Applied Soil Ecology 85 (2014) 30–37

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Arbuscular mycorrhizal fungal composition in high montane forests with different disturbance histories in central Argentina

Florencia Soteras *, Gabriel Grilli, María Noelia Cofré, Nicolás Marro, Alejandra Becerra

Instituto Multidisciplinario de Biología Vegetal (IMBIV), CONICET, Universidad Nacional de Córdoba, CC 495, 5000 Córdoba, Argentina

ARTICLE INFO

Article history:
Received 30 April 2014
Received in revised form 23 August 2014
Accepted 3 September 2014
Available online xxx

Keywords:
Glomeromycota
Rhizosphere community
Root colonization
Mountain forest

ABSTRACT

The aim of this work was to describe and compare the arbuscular mycorrhizal fungal (AMF) morphospecies community and root colonization in three *Polylepis australis* forest disturbance types (degraded forest, young forest and mature forest). Rhizosphere soil samples were collected during wet and dry seasons in three sites located at the high mountains of central Argentina. A highly diverse AMF community was detected with 32 different morphospecies. AMF richness, density, Shannon diversity and evenness were neither influenced by forest disturbance type nor by season. Nevertheless, indicator species analyses showed two AMF taxa mostly associated with the degraded forest, one with the young forest and two linked preferentially to the mature forest. Moreover, the latter forest type showed the highest biovolume of *Gigaspora* spp., a genus representative of conserved ecosystems. *P. australis* root colonization was similar among forest disturbance types and seasons. However, higher abundance of vesicles was observed during the dry season than during the wet season. This study showed that AMF community composition was relatively similar among forests with distinct structural complexity. These results suggest that the AMF community may be resistant to the kind of disturbances that shaped the forests compared, or that natural successional processes may permit AMF to recover from these disturbances.

1. Introduction

Soil microorganisms represent a great part of global biodiversity and play a crucial role in ecosystem functioning (Fitter et al., 2005; Johnson et al., 2013). Arbuscular mycorrhizal fungi (AMF; Phylum Glomeromycota) (Schüßler et al., 2001) are one of the most relevant soil microorganisms due to their direct influence on essential processes between plants and soil (Fitter et al., 2005). AMF are obligate symbionts that associate with ~80% of the studied vascular plants (Brundrett, 2009; Wang and Qiu, 2006), improving soil exploration, mineral acquisition, water relations and root pathogen resistance in their hosts (Smith and Read, 2008). During the last years AMF spore community variation in response to the original plant community changes (e.g., through disturbances as fire, habitat fragmentation or agricultural practices) has been widely evidenced (Grilli et al., 2012; Longo et al., 2014; Stürmer and Siqueira, 2011).

Forest structural changes that are caused by anthropogenic perturbation might indirectly influence AMF morphospecies communities (i.e., spore density, morphospecies diversity and richness) and root mycorrhizal colonization through variation of the vegetation, micro-climatic conditions, soil physical–chemical characteristics, etc. For instance, plant cover reduces soil erosion while its removal exposes soil to increase radiation (Cingolani et al., 2003; FAO, 2005; Renison et al., 2004) affecting AMF composition (Carpenter et al., 2001; Dumbrell et al., 2010; Lopes Leal et al., 2013) and root colonization (Entry et al., 2002; Haugen and Smith, 1992).

There is contradictory evidence about the influence on AMF communities of disturbance history that results in structural changes to forests, some reporting AMF resilience (Johnson and Wedin, 1997; Picone, 2000) while others reporting changes in AMF communities compared to the original forest (Grilli et al., 2012; Longo et al., 2014; Stürmer and Siqueira, 2011; Zhang et al., 2004). In addition, AMF community seasonality has been demonstrated and some morphospecies may be dominant depending on the time of year (Becerra et al., 2009; Lee and Koske, 1994; Lugo and Cabello, 2002; Merryweather and Fitter, 1998; Soteras et al., 2012). Also, root colonization by AMF is usually higher during the growing season (Lugo et al., 2003).

High mountain forests of *Polylepis australis* Bitt. (Rosaceae), the southernmost species of *Polylepis* spp. (Simpson, 1979), are highly

* Corresponding author.
E-mail addresses: fsoteras@conicet.gov.ar, florsoteras@hotmail.com (F. Soteras).

http://dx.doi.org/10.1016/j.apsoil.2014.09.004
0929-1393/

impacted by anthropogenic disturbance (Cingolani et al., 2008). Forest degradation has occurred mainly due to the influence of anthropogenic changes (livestock rearing and intentional fires) since the XVII century (Cingolani et al., 2003). Nowadays, structural complexity differences of the forest remnants of this species might be related to the extent of disturbance (Renison et al., 2011) together with topographic characteristics (e.g., altitude) (Marcora et al., 2008) and other particularities of the species (e.g., Pollice et al., 2013; Renison et al., 2004; Renison et al., 2011). The influence of *P. australis* forest structural changes on physical soil conditions has been evidenced (Renison et al., 2010). However, whether these forests changes affect belowground organisms and, especially AMF community, remains unknown.

The aims of this work were to describe and compare the AMF spore community composition and to determine the mycorrhizal root colonization of *P. australis* in three forest types varying in their structural complexity (degraded forest, young forest and mature forest) at three sites, during two seasons. Considering that the variation of the original plant community could be related to both AMF community composition and root colonization changes and that AMF usually shows seasonal variations, we hypothesized that forests disturbance types and seasonality affect AMF spore community and root colonization.

2. Materials and methods

2.1. Study area

Three *P. australis* forest types with different disturbance history, described and georeferenced by Renison et al. (2011), hereafter called "degraded forest", "young forest" and "mature forest", were chosen at each of three sites ("Los Gigantes" (1800–1900 m asl, 31°23′S, 64°48′W);"Los Molles" (1800–2000 m asl, 31°58′S, 64°56′W) and "Santa Clara" (2000 to 2200 m asl, 31°44′S, 64°47′W)) (Fig. 1). According to the conservation degree the three sites could be ordered from the least to the most preserved as (1) Los Gigantes, (2) Los Molles, and (3) Santa Clara (Renison et al., 2006).

Mean temperature for the coldest and warmest months are 5 °C and 11.4 °C, respectively, with no frost-free period (Cabido, 1985). Mean annual precipitation is 840 mm, being concentrated in the warmest months (October to April) (Cabido et al., 1987). Soils characteristics of the three forest structural types were previously determined by Renison et al. (2010) (Table S1 Table S1).

Supplementary material related to this article found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2014.09.004.

The landscape includes distinctive units differing in their slope, relief and percentage of rocky outcrops, including hilly uplands, plateaus, ravines and valley bottoms (Cabido et al., 1987). Vegetation consists of a mosaic of tussock grasslands and grazing lawns mostly represented by *Deyeuxia hieronymi* (Hack.) Türpe, *Festuca tucumanica* Alexeev, *Poa stuckertii* (Hack.) Parodi, *Alchemilla pinnata* Ruiz & Pav. and *Carex fuscula* Urv. intermingled with granite outcrops and eroded areas with exposed rocky surfaces. Interspersed among the grasslands are *P. australis* shrublands and woodlands, together with isolated *Maytenus boaria* Molina trees, *Berberis hieronymi* Scheid shrubs and fern communities (Cabido, 1985; Cingolani, 2004). Since the beginning of the XVII century the main economic activity has been livestock rearing, cattle and sheep, that have completely replaced the native herbivores (i.e., *Lama guanicoe* Müller) (Cabido et al., 1987; Díaz et al., 1994). Livestock and intentional fire management to promote grass regrowth have created different forest disturbance types varying in their structural complexity (Renison et al., 2011). Therefore, the most conserved mature forest type is now represented as small remnants restricted to rocky outcrops with steep slopes, where the impact of both livestock and fires is less frequent (Cingolani et al., 2008; Renison et al., 2006). This forest type has a mean canopy cover of 72%; shows some isolated individuals of more than 800 cm in height and mean age of the largest living tree is 67 years. The young forest stand shows evidence of previous disturbances but is regenerating naturally, with a mean canopy cover of 54%. Young trees are from 116 to 200 cm in height and mean age of the largest living tree is 37 years. The degraded forest type is characterized by sparse trees with mean cover of 8%; shows low regeneration rates, evidence of previous fire events and soil erosion; and the mean age of the largest living tree is 43 years (Renison et al., 2011).

2.2. Experimental design

During the wet (spring – October 2010) and dry (autumn – May 2011) seasons, soil samples (20 cm depth) were collected with a trowel from the rhizosphere of six randomly selected *P. australis* trees, in each forest type (6 replicates per forest type) at the three

Fig. 1. Sites (arrowheads) located at the high mountains of central Argentina: Los Gigantes, Los Molles and Santa Clara from the degraded to the most preserved. In each site, three *P. australis* forest types (degraded forest, young forest and mature forest) were sampled, during wet and dry seasons.

sites, totaling 54 soil samples for each season (6 replicates × 3 forest types × 3 sites × 2 seasons, total = 108).

At each site, different trees, separated by at least 20 m distance, belonging to the same height class and representative of each forest type (following Renison et al. (2011) characterization), were chosen during both seasons. Roots from each tree were carefully excavated, taking care that only *P. australis* lateral roots, attached to the main trunk, were collected. Samples were placed in plastic bags and stored at 4 °C.

2.3. Arbuscular mycorrhizal fungal morphospecies community

Soil samples were sieved through a 1 cm mesh size to remove litter, stones and sticks. AMF spores were extracted by wet sieving and decanting of 100 g of dry soil, followed by centrifugation in sucrose (Walker et al., 1982). A fine sieve (38 μm) was used to collect small spores and the top sieve (125 μm) was also checked for sporocarps and larger spores. Only apparently healthy spores were isolated by direct observations with stereomicroscope. For quantification and taxonomic identification, fungal spores were mounted onto slides using PVA with and without Melzer's reagent (Omar et al., 1979) and examined with a compound microscope (Nikon, E200). AMF morphospecies identification was based on current species classification (Redecker et al., 2013) and the identification manuals of Schenck and Perez (1990) and INVAM (http://invam.caf.wvu.edu/fungi/taxonomy/speciesID.htm).

Total spore density was determined as the AMF spore number per 100 g of soil dry weight. Also, as an approximation of the soil volume occupied by spores, biovolume of each morphospecies was calculated (Egerton-Warburton et al., 2007; van Veen and Paul, 1979).

2.4. Arbuscular mycorrhizal colonization

In order to assess the percentage of arbuscular mycorrhizal colonization, roots were cleared with 10% KOH (15 min at 90 °C), acidified with 1% HCL (1 min, room temperature) and stained in 0.05% aniline blue, following the techniques described by Phillips and Hayman (1970) and Grace and Stribley (1991). For the determination of the percentage of total arbuscular mycorrhizal colonization (AMC) and of intra-radical structures colonization (arbuscules, vesicles and coils), five permanent slides per sample were mounted and 100 line intersections were counted at 400× magnification under a compound microscope, following McGonigle et al. (1990) magnified intersection method.

2.5. Statistical analysis

Shannon diversity index, richness, Jackknife 1 estimator of richness and evenness (Magurran and McGill, 2011) were obtained in R 2.13.2 (R Development Core Team, 2011) with the function *diversityresult()* of the package BiodiversityR (Kindt, 2013).

To evaluate the strength of association between forest types and AMF taxa, an indicator species analysis was applied with the function *indval()* from the R package labdsv (Dufrêne and Legendre, 1997; Roberts, 2013).

Non-metric multidimensional scaling (NMDS) was performed with *metaMDS()* function of the R package vegan (Oksanen et al., 2012) to evaluate the ordination of arbuscular mycorrhizal fungal community, considering morphospecies presence–absence and the fixed factors (forest types and seasons) in related to the two dimensional ordination space (Kenkel and Orlóci, 1986). NMDS analysis was performed with the Bray Curtis dissimilarity measure. PERMANOVA analysis was done in order to assess the significance of the fixed factors with the function *adonis()* of the vegan package of R with 999 permutations and using Bray Curtis dissimilarity as the measure of distance between pair of morphospecies. PERMANOVA analysis was also used for density and biovolume comparisons among fixed factors.

To determine the differences of Shannon index, evenness and AMF root colonization among forest types and seasons, generalized linear mixed models (GLMM) were fitted in the R package lme4 (Bates et al., 2012), with forest type (three levels: degraded forest, young forest, and mature forest) and season (two levels: wet and dry) as fixed factors and including the interaction term. The sampled individual trees within each forest type and permanent slides per root system (pseudoreplicates) were nested in sites and considered as a random term. The best fit and the significance of model terms were determined comparing the Akaike information criterion (AIC) using chi-squared (χ^2) test, with a significance level of 0.05. Total root colonization and colonization by arbuscules, vesicles and coils (proportions) were fitted with a binomial error structure and log link. Shannon diversity index and evenness were fitted with a Gaussian error structure and identity link.

To determine the relationship between AMF richness and spores density, a linear regression model was fitted. Spore density was log-transformed before analysis.

3. Results

3.1. Arbuscular mycorrhizal fungal spore community

In total 32 AMF morphospecies were identified in the rhizosphere soil samples of the three forest disturbance types of *P. australis*. Among them, 29 were assigned to known species while the remaining were identified to genus level (Table 1). The most frequent morphospecies recovered were *Acaulospora mellea*, *A. scrobiculata*, *Glomus brohultii* and *Rhizophagus intraradices* in all the forest types compared. The highest value of richness per forest type detected was 22. Meanwhile, according to Jackknife 1 estimator of richness the highest expected number of morphospecies per forest type was 30 (Table 1).

Indicator species analyses revealed five significant AMF morphospecies. During the wet season, *Funneliformis geosporum* was mostly present in the degraded forest (indicator value = 0.19; $P = 0.009$). During the dry season, *Dentiscutata biornata* was preferentially in the degraded forest (indicator value = 0.15, $P = 0.028$), *Rhizophagus clarus* in the young forest (indicator value = 0.27, $P = 0.041$) and both *F. mosseae* and *Entrophospora infrequens* in the mature forest (indicator values = 0.25 and 0.18; $P = 0.005$ and 0.035, respectively).

AMF community composition (morphospecies presence–absence) was similar among forest types (PERMANOVA wet season: pseudo-F = 1.41, $P = 0.16$; PERMANOVA dry season: pseudo- F = 1.57, $P = 0.08$) (Fig. 2) and seasons (Table 2). The same response was observed for morphospecies density, showing similar values in the three forest structural types and during both seasons (Table S2).

Supplementary material related to this article found, in the online version, at http://dx.doi.org/10.1016/j.apsoil.2014.09.004.

Because the differences in size among AMF genera, spore biovolume was calculated. Mean spore biovolume of *Acaulospora* was 9.2×10^{-4} mm^3, of *Ambispora* was 3.7×10^{-3} mm^3, of *Claroideoglomus* 1.9×10^{-4} mm^3, of *Entrophospora* 7.1×10^{-4} mm^3, of *Gigaspora* 0.01 mm^3, of *Scutellospora* 0.01 mm^3, of *Funneliformis* 8.2×10^{-4} mm^3, of *Glomus* 2.2×10^{-4} mm^3, of *Rhizophagus* 1.4×10^{-4} mm^3 and of *Pacispora* 6.8×10^{-4} mm^3. Although *Glomus* was one of the most abundant genera (wet season: mean = 41.96, s.e. = 13.98; dry season: mean = 127.41, s.e. = 25.15) contributed with almost the same biovolume (wet season: mean = 0.01, s.e. = 0.003 soil; dry season: mean = 0.03, s.e. = 0.01) as *Gigaspora* (wet season: mean = 0.03, s.e. = 0.01; dry season: mean = 0.02,

Table 1
Occurrence (+) of arbuscular mycorrhizal fungi morphospecies in the rhizosphere of three *P. australis* forest types (degraded forest (DF), young forest (YF) and mature forest (MF)), at each sampling site (Los Gigantes, Los Molles, and Santa Clara) during two seasons (wet and dry).

	Los Gigantes						Los Molles						Santa Clara					
	Wet season			Dry season			Wet season			Dry season			Wet season			Dry season		
	DF	YF	MF	DF	YF	MF	DF	YF	MF	DF	YF	MF	DF	YF	MF	DF	YF	MF
Acaulosporaceae																		
Acaulospora alpina Oehl, Sýkorová and Sieverd.	+	+	+	+	–	+	+	+	–	–	+	+	+	+	+	+	+	+
A. bireticulata Rothwell and Trappe	+	–	+	+	+	–	–	+	–	+	–	–	–	–	+	–	–	–
A. excavata Ingleby and Walker	+	+	+	+	+	+	+	+	–	+	+	+	+	+	+	+	+	+
A. foveata Rothwell and Trappe	–	–	–	–	+	–	+	–	–	–	–	–	–	+	+	–	–	+
A. mellea Spain and Schenck	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
A. rehmii Sieverd. and Toro	+	–	+	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–
A. rugosa Morton	–	+	+	+	+	+	–	+	–	–	+	+	+	+	+	+	+	–
A. scrobiculata Trappe	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
A. spinosa Walker and Trappe	–	+	+	–	+	+	–	+	+	+	+	+	+	–	–	+	–	+
A. undulata Sieverd.	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	+	+	+
A. lacunosa Morton	+	+	+	–	+	+	+	+	+	–	–	–	+	+	+	+	+	+
Acaulospora sp. 1	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	+	–
Ambisporaceae																		
Ambispora leptoticha (Schenck and Sm.) Walker, Vestberg and Schüßler	–	+	–	+	–	–	–	–	–	+	–	+	+	+	+	+	+	+
A. appendicula (Spain, Sieverd. and Schenck) Walker	+	+	+	–	–	+	+	–	+	+	–	–	–	–	+	+	+	+
Claroideoglomeraceae																		
Claroideoglomus claroideum (Schenck and Sm.) Walker and Schüßler	–	–	–	–	+	+	–	–	+	–	+	–	+	–	–	–	–	–
C. luteum (Kenn., Stutz and Morton) Walker and Schüßler	–	+	–	+	–	–	+	–	–	+	+	–	+	+	–	+	+	+
Entrophosporaceae																		
Entrophospora infrequens (Hall) Ames and Schneid.	–	–	+	+	+	+	–	–	–	–	–	–	+	–	+	+	+	+
Entrophospora sp. 1	+	–	–	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–
Gigasporaceae																		
Gigaspora margarita Becker and Hall	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	+	+
G. rosea Nicolson and Schenck	+	–	–	–	–	+	–	+	–	–	+	–	–	–	–	–	–	–
Dentiscutata biornata (Sieverd. and Toro) Sieverd., Souza and Oehl	–	–	–	–	–	–	–	–	–	–	–	–	+	+	–	+	–	–
Glomeraceae																		
Funneliformis badium (Oehl, Redecker and Sieverd.) Walker and Schüßler	–	+	+	+	–	–	+	–	+	+	+	–	+	–	–	+	–	+
F. geosporum (Nicolson and Gerd.) Walker and Schüßler	+	–	–	–	–	–	+	–	–	+	–	–	–	–	–	–	–	–
F. mosseae (Nicolson and Gerd.) Walker and Schüßler	+	+	–	+	+	+	+	+	+	+	–	+	–	–	+	–	+	+
Glomus brohultii Sieverd. and Herrera	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
G. fuegianum Trappe and Gerd.	+	–	+	+	+	+	+	+	+	+	+	–	–	–	–	+	+	+
Glomus sp. 1	–	+	–	–	–	–	–	–	+	–	–	–	–	–	–	–	+	+
Rhizophagus clarus (Nicolson and Schenck) Walker and Schüßler	–	+	+	+	+	+	–	+	–	+	+	–	+	+	+	+	+	+
R. intraradices (Schenck and Sm.) Walker and Schüßler	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Pacisporaceae																		
Pacispora patagonica (Novas and Fracchia) Walker, Vestberg and Schüßler	+	+	+	–	+	+	+	+	–	+	–	+	–	+	–	–	–	+
P. dominikii (Blaszk.) Sieverd. and Oehl	–	–	–	–	+	+	–	–	+	+	+	+	+	–	–	+	–	+
P. robigina Sieverd. and Oehl	–	–	+	–	+	–	+	+	+	+	+	+	–	–	–	+	+	–
Total no. of morphospecies	17	18	19	19	20	20	17	17	16	20	17	15	16	15	16	21	20	22
Jackknife estimator 1	23	25	22	25	25	25	24	23	21	25	23	18	18	20	24	25	26	30

s.e. = 0.01) and *Scutellospora* (wet season: mean = 0; dry season: mean = 0.01, s.e. = 0.01). Meanwhile, *Acaulospora* was highly abundant (wet season: mean = 208.54, s.e. = 124.20; dry season: mean = 165.27, s.e. = 32.08) and occupied high soil volume (wet season: mean = 0.09, s.e. = 0.04; dry season: mean = 0.07, s.e. = 0.01).

The volume in soil occupied by each morphospecies genus (mm^3/100 g of dry soil) was not significantly different among forest types (PERMANOVA wet season: pseudo-F = 1.14, $P = 0.31$; PERMANOVA dry season: pseudo- F = 0.56, $P = 0.93$). However, higher spore biovolume of *Gigaspora* spp. was observed in the mature forest during both seasons (wet season: degraded forest = 0.02 ± 0.01, young forest = 0.02 ± 0.01, mature forest = 0.04 ± 0.02; dry season: degraded forest = 0.01 ± 0.004, young forest = 0.03 ± 0.01, mature forest = 0.03 ± 0.02).

Shannon diversity index and evenness were not significant different among forest types (Shannon Gaussian GLLM: $\chi^2 = 1.22$, $P = 0.54$; evenness Gaussian GLLM: $\chi^2 = 0.13$, $P = 0.94$) nor among seasons (Shannon Gaussian GLLM: $\chi^2 = 1.20$, $P = 0.27$; evenness Gaussian GLLM: $\chi^2 = 1.75$, $P = 0.19$).

Regression analysis indicated that AMF mean richness was positively related to spore density ($P < 0.001$) (Fig. 3).

3.2. Arbuscular mycorrhizal colonization

P. australis roots from every forest type and during both seasons showed colonization by AMF. Total root colonization percentages during the wet season varied from 16.05 to 95% in the degraded forest, from 4 to 92% in the young forest and from 6 to 88.07% in the

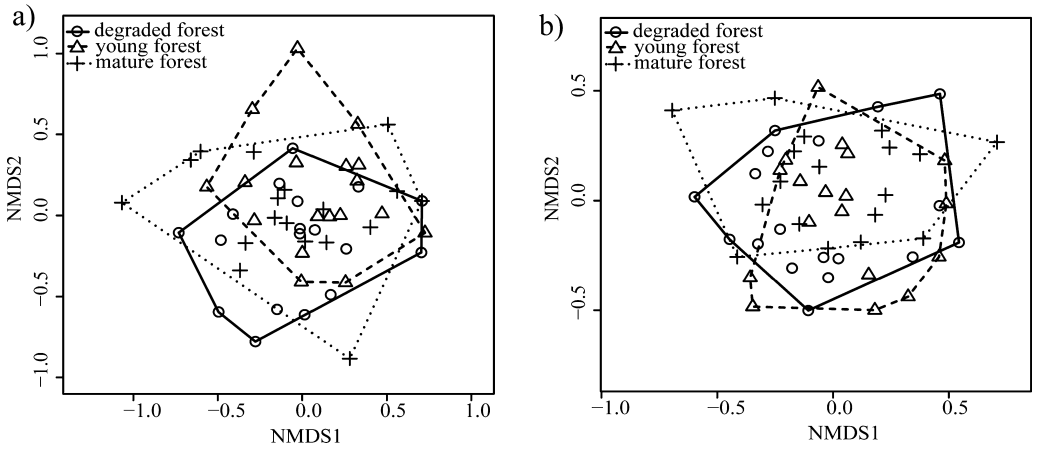

Fig. 2. Two dimensional non-metric multidimensional scaling (NMDS) plot of arbuscular mycorrhizal fungal community composition in three forest structural types (degraded, young and mature) during (a) wet and (b) dry seasons.

mature forest. Meanwhile during the dry season varied from 31.64 to 100% in the degraded forest, from 10.96 to 90% in the young forest and from 16.39 to 93.15% in the mature forest. Although the higher values were observed during the dry than during the wet season, root colonization was not significantly different among seasons (Table 3).

Among intra-radical structures, only vesicles showed significantly higher values during the dry than during the wet season (Table 3). Nevertheless, colonization of intra-radical structures did not show significant differences among forest types (Table 3).

4. Discussion

In this study for the first time, to the best of our knowledge, the influence of different *P. australis* forest disturbance types on the community composition of AMF morphospecies and on mycorrhizal root colonization were evaluated. The total number of AMF morphospecies identified (32) was in the range of values reported for other mountain forest ecosystems. In the high altitudinal forests of Kenia, Jefwa et al. (2009) detected 11 AMF morphospecies; 20 morphospecies were identified in *P. australis* forests of central Argentina (Menoyo et al., 2009) and 40 AMF taxa were isolated from forests of the Tibetan Plateau (Qing-Ming and Liang-Dong, 2010).

The previous work in *P. australis* forests (Menoyo et al., 2009) identified most of the morphospecies detected in this study. The following morphospecies represent new records for the high mountain forests of central Argentina: *Acaulospora alpina*, *Acaulospora foveata*, *A. rehmii*, *A. rugosa*, *A. undulata*, *A. lacunosa*, *Ambispora leptoticha*, *Claroideoglomus luteum*, *Gigaspora margarita*, *Gi. rosea*, *Funneliformis badium*, *F. mosseae*, *Glomus brohultii*, *Rhizophagus clarus*, *Pacispora patagonica*, *P. dominikii* and *P. robigina*. However, many of these taxa have been previously identified in the high mountain grasslands of central Argentina (Lugo and Cabello, 2002). The formal species identification based on spore morphology, as performed in this study, may not be equated directly with the species recovered through spores sequencing (Lanfranco et al., 2001). The use of both morphology and molecular methods may be the most appropriate description approach (Redecker et al., 2013), thus further use of molecular techniques could help to improve the AMF community characterization (Öpik et al., 2010).

Contrary to the initial hypothesis and to other studies (Grilli et al., 2012; Longo et al., 2014; Lopes Leal et al., 2013; Stürmer and Siqueira, 2011; Zhang et al., 2004), AMF richness, spore density, Shannon diversity and evenness were not affected by forest

Table 2
PERMANOVA outputs of arbuscular mycorrhizal fungal community composition variation during wet and dry seasons.

Model/parameter	df[a]	SD[b]	MS[c]	pseudo-F	R^2	P
Degraded forest						
Season	1	0.27	0.27	1.73	0.05	0.11
Residuals	34	5.26	0.15		0.95	
Total	35	5.53			1	
Young forest						
Season	1	0.26	0.26	1.76	0.05	0.13
Residuals	34	5.02	0.15		0.95	
Total	35	5.28			1	
Mature forest						
Season	1	0.26	0.26	1.76	0.05	0.09
Residuals	34	5.02	0.15		0.95	
Total	35	5.28			1	

[a] df: degrees of freedom.
[b] SD: sums of squares.
[c] MS: mean squares.

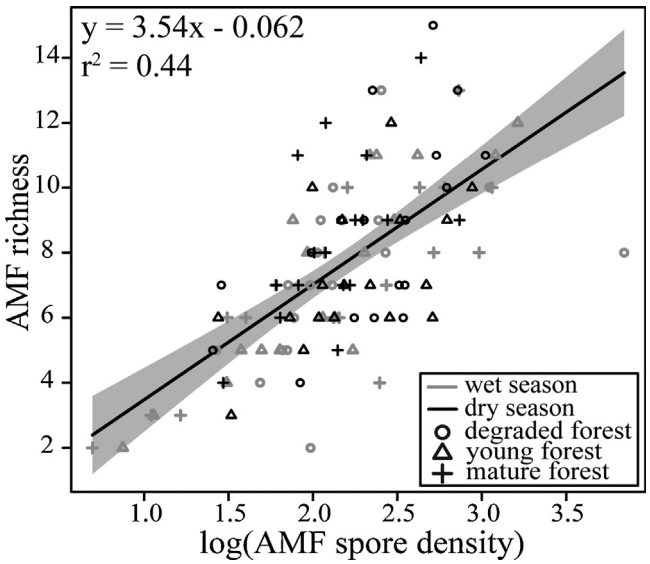

Fig. 3. Relationship between AMF richness (number of morphospecies) and spores density (number of spores/100 g of dry soil) of arbuscular mycorrhizal fungi (AMF) present in three forest structural types (degraded, young and mature) during wet and dry seasons. Shaded band represents 95% intervals of confidence around the regression line fitted (solid line).

Table 3
Mean percentage value (standard error) and generalized linear mixed model (GLLM) outputs of total arbuscular mycorrhizal colonization (AMC), root colonization by arbuscules (A), vesicles (V) and coils (C) of *P. australis* roots of three forest types (degraded forest, young forest and mature forest) during two seasons (wet and dry).

		AMC	A	V	C
Mean (s.e.)					
Wet season	Degraded forest	57.82 (1.89)	0.40 (0.11)	16.16 (1.21)	0.64 (0.12)
	Young forest	56.23 (1.85)	0.23 (0.07)	12.13 (1.08)	0.37 (0.09)
	Mature forest	49.71 (1.86)	0.17 (0.06)	8.99 (0.69)	0.63 (0.15)
Dry season	Degraded forest	68.16 (1.58)	2.07 (0.32)	31.29 (1.28)	0
	Young forest	59.58 (1.80)	0.60 (0.13)	20.49 (1.33)	0
	Mature forest	64.22 (1.70)	0.91 (0.18)	24.35 (1.10)	0.01 (0.01)
Term/GLLM output					
Forest type	df[a]	4	4	4	4
	Deviance	0.952	0.952	3.94	0.103
	P	0.92	0.92	0.41	0.99
Season	df[a]	3	3	3	3
	Deviance	1.760	1.760	12.962	1.959
	P	0.620	0.62	0.005	0.58
Season × forest type	df[a]	2	2	2	2
	Deviance	0.048	0.048	0.766	0.019
	P	0.98	0.98	0.68	0.99

[a] df: degrees of freedom of fixed factors: forest type (3 levels) * season (2 levels) + random term: five permanent slides nested within forest type, nested within three sampling sites.

disturbance types. The similarity of the AMF community among forest types was also evidenced by the NMDS and PERMANOVA analyses. The ordination plots revealed overlapping groups for the different forest types. There are four potential hypotheses that could explain the lack of differences observed in AMF communities. First, the spore dispersion process might facilitate AMF communities' recovery as *P. australis* woodlands and shrublands are interspaced among grasslands that shared most of the morphospecies (Friese and Koske, 1991; Lekberg et al., 2007; Lugo and Cabello, 2002).

Second, the kind of disturbances (i.e., livestock rearing and fire) that shaped the three forests types could not be severe enough to affect soil communities. It has been revealed that when organic matter remains, the soil ecosystem is not affected comparing with agricultural practices where soil overturn highly alters belowground ecosystem (Carrera et al., 2007; Kladivko, 2001). Moreover, due to the long evolutionary history of livestock rearing in the high mountains of central Argentina, grazing could be considered as an intrinsic factor rather than as a disturbance of the ecosystem (Díaz et al., 1994). In accordance with this, Menoyo et al. (2009) found that livestock impact did not affect the AMF community of *P. australis* forests.

Third, other possible explanation is that, mycorrhizal community may be resilient (Johnson et al., 2013; Urcelay et al., 2009), and natural successional processes will enable AMF to recover from these disturbances.

Finally, it has been widely acknowledged that AMF communities are influenced by soil physico- chemical characteristics (Bever et al., 2001; Egerton-Warburton et al., 2007; Grilli et al., 2012). Generally, high inorganic soil phosphorous concentrations limit AMF occurrence, and some AMF taxa are favored by particular soil properties (Smith and Read, 2008). Therefore, the similarities of soil properties among forest types could be explaining the absence of effect of forest disturbances on AMF community.

Jackknife 1 estimator showed that there remain to be detected 2–7 morphospecies in the degraded forest, 5–7 in the young forest and 3–8 in the mature forest. Further studies using trap plant cultures should be carried out to determine non- sporulating spores at sampling time (Stürmer et al., 2013).

Despite the lack of general differences in the AMF community among forest types, indicator species analyses showed two morphospecies mostly associated with the degraded forest, one preferentially linked to the young forest and two AMF taxa to the mature forest type. Therefore, slight variations of the AMF community that could be increase with greater anthropogenic disturbance (e.g. recently burnt forests (Longo et al., 2014)), were observed. Moreover, the mature forest type showed a higher biovolume of *Gigaspora* spp., a genus representative of conserved environments and late successional ecosystems (Allen et al., 2003; Hart and Reader, 2002).

In consistence with worldwide researches (e.g., Qing-Ming and Liang- Dong, 2010; Stürmer and Siqueira, 2011; Zhang et al., 2004), the genera *Glomus* and *Acaulospora* were the most abundant. Furthermore, while *Acaulospora* spp. occupied high volume in soil, *Glomus* showed the same biovolume as other larger but less abundant AMF taxa. These results highlight the importance of considering spore biovolume measurements to determine the biomass contribution of each genus to the soil AMF community (Allen et al., 2003; Egerton-Warburton et al., 2007; Qing-Ming and Liang-Dong, 2010).

Local species richness might be influenced by biotic and abiotic factors (not mutually exclusive) as competition for niche space, resource availability or host-symbionts functional traits (Chagnon et al., 2013; Gotelli and Colwell, 2001; Caley and Schluter, 1997). In this study a relationship between AMF richness and spore density has been observed. As the number of spore enhances, rare taxa or those that sporulate under suitable conditions are recorded, thus this increase might be evidencing the greater AMF community richness.

It has been reported that AMF community show seasonal variations (Lugo and Cabello, 2002; Merryweather and Fitter, 1998; Pringle and Bever, 2002). However, AMF spore diversity, density and richness were similar among seasons. Similar results were recorded by Davison et al. (2012), who using pyrosequencing to describe soil communities, observed spatial variation of AMF community composition but not seasonal changes.

In consistence with Menoyo et al. (2009) results in *P. australis* forests with different livestock density, total arbuscular mycorrhizal colonization did not vary among forest structural types. In our study this variable neither showed seasonal variation, in opposite to other author's findings (Lugo et al., 2003; Zangaro et al., 2013). Nevertheless, significantly higher percentage of root colonization by vesicles during the dry than during the wet season was observed. During the dry season, when soil drought enhance and plant metabolic activity decrease, the abundance of these storage structures, developed by some AMF

genera, tends to increase (Smith and Read, 2008). Although in low percentages, arbuscules and coils, the latter also described as exchange interfaces (Smith and Smith, 2011), were found during both seasons and in all the forest types thus indicating the symbiosis functioning.

5. Conclusions

P. australis forests represent one of the most endangered high mountain ecosystems mostly due to the effect of livestock rearing and intentional fires, leading it conservation as a priority. Therefore, several studies have been focused on the description of their biodiversity. However one of the most important soil microorganisms, AMF, has rarely been evaluated. This study showed that *P. australis* high mountain forests harbor a highly diverse AMF community. The relatively high similarity of morphospecies composition among forests with different degrees of disturbance could be attributed to a number of potential explanations. First, spore dispersal processes. Grassland species that are part of the vegetation mosaic and replace *P. australis* during early succession harbor a highly similar AMF community as *P. australis* forests. Second, the AMF community may not be impacted by these disturbances, which could have become an intrinsic factor of the ecosystem. Third, AMF community may be resilient to the kind of disturbances that shaped the forests compared, and natural successional processes may permit AMF to recover from these disturbances. Finally, the similarities of soil properties among forest types could be explaining the absence of effect of forest disturbances on AMF community.

Acknowledgements

This work was financially supported by Agencia de Promoción Científica y Tecnológica – PICT438-2006, Consejo Nacional de Investigaciones Científicas y Técnicas – PIP0269, Ministerio de Educación de la Nación (Secretaría de Políticas Universitarias-Res. 474), Secretaría de Ciencia y Técnica de la Universidad Nacional de Córdoba (Res. 162/12; 124/13), Argentina and Idea Wild Foundation. F.S., G.G., N.C. and N.M are grateful to CONICET for providing their fellowship. A.B. is researcher of CONICET. This research would not have been possible without numerous volunteers (especially Barberá I., Berizzo A., Bernaschini M.L., Domínguez J., Farias G., Flores S., Galli E., Gatica L., Peralta G., Renison D., Street E., and researchers and Ph.D. students of the Laboratorio de Micología (IMBIV)) who provided exceptional field assistance. We thank Dr. Robledo G. for helping with map design. The authors gratefully acknowledge to Longo S. and to Profs. Drs. Allen E.B. and Allen M.F. for critically reading a previous version of the manuscript.

References

Allen, E.B., Allen, M.F., Egerton-Warburton, L., Cordiki, L., Gómez-Pompa, A., 2003. Impacts of early- and late-seral mycorrhizae during restoration in seasonal tropical forest, Mexico. Ecol. Appl. 13, 1701–1717.

Bates, D.B., Maechler, M., Bolker, B., 2012. lme4: Linear Mixed-Effects Models Using S4 Classes. Version 0.999999-0. http://lme4r-forge.r-project.org/.

Becerra, A.G., Cabello, M., Zak, M.R., Bartoloni, N., 2009. Arbuscular mycorrhizae of dominant plant species in Yungas forests, Argentina. Mycologia 101, 612–621.

Bever, J.D., Schultz, P.A., Pringle, A., Morton, J.B., 2001. Arbuscular mycorrhizal fungi: more diverse than meets the eye, and the ecological tale of why. BioScience 51, 923–932.

Brundrett, M.C., 2009. Mycorrhizal associations and other means of nutrition of vascular plants: understanding the global diversity of host plants by resolving conflicting information and developing reliable means of diagnosis. Plant Soil 320, 37–77.

Cabido, M., Breimer, R., Vega, G., 1987. Plant communities and associated soil types in a high plateau of the Cordoba Mountains, central Argentina. Mt. Res. Dev. 7, 25–42.

Cabido, M., 1985. Las comunidades vegetales de Pampa de Achala Sierras de Córdoba Argentina. Doc. Phytosociol. 9, 431–443.

Caley, M.J., Schluter, D., 1997. The relationship between local and regional diversity. Ecology 78, 70–80.

Carpenter, F.L., Mayorga, S.P., Quintero, E.G., Schroeder, M., 2001. Land-use and erosion of a Costa Rican Ultisol affect soil chemistry: mycorrhizal fungi and early regeneration. Forest Ecol. Manag. 144, 1–17.

Carrera, L.M., Buyer, J.S., Vinyard, B., Abdul-Baki, A.A., Sikora, L.J., Teasdale, J.R., 2007. Effects of cover crops compost and manure amendments on soil microbial community structure in tomato production systems. App. Soil Ecol. 37, 247–255.

Chagnon, P.-L., Bradley, R.L., Maherali, H., Klironomos, J.N., 2013. A trait-based framework to understand life history of mycorrhizal fungi. Trends Plant Sci. 18, 484–491.

Cingolani, A.M., Cabido, M.R., Renison, D., Solís Neffa, V., 2003. Combined effects of environment and grazing on vegetation structure in Argentine granite grasslands. J. Veg. Sci. 14, 223–232.

Cingolani, A.M., Renison, D., Tecco, P.A., Gurvich, D.E., Cabido, M., 2008. Predicting cover types in a mountain range with long evolutionary grazing history: a GIS approach. J. Biogeogr. 35, 538–551.

Cingolani, A., 2004. Mapping vegetation in a heterogeneous mountain rangeland using landsat data: an alternative method to define and classify land-cover units. Remote. Sens. Environ. 92, 84–97.

Díaz, S., Acosta, A., Cabido, M., 1994. Community structure in montane grasslands of central Argentina in relation to land use. J. Veg. Sci. 5, 483–488.

Davison, J., Opik, M., Zobel, M., Vasar, M., Metsis, M., Moora, M., 2012. Communities of arbuscular mycorrhizal fungi detected in forest soil are spatially heterogeneous but do not vary throughout the growing season. PLoS One 7, e41938.

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

Dumbrell, A.J., Nelson, M., Helgason, T., Dytham, C., Fitter, A.H., 2010. Idiosyncrasy and overdominance in the structure of natural communities of arbuscular mycorrhizal fungi: is there a role for stochastic processes? J. Ecol. 98, 419–428.

Egerton-Warburton, L.M., Johnson, N.C., Allen, E.B., 2007. Mycorrhizal community dynamics following nitrogen fertilization: a cross-site test in five grasslands. Ecol. Monogr. 77, 527–544.

Entry, J.A., Rygiewicz, P.T., Donnellyc, P.K., Watrudb, L.S., 2002. Influence of adverse soil conditions on the formation and function of arbuscular mycorrhizas. Adv. Environ. Res. 7, 123–138.

FAO, 2005. Protective functions of forest resources. Progress Towards Sustainable Forest Management, Global Forest Resources Assesment. Food and Agriculture Organization of the United Nations, pp. 95–103.

Fitter, A.H., Gilligan, C.A., Hollingworth, K., Kleczkowski, A., Twyman, R.M., Pitchford, J.W., Programme, T.m.o.t.N.S.B., 2005. Biodiversity and ecosystem function in soil. Funct. Ecol. 19, 369–377.

Friese, Koske, R.E., 1991. The spatial dispersion of spores of vesicular–arbuscular mycorrhizal fungi in a sand dune: microscale patterns associated with the root architecture of American beachgrass. Mycol. Res. 95, 952–957.

Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4, 379–391.

Grace, C., Stribley, D.P., 1991. A safer procedure for routine staining of vesicular–arbuscular mycorrhizal fungi. Mycol. Res. 95, 1160–1162.

Grilli, G., Urcelay, C., Galetto, L., 2012. Forest fragment size and nutrient availability: complex responses of mycorrhizal fungi in native–exotic hosts. Plant Ecol. 213, 155–165.

Hart, M.M., Reader, R.J., 2002. Taxonomix basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. New Phytol. 153, 335–344.

Haugen, L.M., Smith, S.E., 1992. The effect of high temperature and fallow period on infection of mung bean and cashew roots by the vesicular–arbuscular mycorrhizal fungus *Glomus intraradices*. Plant Soil 145, 71–80.

Jefwa, J.M., Mung'atu, J., Okoth, P., Muya, E., Roimen, H., Njuguini, S., 2009. Influence of land use types on occurrence of arbuscular mycorrhizal fungi in the high altitude regions of Mt. Kenya. Trop. Subtrop. Agroecosyst. 11, 277–290.

Johnson, N.C., Wedin, D.A., 1997. Soil carbon nutrients and mycorrhizae during conversion of dry tropical forest to grassland. Ecol. Appl. 7, 171–182.

Johnson, N.C., Angelard, C., Sanders, I.R., Kiers, T.E., 2013. Predicting community and ecosystem outcomes of mycorrhizal responses to global change. Ecol. Lett. 16, 140–153.

Kenkel, N.C., Orlóci, L., 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. Ecology 67, 919–928.

Kindt, R., 2013. BiodiversityR: GUI for biodiversity, suitability and community ecology analysis. Version 2.1. http://www.r-project.org, http://www.worldagroforestry.org/resources/databases/tree-diversity-analysis.

Kladivko, E.J., 2001. Tillage systems and soil ecology. Soil Till. Res. 61, 61–76.

Lanfranco, L., Bianciotto, V., Lumini, E., Souza, M., Morton, J.B., Bonfante, P., 2001. A combined morphological and molecular approach to characterize isolates of arbuscular mycorrhizal fungi in *Gigaspora* (Glomales). New Phytol. 152, 169–179.

Lee, P.J., Koske, R.E., 1994. *Gigaspora gigantea*: seasonal abundance and ageing of spores in a sand dune. Mycol. Res. 98, 453–457.

Lekberg, Y., Koide, R.T., Rohr, J.R., Aldrich-Wolfe, L., Morton, J., 2007. Role of niche restrictions and dispersal in the composition of arbuscular mycorrhizal fungal communities. J. Ecol. 95, 95–105.

Longo, S., Nouhra, E., Goto, B.T., Berbara, R.L., Urcelay, C., 2014. Effects of fire on arbuscular mycorrhizal fungi in the Mountain Chaco Forest. Forest Ecol. Manag. 315, 86–94.

Lopes Leal, P., Siqueira, J.O., Stürmer, S.L., 2013. Switch of tropical Amazon forest to pasture affects taxonomic composition but not species abundance and diversity of arbuscular mycorrhizal fungal community. App. Soil Ecol. 71, 72–80.
Lugo, M.A., Cabello, M.N., 2002. Native arbuscular mycorrhizal fungi (AMF) from mountain grassland (Córdoba Argentina) I. Seasonal variation of fungal spore diversity. Mycologia 94, 579–586.
Lugo, M.A., González Maza, M.E., Cabello, M.N., 2003. Arbuscular mycorrhizal fungi in a mountain grassland II: seasonal variation of colonization studied, along with its relation to grazing and metabolic host type. Mycologia 95, 407–415.
Magurran, A.E., McGill, B.J., 2011. Ecological Diversity: Frontiers in Measurement and Assessment. Oxford University Press.
Marcora, P., Hensen, I., Renison, D., Seltmann, P., Wesche, K., 2008. The performance of *Polylepis australis* trees along their entire altitudinal range: implications of climate change for their conservation. Divers. Distrib. 14, 630–636.
McGonigle, T.P., Millers, M.H., Evans, D.G., Fairchild, G.L., Swan, J.A., 1990. A new method which gives an objective measure of colonization of roots by vesicular–arbuscular mycorrhizal fungi. New Phytol. 115, 495–501.
Menoyo, E., Renison, D., Becerra, A.G., 2009. Arbuscular mycorrhizas and performance of *Polylepis australis* trees in relation to livestock density. Forest Ecol. Manag. 258, 2676–2682.
Merryweather, J., Fitter, A.H., 1998. The arbuscular mycorrhizal fungi of *Hyacinthoides non-scripta* II: seasonal and spatial patterns of fungal populations. New Phytol. 138, 131–142.
Oksanen, J., Blanchet, F.G.K., Roeland Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2012. vegan: Community Ecology Package. Version 2.0-5. http://cran.r-project.org, http://vegan.r-forge.r-project.org/.
Omar, M.B., Bolland, L., Heather, W.A., 1979. P.V.A. (polivinil alcohol). A permanent mounting medium for fungi. Bull. Br. Mycol. Soc. 13, 31–32.
Öpik, M., Vanatoa, A., Vanatoa, E., Moora, M., Davison, J., Kalwij, J.M., Reier, U., Zobel, M., 2010. The online database MaarjAM reveals global and ecosystemic distribution patterns in arbuscular mycorrhizal fungi (Glomeromycota). New Phytol 188, 223–241.
Phillips, J.M., Hayman, D.S., 1970. Improved procedures for clearing roots and staining parasitic and vesicular arbuscular mycorrhizal fungi for rapid assessment of infection. Trans. Br. Mycol. Soc. 55, 158–161.
Picone, C., 2000. Diversity and abundance of arbuscular-mycorrhizal fungus spores in tropical forest and pasture. Biotropica 32, 734–750.
Pollice, J., Marcora, P., Renison, D., 2013. Seed production in *Polylepis australis* (Rosaceae) as influenced by tree size: livestock and interannual climate variations in the mountains of central Argentina. New Forest 44, 233–247.
Pringle, A., Bever, J.D., 2002. Divergent phenologies may facilitate the coexistence of arbuscular mycorrhizal fungi in a North Carolina grassland. Am. J. Bot. 89, 1439–1446.
Qing-Ming, G., Liang-Dong, G., 2010. A comparative study of arbuscular mycorrhizal fungi in forest, grassland and cropland in the Tibetan Plateau, China. Mycology 3, 163–170.
Redecker, D., Schüßler, A., Stockinger, H., Stürmer, S., Morton, J., Walker, C., 2013. An evidence-based consensus for the classification of arbuscular mycorrhizal fungi (Glomeromycota). Mycorrhiza 1–17.
Renison, D., Hensen, I., Cingolani, A.M., 2004. Anthropogenic soil degradation affects seed viability in *Polylepis australis* mountain forests of central Argentina. For. Ecol. Manag. 196, 327–333.
Renison, D., Hensen, I., Suarez, R., Cingolani, A.M., 2006. Cover and growth habit of *Polylepis* woodlands and shrublands in the mountains of central Argentina: human or environmental influence? J. Biogeogr. 33, 876–887.
Renison, D., Hensen, I., Suarez, R., Cingolani, A.M., Marcora, P., Giorgis, M.A., 2010. Soil conservation in *Polylepis* mountain forests of central Argentina: is livestock reducing our natural capital? Austral Ecol. 35, 435–443.
Renison, D., Hensen, I., Suarez, R., 2011. Landscape structural complexity of high-mountain *Polylepis australis* forests: a new aspect of restoration goals. Restor. Ecol. 19, 390–398.
Roberts, D.W., 2013. labdsv: ordination and multivariate analysis for ecology package. Version 1.6-1. http://cran.r-project.org/web/packages/labdsv.
Schenck, N.C., Perez, Y., 1990. Manual of identification of vesicular-arbuscular mycorrhizal fungi. INVAM, University of Florida, Gainesville, Fla, USA.
Schüßler, A., Schwarzott, D., Walker, C., 2001. A new fungal Phylum: the Glomeromycota: phylogeny and evolution. Mycol. Res. 105, 1413–1421.
Simpson, B.B., 1979. A Revision of the Genus *Polylepis* (Rosaceae: Sanguisorbeae). Smithsonian Institution Press, Washington.
Smith, S.E., Read, D., 2008. Mycorrhizal Symbiosis. Academic Press, Great Britain, pp. 815.
Smith, S.E., Smith, F.A., 2011. Roles of arbuscular mycorrhizas in plant nutrition and growth: new paradigms from cellular to ecosystem scales. Annu. Rev. Plant Biol. 62, 227–250.
Soteras, F., Becerra, A., Cofré, N., Bartoloni, J., Cabello, M., 2012. Arbuscular mycorrhizal fungal species in saline environments of central Argentina: seasonal variation and distribution of spores at different soil depths. Sydowia 64, 301–311.
Stürmer, S.L., Siqueira, J.O., 2011. Species richness and spore abundance of arbuscular mycorrhizal fungi across distinct land uses in Western Brazilian Amazon. Mycorrhiza 21, 255–267.
Stürmer, S.L., Stürmer, R., Pasqualini, D., 2013. Taxonomic diversity and community structure of arbuscular mycorrhizal fungi (Phylum Glomeromycota) in three maritime sand dunes in Santa Catarina state, south Brazil. Fungal Ecology 6, 27–36.
Urcelay, C., Díaz, S., Gurvich, D.E., Chapin III, F.S., Cuevas, E., Domínguez, L.S., 2009. Mycorrhizal community resilience in response to experimental plant functional type removals in a woody ecosystem. J. Ecol. 97, 1291–1301.
van Veen, J., Paul, E.A., 1979. Conversion of biovolume measurements of soil organisms grown under various moisture tensions to biomass and their nutrient content. App. Environ. Microbiol. 37, 686–692.
Walker, C., Mize, W., McNabb, H.S., 1982. Populations of endogonaceous fungi at two populations in central Iowa. Can. J. Bot. 60, 2518–2529.
Wang, B., Qiu, Y.-L., 2006. Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 16, 299–363.
Zangaro, W., Rostirola, L.V., de Souza, P.B., de Almeida Alves, R., Lescano, L.E., Rondina, A.B., Nogueira, M.A., Carrenho, R., 2013. Root colonization and spore abundance of arbuscular mycorrhizal fungi in distinct successional stages from an Atlantic rainforest biome in southern Brazil. Mycorrhiza 23, 221–233.
Zhang, Y., Guo, L.-D., Liu, R.-J., 2004. Survey of arbuscular mycorrhizal fungi in deforested and natural forest land in the subtropical region of Dujiangyan, southwest China. Plant Soil 261, 257–263.