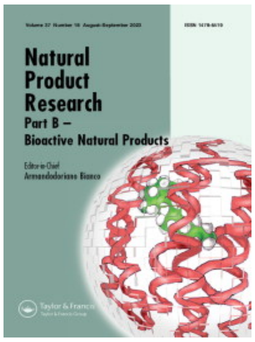

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ABSTRACT

Fungi have a unique metabolic plasticity allowing them to produce a wide range of natural products. Since the discovery of penicillin, an antibiotic of fungal origin, substantial efforts have been devoted globally to search for fungal-derived natural bioactive products. Andean region forests represent one of the few undisturbed ecosystems in the world with little human intervention. While these forests display a rich biological diversity, mycological and chemical studies in these environments have been scarce. This review aims to summarise all the efforts regarding the chemical or bioactivity analyses of Agaricomycetes (Basidiomycota) from southern South America environments. Overall, herein we report a total of 147 fungal species, 21 of them showing chemical characterisation and/or biological activity. In terms of chemical cores, furans, chlorinated phenol derivatives, polyenes, lactones, terpenes and himanimides have been reported. These natural products displayed a range of biological activities including antioxidant, antimicrobial, antifungal, neuroprotective and osteoclast-forming suppressing effects.

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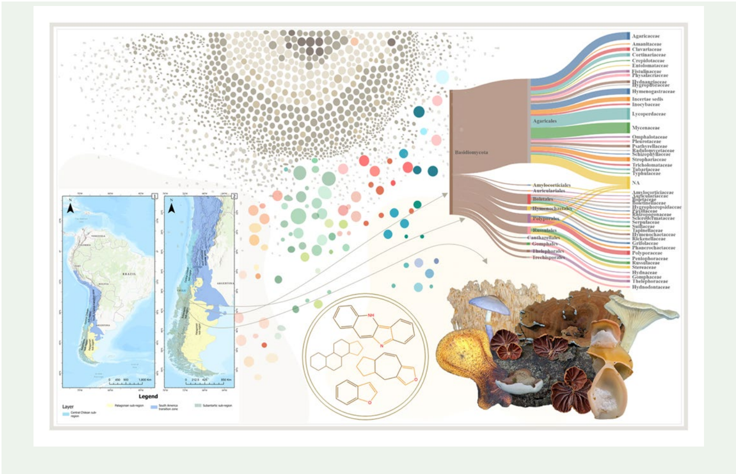

1. Introduction

Fungi represent one of the largest groups of organisms (Dighton 2018). Recent estimations indicate there are 2.2–13.2 million species of fungi on our planet (Hawksworth and Lücking 2017; Kew RBG Wu et al. 2019; Antonelli et al. Baldrian et al. 2022). To date, 120,000–148,000 species have been documented, mainly from Ascomycota (Wijayawardene et al. 2017) and Basidiomycota (He et al. 2022), which correspond to 3%–9% of the total pool of fungal species (Hawksworth and Lücking 2017; Antonelli et al). They are widely distributed across different ecosystems on our planet. In addition, these organisms are entirely heterotrophic as they are unable to perform photosynthesis (Webster and Weber 2007). Consequently, they have developed a unique metabolic plasticity allowing them to rapidly adapt and survive through the biosynthesis of an array of natural products (Sandargo et al. 2019). Fungal-derived natural products are pharmaceutically prolific and have been developed into several important biological applications ranging from highly potent toxins to approved drugs. Fungi are vast and yet untapped sources for pharmaceutically relevant molecules displaying a range of bioactivity including anticancer, antioxidant, hepatoprotective, antibacterial, antidiabetic and anti-inflammatory capabilities (Hyde et al. 2019).

Basidiomycota comprises approximately 40,000 spp. (He et al. 2022) and presents ecologically diverse species (Põlme et al. 2020). They can be saprophytes (Baldrian 2006; Baldrian and Valášková 2008; Fukasawa 2021), parasites (Zhao et al. 2019), mutualistic symbionts with insects (Li et al. 2021b), green algae and cyanobacteria (Oberwinkler 2012), even these organisms can also form mycorrhizae with plants and trees (Tedersoo et al. 2010, 2020; Tedersoo and Smith 2013; Rimington et al. 2020). Chile, which covers a great part of Andean region environments, hosts a large fungal diversity, accounting for approximately 4000 spp. (Instituto de Asuntos Públicos 2016). Almost half of them corresponds to Basidiomycota and even more are yet to be described (Boonmee et al. 2021; Caiafa et al. 2021; Garnica et al.

2021; Nouhra et al. 2021; Rajchenberg et al. 2021). On the other hand, in Argentina, between 1300 and 3600 species of fungi have been recorded according to Biodiversity Information System of the National Parks Administration (SIB 2022).

Andean region (also known as Andean-Patagonian dominion) represents one of the few undisturbed ecosystems in the world with little human intervention. According to Morrone (2018), the Andean region, for southern South America comprises the central Chilean, Subantarctic and Patagonian subregion, covering a vast extension of 6.5 million hectares of land in South America. This region is located between 37°S and 55°S, which include territories from southern Chile and Argentina (Morrone 2018). An important part of Andean region is the biodiversity hotspot of Central Chile (Myers 2000), later called Chilean Winter Rainfall-Valdivian Forests biodiversity hotspot (Mittermeier et al. 2004). Ecologically, these ecosystems have no equivalent in the northern hemisphere and are highly conserved territories displaying unique microclimates, creating favourable conditions for endemism (Luebert and Pliscoff 2019, 2022). Due to the close association between fungi, environment and flora, the Andean region forests can host a wide range of fungal biodiversity (Mueller et al. 2007).

The southern Chilean and Argentinean Basidiomycota has attracted much attention because of its peculiar biogeographical connections with the southern landmasses and because of its high levels of endemism of different fungal groups (Toledo et al. 2016). A great portion of the Agaricomycetes species inhabiting Andean region ecosystems belongs to the orders Agaricales, Hymenochaetales, Polyporales and Russulales within the phylum Basidiomycota (Figure 1). Several of these species have been shown to produce biologically privileged natural products.

2. Methodology

This review presents data on the chemical diversity of native and introduced Agaricomycetes collected and/or isolated from the Andean region. The information was collected from scientific databases and cover from 1966 up to 2022. The following electronic databases were used: SciFinder, Science Direct, Scopus, Web of Science and Google Scholar. The search terms used for this review included keywords, such as ‘metabolites’, ‘Fungi’, ‘Andean’, ‘chemical’, ‘Chile’ and ‘Argentina’. Supplementary Tables S1 and S2 report the chemodiversity of Agaricomycetes collected in the Andean region of Argentina and Chile.

3. Basidiomycota bioprospection from Chile and Argentina

The first mycological campaigns to explore fungal diversity in Southern South America took place in the XVIII century and was led by European naturalists (cf. Garrido et al. 1985; Gamundí and Amos 2007). After this, Claude Gay and Camille Montagne extensively compiled the knowledge about Chilean macrofungi and lichens to the date, including Ascomycota and Basidiomycota (Montagne 1850, 1852). However, it was Carlo Luigi Spegazzini who led a systematic investigation regarding fungi from Andean

Figure 1. Fungal diversity of Andean region.

region in Argentina (Spegazzini 1880) and Chile (Spegazzini 1910, 1921). Also, in the second half of the twentieth century, the work of Rolf Singer, Meinhard Moser, Egon Horak and Norberto Garrido increased the knowledge about Agaricomycetes from Southern South America (Singer et al. 1965; Singer 1969; Moser and Horak 1975; Horak 1979; Garrido 1988).

Palacios (1966) pioneered on incorporating the biological activity of Agaricomycetes collected in Chile. Then, several efforts to investigate the Agaricomycetes species of Southern South America revealed a range of biological activities including antimicrobial (Garrido et al. 1982; Aqueveque et al. 2002, 2015), antifungal (Schalchli et al. 2011, 2015; Aqueveque et al. 2016; Otto et al. 2016), antioxidant (De Bruijn et al. 2008; Torres et al. 2016, 2019; Albornoz et al. 2022), neuroprotection (González-Ramírez et al. 2018; Cabrera-Pardo et al. 2019) and structural determination of natural products (Clericuzio et al. 2004; Aqueveque et al. 2006; Wu et al. 2011; Alarcón et al. 2013; Choi et al. 2013; Reinoso et al. 2013; Riquelme et al. 2020). In Argentina, main studies focused on the nutritional, chemical and antioxidant aspects of fungal extracts (Di Anibal et al. 2015; Postemsky and Curvetto 2015; Toledo et al. 2016; Molares et al. 2020; Gallo et al. 2022; Rugolo et al. 2022).

The discovery of new fungal taxa with biological applications and medicinally relevant natural products have been a prolific niche for drug development endeavors (Abraham 2001; Dai et al. 2010; Spiteller 2015; Stadler and Hoffmeister 2015). Due to the unique biodiversity and climate conditions, the central Chilean, Subantarctic and Patagonian subregion, located in the Andean region are privileged ecosystems where a vast new fungal species and sophisticated chemical structures with broad applications are yet to be discovered (Aqueveque et al. 2017; Rosenberger et al. 2018). Overall, we report a total of 147 fungal species of Agaricomycetes. However, only 21 of them are reported with chemical and/or bioactivity studies. An extended list of fungi identified in southern South America is shown is Supplementary table 1.

4. Agaricales Underw

Globally, this order has 13,233 spp. and 33 families (Kirk et al. 2008). *Amanita muscaria* (L.) Lam. (Deja et al. 2014) and *Agaricus bisporus* (J.E.Lange) Imbach (Muszyńska et al. 2017) are well known species worldwide, with representatives of each genus native to southern South America and naturalised introduced species. The genus *Cortinarius* (Pers.) Gray is an ectomycorrhizal fungus, commonly found in *Nothofagus* forests in southern South America (Moser and Horak 1975; Horak 1979; Garrido 1988; Arnold et al. 2012). A substantial number of the species in this group are edible or have biotechnological properties (Li et al. 2021a).

In southern South America, the Agaricales order constitute more than 50% of the taxa that has been chemically and biologically investigated. This is probably due to their conspicuousness and are distributed in 19 families. Belonging to the Agaricaceae Chevall. family, *Agaricus arvensis* Schaeff and *Macrolepiota bonaerensis* (Speg.) Singer have shown antibacterial activity and *Agaricus augustus* Fr. has been used for the biotransformation of pesticides (Donoso et al. 2008). *Cortinarius xiphidipus* M.M. Moser & E. Horak (Cortinariaceae) has been subjected to chemical studies to determine steroid composition. Additionally, biological studies have been performed to assess the cytotoxic ability of this fungal strain (Torres et al. 2017). For Hymenogastraceae Vittad., *Gymnopilus junonius* (Fr.) P.D., *Gymnopilus purpuratus* (Cooke & Massee) Singer and *Hebeloma crustuliniforme* (Bull.) Quél. have been evaluated in several assays including antibacterial, antifungal, cytostatic, antiviral and biotransformation of pesticides (Garrido 1982; Aqueveque et al. 2006; Donoso et al. 2008; Schalchli et al. 2011; Reinoso et al. 2013; Schalchli et al. 2015).

5. Boletales E.-J. Gilbert

This order has 1316 spp. and 17 families, worldwide (Kirk et al. 2008). The genus *Boletus* L. is known to have many edible species, including *Boletus loyo* Phillippi (syn. *Butyriboletus loyo* (Phillippi) Mikšík) present in Chile and Argentina (Singer and Digilio 1957; Riquelme et al. 2019; Li et al. 2021a; Rivas-Ferreiro et al. 2023). *In vitro* assays on *Boletus aereus* Bull., *B. badius* Pers., *B. edulis* Bull., *B. pinophilus* Pilát & Dermek have shown the presence of metabolites with antioxidant activity (Robaszkiewicz et al. 2010; Sun et al. 2014). *Suillus* Gray is a biomedically relevant genus due to the biosynthesis of the terpene suillin, which has been reported to display several biological activities including cytotoxic, antitumoral and neuroprotective (*in vivo* and *in vitro*). Some common species from this genus are *S. bellinii* (Inzenga) Kuntze, *S. granulatus* (L.) Roussel and *S. luteus* (L.) Roussel (Fernández et al. 2012; Jia et al. 2014; Venditti et al. 2017; Yan et al. 2021; Andrade et al. 2022).

In southern South America, seven families of Boletales have been identified and their antimicrobial activity evaluated: Boletaceae Chevall., Boletinellaceae P.M. Kirk, P.F. Cannon & J.C. David, Rhizopogonaceae Gäum. & C.W. Dodge, Sclerodermataceae Corda, Suillaceae Besl & Bresinsky and Tapinellaceae C. Hahn (Garrido et al. 1982). Furthermore, *Serpula himantioides* (Fr.) P. Karst., from Serpulaceae Jarosch & Bresinsky, has been reported to synthesise pigments displaying UV-photoprotective abilities (Torres et al. 2019). Species from Suillaceae are not only a food resource exploited in rural areas (Fernández et al. 2012; Jacinto-Azevedo et al. 2021), but also have been linked to the spread of invasive conifer species (Policelli et al. 2019; Pildain et al. 2021).

6. Polyporales Gäum

Worldwide, Polyporales have 13 families and 1801 spp. (Kirk et al. 2008). Common species of this order are *Trametes versicolor* (L.) Lloyd (Tišma et al. 2021) and *Ganoderma australe* (Fr.) Pat. (Richter et al. 2015).

In southern South America, three families have been prospected. *Grifola gargal* Singer (Grifolaceae Jülich) is an endemic species of the *Nothofagus* forest of southern Chile and Argentina (Rajchenberg 2002) and has exhibited antioxidant properties as well as the ability to suppress osteoclasts formation (De Bruijn et al. 2008, 2009; Wu et al. 2011; Choi et al. 2013; Harada et al. 2015). In addition, *T. versicolor* (Polyporaceae) has shown remarkable abilities to biodegrade pesticides and it has also been reported to display antifungal activity (Donoso et al. 2008; Schalchli et al. 2015). Also, *Ganoderma australe* mycelial cultures isolated from Argentina have shown *in vitro* immunomodulatory and antioxidant activities (Gallo et al. 2022).

7. Hymenochaetales Oberw

Globally, Hymenochaetales are represented by two families, 48 genera and 610 spp. (Kirk et al. 2008). Some species from Hymenochaetaceae Donk are tree pathogens, white rot fungi, that seriously affect the forestry industry. For example, *Phellinus igniarius* (L.) Quél. and the genus *Arambarria* Rajchenb. & Pildain have been reported as pathogens of grapevine (Cloete et al. 2016; Pildain et al. 2017; Del Frari et al. 2021).

There are also specimens with medicinal properties such as *Fomitiporia punctata* (P. Karst.) Murrill, which has shown antioxidant activities *in vitro* (Liu et al. 2017). Furthermore, *Inonotus obliquus* (Fr.) Pilát produces inotodiol, a compound that has a remarkable cytotoxic activity *in vitro* (Zhao and Zheng 2021).

In southern South America, the family Hymenochaetaceae is the only representative addressed. *Phylloporia boldo* Rajchenb. & Pildain has recently been described as a new endemic species associated with *Peumus boldus* (Rajchenberg et al. 2019). Incipient efforts exploring the chemistry of this newly discovered species have revealed a range of chlorinated compounds (Riquelme et al. 2020).

8. Russulales kreisel ex P.M. Kirk, P.F. Cannon, & J.C. David

This order contains 12 families with 1767 spp. worldwide (Kirk et al. 2008). Due to its relevant bioactivities known, *Hericium erinaceus* (Bull.) Pers. is one of the most studied fungi around the world (Thongbai et al. 2015).

In southern South America, two families have been addressed. The first studies conducted on this order were on species from Russulaceae Lotsy. Specifically, *Lactarius deliciosus* (L.) Gray and *Russula sardonia* Fr. where their antibiotic activity was evaluated (Garrido et al. 1982). Furthermore, ceramides and terpenes have been isolated from fruiting bodies of *Russula austrodelica* Singer (Alarcón et al. 2013). From Stereaceae Pilát family, it is important to highlight *Stereum hirsutum* (Willd.) Pers., which has shown antioxidant (Torres et al. 2016), antifungal (Aqueveque et al. 2016) and antibacterial activities (Aqueveque et al. 2015). Finally, *Aleurodiscus vitellinus* (Lév.) Pat. (syn. *Gloeosoma vitellium* (Lév.) Bres.) has been reported to display remarkable neuroprotective activity in Alzheimer's cell-based models (González-Ramírez et al. 2018).

9. Bioactive natural products from Agaricomycetes of the Andean region

In this section, we will focus on providing an overview of fungal natural products, characterised by NMR and X-ray crystallography, and their reported biological activity. Natural products identified by mass spectrometry are described in the Supplementary Material. Figure 2 shows natural products isolated from Agaricomycetes in the Andean region. Several furan containing natural products have been reported over the years (Figure 2(a)). González-Ramírez et al. (2018) isolated a natural benzofuran, fomannoxin (1), from the Andean region fungus *Aleurodiscus vitellinus*. Fomannoxin showed remarkable neuroprotective abilities while undetectable cytotoxic effects on PC12 cells. This fungal benzofuran displayed a concentration-dependent protection on the Aβ-induced toxicity on PC-12. Fomannoxin also showed beneficial effects on the frequency of cytosolic Ca^{2+} transients in rat hippocampal neurons. During the chemical studies of *Hypholoma sublateritium,* Aqueveque et al. (2006) reported the presence of marasmal (2), a naphthofuran. Biological studies on marasmal revealed reasonable antimicrobial activity against *Bacillus* and *Staphylococcus* strains. NMR studies on *Serpula himantioides* revealed the presence of xerocomic acid (3), a red-orange pigment present in Boletales. Biological evaluation of xerocomic acid revealed high antioxidant capacity as well as

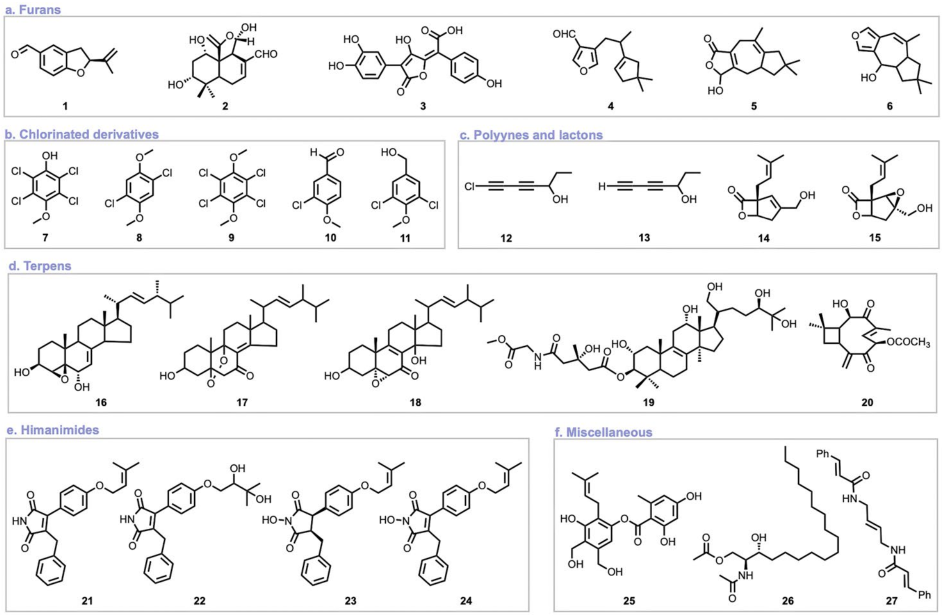

Figure 2. A selection of natural products from Agaricomycetes isolated from Andean region forests.

remarkable levels of photoprotection against UV-C radiation on HEK293 cell assays (Torres et al. 2019). A range of furan containing terpenoids (4–6) were characterised by Alarcón et al. (2013) at the University of Bío-Bío in Chillán, Chile. Chlorinated compounds (Figure 2(b)) have also been isolated from Andean region fungi. Riquelme et al. (2020) investigated the chemistry of *Phylloporia boldo*, a recently discovered fungi, and found several chlorinated hydroquinone metabolites including drosophilin A (7), chloroneb (8) and drosophilin A methyl ether (9). Other chlorinated metabolites such 3-chloro-p-anisaldehyde (10) and 3,5-dichloro-4-metoxi-benzyl alcohol (11) have been isolated from *Hypholoma capnoides* and *Hypholoma fasciculare*, respectively (Aqueveque et al. 2006). Polyynes and lactones scaffolds have also been identified in Basidiomycota from the Andean region (Figure 2(c)). The propargyl alcohols 12 and 13 were isolated from *Gymnopilus junonius* and showed interesting antimicrobial and antifungal activities (Aqueveque et al. 2006). Vibralactone (14) and vibralactone B (15) were isolated from *Stereum hirsutum* and also displayed antimicrobial activities (Aqueveque et al. 2015). A range of terpenes has also been reported (Figure 2(d)). Gargalols A-C (16-18) were characterised from *Grifola gargal*, an edible mushroom from the south of Chile and Argentina (Wu et al. 2011). These sterols showed beneficial effects against osteoporosis. Fasciculol E (19), a lanostane triterpenoid conjugated to a depsipeptide unit, was isolated from fruiting bodies of *Pholiota spumosa* (Clericuzio et al. 2004). Naematolon (20), isolated from *Hypholoma fasciculare*, showed modest antimicrobial activities (Aqueveque et al. 2006). Several himanimides (Figure 2(e), 21–24) were reported from cultures of *Serpula himantioides* (Aqueveque et al. 2006). Antimicrobial evaluation of these molecules showed promising results. Polyphenolic compounds (25) were also observed in *Stereum hirsutum* (Aqueveque et al. 2015).

Grifola gargal also produces novel sphingosines (26) with remarkable osteoclast-forming suppressing activity (Choi et al. 2013). Finally, (E)-2,3-dehydroputrescine-1,4-dicinnamamide (27) was isolated from fruiting bodies of *Pholiota spumosa* and characterised by X-ray crystallography (Clericuzio et al. 2004). An extended list of bioactive molecules, identified by mass spectrometry and isolated from Andean region fungi is displayed in Supplementary Tables 2 and 3.

10. Conclusion

This review gathers information regarding Agaricomycetes investigated from the Andean region, which comprises large territories from Chile and Argentina (Morrone 2018). Basidiomycota are still a prolific source of bioactive fungal natural products (Reck and Spiteller 2015). southern South America represents a distinct biogeographic zone with endemic flora that creates the perfect conditions for the development of unique fungi species with relevant biomedical activities. To the best of our knowledge, this review covers all the chemical studies about Basidiomycota fungi investigated from southern South America. Herein, we report a total of 147 fungal species of Agaricomycetes. However, natural product chemistry and/or bioactivity studies are reported only in 21 of them. Fungal species from the following orders have been reported in southern South America: Agaricales, Boletales, Hymenochaetales, Polyporales and Russulales. In terms of fungal natural scaffolds, several furans, chlorinated phenol derivatives, polyenes, lactones, terpenes and himanimides have been reported. These natural products displayed a range of biological activities including antimicrobial, antifungal, neuroprotective and osteoclast-forming suppressing effects. Finally, more efforts are needed to uncover the biomedically relevant chemical space in fungi from southern South America. These endeavors will pave the path to open new venues for drug development campaigns.

Disclosure statement

No potential conflict of interest was reported by the authors.

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