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# Rescuing the ectomycorrhizal biodiversity associated with South American *Nothofagaceae* forest, from the 19th century naturalists up to molecular biogeography

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The southernmost portion of the Andes in South America hosts *Nothofagaceae* forests that form ectomycorrhizal (EcM) associations. We compiled all the published reports of EcM taxa from these woodlands, based on fruit-body collections and molecularly identified root tips. This resulted in 87 peer-reviewed research papers dealing with EcM associations from *Nothofagaceae* forests published over the past 62 years. Based on these papers the EcM richness and its association with *Nothofagaceae* species was analyzed. Represented by 45 genera (34 Basidiomycetes and 11 Ascomycetes), 479 EcM taxa have been recorded, plus an additional 46 EcM taxa which are potentially EcM. *Cortinarius* was the most frequent and diverse genus, with 64.9% of total species. *Nothofagus dombeyi* had the highest number of unique EcM species, followed by *N. pumilio*, *N. antarctica* and *Lophozonia obliqua*. The EcM community associated with *Nothofagus* species, except *N. nitida,* showed higher similarities among themselves, than with *Lophozonia* and *Fuscospora* species. Beta diversity indexes showed EcM *Nothofagus* species have 29–42% niche overlap, while *Nothofagus—Lophozonia* only had 1–16%. The assessment of the accuracy of the EcM diversity, host specificity and community structure deserve further studies combining phylogenetic analysis based on broad ecological surveys. On the basis of pre-selected criteria *Austropaxillus statuum, Cortinarius fragilis, Cortinarius xiphidipus* and *Hallingea purpurea* are proposed as candidates for nursery spore inoculations, and should be subject to scientific evaluation to determine costs and benefits.

## Introduction

The Andean-Patagonian region, along the southernmost portion of the Andes Mountains in South America, nourishes forests dominated by *Nothofagaceae* Kuprian species (Cabrera, 1976), distributed between 30 to 56° S on both sides of the Andes mountains. The region comprises 11 species of *Nothofagaceae* from three genera: *Nothofagus, Lophozonia* and *Fuscospora,* forming extensive monospecific and mixed forests (Dimitri and Orfila, 1985; Donoso Zegers, 2006; Heenan and Smissen, 2013). Ectomycorrhizal (EcM) associations play a key role in the functioning of all these forests (Singer and Morello, 1960; Valenzuela Flores, 1993; Fontenla *et al*., 1998).

*Nothofagaceae* forests are characterized by low atmospheric pollution (Perakis and Hedin, 2002), poorly developed volcanic soils (Satti *et al*., 2007) with low availability of phosphorous (P) and a high capacity to store water and buffer pH changes (Diehl *et al*., 2003). *Nothofagus pumilio* (Poepp. & Endl.) Krasser is distributed from 35 to 56° S on both sides of the Andes, and occupies the upper limit of the mountain forest. *Nothofagus antarctica* (G. Forst.) Oerst. shares the *N. pumilio* distribution, but due to its drought resistance, it is mostly present in the forest-steppe ecotone area. *Lophozonia obliqua* (Mirb.) Heenan & Smissen and *L. alpina* (Poepp. & Endl.) Heenan & Smissen, both with very high wood quality, have more restricted distributions, growing from 30 to 41° S and 35 to 40.5° S respectively in both Chile and Argentina. Evergreen *N. dombeyi* (Mirb.) Oerst. grows from 30 to 47° S in Argentina and Chile, forming the main type of forest in areas with high humidity, close to lakes and river margins, in pure stands as well as associated with all the other *Nothofagaceae* species except *N. betuloides* (Mirb.) Oerst.; the latter is distributed from 40 to 56° S (Dimitri and Orfila, 1985; Donoso Zegers, 2006). Chile has five other species restricted to the west side of the Andes: *Fuscospora alessandri* (Espinosa) Heenan & Smissen, *L. glauca* (Phil.) Heenan & Smissen, *L. macrocarpa* (A. DC.) Heenan & Smissen and the hybrid *L. x leonii* Espinosa, all with very narrow distributions (from 35 to 36.5° S), and *N. nitida* (Phil.) Krasser forming oceanic forests distributed from 40 to 49° S (Dimitri and Orfila, 1985; Donoso Zegers, 2006).

Studies have shown that the establishment of *Nothofagaceae* forests in Argentina and Chile depends on EcM associations (Singer and Morello, 1960; Singer and Moser, 1965; Garrido 1988; Carrillo *et al.*, 1992; Valenzuela Flores, 1993), reporting EcM colonization rates higher than 70% (Diehl *et al.*, 2008; Longo *et al.*, 2011). High colonization rates together with the fact that *Nothofagaceae* species do not show a P deficit, suggests that EcM constitute an effective adaptation mechanism of *Nothofagaceae* to P-deficient soils (Diehl *et al.*, 2003, 2008; Agüero *et al.*, 2014), making trees more aggressive and resistant to adverse conditions, well adapted to disturbances and also have the ability to act as pioneers (Garrido, 1988; Valenzuela Flores, 1993).

The EcM fungal species richness associated with a tree species over its natural distribution provides important information needed for ecological studies, management decisions and selection of appropriate EcM fungal species for inoculation programs. The assessment of the EcM biota associated to South American *Nothofagaceae* started with the exploration campaigns and first taxa descriptions from C. Spegazzini (1887a, b) at the end of the 19th century. These pioneering studies were followed by diverse taxonomical reports and ecological studies up to until the modern era, including molecular tools for EcM detection and identification. However, all of this information is scattered and has not yet been compiled, organized and published.

Species of *Nothofagaceae* forests in South America, particularly *N. pumilio,* exhibit extensive degraded areas as it has been widely exploited for its timber. Herbivory by both cervids and cattle (Veblen *et al.*, 1996; Vázquez, 2002), and the increased frequency of forest fires during recent decades are preventing regeneration of these valuable forests. Sustainable silvicultural management, conservation decisions and restoration actions promoted by state institutions and land-owners/private investors have been initiated recently, as has the mass production of seedlings to support regeneration and the establishment of new forests (Barroetaveña *et al.*, 2009). Knowledge about EcM richness, which species are shared, and which are specific to each *Nothofagaceae*, is necessary to build distribution models that support conservation decision making, together with defining suitable species to incorporate EcM inoculation programs in nurseries producing *Nothofagaceae*.

This aims of this review were to: (1) compile the reported EcM taxa associated with *Nothofagaceae* species growing in South America, based on fruiting body collections and molecularly identified root tips, from published accounts; (2) to examine the EcM species richness by fungal genera, along with their associations with *Nothofagaceae*; (3) propose EcM species to be scientifically and technically evaluated as candidates in inoculations (via spores) of *Nothofagaceae* species.

## Material and methods

A total of 87 research articles on EcM from *Nothofagaceae* forests, published in Spanish, German and English language from peer-reviewed research journals and books over the past 62 years, was located using online database searches using the keyword phrases ‘ectomycorrhizal fungi’, ‘*Nothofagus* mycorrhizas’, ‘*Nothofagus* forest’, ‘Ectomycorrhizae Patagonia’. Publications that compiled EcM records but did not provide novel citations were not included in the database and the subsequent analysis.

The EcM fungal species and their references were listed for each *Nothofagaceae* species in South American forests (Supplementary Table S1). Records were obtained from all the published information about EcM fungal taxa, both from fruiting bodies records or molecularly identified EcM root tips. Molecular identifications were included at species level only with BLAST >98% and at genus level with BLAST >90% (Schoch *et al.*, 2014). The complete lists of taxa include infrageneric records; varieties are included separately. All EcM fungal species reported were from forests clearly dominated by the reported species. When records came from mixed forests, all species present were recorded in the analysis. Potential Basidiomycetes and Ascomycetes EcM taxa that belong to a genus whose EcM condition is still under discussion (Rinaldi *et al.*, 2008; Tedersoo and Smith, 2013, 2017; Águeda-Hernández, 2014; Kõljalg *et al.*, 2013) were also compiled and highlighted in Supplementary Table S1.

The EcM status of all taxa, at least at genus level, are included in the concept of lineages by Tedersoo and Smith (2013, 2017), and checked with Rinaldi *et al.* (2008), Águeda-Hernández (2014) and UNITE (Kõljalg *et al.*, 2013). Taxa currently known to be saprophytic were excluded. Names and authors of each taxon follow the Index Fungorum database (http://www.indexfungorum.org/Index.htm); if the name had changed, the currently accepted name was underlined (Supplementary Table S1). The sporocarp habit of each taxon was classified as: epigeous, hypogeous, corticioid (C, fruitbodies resupinated), or subhypogeous.

The total number of citations of each EcM species by tree species, summarized in Supplementary Table S2 was used as a preliminary indicator of frequency to estimate EcM richness, shared species, beta diversity indices, cluster analysis and niche overlap by host tree. Ambiguous species (when associated tree species was not specified by the author) and potential EcM registers were not included. Alpha diversity was estimated by Richness and Chao richness. Differences in these indices between tree species were analyzed by non-parametric ANOVAs with Kruskall Wallis test at 0.05 significance level. All the analyses were performed with the statistical package InfoStat for Windows 10 (Di Rienzo *et al.*, 2017). Niche overlap by tree species and beta diversity were estimated by Jaccard, Sorensen, Morisita-Horn and Bray-Curtis indices using EstimateS (Colwell, 2013).

To examine similarities between tree species considering their associated EcM communities, a Cluster analysis was performed using InfoStat for Windows 10 (Di Rienzo *et al.*, 2017). The outcome of these results was used to consider integrating the biogeographical district classification proposed by Cabrera and Willink (1980) for South American *Nothofagaceae* forests: *Maulino district* from coastal and humid Chilean zones (from 34.9 to 37.3° S latitude) including *F. alessandri*, *L. x leonii*, *L. glauca*, *L. macrocarpa*, *L. obliqua* and *N. dombeyi*; *Maguellanic district* from Argentina and Chile (from 47 to 56° S latitude) including *N. betuloides*, *N. antarctica*, *N. pumilio*, *N. nitida*; *Deciduous forest district* from east xeric Argentina and Chile (from 37 to 44° S latitude) including *N. antarctica*, *N. pumilio*; *Pehuen district* from Argentina and Chile (from 37.5 to 40.2° S latitude) including *N. antarctica*, *N. pumilio* and *L. obliqua* associated with *Araucaria*

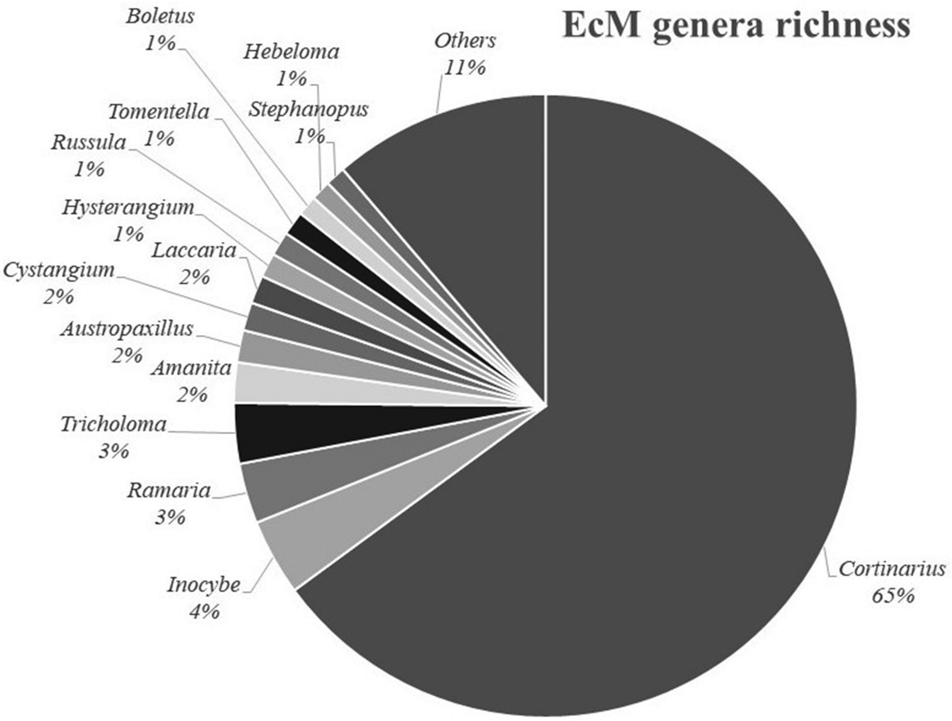

**Figure 1** Ectomycorrhizal fungi genera richness.

*araucana* and *Valdivian district* from Argentina and Chile humid zones (from 37.3 to 47° S latitude) including *N. dombeyi*, *N. nitida*, *L. alpina* and *L. obliqua*.

The selection of EcM candidate species for spore inoculations was based in Barroetaveña (2004) and Bassani *et al.* (2013), considering the following characteristics: (a) ease of harvesting fruiting bodies, determined by size and fruiting habit (epigeous and/or sub-hypogeus considered easy to find; hypogeous considered difficult to find); (b) fruiting abundance, determined by frequency of observations in the field, citations in the present review, and size of fruiting bodies; (c) fruiting period throughout the year; (d) spore density (spores per unit of fruiting body weight, considering complete fruit bodies for hypogeous species, and only the pileus for epigeous or sub-hypogeous species); (e) tree species reported as hosts; (f) previous reports in seedlings.

## Results

### EcM taxa associated with Nothofagaceae in Patagonia: species richness, frequency, specific and shared species

The overall analysis showed that 479 taxa were recorded for *Nothofagaceae* distributed in South American forest (Supplementary Table S1), represented by 45 genera, 34 of them Basidiomycetes and 11 Ascomycetes (Figure 1). There are 17 Basidiomycetes species from 5 genera and 29 Ascomycetes from 9 genera that are potentially EcM (Supplementary Table S1). *Cortinarius* represents the most diverse genus, with 311 species and another 11 registered from root tips at generic level (BLAST between 89–97%) (Nouhra *et al.*, 2013). *Inocybe* presented 19 species, followed by *Tricholoma* and *Ramaria* with 15 species each, *Amanita* with 10 species, *Austropaxillus* with 8 species, *Cystangium* and *Laccaria* with 7 species, *Russula, Tomentella* and *Hysterangium* with 6 species, *Boletus, Hebeloma* and *Stephanopus* with 5 species each, while the remaining 31 genera had less than 5 species (Figure 1). Of all the taxa reported, 89.8% are epigeous, 6.3% are hypogeous, 1.9% are sub-hypogeous and 2.1% are corticioid (Supplementary Table S1).

The total number of EcM species by *Nothofagaceae* ranged between 22 for *L. x leonii* and 320 for *N. dombeyi* (Table 1). *Nothofagus dombeyi* and *N. pumilio* yielded a high number of exclusive EcM species (115 and 44 respectively) representing 36 and 18% of their total EcM species, while *L. x leonii* and *F. alessandri* showed no unique species (Table 1). *Austropaxillus boletinoides* Singer and *A. statuum* (Speg.) Bresinsky & Jarosch were the most reported ones (20 records), followed by *Cortinarius austrolimonius* Moser & Horak, *C. flammuloides* Moser & Horak. and *C. magellanicus* Speg. with 17 records (Figure 2; Supplementary Table S2). Of the EcM compiled species, 37.6% had only one record (Supplementary Table S2).

The EcM richness (S) was significantly different among tree species (Kruskal Wallis, $H = 1079.33$; $P < 0.0001$, Table 1), *N. dombeyi* being the richest (307 species) and *L. x leonii* the least rich (7 species) (S index, Table 1). Similar results were found for the Chao richness index (Kruskal Wallis, $H = 1011$; $P < 0.0001$, Table 1).

The EcM community associated whit *Nothofagus,* except *N. nitida,* showed higher similarities among themselves compared with *Lophozonia* and *Fuscospora* species (Figure 3). *Lophozonia alpina* and *L. obliqua* clustered together close to the unique

**Table 1** Number of EcM cited, exclusive species, potential EcM species and alpha diversity by *Nothofagaceae* species.

| Tree species | Cited species | Exclusive EcM species | Exclusive EcM % | Potential species | S | S Chao | Biogrografical distict |
|---|---|---|---|---|---|---|---|
| *F. alessandri* | 43 | 0 | 0.00 | 8 | 29$^{a}$ | 33.31$^{a}$ | Maulino |
| *L. alpina* | 58 | 2 | 3.45 | 17 | 43$^{b}$ | 42.31$^{b}$ | Valdivian |
| *L. glauca* | 57 | 3 | 5.26 | 8 | 43$^{b}$ | 47.82$^{b}$ | Maulino |
| *L. macrocarpa* | 26 | 2 | 7.69 | 8 | 11$^{a,c}$ | 12.82$^{c}$ | Maulino |
| *L. obliqua* | 84 | 13 | 15.48 | 23 | 69$^{d}$ | 73.08$^{d}$ | Maulino, Pehuen, Valdivian |
| *L. x leonii* | 22 | 0 | 0.00 | 8 | 7$^{c}$ | 7.05$^{c}$ | Maulino |
| *N. antarctica* | 165 | 16 | 9.70 | 16 | 150$^{e,f}$ | 147.11$^{e,f}$ | Maguellanic, Desiduous, Pehuen |
| *N. betuloides* | 128 | 1 | 0.78 | 20 | 113$^{d,e}$ | 111.18$^{d,e}$ | Maguellanic |
| *N. dombeyi* | 320 | 115 | 35.94 | 16 | 307$^{g}$ | 295.45$^{g}$ | Maulino, Valdivian |
| *N. nitida* | 54 | 7 | 12.96 | 8 | 39$^{b}$ | 41.11$^{a,b}$ | Maguellanic, Valdivian |
| *N. pumilio* | 248 | 44 | 17.74 | 31 | 233$^{f,g}$ | 227.54$^{f,g}$ | Maguellanic, Desiduous, Pehuen |

*Different letter means significant differences at $P < 0.05$ (Kruskall Wallis).

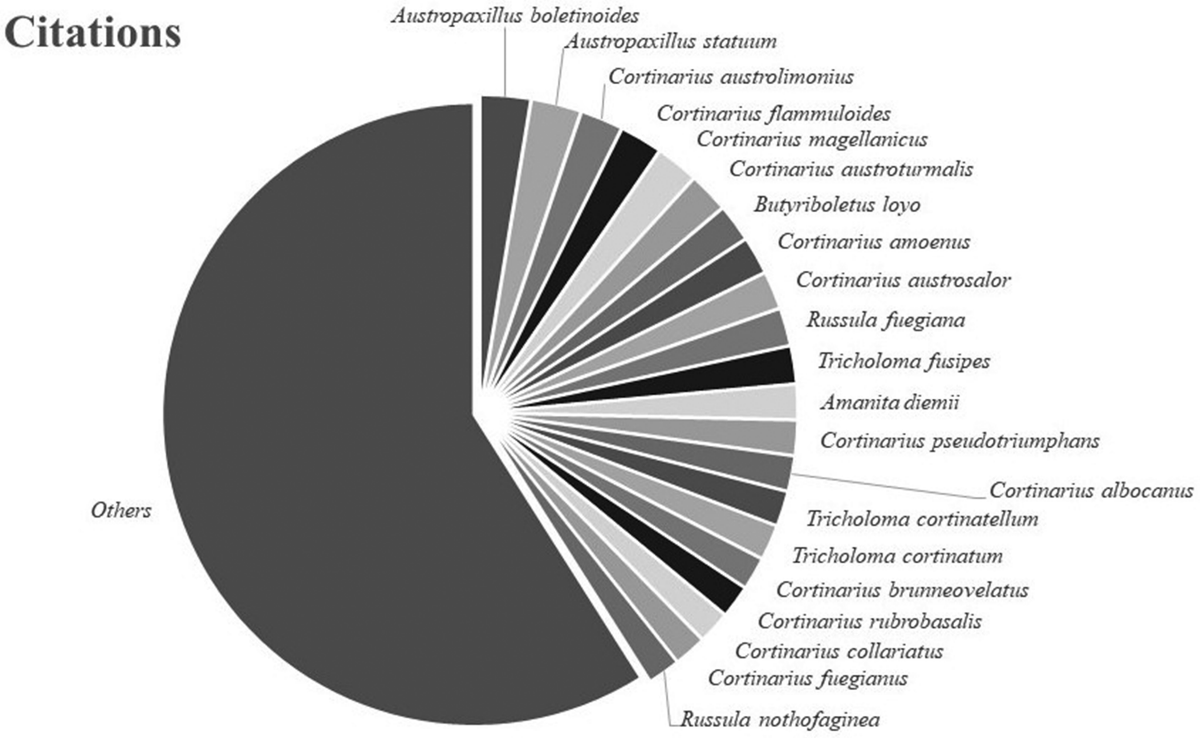

**Figure 2** Ectomycorrhizal genera representativeness (%).

Chilean *Nothofagaceae* species (Figure 3). In the same sense, the beta diversity indexes of the EcM *Nothofagus* species had 29 to 42% niche overlap, while *Nothofagus—Lophozonia* only had 1 to 16% (Jaccard index, Table 2), confirmed by the other beta diversity indices.

## Selection of fungal candidate species for EcM spore inoculations

Applying the selected assessment criteria based on reviewed publications, the following species are proposed as potential candidates for nursery inoculations:

***Austropaxillus statuum*** : harvest of fruiting bodies is easy given that it is an epigeous species, with pileus diameter between 5 and 10 cm. Fruiting abundance is high (Bassani *et al.*, 2013), with 20 citations in the database (Table 1, S1). Fruiting occurs from March to April, more abundantly early in the season. Spore density is intermediate, with good viability conservation (Bassani *et al.*, 2013). Hosts are *Nothofagus pumilio, N. dombeyi, N. antarctica, N nitida, L. glauca, F. alessandri. Austropaxillus* mycorrhizas have been reported by Godoy and Palfner, (1997) from nursery *L. alpina* seedlings and from successful axenical synthesis with all Patagonian *Nothofagaceae* with colonization rates between 51–100% (Garrido, 1988). Edibility: not edible (Gamundí and Horak, 1993).

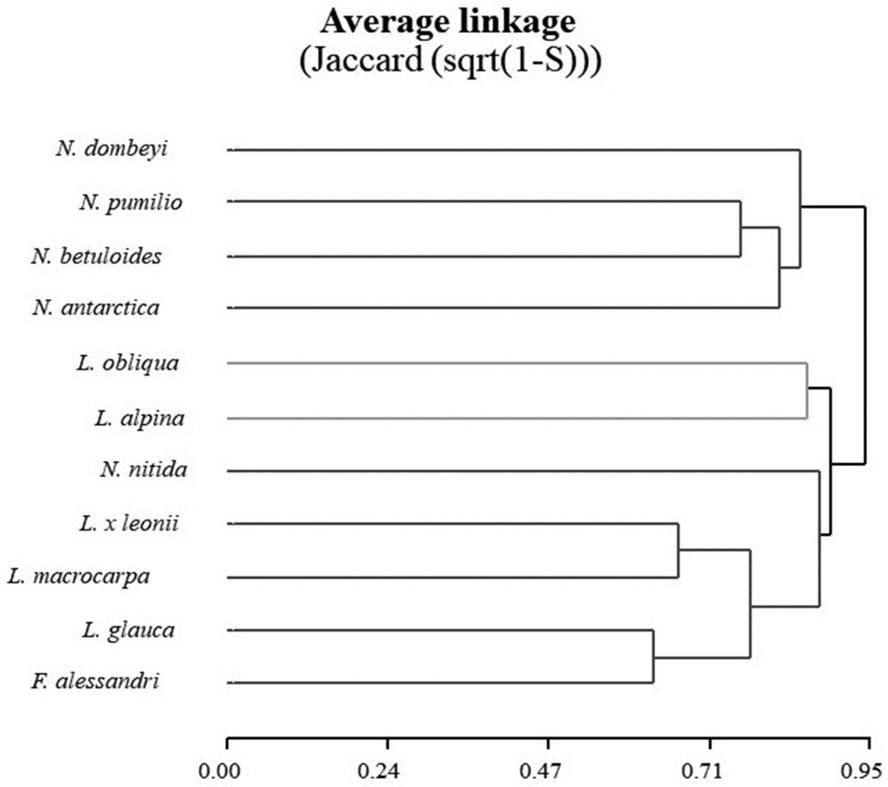

**Figure 3** Cluster analysis showing similarities between *Nothofagaceae* considering their associated EcM communities.

***Cortinarius fragilis*** : harvest of fruiting bodies is easy given that it is a sub-hypogeous species, with pileus diameter up to 4 cm. Fruiting abundance is intermediate (Bassani *et al.*, 2013), with 8 citations in the database (Table 1, S1). Fruiting occurs from March to May. Spores density is intermediate, with good viability conservation (Bassani *et al.*, 2013). Hosts are *N. pumilio*, *N. dombeyi*, *N. antarctica*, *L. alpina* and *L. obliqua*. *Cortinarius* has been reported from *L. alpina* seedlings (Fernández *et al.*, 2015) and from *N. antarctica* seedlings (Salgado Salomón *et al.*, 2018a). Edibility: unknown.

***Cortinarius xiphidipus*** : harvest of fruiting bodies is easy given that it is an epigeous species, with pileus diameter between 5 and 10 cm. Fruiting abundance is low (Bassani *et al.*, 2013), with 6 citations in the database (Table 1, S1). Fruiting occurs from March to May. Spores density is low, with medium viability conservation (Bassani *et al.*, 2013). Hosts are *N. antarctica*, *N. dombeyi*, *N. pumilio*. *Cortinarius* has been reported from *L. alpina* seedlings (Fernández *et al.*, 2015) and from *N. antarctica* seedlings (Salgado Salomón *et al.*, 2018a). The species is reported as edible (Toledo *et al.*, 2014; Gamundí and Horak, 1993).

***Hallingea purpurea*** : harvest of fruiting bodies is hard, given that it is an hypogeous species with fruiting diameter less than 1.5 cm, although forming nests with several bright violet fruit bodies, which are easy to observe and locate. Fruiting abundance is medium to low (Bassani *et al.*, 2013), with 8 citations in the database (Table 1, S1). Fruiting occurs from March to May. Spore density is high although with low viability conservation (Bassani *et al.*, 2013). Hosts are *N. dombeyi*, *N. pumilio* and *N. betuloides*. No records from *Nothofagaceae* seedlings have been found. Edibility*:* unknown.

## Discussion

The 45 EcM genera detected for South American *Nothofagaceae* represent 17.6% of 256 EcM genera worldwide revised by Tedersoo and Smith (2013), Rinaldi *et al.* (2008) and Tedersoo *et al.* (2010). Although our records of Ascomycetes genera correspond to 17.2% of worldwide reported genera, we have listed another 29 Ascomycetes species from 9 genera that could be EcM.

*Nothofagus dombeyi* showed the highest number of EcM species, probably because of its wide distribution (Donoso Zegers, 2006) mostly in areas with high humidity, close to lakes and river margins with temperatures favorable for fungal fruiting. Moreover, its accessibility has made it one of the most studied species, followed by *N. pumilio*, also widely distributed in Patagonian forests (Donoso Zegers, 2006).

The analyses of similarities between the EcM biota associated to each *Nothofagaceae*, with the biogeographical distribution of each tree and their associations in the territory, using the district classification, showed correspondence with trees biogeographical distributions. The highest niche overlapping occurs in the Magellanic district, where *N. pumilio* forms mixed forests with *N. betuloides*, a species restricted to this district. *Lophozonia obliqua* form a single cluster with *L. alpina*, but their niche overlapping

**Table 2** Beta diversity indices by *Nothofagaceae* species.

| First sample | Second sample | Shared species observed | Jaccard classic | Jaccard % | Sorensen classic | Morisita-Horn | Bray-Curtis |
|---|---|---|---|---|---|---|---|
| *L. alpina* | *L. glauca* | 8 | 0.105 | 10.5 | 0.19 | 0.191 | 0.159 |
| *L. alpina* | *L. macrocarpa* | 2 | 0.041 | 4.1 | 0.078 | 0.065 | 0.056 |
| *L. alpina* | *L. obliqua* | 18 | 0.196 | 19.6 | 0.327 | 0.367 | 0.305 |
| *L. alpina* | *L. x leonii* | 0 | 0 | 0 | 0 | 0 | 0 |
| *L. alpina* | *N. antarctica* | 20 | 0.118 | 11.8 | 0.211 | 0.196 | 0.164 |
| *L. alpina* | *N. betuloides* | 14 | 0.1 | 10 | 0.182 | 0.225 | 0.169 |
| *L. alpina* | *N. dombeyi* | 34 | 0.109 | 10.9 | 0.196 | 0.272 | 0.19 |
| *L. alpina* | *N. nitida* | 6 | 0.082 | 8.2 | 0.152 | 0.168 | 0.122 |
| *L. alpina* | *N. pumilio* | 23 | 0.092 | 9.2 | 0.168 | 0.193 | 0.139 |
| *L. glauca* | *L. macrocarpa* | 2 | 0.041 | 4.1 | 0.078 | 0.106 | 0.066 |
| *L. glauca* | *L. obliqua* | 16 | 0.17 | 17 | 0.291 | 0.386 | 0.286 |
| *L. glauca* | *L. x leonii* | 5 | 0.119 | 11.9 | 0.213 | 0.207 | 0.179 |
| *L. glauca* | *N. antarctica* | 16 | 0.092 | 9.2 | 0.168 | 0.22 | 0.134 |
| *L. glauca* | *N. betuloides* | 16 | 0.116 | 11.6 | 0.208 | 0.262 | 0.178 |
| *L. glauca* | *N. dombeyi* | 35 | 0.112 | 11.2 | 0.202 | 0.315 | 0.162 |
| *L. glauca* | *N. nitida* | 6 | 0.082 | 8.2 | 0.152 | 0.149 | 0.115 |
| *L. glauca* | *N. pumilio* | 21 | 0.083 | 8.3 | 0.154 | 0.232 | 0.101 |
| *L. macrocarpa* | *L. obliqua* | 4 | 0.055 | 5.5 | 0.104 | 0.114 | 0.081 |
| *L. macrocarpa* | *L. x leonii* | 0 | 0 | 0 | 0 | 0 | 0 |
| *L. macrocarpa* | *N. antarctica* | 3 | 0.019 | 1.9 | 0.038 | 0.057 | 0.035 |
| *L. macrocarpa* | *N. betuloides* | 2 | 0.017 | 1.7 | 0.033 | 0.103 | 0.035 |
| *L. macrocarpa* | *N. dombeyi* | 4 | 0.013 | 1.3 | 0.025 | 0.021 | 0.017 |
| *L. macrocarpa* | *N. nitida* | 0 | 0 | 0 | 0 | 0 | 0 |
| *L. macrocarpa* | *N. pumilio* | 3 | 0.013 | 1.3 | 0.025 | 0.039 | 0.018 |
| *L. obliqua* | *L. x leonii* | 1 | 0.014 | 1.4 | 0.027 | 0.041 | 0.021 |
| *L. obliqua* | *N. antarctica* | 29 | 0.155 | 15.5 | 0.269 | 0.241 | 0.221 |
| *L. obliqua* | *N. betuloides* | 16 | 0.098 | 9.8 | 0.178 | 0.214 | 0.167 |
| *L. obliqua* | *N. dombeyi* | 44 | 0.134 | 13.4 | 0.236 | 0.362 | 0.225 |
| *L. obliqua* | *N. nitida* | 6 | 0.061 | 6.1 | 0.114 | 0.142 | 0.113 |
| *L. obliqua* | *N. pumilio* | 29 | 0.107 | 10.7 | 0.194 | 0.226 | 0.143 |
| *L. x leonii* | *N. antarctica* | 1 | 0.007 | 0.7 | 0.013 | 0.009 | 0.009 |
| *L. x leonii* | *N. betuloides* | 1 | 0.009 | 0.9 | 0.017 | 0.012 | 0.012 |
| *L. x leonii* | *N. dombeyi* | 3 | 0.01 | 1 | 0.019 | 0.026 | 0.013 |
| *L. x leonii* | *N. nitida* | 0 | 0 | 0 | 0 | 0 | 0 |
| *L. x leonii* | *N. pumilio* | 1 | 0.004 | 0.4 | 0.008 | 0.022 | 0.004 |
| *N. antarctica* | *N. betuloides* | 51 | 0.244 | 24.4 | 0.392 | 0.428 | 0.362 |
| *N. antarctica* | *N. dombeyi* | 96 | 0.269 | 26.9 | 0.424 | 0.513 | 0.414 |
| *N. antarctica* | *N. nitida* | 8 | 0.045 | 4.5 | 0.086 | 0.143 | 0.089 |
| *N. antarctica* | *N. pumilio* | 104 | 0.378 | 37.8 | 0.549 | 0.617 | 0.493 |
| *N. betuloides* | *N. dombeyi* | 74 | 0.216 | 21.6 | 0.355 | 0.428 | 0.324 |
| *N. betuloides* | *N. nitida* | 20 | 0.155 | 15.5 | 0.268 | 0.323 | 0.259 |
| *N. betuloides* | *N. pumilio* | 101 | 0.417 | 41.7 | 0.589 | 0.564 | 0.452 |
| *N. dombeyi* | *N. nitida* | 18 | 0.056 | 5.6 | 0.105 | 0.151 | 0.095 |
| *N. dombeyi* | *N. pumilio* | 134 | 0.333 | 33.3 | 0.5 | 0.598 | 0.491 |
| *N. nitida* | *N. pumilio* | 14 | 0.055 | 5.5 | 0.104 | 0.138 | 0.085 |

was low. The fact that *L. obliqua* is distributed in 3 districts, growing together with *L. alpina* only in the Valdivian district, could explain why the former has more citations and exclusive EcM species, determining their differences in diversity. *Lophozonia* and *Fuscospora* species restricted to the Maulino district appear clustered together along with *N. nitida*. This fact suggests that the observed EcM community similarity is associated more with the biogeographical distribution of the tree than with *Nothofagaceae* speciation. On the other hand, 42.4% of the total EcM compiled are exclusive to one tree species, with 78.3% associated to the most studied *N. dombeyi* and *N. pumilio*. This evidence suggests that more surveys are needed for the other *Nothofagaceae* and also that most of the species reported in this review need combined population genetics analyses and wide-ranging studies of phylogeography, as the increased reproductive isolation with longer distances can lead to lineage divergence, or even hide cryptic speciation (Vincenot and Selosse, 2017).

It is currently accepted that dispersal limitation, host dependency and specificity, plant-soil feedback, and effects of EcM common mycelium networks could drive EcM fungal succession (Dickie *et al*., 2013; Teste and Dickie, 2017). The shift in EcM community associated with growth stages for South American *Nothofagaceae* forests has not yet been elucidated, nor the effects of site conditions or anthropogenic impacts. It has been reported that seedlings could present a reduced diversity of EcM communities compared to mature stands (Ważny and Kowalski, 2017), that some EcM species can be present at any stage of ecosystem development (Matsuda and Hijii, 2004; Twieg *et al*., 2007), while others has high association with seedling stages (Cline *et al*., 2005; Ważny and Kowalski, 2017). All these considerations should be taken in account to select candidate species for inoculation programs. We reviewed a group of species proposed as spore inoculum from a practical perspective, underlining that they are easy to apply, do not require expensive infrastructure nor qualified personnel for their production, are very abundant, low volume, easy to handle and tolerate long storage periods (Rincón *et al*., 2007; Bassani *et al*., 2013). Moreover, given the importance of edible fruiting bodies as a highly profitable non-timber forest product for Patagonian native forests, profuse fruiting is a desirable characteristic to prioritize edible mycorrhizal species. We consider spore inoculation is the most realistic option for local nurseries that probably cannot afford the cost of mycelium production or purchase. Nonetheless, EcM taxa other than those proposed here have been reported from nurseries and naturally established *Nothofagaceae* seedlings as *Descolea* (Palfner *et al*., 2008; Valenzuela Flores *et al*., 2008; Álvarez *et al*., 2009; Fernández *et al*., 2015; Salgado Salomón *et al*., 2018a), *Hebeloma* (Fernández *et al*., 2015; Salgado Salomón *et al*., 2018a), *Sebacina*, *Inocybe*, *Laccaria*, *Genea* (Fernández *et al*., 2015; Marín *et al*., 2018), *Tomentella* (Kuhar *et al*., 2016; Fernández *et al*., 2013, 2015; Salgado Salomón *et al*., 2017, 2018a), Clavulinaceae (Fernández *et al*., 2015), Thelephorales (Fernández *et al*., 2015), Pyrenomataceae (Fernández *et al*., 2013; Salgado Salomón *et al*., 2018a). To broaden the perspective of EcM species best suited to inoculate nursery plants, especially for those with low fruiting frecuency, small spores production or corticioid habit, mycelium inoculum production, mycorrhizal infection and field performance tests will be required. Furthermore, vegetative inoculum has been reported as more convenient for certain species (Kuek, 1994; Brundrett *et al*., 2005). Other edible EcM species not suitable for spores inoculation, such as those from the *Cortinarius magellanicus* complex and *Ramaria patagonica* (Toledo *et al*., 2014; Barroetaveña and Toledo, 2016; Salgado Salomón *et al*., 2018b) could be tested with this technology.

Subsequent to the important work reported by Moser and Horak (1975; 278 taxa) from Patagonia, comparatively few species have been described from Australia and New Zealand *Nothofagaceae* species (Gasparini and Soop, 2008). Only 61 species (including the genus *Dermocybe*) were reported in Fungi of Australia (May and Wood, 1997), with at least 16 taxa doubtfully determined (Gasparini and Soop, 2008). According to Segedin and Pennycook (2001), 98 species have been reported from New Zealand (including the genera *Dermocybe*, *Cuphocybe*, *Rapacea*, *Rozites* and *Thaxterogaster*, now considered as *Cortinarius)* (McKenzie *et al*., 2000). Since these checklists were available, 32 *Cortinarius* taxa have been published from Australia (Gasparini, 2001, 2004, 2007) and 98 from New Zealand (Soop, 2001, 2002, 2003, 2005, 2013, 2014, 2016; soop *et al*., 2018), and many more EcM taxa are likely to be found in unexplored ecosystems from southern temperate forest (Tedersoo and Smith, 2013). Shared species with New Zealand *Nothofagaceae* forests includes *Cenococcum geophilum*, *Cortinarius melleomitis* and *Laccaria tetraspora* (McKenzie *et al*., 2000), while *Laccaria laccata*, *Cenococcum geophilum*, *Cortinarius teraturgus* and *C. amoenus* are shared with Australian *Nothofagaceae* forests (Tedersoo *et al*., 2009, Horton *et al*., 2017).

The dominant and rich genus *Cortinarius* associated with *Nothofagaceae* species included in this review, is a large and complex genus within the Agaricales, with synonymized genera present in Patagonia previously classified as *Thaxterogaster*, *Rozites* and *Dermocybe* (Peintner *et al*., 2001, 2002). It is the most diverse EcM genus of *Nothofagaceae* forests in all its distribution (Moser and Horak, 1975; Garrido, 1986; Dickie *et al*., 2009; Nouhra *et al*., 2013). Horton *et al*. (2017) have proposed that Cortinariaceae dominate temperate *Eucalyptus* forests irrespective of forest type, and that the lack of host specificity may partly account for their diversity and abundance, which seems similar to what happens in *Nothofagaceae* forests in Patagonia, with a high number of shared species. On the other hand, recent studies show that *C. magellanicus*, previously reported as widely distributed and shared between *Nothofagaceae* in the Southern Hemisphere (Horak, 1967; Moser and Horak, 1975; Horak and Wood, 1990; Palfner, 2001; Segedin and Pennycook, 2001; Garnica *et al*., 2003; Toledo *et al*., 2014), is a complex of species composed of at least four phylogenetic lineages, each with strong regionalism and distinct host associations (Salgado Salomón *et al*., 2018b). Vouchers morphologically identified as *C. magellanicus* from N. Zealand are now *C. vitreopileatus* var. *similissimus* Peintner & Horak (Salgado Salomón *et al*., 2018b) questioning the specific taxonomy of others *Cortinarius* species reported as Gondwanically distributed. The fact that BLAST searches of South America *Cortinarius* sequences from type material in UNITE and NCBI do not give any results with similarities higher than 95% for most of them (Frøslev *et al*., 2007; Nouhra *et al*., 2013), highlights again a huge gap concerning South American reference data.

Corticioid fungi commonly produce their flat, sheet-like fruiting bodies on the underside of dead wood, twigs and similar plant litter on the forest floor. The mycorrhizal nature of a few of those hundred corticioid species in the Northern Hemisphere has been known for a long time, but in most cases the mycorrhizal evidence was discovered in the late 1900s. Confirmed ectomycorrhizal genera include *Amphinema*, *Byssocorticium*, *Byssoporia*, *Piloderma*, *Pseudotomentella*, *Tomentella*, *Tylospora* (Tedersoo and Smith, 2013). Corticioid genera suspected to contain ectomycorrhizal species are *Sistotrema,* and *Trechispora* (Erland and Taylor, 1999, Rinaldi *et al*., 2008; Tedersoo *et al*., 2010; Tedersoo and Smith, 2013). In boreal forests, *Tomentella sublilacina* (Ellis & Holw.) Wakef., *Amphinema byssoides* complex and *Tylospora fibrillosa* Donk. are promiscuous species among the most abundant members of EcM fungal communities (Iwanski and Rudawska, 2007; Tedersoo *et al.*, 2008). In Australia, *Tomentella-Thelephora* (Thelephorales) prevailed on isolated seedlings of *Lophozonia cunninghamii* (Hook.f.) Heenan & Smissen. Studies in Patagonia (Argentina) also showed that the/*tomentella -thelephora* (5 spp.), /*tullasnella* (2 spp.) and/*sebacina* (3 spp.) lineages were present in the fungal community of *Nothofagus dombeyi*, *L. obliqua* and *L. alpina* forests (Fernández *et al.*, 2013, 2015; Kuhar *et al.*, 2016; Nouhra *et al.*, 2013, Salgado Salomón *et al.*, 2018a).

Numerous unpublished sequences from *Nothofagacaeae* environmental samples have been uploaded to UNITE, belonging to EcM lineages as/*cortinarius* (103), /*inocybe* (66 seq.), /pyronemataceae (49 seq., including the/*pulvinula*, /*Ootidea*, /*tarzetta*, /*genea-humaria*, and/*wilcoxina* lineages), /*tomentella-thelephora* (46 seq.), /*tullasnella* (19 seq,), /*tuber-helvella* (19 seq.), /*descolea* (17 seq.), /*pachyphloeus-amylascus* (14 seq.), /*terfezia-peziza depressa* (14 seq in UNITE)/*clavulina* (10 seq in UNITE), /*sebacina* (7 seq in UNITE), /*tremellodendropsis* (6 seq.), /*hebeloma-alnicola* (6 seq.), /*tricholoma* (5 seq.) and/*hysterangium* (2 seq.), although identified at genus or family level. The genus *Tremellodendropsis* has been reported by Truong *et al.* (2017a) for *N. dombeyi* roots with low similarity and therefore deserves further analysis. Also, several species groups of the Pezizales could not be matched with any of the known ectomycorrhizal or non-mycorrhizal taxa (Tedersoo *et al.*, 2010, 2013).

Considering the gaps in South American reference data about EcM diversity, it is necessary to move forward incorporating sequences from type materials or from accurately determined vouchers to confirm the richness of fungal species in mutualism. Future research combining phylogenetic analysis based on wide ecological surveys would allow revising the real diversity, host specificity and community structure of the EcM biota associated to *Nothofagaceae* forests in South America.

## Supplementary data

Supplementary data are available at *Forestry* online.

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## Conflict of interest statement

None declared.

## References

Águeda-Hernández, B. 2014 *Boletus edulis and Cistus ladanifer: characterization of its ectomycorrhizae, in vitro synthesis, and realized niche*. Ph.D. thesis, Universidad de Murcia.

Agüero, M.L., Puntieri, J., Mazzarino, M.J., Grosfeld, J. and Barroetaveña, C. 2014. Seedling response of *Nothofagus* species to N and P: linking plant architecture to N/P ratio and resorption proficiency. *Trees* **28(**4**)**, 1185–1195.

Álvarez, M., Huygens, D., Fernández, C., Gacitúa, Y., Olivares, E., Saavedra, I. *et al.* 2009 Effect of ectomycorrhizal colonization and drought on reactive oxygen species metabolism of *Nothofagus dombeyi* roots. *Tree Physiol.* **29**, 1047–1057.

Bassani, V.N. 2010 *Conservación y actividad de esporas de hongos ectomicorrícicos seleccionados para inocular lenga y coníferas exóticas*. Universidad Nacional de la Patagonia, Argentina, Undergraduate final seminar.

Bassani, V.N., Barroetaveña, C. and Rajchenberg, M. 2013. Spores of ectomycorrhizal fungi as inoculants for *Nothofagus pumilio* and exotic conifer seedlings in Patagonia, Argentina: their activity and conservation. *New For.* **44**, 471–485.

Barroetaveña, C. 2004 *Estudio de las Ectomicorrizas de plantines y plantaciones de pino ponderosa (Pinus ponderosa Doug. ex Laws.) y pino oregón (Pseudotsuga menziesii (Mirb.) Blanco) en la región Andino Patagónica*. Ph.D. thesis. Universidad Nacional del Comahue.

Barroetaveña, C., Schinelli, C., Bassani, V.N., Tejera, L. and Gallo, L. 2009 Inoculación ectomicorrícica de *Nothofagus* spp. Proyecto Domesticación de especies Forestales Nativas, INTA. Technical report. 19p. Available at: https://inta.gob.ar/portada-documentos/articulos-e-informes

Barroetaveña, C. and Toledo, C.V. 2016. Hongos silvestres comestibles Novedosos en el Bosque Nativo y en las Plantaciones de Patagonia Andina, Argentina. *Cienc. Invest. For.* **22 (**3**)**, 73–88. ISSN: 0716-5994.

Bonito, G., Smith, M.E., Nowak, M., Healy, R.A., Guevara, G., Cázares, E., *et al.* 2013. Historical biogeography and diversification of truffles in the Tuberaceae and their newly identified southern hemisphere sister lineage. *PLoS One* **8(**1**)**, e52765. doi: 10.1371/journal.pone.0052765

Brundrett, M., Malajczuk, N., Mingqin, G., Daping, X., Snelling, S. and Dell, B. 2005 Nursery inoculation of *Eucalyptus* seedlings in Western Australia and southern China using spores and mycelial inoculum of diverse ectomycorrhizal fungi from different climatic regions. *For. Ecol. Manag.* **209**, 193–205.

Cabrera, A. 1976 *Regiones Fitogeográficas Argentinas. Enciclopedia Argentina de Agricultura y Jardinería*. Vol. **1**. A.C.M.E. SACI, Buenos Aires.

Cabrera, A.L. and Willink, A. 1980 *Biogeografía de América Latina. Serie de Biología, Monografía 13*. The General Secretariat of the Organization of American States, Washington, DC, 122p.

Carrillo, R., Godoy, R. and Peredo, H. 1992 Simbiosis micorrícica en comunidades boscosas del Valle Central en el sur de Chile. *Bosque* **13(**2**)**, 57–267.

Castellano, M. and Muchojev, J. 1996 Truffle-like from South America: *Hysterangium* sensu lato. *Mycotaxon* **57**, 329–345.

Cline, E.T., Ammirati, J.F. and Edmonds, R.L. 2005 Does proximity to mature trees influence ectomycorrhizal fungus communities of Douglas-fir seedlings? *New Phytol.* **166**, 993–1009.

Colwell, R.K. 2013 *Estimates: Statistical Estimation of Species Richness and Shared Species from Samples*. Version 9 and earlier. User's Guide and application. Available at: http://purl.oclc.org/estimates

Corner, E.J.H. 1957. Some *Clavarias* from Argentina. *Darwin* **11(**2**)**, 193–206.

Di Rienzo, J.A., Casanoves, F., Balzarini, M.G., Gonzalez, L., Tablada, M. and Robledo, C.W. 2017 *InfoStat Versión 2017*. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina. URL: http://www.infostat.com.ar.

Dickie, I.A., Martínez-García, L.B., Koele, N., Grelet, G.-A., Tylianakis, J.M., Peltzer, D.A. *et al.* 2013 Mycorrhizas and mycorrhizal fungal communities throughout ecosystem development. *Plant Soil* **367**, 11–39.

Dickie, I.A., Richardson, S.J. and Wiser, S.K. 2009 Ectomycorrhizal fungal communities and soil chemistry in harvested and unharvested temperate *Nothofagus* rainforests. *Can. J. For. Res.* **39**, 1069–1079.

Diehl, P., Mazzarino, M.J., Funes, F., Fontenla, S., Gobbi, M. and Ferrari, J. 2003 Nutrient conservation strategies in native Andean-Patagonian forests. *J. Veg. Sci.* **14**, 63–70.

Diehl, P., Mazzarino, M.J. and Fontenla, S. 2008 Plant limiting nutrients in Andean–Patagonian woody species: effects of interannual rainfall variation, soil fertility and mycorrhizal infection. *For. Ecol. Manag.* **255**, 2973–2980.

Dimitri, M.J. and Orfila, E.N. 1985 *Tratado de morfología y sistemática vegetal*. Acme S.A.C.I, Buenos Aires. 489 p.

Donoso Zegers, C. 2006 *Las especies arbóreas de los bosques templados de Chile y Argentina, Autoecología*. Marisa Cuneo Ediciones Valdivia, Chile, 678 p.

Erland, S. and Taylor, A.F.S. 1999 Resupinate ectomycorrhizal fungal genera. In *Ectomycorrhizal Fungi: Key Genera in Profile*. J.W.G., Cairney, S.M., Chambers (eds.). Springer-Verlag, Berlin, Germany. pp. 347–363.

Frøslev, T.G., Jeppesen, T.S., Lassoe, T. and Kjoller, R. 2007 Molecular phylogenetics and delimitation of species in *Cortinarius* section *Calochroi* (Basdiomycota, Agaricales) in Europe. *Mol. Phylogenet. Evol.* **44**, 217–277.

Fernández, N.V., Marchelli, P. and Fontenla, S.B. 2013 Ectomycorrhizas naturally established in *Nothofagus nervosa* seedlings under different cultivation practices in a forest nursery. *Microb. Ecol.* **66**, 581–592.

Fernández, N.V., Marchelli, P., Gherghel, F., Kost, G. and Fontenla, S.B. 2015 Ectomycorrhizal fungal communities in *Nothofagus nervosa* (Raulí): a comparison between domesticated and naturally tablished specimens in a native forest of Patagonia, Argentina. *Fun. Ecol.* **18**, 36–47.

Fontenla, S., Godoy, R., Rosso, P. and Havrylenko, M. 1998 Root associations in *Austrocedrus* forests and seasonal dynamics of arbuscular mycorrhizas. *Mycorrhiza* **8**, 29–33.

Gamundí, I. 1962a. Discomycetes inoperculados del Parque Nacional Nacional Huapi (Argentina). *Darwiniana* **12(**3**)**,385–445.

Gamundí, I. 1962b. Discomycetes operculados del Parque Nacional Nacional Huapi (Argentina). *Darwiniana* **13(**2–4**)**, 568–606.

Gamundí, I. 1971. Discomycetes de Chile. *Bol. Soc. Ar. Bot.* **13(**4**)**, 260–289.

Gamundi, I. 1975. Flora criptogamica de Tierra de Fuego. Pezizales. In S. A., Guarrera, I., Gamundí, C. M., Matteri (eds.), Flora Criptogámica de Tierra Fuego, **10(**3**)**, 1–187. Fundación para la Educación, la Ciencia y la Cultura, Buenos Aires.

Gamundí, I. and Giaiotti, A.L. 1998 Nota sobre los discomycetes AndinoPatagónicos II. Novedades Taxonómicas. *Darwiniana* **35**, 49–60.

Gamundí, I. and Horak, E. 1993 *Hongos de los bosques Andino-Patagonicos*. Vazquez Mazzini Editores, Buenos Aires.

Gamundí, I., Minter, D.W., Romero, A.I., Barrera, V.A., Giaiotti, A.L., Messuti, M.I. *et al.* 2004. Catálogo de los Discomycetes (fungi) de Patagonia, Tierra del Fuego y áreas antárticas adjacentes. *Darwiniana* **42**(1–4), 63–164.

Garnica, S., Weiß, M. and Oberwinkler, F. 2002. New *Cortinarius* species from *Nothofagus* forests in South Chile. *Mycologia,* **94(**1**)**, 136–145.

Garnica, S., Weiß, M., and Oberwinkler, F. 2003. Morphological and molecular phylogenetic studies in south American *Cortinarius* species. *Mycol. Res.* **107 (**10**),** 1143–1156.

Garrido, N.N. 1986 Survey of ectomycorrhizal fungi associated with exotic forest trees in Chile. *Nova. Hedw.* **43**, 423–442.

Garrido, N.N. 1988 Agaricales s. l. und ihre Mykorrhizen in den *Nothofagus*-Waldern Mittelchiles. *Bibl. Mycol.* **120**, 1–528.

Garrido, N.N. and Bresinsky, A. 1985 *Amanita merxmuelleri* (Agaricales), eine neue art aus *Nothofagus*-Wäldern Chiles. *Bot. Jahrb. Syst.* **107**, 521–540.

Gasparini, B. 2001 A contribution to the knowledge of *Cortinarius* and allied genera of southern Tasmania, Australia; *Cortinarius* subgenus *Cortinarius*. *Australas. Mycol.* **20**, 41–54.

Gasparini, B. 2004 *Cortinarius* subgenus *Orellani* in Australia and in the world. *Australas. Mycol.* **23**, 62–76.

Gasparini, B. 2007 Genus *Cortinarius*, subgenus *Phlegmacium* in Tasmania. *N. Z. J. Bot.* **45**, 155–236.

Gasparini, B. and Soop, K. 2008 Contribution to the knowledge of *Cortinarius* [Agaricales, Cortinariaceae] of Tasmania (Australia) and New Zealand. *Austral. Mycol.* **27**, 173–203.

Greslebin, A. 2002. Fungi, Basidiomycota, Aphyllophorales: Coniophoraceae, Corticiaceae, Gomphaceae, Hymenochaetaceae, Lachnocladiaceae, Stereaceae, Thelephoraceae. Tulasnellales: Tulasnellaceae. In S. A., Guarrera, I., Gamundí, C. M., Matteri (eds.), Flora Criptogámica de Tierra Fuego, 11: 1–212. Fundación para la Educación, la Ciencia y la Cultura, Buenos Aires.

Godoy, R. and Palfner, G. 1997 Ectomicorrizas en *Nothofagus alpina* (P. et E.) Oerst y *N. dombeyi* (Mirb.) Oerst. del Sur de Chile. *Bol. Micol.* **12**, 55–61.

Heenan, P.B., Smissen, R.D. 2013. Revised circumscription of *Nothofagus* and recognition of the segregate genera *Fuscospora*, *Lophozonia*, and *Trisyngyne* (*Nothofagaceae*). *Phytotaxa* **146 (**1**)**, 1–31.

Horak, E. 1964a Fungi Austroamericani. 1. *Tricholoma* (Fr) Quelet. *Sydowia* **17**, 153–167.

Horak, E. 1964b Fungi Austroamericani. 5. Beitrag zur Kenntnis der Gattungen Hysterangiun Vitt., Hymenogaster Vitt., Hydnangium Wallr. Und melanogaster Cda. In Sudamerika (Argentinien, Uruguay). *Sydowia* **17**, 197–205.

Horak, E. 1964c Fungi Austroamericani. 6. Beitrag zur Kenntnis der Gattungen *Martellia* Matt., *Elasmomyces* Cav., und *Cystangium* sing. Y. *Sydowia* **17**, 206–213.

Horak, E. 1964d Fungi Austroamericani 7. *Hypogaea* gen. Nov. Aus dem *Nothofagus*-wald der patagonichen Anden. *Sydowia* **17**, 297–301.

Horak, E. 1967 Fungi Austroamericani IV. Revisión de los hongos superiores de Tierra del Fuego o Patagonia en el Herbario de C. Spegazzini en La Plata. *Darwiniana* **14**, 355–385.

Horak, E. 1971. Studies on the genus *Descolea* sing. *Persoonia* **6(**2**)**, 231–248.

Horak, E. 1977 New and rares *Boletus* from Chile. *Bol. Soc. Argent. Bot.* **18**, 97–109.

Horak, E. 1979. Fungi, Basidiomycetes. Agaricales y Gasteromicetes secotioides. In S. A., Guarrera, I., Gamundí, C. M., Matteri (eds.), Flora Criptogámica de Tierra Fuego, **11(**6**)**, 1–524. Fundación para la Educación, la Ciencia y la Cultura, Buenos Aires.

Horak, E. 1980. *Inocybe* (Agaricales) in Indomalaya and Australasia. *Persoonia* **11(**1**)**, 1–37.

Horak, E. 1981 Notes and taxonomy and biogeography of *Rozites* Karsten. *Sydowia* **24**, 94–108.

Horak, E. 1983 Mycogeography in the South Pacific region: Agaricales, Boletales. *Austral. J. Bot. Suppl.* **10**, 1–41.

Horak, E. and Wood, A.E. 1990 *Cortinarius* Fr. (Agaricales) in Australasia. 1. Subgen. *Myxacium* and subgenus *Paramyxacium*. *Sydowia* **42**, 88–168.

Horak, E. and Moser, M. 1965 Fungi austroamericani. 12. Studien zur Gattung *Thaxterogaster* Singer. *Nova Hed* **10**, 211–242.

Horak, E. and Moser, M. 1966 Fungi austroamericani. 8. Uberneue Gastroboletaceae aus Patagonien: *Singeromyces* Moser, *Pasillogaster* Horak und *Gymnopaxillus* Horak. *Nova Hed* **10**, 329–338.

Horton, B.M., Glen, M., Davidson, N.J., Ratkowsky, D.A., Close, D.C., Wardlaw, T.J. *et al.* 2017. An assessment of ectomycorrhizal fungal communities in Tasmanian temperate high-altitude *Eucalyptus delegatensis* forest reveals a dominance of the Cortinariaceae. *Mycorrhiza* **27(**1**)**, 67–74.

Iwanski, M. and Rudawska M, 2007. Ectomycorrhizal colonization of naturally regenerating *Pinus sylvestris* L. seedlings growing in different microhabitats in boreal forest. *Mycorrhiza* **17**, 461–467.

Jackson, L. and Driver, C. 1969 Morphology of mycorrhizae on deciduous forests tree species. *Castanea (Morgantown)* **34**, 230–235.

Kõljalg, U., Nilsson, R.H., Abarenkov, K., Tedersoo, L., Taylor, A.F.S., Bahram, M. *et al*. 2013. Towards a unified paradigm for sequence-based identification of fungi. *Mol. Ecol.* **22**, 5271–5277.

Kuek, C. 1994 Issues concerning the production and use of inocula of ectomycorrhizal fungi in increasing the economic productivity of plantations. In *Management of Mycorrhizas in Agriculture, Horticulture and Forestry*. A.D., Robson, L.K., Abbott, N., Malajczuk (eds.). Kluwer, The Netherlands, pp. 221–230.

Kuhar, F., Barroetaveña, C. and Rajchenberg, M. 2016. New species of *Tomentella* (Thelephorales) from the Patagonian Andes forests. *Mycologia* **108(**4**)**, 780–790.

Kuhar, F., Smith, M.E., Mujic, A., Truong, C. and Nouhra, E. 2017. A systematic overview of *Descolea* (*Agaricales*) in the *Nothofagaceae* forests of Patagonia, *Fungal Biol.* **12(**10**)**, 876–889.

Longo, M.S., Urcelay, C. and Nouhra, E. 2011 Long term effects of fire on ectomycorrhizas and soil properties in *Nothofagus pumilio* forests in Argentina. *For. Ecol. Manag.* **262**, 348–354.

Lorenzo, L.E. and Messuti, M.I. 2013. *Leotia lubrica* (Ascomycota, Leotiaceae) hallada en la Patagonia, Argentina. *Darwiniana* **1(**2**)**, 237–240.

Marín, C., Valenzuela, E., Godoy, R. and Palfner, G. 2018. Diversity and growth-effects of ectomycorrhizal fungi of a *Nothofagus pumilio* forest in the Andes of southern Chile. *Bol. Micol.* **33(**1**)**, 9–20

Matsuda, Y. and Hijii, N. 2004 Ectomycorrhizal fungal communities in an *Abies firma* forest, with special reference to ectomycorrhizal associations between seedlings and mature trees. *Can. J. Bot.* **82**, 822–829.

May, T.W. and Wood, A.E. 1997 Basidiomycota. *Fungi Aust.* **2**, 49–55.

McKenzie, E.H.C., Buchanan, P.K. and Johnston, P.R. 2000. Checklist of fungi on *Nothofagus* species in New Zealand. *N. Z. J. Bot.* **38(**4**)**, 635–720.

Mikola, P. 1970 Mycorrhizal inoculation in afforestation. *Intern. Rev. Forestry Research* **3**, 123–196.

Moser, M. and Horak, E. 1975 *Cortinarius* Fr. Und nahe verwandte Gattungen in Sçudamerika. Beih. *Nova Hedw.* **52**, 1–628.

Nouhra, E.R., Hernandez Caffot, M.L., Pastor, N. and Crespo, E.M. 2012a. The species of Scleroderma from Argentina, including a new species from the *Nothofagus* forest. *Mycologia* **104(**2**)**, 488–495.

Nouhra, E.R., Urcelay, C., Longo, M.S., Fontenla, S. 2012b. Differential hypogeous sporocarp production from *Nothofagus dombeyi* and *N. pumilio* forests in southern Argentina. *Mycologia* **104(**1**)**, 45–52.

Nouhra, E., Urcelay, C., Longo, S. and Tedersoo, L. 2013. Ectomycorrhizal fungal communities associated to *Nothofagus* species in northern Patagonia. *Mycorrhiza* **23(**6**)**, 487–496.

Peintner, U., Moser, M. and Vilgalys, R. 2001 *Thaxterogaster* is a synonym of *Cortinarius*: new combinations and new names. *Mycotaxon* **81**, 177–184.

Peintner, U., Horak, E., Moser, M. and Vilgalys, R. 2002 *Rozites*, *Cuphocybe* and *Rapacea* are taxonomic synonyms of *Cortinarius*: new combinations and new names. *Mycotaxon* **83**, 447–451.

Palfner, G. 1996 *Thaxterogaster albocanus* Moser and *Nothofagus* & Moser and *Nothofagus pumilio* (Poepp. Et Endl.) Krasser. *Descr. Ectomycorrhizae* **1**, 155–160.

Palfner, G. 1997 *Descolea antarctica* Singer and *Nothofagus alpina* (Poepp. et Endl.) Oerst. *Descr Ectomycorrhizae* **2**, 7–12.

Palfner, G. 2002a *Austropaxillus boletinoides*. In *Colour Atlas of Ectomycorrhizae*. R., Agerer (ed.). Einhorn Verlag, Schwäbisch Gmünd, plate 151.

Palfner, G. 2001 Taxonomische Studien an Ektomykorrhizen aus den *Nothofagus*-Wäldern Mittelsüdchiles (Estudios taxonómicos sobre ectomicorrizas de los bosques de *Nothofagus* del Centro Sur de Chile). *Bibl. Mycol.* **190**, 1–243.

Palfner, G. 2002b *Cortinarius austrosalor*. In *Colour Atlas of Ectomycorrhizae*. R., Agerer (ed.). Einhorn Verlag, Schwäbisch Gmünd, plate 152.

Palfner, G., Canseco, M.I. and Casanova-Katny, M.A. 2008 Post-fire seedlings of *Nothofagus alpina* in southern Chile show strong dominance of a single ectomycorrhizal fungus and a vertical shift in root architecture. *Plant Soil* **313**, 237–250.

Palfner, G. and Godoy, R. 1996 *Russula fuegiana* and *Nothofagus pumilo* (Poepp. Et Endl.) Krasser. *Descr Ectomycorrhizae* **1**, 131–136.

Palfner, G., Horak, E. 2000. *Gautieria inapire* sp. nov., a new hypogeous species from *Nothofagus* forest in southern Central Chile. *Sydowia*. **5(**1**)**, 140–151.

Perakis, S.S. and Hedin, L.O. 2002. Nitrogen loss from unpolluted south American forests mainly via dissolved organic compounds. *Nature* **415(**24**)**, 416–419.

Poitou, N., Mamoun, M. and Delmas, J. 1982 Quelques résultats obtenus, concernant la mycorhization de plantes-hôtes par les champignons mycorhiziens comestibles. In *Les mycorhizes, partie intégrante de la plante: Biologie et perspectives d'utilization*. S., Gianinazzi, V., Gianinazzi-Pearson, A., Trouvelot (eds.). Les Colloques de l'INRA, pp. 295–301.

Raithelhuber, J. 1950 Les Russules de l'Argentine. *Rev. Mycol. (Paris)* **15**, 125–137.

Raithelhuber, J. 1972a. Lateinische Kurzdiagnose der auf der Dreiländertagung in Neubulach vorgestellten Pilzarten aus Argentinien. *Metrodiana* **3(**1**)**, 27–29.

Raithelhuber, J. 1972b. Neue oder wenig bekannte Tricholomataceae Argentiniens. *Metrodiana* **4(**1**)**, 1–28.

Raithelhuber, J. 1974 Lateinische Diagnosen bisher unveröffentlichter Pilzarten. *Metrodiana* **5**, 71–73.

Rinaldi, A.C., Comadini, O. and Kuyper, T.W. 2008 Ectomycorrhizal fungal diversity: separating the wheat from the chaff. *Fungal Divers.* **33**, 1–45.

Rincón, A., de Felipe, M. and Fernández-Pascual, M. 2007 Inoculation of *Pinus halepensis* mill. With selected ectomycorrhizal fungi improves seedling establishment 2 years after planting in a degraded gypsum soil. *Mycorrhiza* **18**, 23–32.

Salazar Vidal, V.E. 2016 *Amanita diemii* Singer y *Amanita merxmelleri* Bresinsky & Garrido (Agaricales, Basidiomycota), las amanitas comestibles de Chile. *Bol. Micol.* **31(**1**)**, 28–35

Salazar Vidal, V.E. and Palfner, G. 2014 Catálogo preliminar de macrohongos asociados a bosque de *Nothofagus* en la Reserva Nacional Los Ruiles, VII Región. In *IX Congreso Nacional de la Asociación de Estudiantes de Biología de Chile (AEBCH)*. Facultad de Recursos Naturales, Universidad Católica de Temuco, Chile.

Salgado Salomón, M.E., Barroetaveña, C., Pildain, M.B., Kuhar, F. and Rajchenberg, M. 2017. *Tomentella* (Thelephorales, Basidiomycota) en bosques de *Nothofagaceae* de Patagonia, Argentina: micorrizas de nuevas especies, *Bol. Soc. Argent. Bot.* **52(**3**)**, 423–434.

Salgado Salomón, M.E., Barroetaveña, C., Pildain, M.B., William, E.A. and Rajchenberg, M. 2018a What happens to the mycorrhizal communities of native and exotic seedlings when *Pseudotsuga menziesii* invades *Nothofagaceae* forests in Patagonia, Argentina? *Acta Oecol.* **91**, 108–119.

Salgado Salomón, M.E., Dresch, P., Horak, E., Galleguillos, F., Barroetaveña, C. and Peintner, U. 2018b. The enigmatic *Cortinarius magellanicus* complex occurring in *Nothofagaceae* forests of the southern hemisphere. *Fungal Biol.*. **22(**11**)**, 1077–1097.

San-Fabian, B., Niskanen, T., Liimatainen, K., Kooij, P.W., Mujic, A.B., Truong, C. *et al*. 2018. New species of *Cortinarius* sect. *Austroamericani*, sect. Nov., from south American *Nothofagaceae* forests. *Mycologia* **11(**6**)**, 1127–1144.

Sánchez-García, M., Matheny, P.B., Palfner, G. and Lodge, D.J. 2014. Deconstructing the Tricholomataceae (Agaricales) and introduction of the new genera *Albomagister*, *Corneriella*, Pogonoloma and Pseudotricholoma, *Taxon* **63(**5**)**, 993–1007.

Satti, P., Mazzarino, M.J., Roselli, L. and Crego, P. 2007 Factors affecting soil P dynamics in temperate volcanic soils of southern Argentina. *Geoderma* **139**, 229–240.

Schoch C.L., Robbertse, B., Robert, V., *et al*. 2014. Finding needles in haystacks: linking scientific names, reference specimens and molecular data for fungi. *Database* **2014**, bau061.

Segedin, B. and Pennycook, S. 2001 A nomenclatural checklist of agarics, boletes, and related secotioid and gasteromycetous fungi recorded from New Zealand. *N. Z. J. Bot.* **39**, 285–348.

Singer, R. 1950 *Descolea antarctica*, género y especies nuevas de Tierra del Fuego. *Lilloa* **23**, 255–258.

Singer, R. 1951a *Thaxterogaster*. A new link between Gasteromycetes and Agaricales. *Mycologia* **43**, 215–228.

Singer, R. 1951b The Agaricales (mushroom) in modern taxonomy. *Lilloa* **22**, 1–832.

Singer, R. 1952 The agaric of the argentine sector of Tierra del Fuego and limitrophous regions of the Magallanes area. Part I: white and pink species groups. *Sydowia* **6**, 165–226.

Singer, R. 1953 The agarics of the argentine sector of Tierra del Fuego and limitrophous regions of the Magallanes area. Part 2. The brown-spored genera (except *Cortinarius*). *Sydowia* **7**, 206–265.

Singer, R. 1954 Agaricales von Nahuel Huapi. *Sydowia* **8**, 100–157.

Singer, R. 1960. Three new species of Secotiaceae from Patagonia. *Persoonia* **1(**3**)**, 385–391.

Singer, R. 1962. Monograph of south American Basidiomycetes, especially those of the east slope of the Andes and Brazil. V. Gastromycetes with agaricoid affinities (secotiaceous Hymenogastrineae and related forms). *Bol. Soc. Argent. Bot.* **10(**1**)**, 52–67.

Singer, R. 1963. Ektrotrph, seine Definiton, geographische Verbreitung, Bedeutung in der Forstökologie-Mykorrhiza. *Intern. Mycorrhiza Symposium, Weimar* **1960**, 223–231.

Singer, R. 1964 Boletes and related groups in South America. *Nova Hedw* **7**, 93–132.

Singer, R. 1966. Monograph of south American Basidiomycetes, specieally those on the east slope of the Andes and Brazil. IX Tricholoma in Brazil and Argentina. *Darwiniana* **14(**1**)**, 19–35.

Singer, R. 1967. Notes Sur le genre Laccaria. *Bull. Soc. Mycol. France* **83(**1**)**, 104–123.

Singer, R. 1968 Nuevos hongos descubiertos en Chile. *Biologica (Santiago)* **49**, 69–71.

Singer, R. 1969 Mycoflora Australis. *Beih. Nova Hedwigia* **29**, 1–406.

Singer, R. 1971a Forest mycology and forest communities in South America II: Mycorrhiza sociology and fungus succession in the *Nothofagus dombeyi-Austrocedrus chilensis* woods of Patagonia. In *Mycorrhizae*. R., Hacskaylo (ed.). Vol. **1189**. USDA Forest Serv., Misc. Publ, pp. 204–215.

Singer, R. 1971b. A revision of the genus *Melanomphalia* as a basis of the phylogeny of the Crepidoteceae. In Peterson R (ed). *Evolution in the Higher Basidiomycetes An International Symposium*. Univ. Tennessee Press. Knoxville. pp. 441–480.

Singer, R.. 1973. Notes on Bolete taxonomy. *Persoonia* **7(**2**)**, 313–320.

Singer, R. 1977 Keys for the identification of the species of Agaricales I. *Sydowia* **30**, 192–279.

Singer, R. 1986 *The Agaricales in Modern Taxonomy*. 4th edn., Koeltz Scientific Books. Koenigstein, Germany, p. 912.

Singer, R. and Digilio, A. 1951 Pródromo de la flora agaricana Argentina. *Lilloa* **25**, 5–461.

Singer, R. and Morello, J. 1960. Ectotrophic forest trees mycorrhizae and forest communities. *Ecology* **41(**3**)**, 549–551.

Singer, R. and Moser, R. 1965. Forest mycology and forest communities in South America. *Mycopathol. Mycol. Appl.* **26(**2–3**)**, 130–191.

Singer, R. and Smith, A.H. 1960. Studies on secotiaceous fungi IX. The astrogastraceous series. *Mem. Torrey Bot. Club.* **21(**3**)**, 1–112.

Soop, K. 2001. Contribution à l'étude de la mycoflore cortinarioïde de Nouvelle-Zélande. *Bull. Soc. Mycol. Fr.* **117(**2**),** 91–132.

Soop, K. 2002. Contribution à l'étude de la mycoflore cortinarioïde de Nouvelle-Zélande II. *Bull. Soc. Mycol. Fr.* **118(**3**)**, 173–194.

Soop, K. 2003. *Cortinaroid Fungi of New Zealand. An Iconography and Key*. 3rd revised edition. Editions Scientrix. Mora, New Zealand. 21pp. ISBN 91-974803-2-0

Soop, K. 2005 A contribution to the study of the cortinarioid mycoflora of New Zealand, III. *N. Z. J. Bot.* **43**, 551–562.

Soop, K. 2013. A contribution to the study of the cortinarioid mycoflora of New Zealand, IV. *Bresadoliana* **1(**2**)**, 17–34.

Soop, K. 2014. A contribution to the study of the cortinarioid mycoflora of New Zealand, VI. *N. Z. J. Bot.* **52(**3**)**, 328–342.

Soop, K. 2016. A contribution to the study of the cortinarioid mycoflora of New Zealand, VII. *N. Z. J. Bot.* **54(**3**)**, 344–365, doi: 10.1080/0028825X.2016.1178149

Soop, K. 2017. A contribution to the study of the cortinarioid mycoflora of New Zealand, VII. *N. Z. J. Bot.* **54(**3**)**, 344–365.

Soop, K., Wallace, M. and Dima, B. 2018. New *Cortinarius* (Agaricales) species described from New Zealand. *N. Z. J. Bot.* **56(**2**)**, 163–182.

Spegazzini, C. 1887a Fungi Patagonici. *Bol. Acad. Nac. Cienc. (Cordoba)* **21**, 5–64.

Spegazzini, C. 1887b Fungi Fuegiani. *Bol. Acad. Nac. Cienc. (Cordoba)* **21**, 135–308.

Tedersoo, L., Arnold, E. and Hansen, K. 2013 Novel aspects in the life cycle and biotrophic interactions in Pezizomycetes (Ascomycota, fungi). *Mol. Ecol.* **22**, 1488–1493.

Tedersoo, L., May, T.W. and Smith, M.E. 2010. Ectomycorrhizal lifestyle in fungi: global diversity, distribution, and evolution of phylogenetic lineages. *Mycorrhiza* **20**, 217–263.

Tedersoo, L., Pärtel, K., Jairus, T., Gates, G., Põldmaa K. and Tamm, H. 2009. Ascomycetes associated with ectomycorrhizas: molecular diversity and ecology with particular reference to the Helotiales. *Environ. Microbiol.* **11(**12**)**, 3166–3178.

Tedersoo, L. and Smith, M.E. 2013 Lineages of ectomycorrhizal fungi revisited: foraging strategies and novel lineages revealed by sequences from belowground. *Fungal Biol. Rev.* **27**, 83–99.

Tedersoo, L. and Smith, M.E. 2017 Ectomycorrhizal fungal lineages: detection of four new groups and notes on consistent recognition of ectomycorrhizal taxa in high-throughput sequencing studies. In *Biogeography of Mycorrhizal Symbiosis*. L., Tedersoo (ed.). Springer Nature, Cham, Switzerland.

Tedersoo, L., Suvi, T., Jairus, T. and Kõljalg, U. 2008. Forest microsite effects on community composition of ectomycorrhizal fungi on seedlings of *Picea abies* and *Betula pendula*. *Environ. Microbiol.* **10(**5**)**, 1189–1201.

Teste, F.P. and Dickie, I.A. 2017. Mycorrhizas across successional gradients. In *Mycorrhizal Mediation of Soil Fertility, Structure, and Carbon Storage*. N.C., Johnson, C., Gehring, J., Jansa (eds.). Elsevier, Cambrige, USA. pp. 67–89. doi: 10.1016/C2015-0-01928-1

Toledo, C.V., Barroetaveña, C. and Rajchenberg, M. 2014 Phenology and environmental variables associated to the fruiting of wild edible mushrooms from Andean-Patagonia forests in Argentina. *Rev. Mex. Biodiv.* **85**, 1093–1103.

Trappe, J. 1964. Mycorrhizal hosts and distribution of *Cenococcum graniforme*. *Lloydia* **27**(2): 100–106.

Trierveiler-Pereira, L., Smith, M.E., Trappe, J.M. and Nouhra, E.R. 2015. Sequestrate fungi from Patagonian *Nothofagus* forests: *Cystangium* (Russulaceae, Basidiomycota). *Mycologia* **107**, 90–103.

Truong, C., Mujic, A.B., Healy, R., Kuhar, F., Furci, G., Torres, D., *et al.* 2017a. How to know the fungi: combining field inventories and DNA-barcoding to document fungal diversity. *New Phytol.* **214(**3**)**, 913–919.

Truong, C., Sanchez-Ramirez, S., Kuhar, F., Kaplan, Z. and Smith, M.E. 2017b The Gondwanan connection-southern temperate *Amanita* lineages and the description of the first sequestrate species from the Americas. *Fungal Biol.* **121**, 638–651.

Twieg, B.D., Durall, D.M. and Simard, S.W. 2007 Ectomycorrhizal fungal succession in mixed temperate forests. *New Phytol.* **176**, 437–447.

Valenzuela Flores, E. 1993 *Estudio Sistemático Corológico y Ecológico de los Agaricales Sensu Lato de los Bosques Autóctonos de la Región de los Lagos en Chile*. Tesis doctoral, Universidad de Alcalá de Henares. Facultad de Ciencias. Sección Biológicas. Departamento de Biología Vegetal.

Valenzuela Flores, E., Barría, D., Martínez, O., Godoy, R. and Oyarzún, C. 2013. Influence of nitrogen fertilization on abundance and diversity of basidiocarps of Agaricales *s.l.* in a temperate forest of *Nothofagus obliqua*. *Bosque* **34(**1**)**, 63–70.

Valenzuela Flores, E., Hipp, J., Alonso, C., Godoy, R., Alberdi, M., Álvarez, M., *et al.* 2008. Physiological-enzymatic characteristics and inoculation of mycelial strains of *Descolea antarctica* sing. in *Nothofagus* seedlings. *Electron. J. Biotechnol.* **11(**2**)**. This paper is available on line at http://www.ejbiotechnology.info/content/vol11/issue2/full/7/

Vázquez, D.P. 2002 Multiple effects of introduced mammalian herbivores in a temperate forest. *Biol. Invasions* **4**, 175–191.

Veblen, T.T., Donoso, C., Kitzberger, T. and Rebertus, A.J. 1996 Ecology of Southern Chilean and Argentinean *Nothofagus* Forests. In *The Ecology and Biogeography of Nothofagus Forest*. T.T., Veblen, R.S., Hill, J., Read (eds.). Yale University Press, New Haven, USA, pp. 293–353.

Vincenot, L. and Selosse, M.A. 2017 Population biology and ecology of ectomycorrhizal fungi. In *Biogeography of Mycorrhizal Symbiosis. Ecological Studies*. L., Tedersoo (ed.). Springer International Publishing, Cham, Switzerland, pp. 39–59.

Ważny, R. and Kowalski, S. 2017. Ectomycorrhizal fungal communities of silver-fir seedlings regenerating in fir stands and larch forecrops. *Trees* **31(**3**)**, 929–939.