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Hypogeous sequestrate fungi in South America – how well do we know them?

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Abstract Collecting and studying hypogeous sequestrate fungi and their particular fruiting biology has always been challenging and intriguing for scientists. However, knowledge of hypogeous taxa has for a long time been limited mainly to the Northern Hemisphere, and more recently, Australia. Nevertheless, cumulative information on sequestrate fungi for South America (SA) has increased considerably over the years, and constitutes by itself, the aim of this review. We have reviewed the available published literature, from 1880 until recent times, to extract information on records, ecology, and morphological characteristics of hypogeous sequestrate fungi from SA. Based on the 172 taxa cited in the available literature, a trend of increasing interest in the study of these fungi in the region is apparent, yet with an uneven distribution among countries, climate belts, and nature of forest habitats. Hypogeous truffle-like species in SA play a key role in regulating nutrient and carbon cycles and in all ecosystem multifunctionality. The symbiotic status is provided for most species listed, and mutualism, especially ectomycorrhizal, is predominant (82 %). The hypogeous sequestrate fungi in SA are an understudied group of fungi, with exceptional anatomical and biological features as well as in many cases intriguing phylogenetic relationships, requiring more attention and analysis from mycologists.

Keywords Ascomycota · Basidiomycota · Ectomycorrhizal truffle-like species · Sequestrate fruit-bodies

1 Introduction

Hypogeous sequestrate fungi are those that produce macroscopic fruit-bodies partially or completely embedded in soil. They comprise many phylogenetically related or unrelated species, all showing morphological features from convergent evolution, resulting as an adaptation to the hypogeous habit. In taxonomic terms they represent true (Ascomycota) and false truffles (Basidiomycota), various gasteroid fungi, a few Zygomycota (*incertae sedis*, Hibbett et al. 2007), some members of the Endogonales and Mortierellales (Kirk et al. 2008; Smith et al. 2013a), and a few sporocarpic species in Glomeromycota (Hibbett et al. 2007), which are for the most part distributed worldwide. A related term, "sequestrate", describes fungi with morphologically more or less enclosed macroscopic fruit-bodies, which evolved from having exposed hymenia and active spore discharge, to an enclosed hymenial structure, and, in most cases, a hypogeous habit, where spores are retained within the fruit-body until dispersal (Trappe 1979; Kendrick 1992; Kirk et al. 2008). A clear separation and therefore easy placement of species into

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hypogeous, epigeous and/or sequestrate categories is not always possible. Thus, most checklists just include easily defined sequestrate fungi (Bougher and Lebel 2001; Castellano et al. 2004; Trappe et al. 2009).

Hypogeous taxa differ from epigeous in their mechanisms to produce and disperse spores. They lack a stem or in many cases do not have a stem robust enough to push the fruit-body up and out of the soil. Therefore, upon maturation spores remain enclosed within the fruit-body peridium and are commonly released by specialized animals (mammals, arthropods, etc.) that feed on the fruit-bodies, or are dispersed by water or wind (Smith and Read 2008; Maser et al. 2010) (Fig. 1). Over time, hypogeous sequestrate fungi have developed numerous ways to attract mycophagous animals. Largely, aromatic luring is involved (Fig. 1), and thus different biochemical attractions have been developed by the fungi (Pacioni et al. 1991; Maser et al. 2010). The animals, in turn, had to develop different ways to find and consume the fungi. In some cases, examples of co-evolution have been observed (Moreno-Arroyo et al. 2005; Maser et al. 2010), and total dependence on this process is recorded for certain species, such as deer and small rodents.

To date, only a few wild animals (mammals) have been identified feeding and transporting remains of hypogeous sequestrate fungi into new locations within natural ecosystems in South America (SA) (Perez Calvo et al. 1989; Nouhra et al. 2005). Recently, non-native mammals have been identified as important dispersal agents of non-native ECM fungi, therefore promoting the transport of certain fungal species into new environments in SA (Nuñez et al. 2013). In eucalypt plantations in the south of Brazil, records confirm that isopods contribute to spore dispersal of truffle-like fungi (Sulzbacher et al. 2015). Several studies carried out in continents other than SA have shown the importance of hypogeous sequestrate fungi in the diet of mycophagous fauna in North America and Australia (Fogel and Trappe 1978; Cázares and Trappe 1994; Claridge and Lindenmayer 1998; Claridge and Trappe 2005; Maser et al. 2010; Schickmann et al. 2012).

The fruit-bodies of hypogeous sequestrate fungi are cryptic due to their habit, and in most cases not easy to find. Past records are based mostly on casual findings. A more developed approach for truffle collecting includes setting transects and plots and then racking the soil organic layer as described by Claridge et al. (2000) and Castellano et al.

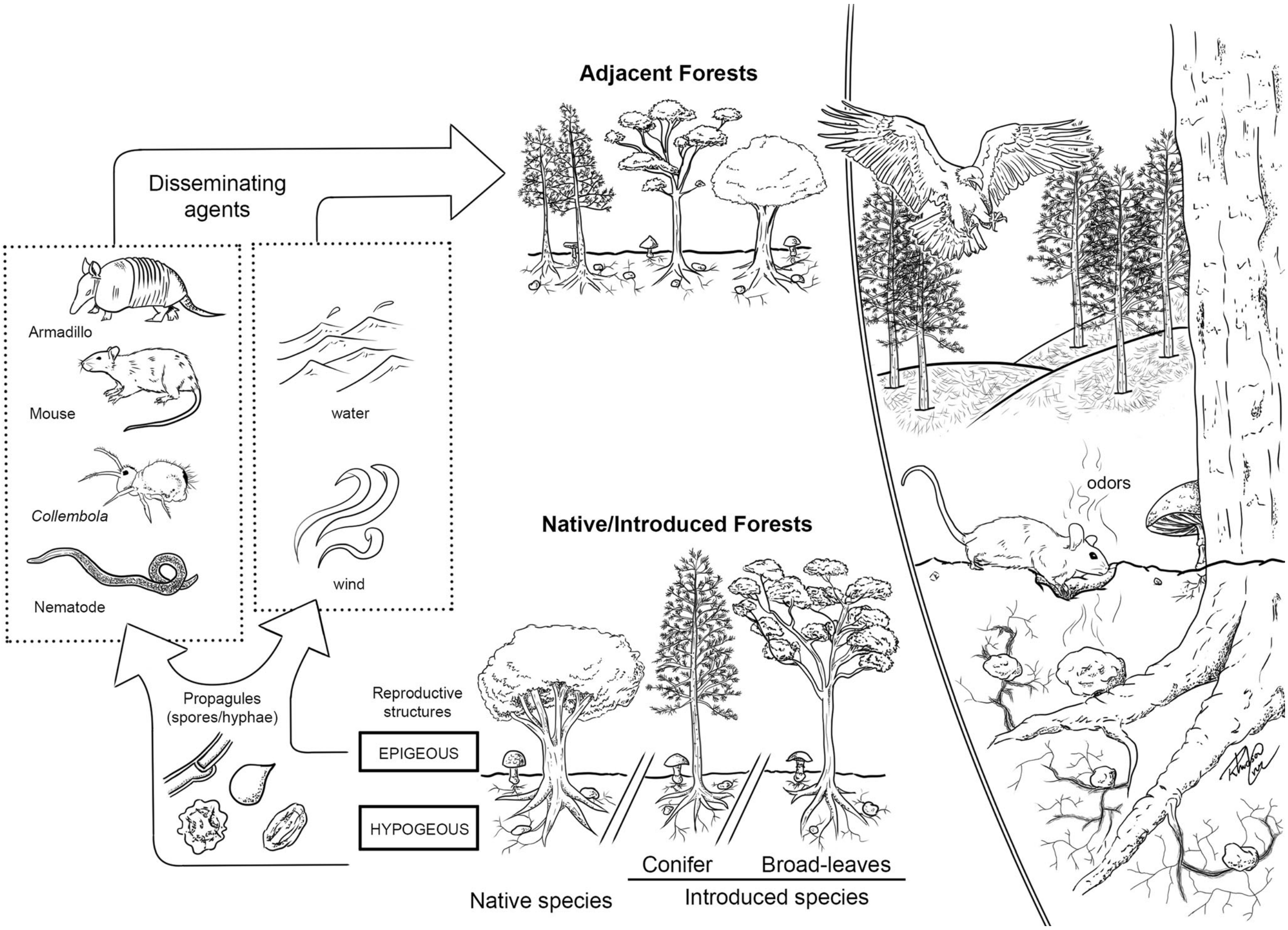

Fig. 1 Hypogeous sequestrate fungi in native and introduced forests showing vectors of propagules dispersal

(2004). Species with prominent flavor (*Balsamia*, *Genea*, *Hymenogaster*, *Melanogaster*, *Tuber*, etc.) can be located by trained animals (dogs, pigs), or simply by tracing the recent digging activities of small mammals, deer, etc.

Some, like true truffles, can be traced back over the years by locating the fungal mats within the soil. Locating the mats is useful for understanding the geographic distribution and physiological aspects of a particular species. Mats are often very sensitive to anthropogenic or fire disturbances, which can easily end or impair the spread of certain fungal species within the soil. Some may take over 15 years to recover after disturbances (Trappe et al. 2012). Therefore, caution is needed when studying the fungi or scratching the soil for the fruit-bodies.

Hypogeous sequestrate fungi are important components of forest ecosystems. They play different roles in the environment, particularly in mutualistic partnerships with plants (Smith and Read 2008; Trappe et al. 2009). More specifically, several hypogeous fungal genera, such as *Chondrogaster*, *Cortinarius* (some species previously included in *Thaxterogaster*), *Descomyces*, *Hydnangium*, *Hysterangium*, *Rhizopogon*, *Scleroderma* and *Tuber* form ectomycorrhizae with plant species. The symbiosis is important for nutrient (mainly N and P), carbon and water cycling. Ectomycorrhizal fungi (ECM) can be responsible for up to 70 % of the P (Simard et al. 2002) and 80 % of the N (Simard et al. 2002; Hobbie and Hobbie 2006, 2008) taken up by plants. Furthermore, mycorrhizal fungi have large impacts on litter decomposition, soil formation and aggregation, in addition to increasing resistance to drought, trace elements, diseases, and stress-related events (Rillig and Mummey 2006; Lindahl et al. 2007; Smith and Read 2008). Mycorrhizal fungi also influence plant productivity and plant diversity, and connect plants below ground via a hyphal network, allowing the movement of resources among coexisting plants (van der Heijden et al. 2015).

The occurrence, distribution and diversity of hypogeous sequestrate fungi have been unevenly studied around the world. While in temperate areas of Europe, North America and Australia hypogeous sequestrate fungi have been extensively studied (Hunt and Trappe 1987; Luoma et al. 1991; Colgan et al. 1999; Montecchi and Sarasini 2000; Smith et al. 2002; Trappe et al. 2009; Danks et al. 2013), there is a scarcity of published scientific works of this group of fungi or voucher collections for most of SA, Southeast Asia, and Africa (Trappe et al. 2009).

Europe was probably the first continent where hypogeous sequestrate fungi were studied to any significant extent, mainly on account of truffles being a centuries-long known delicacy for Sumerian, Greek, and Roman cuisines (Moreno-Arroyo et al. 2005; Trappe et al. 2009). The exact number of species in Europe is difficult to estimate, but at least 53 hypogeous genera are known (excluding Zygomycota) (Montecchi and Sarasini 2000). For Africa, only scattered publications are available citing a few genera. Among them are *Arcangeliella*, *Aroramyces*, *Austrogautieria*, *Cystangium*, *Elaphomyces*, *Elasmomyces*, *Hydnangium*, *Lactarius*, *Richoniella*, *Sclerogaster* (Dring and Pegler 1978; Pegler 1982; Thoen and Bâ 1989; Sanon et al. 1997; Castellano et al. 2000, 2016; Eberhardt and Verbeken 2004; Verbeken and Walleyn 2004; Bâ et al. 2012; Ducousso et al. 2012). For Asia, the majority of studies have focused on the genus *Tuber* (Huang et al. 2009; Chen et al. 2011) or on boletoid representatives (Lumyong et al. 2003; Lebel et al. 2012; Orihara et al. 2012; Mujic et al. 2014). Other groups have been accorded only minimal attention (Corner and Hawker 1953; Zhang and Yu 1990; Tao et al. 1993; Verbeken et al. 2014).

For the Southern Hemisphere (including South America, Australia, Africa, and Southeast Asia), Castellano and Trappe (1990) presented a preliminary nomenclatural list of truffle-like fungi including 322 references to type descriptions and 154 additional citations. Additional data revealed high diversity of hypogeous sequestrate fungi for Australia and New Zealand: between 1,278 and 2,450 species estimated for Australia, and 193 to 232 species for New Zealand. Among them, 12–30 % have already been cited or described (Bougher and Lebel 2001). Truffle-like fungi are highly endemic in Australia compared to other regions of the world (Danks et al. 2010, 2013). List of hypogeous sequestrate fungi are not always available for many areas on the globe. This is the case for SA, despite the existing references on hypogeous records from various types of forests ranging from the northern tropical and subtropical regions, downwards to the colder mountains and plains of Patagonia.

Therefore, the objective of this review is to present a compilation of the available published records on hypogeous sequestrate fungi from SA, with particular focus on species occurrence, distribution and ecology. Furthermore, the review suggests a critical estimation of hypogeous fungal species diversity associated with different forest types in SA.

2 Materials and methods

The term hypogeous sequestrate fungi is used for sequestrate fungi (sensu Kendrick 1992) with hypogeous or subhypogeous fruiting. References of hypogeous and subhypogeous fungi in the Ascomycota and Basidiomycota, based on true sexual fruit-body collections from SA, are included in this review (Table S1). The study reviewed all research articles dating from 1880 to September 2016, and included species descriptions and species citations on the above-mentioned groups. Species names and their taxonomic status are given following information in Mycobank (http://www.mycobank.org/MycoTaxo.aspx) or Index Fungorum (http://www.indexfungorum.org/names/names.asp).

Additional information including distribution by country, native or non-native status, and ecological affinities were retrieved from the literature cited (Table S1). The ecological modes of species are given based on extant field observations, supplemented by the literature, and considering their taxonomic position in relation to previously described ECM lineages (Rinaldi et al. 2008; Tedersoo et al. 2010; Tedersoo and Smith 2013). Table S1 shows a list of fungal taxa registered according to the literature. Some specimens are cited as "indeterminate and undescribed", principally because taxa were not formally described in the original source. The study represents all SA countries, even though we found records for hypogeous or sequestrate fungi only for Argentina, Brazil, Chile, Colombia, Ecuador, Guyana and Uruguay (Fig. 2).

3 Results

3.1 South American hypogeous sequestrate fungal diversity

This compilation shows that 175 taxa of hypogeous and subhypogeous fungi were described or cited in the literature for SA (Table S1), with uneven distribution over the continent (Fig. 1). Argentina (102) is the country with the highest number of cited species, followed by Chile (42) and Brazil (38). Other countries, such as Guyana (15), Uruguay (9), Ecuador (6), and Colombia (1), have fewer recorded species. We were not able to find any records of hypogeous sequestrate fungi for other South American locations (Fig. 1).

Fig. 2 Map of South America showing hypogeous sequestrate fungi sampling locations

Eleven species were recorded only once from the type locality during the 19th century, with no additional collections made afterward. In most cases, these original descriptions lack information about morphology, substrate affinity, and/or mycorrhizal status of the recorded taxa (Table S1). The tropical Guiana Shield forests host a high diversity of truffle-like fungi, most of them recently described as new to science (Henkel et al. 2010; Castellano et al. 2012, 2016; Smith et al. 2015). From the list, 104 species are considered native, especially in the temperate regions of Argentina and Chile, while 62 are considered allochthonous, introduced with the mycorrhizal host plants. Nine are referred to as unknown and no information about their origins is available in the literature.

3.2 The ecological mode

For most species (157), the ecological mode was estimated based on extant field observations and supplemented by information from the literature. 144 out of 175 listed species (82 %) are biotrophic, establishing ECM symbioses with a range of tree species (Table S1). Only 13 are listed as saprotrophic, and 18 are unknown.

Similarly to other ECM taxa, hypogeous sequestrate fungi are derived from diverse lineages of saprotrophic ancestors (Tedersoo et al. 2010; Tedersoo and Smith 2013; Ge and Smith 2013). The most common and abundant hypogeous genera in SA are included in various ECM lineages such as *Cortinarius* (/cortinarius lineage, including ex *Thaxterogaster* species), represented by 37 taxa, *Cystangium* (/russula-lactarius lineage) and *Hymenogaster* (/hebeloma-alnicola lineage), each one including seven taxa, *Hydnangium* (/laccaria lineage) with five taxa, *Hysterangium* (/hysterangium lineage) with 21 taxa, *Rhizopogon* (/suillus-rhizopogon lineage) with 11 taxa, and *Tuber* (/tuber-helvella lineage) represented by nine taxa.

4 Discussion

South America has a wide variety of unique biomes ranging from the northern tropical Andes in Colombia and Ecuador, to the lowland forests of the Caribbean coast, down to the south and east, through the Amazon basin, the Guiana Shield, the drylands, and the Atlantic forest in Brazil and Paraguay. In the south are the high "altiplanos", "Yungas" and drylands of Peru, Bolivia, Chile and Argentina, down to the Pampas and into Patagonia. In all these regions and biomes, the diversity of landscapes, soil and climatic conditions have deeply affected plant composition, thus contributing to a high diversity of fungi. However, the diversity of hypogeous and sequestrate fungi in SA remains poorly studied. The hypogeous and cryptic habit of most species, in addition to the scant number and unbalanced distribution of mycologists, is probably the main reason behind the observed patterns. Thus, for many regions of SA the real hypogeous fungal diversity remains to be discovered, and the diversity of taxa with this habit remains poorly known (Fig. 3).

In Patagonia, the ectotrophic forest dominated by *Nothofagus* seems to host the highest hypogeous diversity known for SA (Horak and Moser1965; Halling 1981; Nouhra et al. 2012a; Trierveiler-Pereira et al. 2015). In this ecosystem, Nouhra et al. (2012a) explored the diversity of hypogeous ECM-forming fungi associated with two *Nothofagus* species: *N. dombeyi* and *N. pumilio*. In total, 25 species belonging to 12 genera in Basidiomycota (9) and Ascomycota (3) were recovered. Among them, *Descomyces* (1), *Gautieria* (1), *Geastrum* (2), *Genea* (2), *Gymnohydnotrya* (1), *Gymnopaxillus* (1), *Hallingea* (1), *Hysterangium* (1), *Scleroderma* (1), *Setchelliogaster* (1) and *Thaxterogaster* (14) taxa were recorded. More recently, various sequestrate taxa in the Russulales have been described (Trierveiler-Pereira et al. 2015), as well as new sequestrate *Cortinarius* species from different *Nothofagus* forest types (Pastor et al. unpublished). Although diverse, the known hypogeous taxa richness of *Nothofagus* forest in Patagonia is still low when compared with other ECM temperate forests. This low fungal diversity could be attributed to the biogeographic isolation of the *Nothofagus* forests in SA, or may be partly due to the short-term sampling of recent exploration studies. Even so, new species are expected to occur in the vast area and varied landscapes of the Andes dominated by *Nothofagus*, as indicated by the various new taxa currently being described for the region within the *Cortinarius* (*Thaxterogaster*), *Descomyces*, *Genea*, *Setchelliogaster* (Nouhra, unpublished data).

The Yungas, a type of tropical and subtropical montane forest located at the eastern slopes of the Andes, has been the focus of a few studies on ECM fungi. In that ecosystem, at least one native hypogeous ECM species (*Alpova*

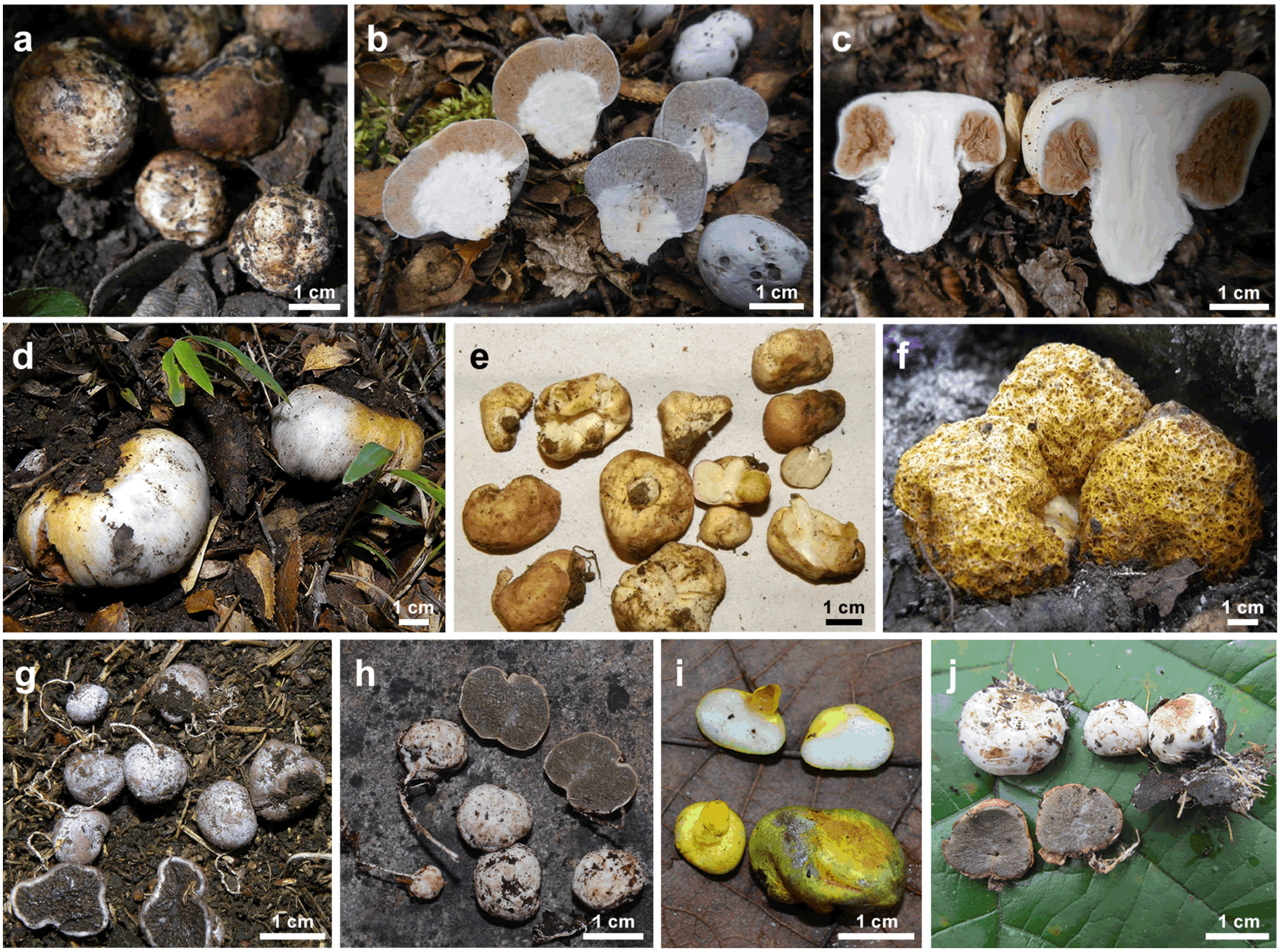

Fig. 3 Native hypogeous fungal diversity frequently sampled in South America (**a** – *Alpova austroalnicola*, **b** – *Cortinarius holojanthinus*, **c** – *Cortinarius* sp., **d** – *Cortinarius* sp., **e** – *Cystangium depauperatum*, **f** – *Gymnopaxillus* sp., **g** – *Hallingea purpurea*, **h** – *Hysterangium crassipariete*, **i** – Undescribed Boletales, **j** – *Hysterangium* sp.)

austroalnicola) have been reported from *Alnus acuminata* dominated forest (Nouhra et al. 2005). No other hypogeous sequestrate fungi have been found in the *A. acuminata* spp. *acuminata* forests of the Andes, and the number of epigeous mushroom species known in the area is relatively low (Becerra 2002; Nouhra et al. 2003), indicating that few highly specialized ECM fungi occur in this ecosystem. Similar data have been reported for other *Alnus*-dominated communities of the world (Molina 1979, 1981; Brunner and Horak 1990). Nevertheless, considering that *Alnus* species are known to host ECM fungi (Trappe 1975; Clemençon 1977; Molina 1979, 1981), more efforts to unveil the real diversity of hypogeous sequestrate fungi in those stands are needed.

In the Guiana Shield region of SA, Smith et al. (2013b) have discovered nine hypogeous ECM-related specimens, either through the collection of fruit-bodies or root tips colonized by the fungi. Among them, species of *Elaphomyces*, *Hysterangium* and several unidentified hypogeous taxa belonging to Boletaceae, mostly ECM-confirmed lineages, (Tedersoo et al. 2010) were described. Moyersoen (2006) studied roots of several individuals of *Pakaraimaea dipterocarpacea* ssp. *nitidum* in Venezuela and confirmed their association with seven species of ECM fungi. Additionally, 31 species of ECM fungi were later identified from the Guiana Shield based on collections of ECM roots and fruit-bodies (Moyersoen 2012). These northern tropical forests, characterized by ectomycorrhizal hosts within Caesalpiniaceae, Dipterocarpaceae and Polygonaceae (Tedersoo et al. 2010), are home to many ECM fungi, including hypogeous species. The recorded genera of hypogeous sequestrate fungi for this ecosystem are *Hysterangium* (Hosaka et al. 2006), *Guyanagaster* (Henkel et al. 2010), *Elaphomyces* (Castellano et al. 2012, 2016), and three new genera in the Boletaceae (Henkel et al. 2012), recently described as *Jimtrappea* T.W. Henkel, M.E. Smith & Aime, *Castellanea* T.W. Henkel & M.E. Sm., and *Costatisporus* T.W. Henkel & M.E. Sm (Smith et al. 2015). In addition to the hypogeous representatives, the seven-year study conducted by Henkel and collaborators (2012) showed a high diversity of epigeous ECM fungi in the *Dicymbe* monodominant forests of the Guiana Shield. Over the sampling period, fruit-bodies of 126 species of putative or confirmed ECM fungi were recovered, representing 13 families and 25 genera of primarily Agaricomycetes, but also Ascomycota (Elaphomycetaceae), the majority of which are new to science (Castellano et al. 2012; Henkel et al. 2012; Castellano et al. 2016). These findings highlight the potential diversity of epigeous and hypogeous ECM fungi in these under-studied, highly specific and remote areas of the globe.

ECM tree hosts such as *Alnus*, *Salix* and *Quercus* naturally occur along the South American Cordilleras (Nixon 2006; Tedersoo et al. 2009). It is likely that these forests are also home for new and as yet undescribed ectomycorrhizal hypogeous species. Recently, new hypogeous species within the Boletales, Hysterangiales and Phallales have been recorded under various native Atlantic forest fragments along the Northern Brazilian Atlantic coast (Sulzbacher et al. 2013; Sulzbacher, unpublished data). These findings highlight the potentially vast diversity of hypogeous sequestrate fungi harbored in these diversified ecosystems.

The occurrence of hypogeous ECM fungi in several South American ecosystems may depend on the distribution of spores mediated by mycophagous animals as the main mechanism of dispersal (Fig. 1). This mechanism has been well documented for other parts of the globe (Fogel and Trappe 1978; Cázares and Trappe 1994; Claridge and Lindenmayer 1998; Claridge and Trappe 2005; Maser et al. 2010; Schickmann et al. 2012). In SA, Nouhra et al. (2005) reported for the first time the mycophagous status of the nine-banded armadillo *Dasypus novemcinctus*. The species is related to the dispersal of *A. austroalnicola* in the *Alnus*-dominated forests of the Argentinian Yungas. Most recently, Nuñez et al. (2013) studied the role of the wild boar *Sus scrofa* in the dispersion of several exotic epigeous and hypogeous fungi, as well as their non-native associated conifer tree hosts in Patagonia. In addition, ongoing experiments have proved the role of these animals in the dispersion of native hypogeous sequestrate fungi associated with *Nothofagus* forests (Soteras et al., unpublished data). Other yet to be discovered relationships among hypogeous sequestrate fungi and animals may help to understand the distribution patterns of these under-studied fungi.

Hypogeous sequestrate fungi can show high levels of endemism (Castellano et al. 2004). This pattern can be described for some South American taxa. Many species are only known from the type locality or were described for specific habitats in SA. In a global diversity review, Mueller et al. (2007) indicated that 95 % of approximately 30 species cited for temperate SA regions are endemic, and estimated that approximately 300 new species remain to be discovered. For the tropical Western Hemisphere regions, the number of cited species with hypogeous habit is close to 30, and at least additional 200 species are predicted to be discovered (Mueller et al. 2007). Further studies are necessary to determine the distribution patterns and levels of endemism of hypogeous sequestrate fungi in SA.

Tedersoo et al. (2010) suggested that some hypogeous taxa are exclusive for SA, especially in the native Patagonian *Nothofagus* forest. In corroboration of this supposition, a significant number of new species of truffle-forming fungi have been or are currently being described from those subantarctic forests (Nouhra et al. 2012a, 2012b; Nouhra, unpublished data). Most recently, Trierveiler-Pereira et al. (2015) described new species of *Cystangium* from Patagonia. Most of these are known only from the type locality. The biogeographic history and diversity of forest ecosystems found in SA suggest that a substantial number of hypogeous species are still unknown. Efforts in sampling and advances in systematics will doubtless unveil many as yet undiscovered hypogeous taxa, and contribute to an understanding of the diversity and distribution of these fungi in the continent.

From a classification perspective, most hypogeous sequestrate fungal taxa reported for SA were formerly assigned to various orders of recognized epigeous taxa as derived forms, mainly based on their morphological features (eg, *Thaxterogaster* to Cortinariales, *Arcangeliella* and *Martellia* to Russulales, etc.). However, with the advent of molecular phylogenetics, several of these taxa have been subsumed under related epigeous genera, mainly based on their ITS sequence similarity and polyphyletic nature, within the context of formerly known epigeous taxa in the same lineage (Miller et al. 2001; Peintner et al. 2002; Tedersoo et al. 2010; Tedersoo and Smith 2013). A good example is the secotioid genus *Thaxterogaster*, subsumed under *Cortinarius* (Peintner et al. 2002). The sequestrate *Arcangeliella* and *Martellia* species have arisen several times from lamellate *Russula* and *Lactarius* (Calonge and Martin 2000; Miller et al. 2001). On the other hand, some authors maintain the generic limits in a more restricted sense (Desjardin 2003; Lebel and Tonkin 2007; Trierveiler-Pereira et al. 2015), using not just phylogenetic relationships, but also anatomical and ecological characters (Lebel and Tonkin 2007; Trierveiler-Pereira et al. 2015). Additional studies including various DNA markers, key diagnostic morphological features, and ecological aspects, are needed to provide a better picture of the relationship between hypogeous-secotioid forms within the containing lineages. Allied to this, extensive field collecting trips will help to unveil the real diversity of hypogeous sequestrate fungi in SA, increasing the number of known taxa and the classification of the organisms within the kingdom.

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