Fig. 2.2). Here, the only ectomycorrhizal tree is *S. humboldtiana* that, as in the subtropical montane forests, is restricted to certain riparian habitats without forming extensive forests.

Table 2.1 Number of native tree species surveyed in each family in Subtropical montane forests in north-west Argentina

Family	No of species	Mycorrhizal type
Fabaceae	12	AM
Myrtaceae	5	AM
Bignoniaceae	3	AM
Lauraceae	3	AM
Anacardiaceae	2	AM
Boraginaceae	2	AM
Rosaceae	2	AM
Urticaceae	2	AM
Adoxaceae	1	AM
Aquifoliaceae	1	AM
Asteraceae	1	AM
Betulaceae	1	AM-ECM
Cannabaceae	1	AM
Juglandaceae	1	AM
Meliaceae	1	AM
Moraceae	1	AM
Papaveraceae	1	AM
Podocarpaceae	1	AM
Rubiaceae	1	AM
Rutaceae	1	AM
Salicaceae	1	AM-ECM
Sapindaceae	1	AM
Solanaceae	1	AM
Tiliaceae	1	AM
Ulmaceae	1	AM

The non-mycorrhizal species is *Boungainvillea stipitata* (Nyctaginaceae) for which no study has assessed its mycorrhizal status. We assigned the mycorrhizal status according to information of the congeneric species *B. spectabilis* (Wang and Qiu 2006). This is also supported by the fact that Nyctaginaceae includes numerous non-mycorrhizal species (Brundrett 2017). The AM tree species of this seasonally dry montane forests (93%) belong to different families among which Fabaceae is also the most numerous (Table 2.2).

In turn, ECM trees are predicted to dominate in temperate forests (Read 1991). Among the 24 native species surveyed in Temperate Andean Patagonian forests, 6 are ECM. However, in terms of species number, AM species show higher values (15 species). In addition, 3 species correspond to NM type (Table 2.3).

The ECM species correspond to the Gondwanic genus *Nothofagus* (Nothofagaceae). Despite being lower in terms of species number, in comparison to AM, the ECM *Nothofagus* spp. species are dominant trees in these forests (e.g. Veblen et al. 1992). The non-mycorrhizal species belong to the Proteaceae, a typical non-mycorrhizal gondwanic family that forms clusters roots specialized in obtaining nutrient in infertile soils (Brundrett 2017). Among AM families, Cupressaceae and Podocarpaceae show the highest numbers with 3 and 2 species, respectively. *Austrocedrus chilensis* (Cupressaceae) cover important parts of this territory (Veblen et al. 1992).

Altogether, these surveys suggest that the importance of ECM and, to a lesser degree, NM trees in montane forests ecosystems increases from subtropical towards temperate region. The results support the proposed models for mycorrhizal distribution in Southern South America.

Table 2.2 Number of native tree species surveyed in each family in Chaquean montane forests in north-west Argentina

Family	No of species	Mycorrhizal type
Fabaceae	10	AM
Rhamnaceae	3	AM
Anacardiaceae	3	AM
Rosaceae	2	AM
Apocynaceae	1	AM
Cannabaceae	1	AM
Celastraceae	1	AM
Euphorbiaceae	1	AM
Myrtaceae	1	AM
Nyctaginaceae	1	NM
Polygonaceae	1	AM
Rutaceae	1	AM
Salicaceae	1	AM-ECM
Santalaceae	1	AM
Zygophyllaceae	1	AM

Table 2.3 Number of native tree species surveyed in each family in Andean patagonian forests in south-west Argentina

Family	No of species	Mycorrhizal type
Nothofagaceae	6	ECM
Cupressaceae	3	AM
Proteaceae	3	NM
Podocarpaceae	2	AM
Aextoxicaceae	1	AM
Anacardiaceae	1	AM
Araucariaceae	1	AM
Asteraceae	1	AM
Atherospermataceae	1	AM
Celastraceae	1	AM
Cunoniaceae	1	AM
Lauraceae	1	AM
Myrtaceae	1	AM
Winteraceae	1	AM

2.4 Mycorrhizal Distribution in Alien Trees Occurring in Montane Forests from Argentina

Our Survey reveal that the Chaquean montane forests show the highest number of invasive alien tree species (34 spp.) when compared with Subtropical montane forests (15 spp.) and Andean patagonian forests (19 spp.). This could be the result of more intense sampling in chaquean forests or because this ecosystem is more susceptible to invasions.

The proportion of mycorrhizal types in alien trees also differ among ecosystems ($\chi^2 = 19.2, p = 0.0007$) and the proportion of ECM type also increases with increasing latitude (Fig. 2.3). Instead, non-mycorrhizal alien trees were only present in subtropical montane forest, represented by only one species (*Grevillea robusta*, Proteaceae).

Among the 15 alien trees species surveyed in subtropical montane forest in northwest Argentina, the majority were AM, albeit two ECM and one NM were also registered. The ECM trees were *Eucalyptus grandis* (Myrtaceae) and *Pinus taeda* (Pinaceae). Both genera are well known by having several ECM invasive tree species (Richardson and Rejmánek 2011). It is worth mentioning that the invasive alien tree species were more evenly distributed among plant families in these forests (Table 2.4) than in the other two regions (see below).

The chaquean montane forests present a wide variety of alien trees species (34 spp, Table 2.5). The majority is AM followed by ECM, with 28 (82%) and 6 (17.6%) species, respectively. Rosaceae is the family with the highest number of alien species. Most of them are AM but *Crataegus monogyna* has been reported to

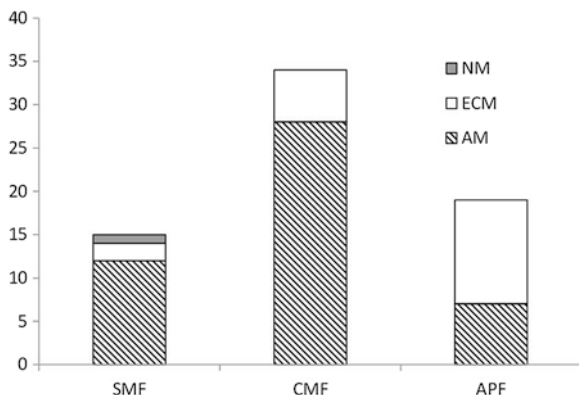


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Table 2.4 Number of alien tree species surveyed in each family in Subtropical montane forests in northwest Argentina

Family	No of species	Mycorrhizal type
Rosaceae	3	AM
Fabaceae	2	AM
Moraceae	2	AM
Myrtaceae	2	1 AM, 1 AM-ECM
Oleaceae	2	AM
Lauraceae	1	AM
Pinaceae	1	ECM
Proteaceae	1	NM
Rutaceae	1	AM

Table 2.5 Number of alien tree species surveyed in each family in Chaquean montane forests in central Argentina

Family	No of species	Mycorrhizal type
Rosaceae	8	7 AM, 1 ECM
Fabaceae	4	AM
Oleaceae	3	AM
Moraceae	2	AM
Pinaceae	2	ECM
Tamaricaceae	2	AM
Anacardiaceae	1	AM
Betulaceae	1	ECM
Bignoniaceae	1	AM
Cannabaceae	1	AM
Euphorbiaceae	1	AM
Meliaceae	1	AM
Myrtaceae	1	AM-ECM
Phytolaccaceae	1	AM
Rutaceae	1	AM
Salicaceae	1	AM-ECM
Sapindaceae	1	AM
Simaroubaceae	1	AM
Ulmaceae	1	AM

Table 2.6 Number of alien tree species surveyed in each family in Andean patagonian forests in southwest Argentina

Family	No of species	Mycorrhizal type
Pinaceae	6	1 AM-ECM, 5 ECM
Betulaceae	3	ECM
Rosaceae	3	2 AM, 1 ECM
Fabaceae	2	AM
Salicaceae	2	1 AM-ECM, 1 ECM
Adoxaceae	1	AM
Cupressaceae	1	AM (ECM)
Sapindaceae	1	AM

be ECM in Europe (Maremmanni et al. 2003). Then we suggest that the mycorrhizal type of this species should be confirmed. The other ECM trees belong to well-known ECM families such as Pinaceae, Betulaceae, Salicaceae and Myrtaceae.

Unlike both neotropical montane ecosystems (Subtropical and Chaquean), in Andean patagonian forests ECM is represented by higher percentage of species than AM (63 and 37%, respectively) (Table 2.6). Pinaceae and Betulaceae showed the highest species number (6 and 3, respectively) (Simberloff et al. 2002). Among

them, *Pseudotsuga menziesii* forms both AM and ECM (Salomón et al. 2018). The other ECM families were Rosaceae and Salicaceae. *Juniperus communis* (Cupressaceae) is mainly cited as AM but ECM has been occasionally reported suggesting a facultative relationship with ECM fungi (Thomas et al. 2007). For this reason, here it is considered as AM but further studies would confirm the mycorrhizal status of this alien plant in subantarctic forests.

Two AM shrubby species were also included due to their importance in terms of abundance and distribution: *Cystus scoparius* (Fabaceae) (Simberloff et al. 2002, 2003) and *Rosa rubiginosa* (Rosaceae) (Simberloff et al. 2002; Zimmermann et al. 2010), both AM species.

The patterns of mycorrhizal distribution in alien trees occurring in montane ecosystems across Argentinian territory also show that ECM species frequency increase with increasing latitude. However, this increase in frequency is notably higher in aliens than in natives. Instead, NM aliens are less represented than NM natives.

2.5 Mycorrhizas and Plant Invasions

In the last 20 years, the importance of belowground mutualistic interactions such as “mycorrhizas” in plant invasions has been widely recognized (e.g. Richardson et al. 2000; Callaway et al. 2003; Dickie et al. 2017). Few studies, however, compared patterns of mycorrhizal distribution in native and alien flora at the biome or regional level (Fitter 2005; Pringle et al. 2009; Menzel et al. 2017).

Our surveys include three floras in montane ecosystems from different biomes. Considering the montane forests altogether, the distribution of mycorrhizal types show a greater proportion of ECM in alien (20/67 cases) than in native (9/101) tree species ($\chi^2 = 12.8$, $p = 0.017$). Inversely, there was a higher proportion of AM and NM in natives (88 and 4, respectively) than in alien trees (46 and 1, respectively). The negligible presence of NM alien trees throughout the montane ranges (i.e. single specie) is in line with Menzel et al. (2017), highlighting the relevance of belowground mutualistic interactions for tree invasion success. The overall prevalence of AM associations among invasive species is in line with Fitter (2005).

The general trend of a higher proportion of ECM in aliens than in natives kept significant within the Temperate Andean Patagonian forests ($\chi^2 = 8.17$, $p = 0.0169$) when analysing each biome separately (Fig. 2.4). However, there were no differences between aliens and natives within the Subtropical and Chaquean montane forests ($\chi^2 = 5.02$, $p = 0.0811$; $\chi^2 = 4.22$; $p = 0.1213$, respectively). These analyses suggest that ECM may have an advantage over AM aliens in expanding their ranges and that this advantage would be higher with increasing latitude (see below).

The non-significant differences in proportion of mycorrhizal types in alien and natives trees in Neotropical region (Subtropical and Chaquean forests) is explained by the majority of AM tree species in both native and aliens in these forests. According to the literature, the most widely studied alien species, and probably more widely distributed, in Subtropical montane forests are AM (*Ligustrum*

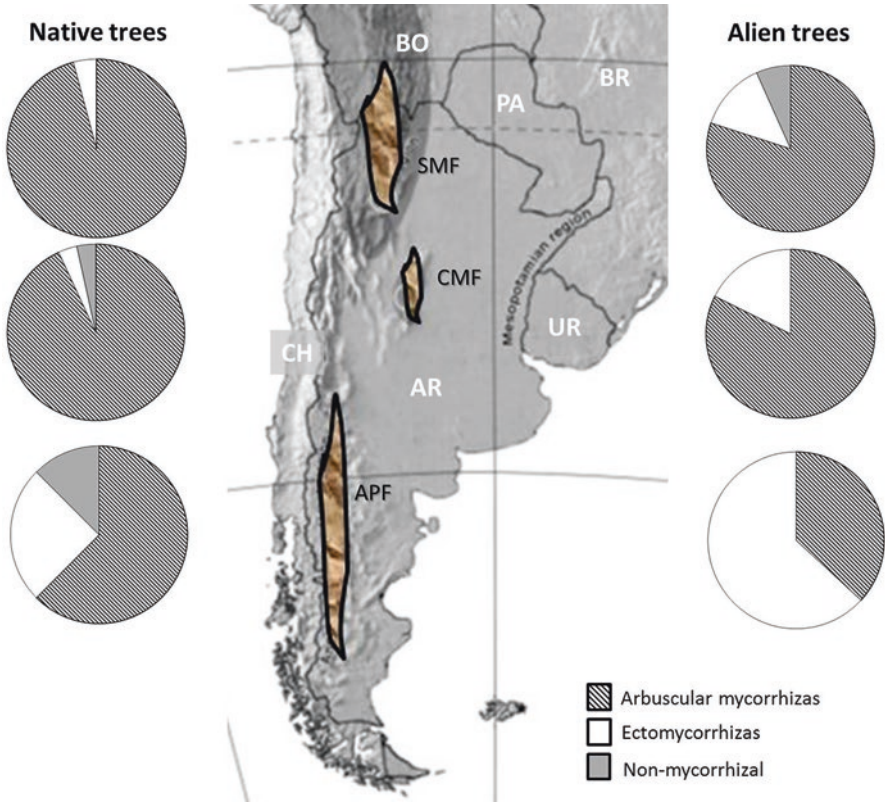


Fig. 2.4 Relative abundance of native and alien tree species forming different mycorrhizal type in Subtropical (SMF), Chaquean (CMF), and Andean Patagonian (APF) montane forests from Southern South America. NM, non-mycorrhizal; ECM, ectomycorrhizal; AM, arbuscular mycorrhizal. AR, Argentina; CH, Chile; UR, Uruguay; BO, Bolivia; PA, Paraguay; BR, Brazil

lucidum, *Morus alba* and *Gleditsia triacanthos*; Aragón and Morales 2003; Fernandez et al. 2017) but the role of mycorrhizal fungi in their success in these forests has not been studied. In Chaquean Montane forest, *Ligustrum lucidum* (Hoyos et al. 2010; Zeballos et al. 2014; Giorgis et al. 2017), *Gleditsia triacanthos* (Giorgis et al. 2011a; Furey et al. 2014; Fernandez et al. 2017; Marcora et al. 2018), and *Pyracantha angustifolia* (Tecco et al. 2007; Zeballos et al. 2014) are the most widely expanded and studied in the region. It has been recently shown that seedling of these alien tree species benefit from AM fungi, mainly for P nutrition, either from already invaded or from non- invaded elevations in these montane ranges (Urcelay et al. 2019). The prevalence of AM association in trees of both neotropical regions could be interpreted as functional convergence in belowground strategies among native and alien trees in these biomes. However, it is worth mentioning that ECM alien trees include some serious invaders such as Pinaceae (Richardson and Rejmánek 2011) that are naturalized in both montane biomes. For example, in

Chaquean mountains *Pinus elliottii* expand outside the afforestations, either to native forests or grasslands, due to its capacity for co-invade with alien ECM symbionts, particularly *Suillus granulatus* and *Rhizopogon pseudoreseolus* (Urcelay et al. 2017). No evidence exists on the symbiotic interactions between *P. elliottii* and native ECM fungi reported for *Salix humboldtiana*, the only ECM native tree in the region (Becerra et al. 2009). The expansion of *Pinus elliottii* is still incipient (Giorgis et al. 2011b; Urcelay et al. 2017) but it is predicted to become a great threat in the near future as occurred in other continents in the southern hemisphere (Richardson 2006).

The higher proportion of ECM alien trees within temperate forests (compared to both the coexisting natives and to aliens of other regions) highlights the advantage of this association for invasion success within this biome. It is further in line with global scale distribution of ECM (Read 1991). Among the invasive aliens in Andean Patagonian forests, *Pseudosuga menziesii* is probably the most widely distributed and studied (e.g. Simberloff et al. 2002; Sarasola et al. 2006; Orellana and Raffaele 2010). Also important are *Pinus ponderosa*, *P. contorta*, *P. radiata*, *P. monticola*, *P. sylvestris*, and *Juniperus communis* (Simberloff et al. 2002; Sarasola et al. 2006; Richardson et al. 2008). *Pseudosuga* and *Pinus* species need to establish ECM symbiosis to succeed in the novel environments. In these species, the specificity for mycorrhizal partners is higher than in AM trees which are assumed to be generalists (Nuñez and Dickie 2014). Thus, ECM trees need alien ECM fungi to expand outside plantations. This was particularly evidenced for *P. menziesii*, *P. contorta*, and *P. ponderosa*. They were found to be associated with the different fungi such as *Suillus luteus*, *S. lakei*, *Amphinema* spp., *Melanogaster* sp., *Rhizopogon* cf. *rogersii*, *R. cf. arctostaphyli*, *R. roseolus*, *R. villosulus*, *Hebeloma mesophaeum*, *Lactarius quieticolor*, *Cortinarius* spp. *Pseudotomentella tristis*, *Wilcoxina* spp., among others. These alien ECM fungi are dispersed either by the wind or by exotic mammals (Nuñez et al. 2009, 2013; Salomón et al. 2011, 2018; Hayward et al. 2015a, b). Inferring convergence or divergence in mycorrhizal association between coexisting alien and natives in temperate forests is not conclusive. There is a prevalence of AM in native species in terms of species number but this underestimate the relevance of ECM in the system in terms of dominance since *Nothofagus* spp. are very relevant in terms of structural cover in this biome (Veblen et al. 1992). Thus, we do not infer divergence out of our results. The analysis of patterns of mycorrhizal distribution ponderated by species' abundance will certainly give a better insight to this question.

2.6 Conclusions

Although not explicitly tested, the results gathered here suggest that the distribution of mycorrhizal types in native trees at a broad geographic scale in South America is mainly driven by climate. From the analyses we conclude that patterns of mycorrhizal distribution in alien and native trees occurring in montane ecosystems from

subtropical to temperate regions, roughly follow those predicted by models of mycorrhizal distribution (e.g. Read 1991). This is seemingly in line with the idea of broad scale environmental filters driving greater predominance of convergences than divergences in the functional strategies of coexisting tree species along these mountain biomes (e.g. Weiher et al. 1998; Cornwell et al. 2006; Cornwell and Ackerly 2009; Lohbeck et al. 2014). Nonetheless, ECM in aliens is in higher proportion compared to natives, particularly in temperate forests. Further studies should incorporate the analyses of the abundance of mycorrhizal types in a given ecosystem, not only the proportion of plant species, in order to estimate their impacts on ecosystem functioning and biogeochemical cycling (Soudzilovskaia et al. 2017). The evidence suggests that ECM trees co-invade with alien mycorrhizal fungi. In the case of Pinaceae, they mainly co-invade with species belonging to the genus *Suillus* and *Rhizopogon* (Policelli et al. 2018). Arbuscular mycorrhizal type shows the highest proportion in native and alien trees from all the ecosystems except for aliens in the Andean-patagonian region. In contrast to ECM trees, it is presumed that AM alien trees form mycorrhizas with native fungi.

It is worth remarking that mainly trees were included in the analyses. This selection can exclude certain mycorrhizal types. For example, the occurrence of small ericoid shrubs is known for the three montane forests. In some of them, indeed, the ERM structures and the identity of symbionts were studied (Urcelay 2002; Selosse et al. 2007; Bruzone et al. 2015). Then, the proportion mycorrhizal types represented in native and alien species may change if other plant life forms were included. In this scenario, a higher proportion ERM and NM could be expected because these types are mainly represented in small shrubs and herbs, respectively.

Since some of the mycorrhizal status lists consulted here may contain errors (see Dickie et al. 2007; Brundrett and Tedersoo 2019), the type of mycorrhiza in certain tree species still should be confirmed. However, the patterns reported here, based on updated and more precise information, do not differ much from those communicated some years ago based on more limited data sets (Urcelay and Tecco 2006, 2008, 2010). This suggests that the patterns of mycorrhizal distribution are robust in face of the addition and/or refinement of the data.

Finally, the effects of mycorrhizal fungi on growth, nutrition, and then expansion and dominance of most native and alien trees in ecosystems of southern South America still remains to be determined. Altogether, these findings suggest that mycorrhizal associations have an unambiguous role in tree invasions in montane forests across different climates but the relative importance of each mycorrhizal type in each ecosystem remains unknown.

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