



Biogeography and uniqueness of filamentous terrestrial fungi in the polar regions

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ABSTRACT

Fungi are widely distributed on our planet, including in extremely harsh habitats, such as the polar regions. The extreme conditions of those habitats limit the number of organisms capable of living there, but some fungi are adapted to the polar conditions and play essential roles in nutrient cycling. However, knowledge about their diversity, distribution, and functioning is fragmented, and approaches used to study them are diverse, often yielding difficult-to-compare results. We present maps with locations of mycological studies in the Arctic and Antarctica, as well as a list of mycelial fungi found on various terrestrial substrates through cultivation on nutrient media and/or molecular methods. These fungi were identified to the species level based on morphological-cultural features or gene-sequence analysis. Analysis of the methods applied to study fungi in different substrates shows that a combination of multiple methods is optimal to study species composition. The taxonomic affiliation of the identified species to different fungal divisions is largely determined by habitat conditions and research methods. The largest number of species belongs to the divisions Ascomycota and Basidiomycota. The predominant ecological groups were saprotrophic and symbiotic fungi. The majority of 1324 discovered fungal species are known as cosmopolitan species. Approximately one-fifth of the fungi were identical between the Arctic and Antarctica, only a few species are known to be endemic to Antarctica or Arctic, and there are 1–6 identified bipolar species. Claims of endemism of polar-region fungi are relatively weakly supported.

1. Introduction

Being the polar regions of our planet, the Arctic and Antarctic regions contain extreme conditions for life (Cox et al., 2016), such as low average annual temperatures, long periods of darkness and light, widespread permafrost, high ultraviolet radiation, frequent freeze and thaw cycles during the vegetation period, and low water and nutrient availability (Canini et al., 2021; Govani et al., 2022; Hassan et al., 2016). However, the polar regions also have significant differences in landscape areas, hydrological features, climatic conditions, types of ice and snow covering, soils and permafrost (Dobinski, 2011; Dobiński, 2020; Govani et al., 2022). The Arctic is often defined as a land of tundra with climatic conditions restricting tree growth (Robinson, 2001; Walker et al., 2005); however, a big part of the areas above the Arctic Circle also contains taiga forests (Montesano et al., 2009). Vast peatland coverage storing huge carbon reserves is a characteristic feature of the arctic region

(Chaudhary et al., 2020; Tarnocai, 2009; Tarnocai and Stolbovoy, 2006). Antarctica is a predominantly rocky continent more than 98% occupied by ice and characterized by irregularly developed soil or its absence (Bockheim and Haus, 2014; Pires et al., 2017). Bockheim and Haus (2014) noted organic, ornithogenic and mineral type of soils storing organic carbon in ice-free Antarctic areas. Arctic permafrost is an uneven environment, generally abundantly moistened and containing mineral and organic soils. In contrast, Antarctic permafrost has large differences between the deep continental and maritime parts and is highly influenced by regional climate, proximity to the glaciers, age, vegetation, snow cover, and surface albedo (Ottoni et al., 2022). Increasing warming in high-latitude regions affects Arctic permafrost peatlands, which are sensitive to climatic changes and provokes permafrost thawing, changing in plant composition and soil microorganism communities (Zhang et al., 2018). In different parts of Antarctica, the processes of climate change are contradictory. The

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Antarctic continental deserts, specifically McMurdo Dry Valleys, are considered the coldest and driest on the World (Goordial et al., 2016) comprising the only permafrost with a dry soil layer over ice-cemented ground (Canini et al., 2021; Ottoni et al., 2022). Intriguingly, Doran et al. (2006) registered the large-scale perennial cooling in this area. However, the increasing warming in the Antarctic Peninsula and some other parts of Maritime Antarctica is reported at the same time (Doran et al., 2006; Pires et al., 2017; Royles et al., 2012). All of the processes in the polar regions generated by climate changing listed above affect the living-organism communities (Makhalanyane et al., 2016) and global carbon fluxes (Jenny Angel et al., 2022; Liu et al., 2022).

An exploration of research articles has shown the presence of fungi in the polar regions on a variety of substrates. Makhalanyane et al. (2016) notified: “in cold environments, microorganisms (bacteria, archaea and fungi) are major constituents of the total biomass, and are estimated to mediate the cycling of key biogeochemical elements such as nitrogen and carbon, with potentially important implications for the productivity of these systems” (Makhalanyane et al., 2016). However, we still have a very limited understanding of fungal diversity and distribution (Eisenhauer et al., 2017; Tedersoo et al., 2021), especially in such extreme habitats as polar regions (Bölter et al., 2002; da Silva et al., 2019; Hassan et al., 2016; Makhalanyane et al., 2016). Additionally, we have insufficient knowledge on the contribution of fungi to carbon fluxes (Tveit et al., 2013), as well as on their ecological role and evolution in the polar regions (Botnen et al., 2020; Cox et al., 2016; da Silva et al., 2019). It is not entirely clear which fraction of the fungi found in the extreme ecosystems of the Arctic and Antarctic is present in a living active mycelial state, and which as spores (Bölter et al., 2002; Robinson, 2001; Schmidt and Bölter, 2002). However, there is a significant part of the work showing that the psychrotolerant¹ species of fungi predominate over psychrophilic² ones in polar regions (Frisvad, 2008; Hassan et al., 2016; Ludley and Robinson, 2008; Nikitin and Semenov, 2022; Robinson, 2001; Zucconi et al., 1996). Furthermore, investigations show that the community structure within the consortia of bacteria, yeasts and fungi is also similar to that of temperate soils (Bölter et al., 2002). Therefore, it is assumed that with warming, the overall activity of microorganisms, including fungi, in the polar regions will increase (Ozerskaya et al., 2008), which presumably boosts the intensity of the nitrogen and carbon cycles (Arenz et al., 2011; Siciliano et al., 2009; Wild et al., 2014).

We found that most past studies present lists of fungi identified both to the species level as well as to higher taxonomic level, such as the genus (Bridge and Spooner, 2012; Penton et al., 2013), family and order (Stephenson et al., 2007). In this work, only names of fungi identified to the species level are included, since the species is the relevant level for our work. Species of a single genus often differ from each other in their physiological characteristics and ecological confinement, which is valuable for understanding the ability of these species, rather than entire genera, to live in such extreme habitats as the polar regions.

This review summarizes our knowledge about the diversity of terrestrial filamentous fungi in Polar regions detected and identified to species names by culture-based and molecular methods. The overall aim of this study was to evaluate the claim that the poles have unique fungal communities with many endemic species. To achieve the aim the following objectives were formulated.

1) to create a comprehensive list of terrestrial filamentous fungi that have been reported from Arctic and Antarctic regions;

¹ Psychrotolerant fungi can grow close to 0 °C, with optimum growth temperatures of >15 °C and maximum growth temperatures of >20 °C (Coleine et al., 2022).

² Psychrophilic can grow at or below 0 °C, with optimum growth temperatures of ≤15 °C and maximum growth temperatures of ≤20 °C (Coleine et al., 2022).

- 2) to analyze methods used for sample storage, detection and identification of fungi from these regions and to discuss the influence of the applied methods on the results obtained;
- 3) to compare the fungal communities of both polar regions with each other and with more global fungal communities;
- 4) to collect information about endemic fungal species in polar regions to evaluate claims of endemism.

2. Information retrieval and processing

In order to compile information about fungi known from the polar regions, we reviewed mycological and ecological manuscripts mainly using Google Scholar searches throughout the research time of fungi in these regions. Additionally, we used a list of fungi and manuscripts from the British Antarctic Survey site (https://legacy.bas.ac.uk/bas_research/data/access/fungi/Speciespublic2.html#Use) in order to find more studies of Antarctic fungi.

We employed the following criteria to compile this list: (1) The report had to be verified in a peer-reviewed publication. Unpublished, mimeographed, and locally distributed reports, herbarium information, anecdotal references, and checklists were not included; (2) The fungi had to be filamentous. (3) The fungi had to be detected by cultural and/or molecular approaches. (4) Fungi had to be identified up to the species level. (5) Only terrestrial fungi and fungi detected in driftwood were included. Generally we included fungi detected on or above/under the boundaries of the Arctic and Antarctic polar circles (66°33'49.3"N and 66°33'49.3"S, respectively), but in several cases we included fungal species of near subpolar locations as well.

In addition to the geographic locations of the investigations we also tried to find information about methods of sample storage, detection and taxonomic identification from the studied manuscripts. Moreover, our list of fungi was intended to serve as a compilation of those fungi that have been found growing in the polar regions from different substrates. We relied mostly on the habitat descriptions of each fungus in the appropriate publications. However, we realize that these data are likely incomplete. In some instances, the above information could not be determined from the available literature; these records are marked as “n. i.” (no information).

Fungal taxonomies follow the Index Fungorum (<http://www.indexfungorum.org>). When the names of the fungal species in the Index Fungorum differed from the name of this species in the articles, we cited both names. If the article indicated the fungal name as the genus sp., which has only one species, according to the Index Fungorum and data from the GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>), then we indicated this species instead of the genus sp. in our list of fungi. There is some of species present in the articles are not in the Index Fungorum or have archaic status, we marked them by * (Tables A.1).

The data were processed using Excel 14.6.1 and SketchBook 8.7.0 softwares. Maps of fungi investigations and sampling were created in open-source software QGIS 3.22. Papers we studied contained three types of georeferencing: geographic coordinates in degree-minutes-seconds format, text descriptions of the place and maps. Only 46% of the descriptions we used had coordinates and thus could be accurately reproduced on the map. Furthermore, 44% of the sources described vast territories in text only and another 10% were also accompanied by maps. In such cases we located points in the centers of research areas or according to the maps.

3. General description of the fungal community obtained by culture-based and molecular methods in both polar regions

The list of filamentous terrestrial fungal species of the polar regions presented in this article was obtained from 221 scientific publications. A greater number of the articles, 145 dealt with the study of fungi in Antarctica, 71 articles with fungi of Arctica, and five research papers with fungi from both poles. A complete list of discovered fungal species

and locations of the investigations is presented in Tables A.1 and on the maps of Figs. 1 and 2. Detailed information about these fungi is given in additional materials, which indicate the places and substrates of detecting the species, methods for their sampling and identification, as well as methods for storing samples (Tables A.1).

Of the analyzed investigations, 1324 identified species of terrestrial filamentous fungi have been reported from Arctic and Antarctic regions (Tables A.1, Fig. 3). Ascomycota and Basidiomycota species form the largest component of this assemblage with ~68% and ~28% of species, respectively; ~4% of species are mucoromycetes, one species is an entomophthoromycete, one species is a glomeromycete, and one species is a zoopagomycete. The presence of multiple types of sterile mycelium detected by cultural methods was pointed out in many studies of both polar regions (Tables A.1).

We found that the majority of fungal species (853) were recorded in the polar regions once, and 471 fungal species were noted in two or more studies (Tables A.1, A.2). *Pseudogymnoascus pannorum* is the most common species in both Polar regions, mentioned in 77 analyzed papers and obtained by all methods described in this article (Tables A.1, A.2). Other taxa commonly isolated in both polar regions that were noted in 45–53 papers (*Cladosporium cladosporioides*, *C. herbarum*, *Penicillium chrysogenum*), 23–40 papers (*Alternaria alternata*, *Antarctomyces psychrotrophicus*, *Aspergillus versicolor*, *Aureobasidium pullulans*, *Cadophora fastigiata*, *C. luteo-olivacea*, *C. malorum*, *Cladosporium sphaerospermum*, *Mortierella alpina*, *Mucor hiemalis*, *Phoma herbarum*, *Penicillium aurantiogriseum*, *P. brevicompactum*, *P. glabrum*, *Thelebolus microsperes*) or in less papers (Tables A.2).

In the process of reviewing the literature on fungal diversity in the polar regions, we identified several difficulties associated with the analysis of available information: i) while some areas have been explored more frequently and in more detail, most have not been explored at all due to inaccessibility; ii) the fungi of the Arctic and Antarctic have been studied with different intensity; iii) different methods of sampling and storage of samples, isolation and determination of fungi were used, which affected the results obtained.

4. Methods used in the investigations

Due to the remoteness of the polar regions, most samples were stored for several weeks or months before laboratory processing. It is also worth noting that a variety of substrates were examined in different studies.

4.1. Substrates from which fungi were obtained

Analysis of the investigations showed that fungi identified in polar regions through molecular and cultural methods included species associated with both living organisms and dead organic matter (Table 1). The majority of species were isolated from substrates formed by bioinert matter which represent materials generated as a result of living organisms activity and inert processes of the biosphere (Ostroumov, 2008; Vernadsky, 1965). Some of the bioinert substrates were dominated by organic matter and others by inorganic matter. Substrates subjected to anthropogenic influence and airborne fungi were classified into distinct categories. Each substrate group added new fungal species to the overall list that were not detected on other materials. The majority of fungal species were isolated from Arctic material, with the exception of species obtained from animal remains and airborne fungi, which predominated in Antarctica (Table 1). A more detailed table with the studied substrates is given in the appendices (Tables A.1).

4.2. Storage of samples, detection and identification of fungi

Only in rare cases was laboratory work with the samples done immediately or in 3–10 days after collection (Baublis et al., 1991; Dunleavy and Mack, 2021; Gonçalves et al., 2012, 2015,

Grum-Grzhimaylo et al., 2018; O.A. Grum-Grzhimaylo et al., 2016; Gunde-Cimerman et al., 2003; Kirtsideli et al., 2011; Poosakkannu et al., 2017). The researchers occasionally did not indicate the duration of sample storage (e.g., Blanchette et al., 2016; Held and Blanchette, 2017; Iliushin et al., 2022a,b; Tosi et al., 2005) or information regarding the storage method (Kirtsideli et al., 2010, 2016; Lapteva et al., 2017; Mercantini et al., 1989; Perini et al., 2019; Zhang and Yao, 2015). The studies we found indicated that researchers mainly stored collected samples until laboratory treatment in one of three ways: freezing, cooling (several degrees above zero), or drying, and in some cases samples were processed in 24 h after collection (Fig. A.1.1; Tables A.1).

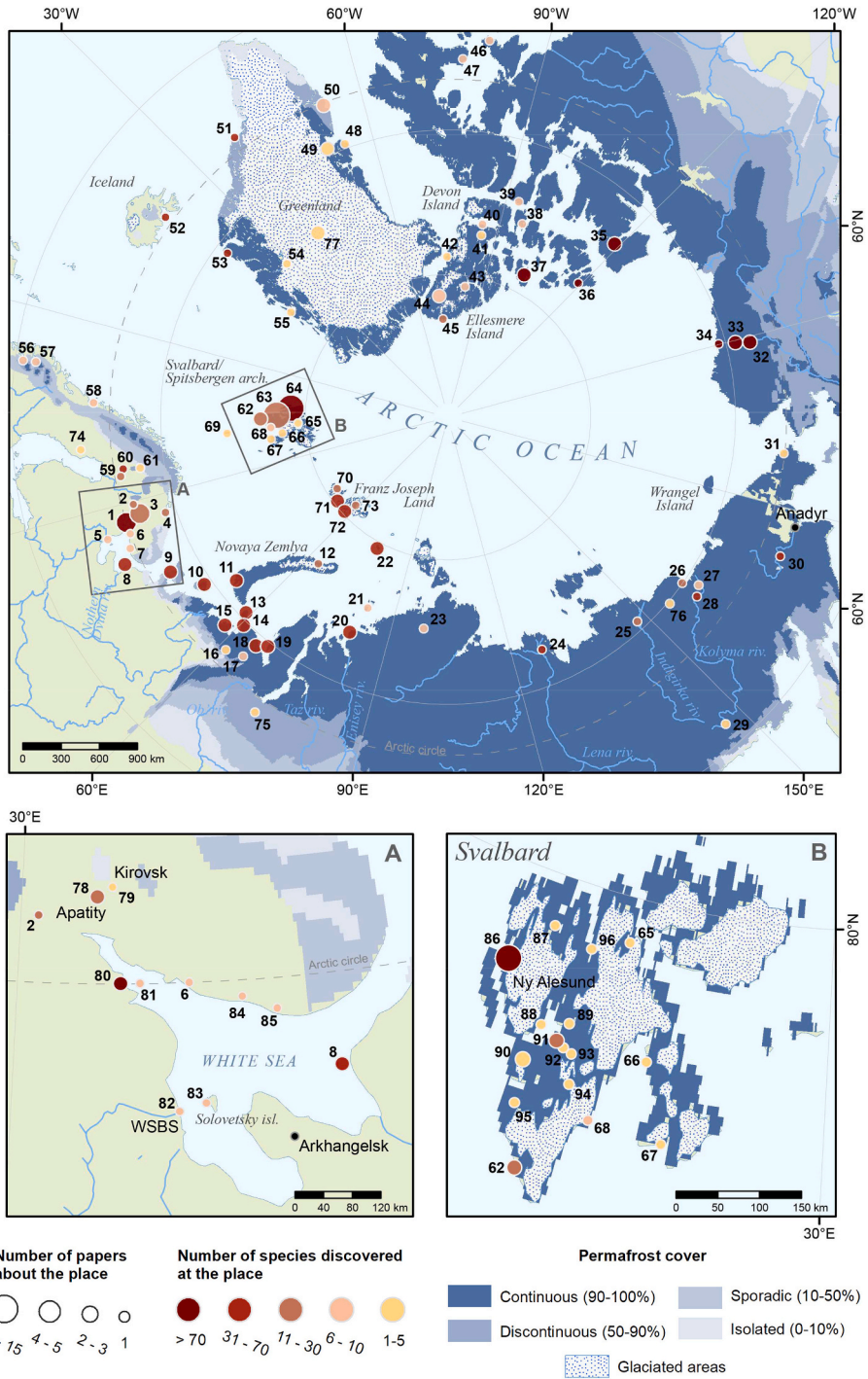
Most fungal species were obtained only from frozen samples, but this was also the most common way to store samples, while drying was the rarest method (Fig. A.1.1, A.1.2; Tables A.1). Furthermore, we observe that many fungal species were discovered only after samples were stored by any one method (Fig. A.1.1, A.1).

We examined studies in which fungi were detected and identified mainly by one of the following methods: direct cultivation of environmental samples on standard and selective media, or metabarcoding after isolation of eDNA from the samples. After cultivation of the samples identification of the fungi were provided by morphological features or ITS or/and LSU regions of the rDNA sequencing. The majority of fungal species were obtained by cultivation and eDNA sequencing (~45% and ~43%, respectively), and ~10% of the species were found with both approaches. However, of studies to detect fungi, cultivation was used in 78%, eDNA was used in 14%, and both approaches were applied in 3% (Fig. A.1.3, A.1.4). Approximately ~59% of the discovered fungi species were identified by the rDNA sequencing method, while ~24% of species were identified using morphological features. Both methods were used to identify ~14% of species (Fig. A.1.5). Approximately equal numbers of fungal species were identified by molecular and morphological methods, while only in 5% of the cases both methods were used (Fig. A.1.5, A.1.6).

4.3. Effect of storage and detection methods on the discovered composition of fungi

The complex of methodological approaches for storing and analysing samples undoubtedly affects the result of detecting and identifying fungi (Bölter et al., 2002; Frisvad, 2008). To reveal the most complete picture of species diversity, distribution, quantity, and ecological role of fungi, long-term studies of the most diverse types of substrates (Kochkina et al., 2012) are needed, in numerous replications and throughout all seasons, as seasonal conditions and vegetation directly affect the fungal community (Wallenstein et al., 2007). Despite the wide range of different sample types studied in polar regions (Tables 1, A1), usually only a small number of them were analyzed in each individual study, and most studies were conducted only once. In addition, a significant part of the polar regions has not been studied at all (Figs. 1 and 2).

The method and duration of storage of samples affect the detection of the fungal community (Cui et al., 2014; Delavaux et al., 2020; Frisvad, 2008). Presumably, during freezing and drying, some species and colony-forming units (CFU) are lost, and during long-term storage of cooled samples the fungal community changes since growth of some species continues. Studies showing the effect of sample drying on the number or detected colonies and fungal species were not found. Nikitin et al. (2017) conducted a study showing the effect of sample storage temperature on the length of mycelium visible under a microscope and the number of fungal spores in soil samples. He recommends dividing each sample into several parts and storing each part at different temperatures (+5, -18 ... -20, -70 ... -80°C) separately. Each of these temperature values had a different effect on the preservation of mycelia length and number of spores (Nikitin et al., 2017). The effect of storing samples at low temperatures on the overall picture of the fungal community may seem unlikely to be significant when studying fungi from the polar regions, since psychrophilic and psychrotolerant species will



(caption on next page)

Fig. 1. The map of Arctic with locations of the investigations; 1 – (Bubnova, 2017; Bubnova and Velikanov, 2004; Grum-Grzhimaylo et al., 2016, 2018); 2 – (Santalahahti et al., 2018); 3 – (Korneykova et al., 2022, 2020; Tkachenko, 2013); 4 – (Bubnova and Konovalova, 2018); 5, 6, 7 – (Bubnova, 2017); 8, 9, 10, 11 – (Kirtsideli et al., 2011, 2016; Nikitin, 2021); 13,14,15 – (Kirtsideli et al., 2011, 2016); 16 – (Lapteva et al., 2017); 17 – (Kirtsideli et al., 2010); 18, 19, 20 – (Kirtsideli et al., 2011, 2016); 21 – (Kirtsideli et al., 2014); 22 – (Kirtsideli et al., 2011, 2016); 23 – (Kirtsideli, 1999); 24 – (Blanchette et al., 2016); 25 – (Miyamoto et al., 2022); 26 – (Ozerskaya et al., 2008); 27 – (Stakhov et al., 2008); 28 – (Bellemain et al., 2013); 29 – (V. Iliushin et al., 2022); 30 – (Bellemain et al., 2013); 31 – (Lydolph et al., 2005); 32 – (Geml et al., 2012; Semenova et al., 2015, 2016; Timling et al., 2014); 33 – (Dunleavy and Mack, 2021; Geml et al., 2012; Timling et al., 2014); 34 – (Timling et al., 2014); 35 – (Geml et al., 2012; Timling et al., 2014); 36 – (Timling et al., 2014); 37 – (Geml et al., 2012; Timling et al., 2014); 38, 39, 40 – (Robicheau et al., 2019); 41 – (Jurgens et al., 2009); 42 – (Day et al., 2006); 43 – (Osono et al., 2012); 44 – (Jurgens et al., 2009; Blanchette et al., 2021; Smith et al., 2004); 45 – (Tsuji et al., 2022); 46, 47 – (Robicheau et al., 2019); 48 – (Meyling et al., 2012); 49 – (Meyling et al., 2012; Pedersen et al., 2020); 50 – (Perini et al., 2019, 2021); 51, 52, 53 – (Blanchette et al., 2016); 54, 55 – (Meyling et al., 2012); 56 – (Borchhardt et al., 2019); 57, 58 – (Bjorbækmo et al., 2010); 59 – (Santalahahti et al., 2018); 60 – (Poosakkannu et al., 2017); 61 – (Juottonen et al., 2020); 62 – (Borzęcka et al., 2022; Botnen et al., 2020); 63 – (Botnen et al., 2020; Iliushin, 2020; V. A. Iliushin et al., 2022; Kurek et al., 2007; Lorberau et al., 2017); 64 – (Botnen et al., 2020; Edwards et al., 2013; Frossard et al., 2021; Geml et al., 2012; Gunde-Cimerman et al., 2003; Perini et al., 2021; Singh et al., 2012, 2015; Tsuji et al., 2016; Zalar et al., 2008; Zhang et al., 2015a, 2015b; Zhang and Yao, 2015; Svalbardkatalogen, 1996); 65, 66, 67 – (Botnen et al., 2020); 68 – (Bjorbækmo et al., 2010); 69 – (Crous et al., 2022); 70 – (Nikitin and Semenov, 2022); 71 – (Bergero et al., 1999; Nikitin and Semenov, 2022); 72 – (Bergero et al., 1999; Kirtsideli et al., 2011; Nikitin and Semenov, 2022); 73 – (Bergero et al., 1999); 74 – (Conery, 2021); 75 – (Yakushev et al., 2019); 76 – (Kochkina et al., 2011); 77 – (Knowlton et al., 2013; Ma et al., 1999); 78 – (Korneykova et al., 2020, 2022); 79 – (Tkachenko, 2013); 80 – (Bubnova and Velikanov, 2004; Grum-Grzhimaylo et al., 2016, 2018); 81 – (Bubnova and Konovalova, 2018); 82, 83, 84, 85 – (Bubnova, 2017); 86 – (Botnen et al., 2020; Edwards et al., 2013; Frossard et al., 2021; Geml et al., 2012; Gunde-Cimerman et al., 2003; Perini et al., 2021; Singh et al., 2012, 2015; Tsuji et al., 2016; Zalar et al., 2008; Zhang et al., 2015a, 2015b; Zhang and Yao, 2015; Svalbardkatalogen, 1996); 87, 88, 89 – (Botnen et al., 2020); 90 – (Iliushin, 2020; V. A. Iliushin et al., 2022); 91 – (Botnen et al., 2020; Lorberau et al., 2017); 92, 93, 94 – (Botnen et al., 2020); 95 – (Kurek et al., 2007); 96 – (Botnen et al., 2020).

be common. However, mesophilic species are active during the growing season in the polar regions. Therefore, when samples are stored at low temperatures, they are suppressed by cold-loving ones, which results in an overall distorted picture. Thus, it is ideal to use all methods of sample storage or to study the samples quickly after collecting to obtain a complete picture of fungal species diversity.

Moreover, the methods of fungal detection in substrates strongly influence the results of fungal species composition (Frisvad, 2008). When using the culture-based approach, only cultivable fungal species are isolated. In practice, 1 % is easily cultivable using standard lab protocols (Frey et al., 2016), although it has been estimated that 2/3 of all fungi can in principle be cultivated (Arenz and Blanchette, 2011). Furthermore, species composition and quantity of isolated fungi using culture-based approaches are affected by the number of samples and their dilution, the repetition of each sample seeding, the composition of nutrient media (Arenz et al., 2006), and cultivation conditions (Kochkina et al., 2012). The temperature of cultivation influences the detection of psychrophilic or mesophilic fungi (e.g., McRae 1999 and Seppelt, 1999; Weinstein, 1997), while different pH values can detect acid-tolerant or acidophilic species (Grum-Grzhimaylo, 2016, 2018). The application of molecular methods has made it possible to understand the non-cultivable fraction (Frey, 2016). By using metatranscriptomic analysis of extremely short-lived mRNA, it is more likely to detect fungi that were in an active stage during sample collection. However, in most studies, samples are analyzed through the extraction of total DNA, which can remain preserved for thousands of years in permafrost soils (Coolen and Orsi, 2015). Additionally, the results of fungal detection by DNA depend on many analytical variables, such as sample volume and amount, DNA extraction methods, primers for PCR and sequencing technology, fungal life cycle stages, and other factors (Tedersoo et al., 2021).

Cultivation methods suffer from several disadvantages. On the one hand, many of the species obtained through cultivation were not in an active state under natural conditions; however, their isolation from the substrate enables a deeper examination of the physiology of these fungi in laboratories (Arai et al., 2022; E. A. Ianutsevich et al., 2023; Elena A. Ianutsevich et al., 2023), as well as sequencing and studying their genomes (Coleine et al., 2017, 2020), creating databases and culture collections (Kochkina et al., 2021). On the other hand, although collection of fruiting bodies of basidiomycetes confirms their activity, it does not give a clear idea of the distribution and biomass, since the fruiting bodies are formed irregularly and it is not clear how much mycelium is present in the material. Furthermore, numerous fungi are in symbiosis with higher plants (Vohník, 2020; Charya and Garg, 2019) and others infect plants (Doehlemann et al., 2017) and animals (Gnat et al., 2021) and these species frequently cannot be cultivated on standard nutrient

media, and their detection and identification is feasible either through direct microscopy or molecular methods, which are constrained by insufficient genomic data and primarily rely on identification to higher taxonomic categories than the species level.

Many studies we examined used either culture methods or eDNA isolation from samples. We were able to find single studies in which several approaches would be applied simultaneously. Arenz et al. (2006) used culture-based and molecular methods to study anthropogenic samples of wood, artifacts including straw, paper, floor, rope, burlap collected butter, biscuits, and soils in Antarctica. They analyzed 164 samples by plating them on three different culture media and 48 of these samples were analyzed using denaturing gradient gel electrophoresis (DGGE). In total, 284 fungal ITS sequences were identified; including 184 from culturing and 100 from DGGE. In summary, 25 taxa were detected by traditional culturing methods and not by DGGE. Conversely, 28 taxa, including the four unknown types, were detected and identified by DGGE and not by culturing (Arenz et al., 2006). Malosso et al. (2006) analyzed soils from Antarctica using molecular methods and by cultivating the same soil samples on nutrient media. Nucleic acids from both the community DNA and colony extracts were amplified using PCR with primers specific to the 18S rRNA gene. Amplicons were separated on denaturing gradient gels (DGGE) or after restriction digestion with endonucleases (ARDRA). The obtained fungal clones, showing unique ARDRA and DGGE bands, were sequenced. The fungal species compositions obtained from the same samples varied depending on the fungal detection method utilized (Malosso et al., 2006). Kochkina et al. (2012) analyzed 36 samples of ancient deposits from Antarctica using a diverse range of culture-based techniques, and for nine samples, they employed both culture-based and molecular approaches. When using culture-based methods, fungi were not found in about half of the samples, and total-DNA was only isolated from one third of the analyzed samples. Both culture-based and molecular methods were able to identify fungi from only one sample, while no common fungal species were identified by both methods. These data indicate that different species are identified using different methods (Kochkina et al., 2012). Pudasaini et al. (2017) explored the microbial diversity of an ice-free Antarctic desert using traditional cultivation methods, an approach of the soil substrate membrane system (SSMS; Ferrari et al., 2005), and culture-independent 454-tag pyrosequencing for 18 soils samples. This study found that fungal OTUs were not shared between culture-dependent and independent techniques. A total of 663 fungal OTUs were recovered using three approaches with distinct methods, yet not a single common OTU was identified across all three methods (Pudasaini et al., 2017). Selbmann et al. (2021) investigated Antarctic cryptoendolithic black fungi using cultivation and the high-throughput sequencing approaches. "Both methods applied showed advantages

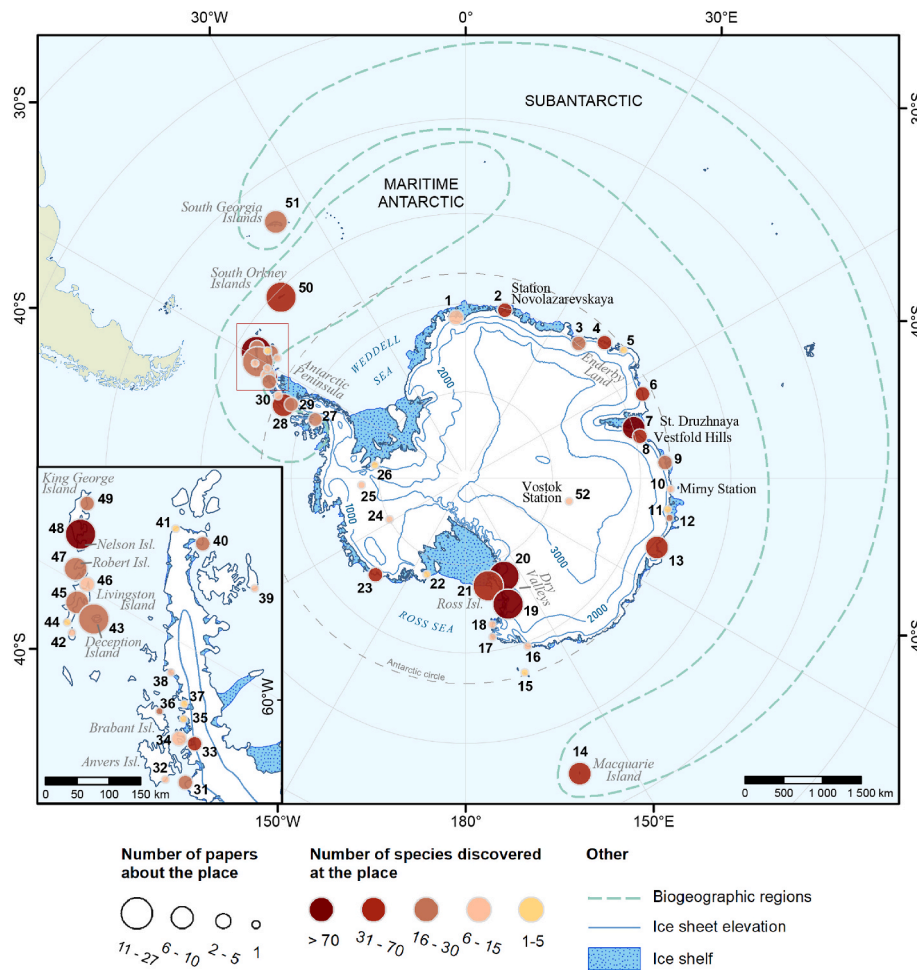


Fig. 2. The map of Antarctica with locations of the investigations; 1 – (Ryan et al., 1989; Steele et al., 1994); 2 – (Kochkina et al., 2012, 2014; Nikitin, 2018; Singh et al., 2006); 3 – (Hirose et al., 2013, 2016; Tsuji et al., 2013; Tubaki, 1961); 4 – (Kochkina et al., 2019; Nikitin, 2018); 5 – (Hirose et al., 2016); 6 – (Fletcher et al., 1985; Kerry, 1990; Line, 1988); 7 – (Brunati et al., 2009; De Hoog et al., 2005; Ellis, 1980; Kerry, 1990; Kochkina et al., 2012, 2014, 2019; Line, 1988); 8 – (Kochkina et al., 2019; Marfenina et al., 2016; Nikitin, 2018); 9 – (Brunati et al., 2009; Kochkina et al., 2012); 10 – (Kochkina et al., 2014); 11 – (Olech and Alstrup, 1996); 13 – (Azmi and Seppelt, 1998; Chambers et al., 1999; Ellis, 1980; Kerry, 1990; McRae et al., 1999; McRae and Seppelt, 1999; Pudasaini et al., 2017); 14 – (Chambers et al., 1999; Ellis, 1980; Kerry, 1990; Kerry and Weste, 1985; Roddam and Rath, 1997); 15 – (Ellis, 1980); 16 – (Kochkina et al., 2014); 17, 18 – (Arenz and Blanchette, 2011); 19 – (Broady et al., 1987; Coleine et al., 2018; Del Frate and Caretta, 1990; Fenice et al., 1997; Held et al., 2006; Mercantini et al., 1989, 1993; Montemartini Corte et al., 2000; Selbmann et al., 2005, 2008, 2021; Tosi et al., 2002, 2004, 2005; Zucconi et al., 1996); 20 – (Arenz et al., 2006, 2011; Baublis et al., 1991; Brunati et al., 2009; Christner et al., 2003; Coleine et al., 2017, 2018; Connell et al., 2006; De Hoog et al., 2005; Fell et al., 2006; Gilichinsky et al., 2005, 2007; Houbraken et al., 2012; Kochkina et al., 2012, 2021; Kudalkar, 2016; Onofri, 1999; Selbmann et al., 2005, 2008, 2021; Sugiyama et al., 1967; Sun et al., 1978; Tubaki and Asano, 1965; Visagie et al., 2016; Vishniac, 1996; Onofri et al., 2000); 21 – (Alias et al., 2013; Arenz and Blanchette, 2011; Blanchette et al., 2004, 2010; Broady et al., 1987; Connell and Staudigel, 2013; Duncan, 2007; Duncan et al., 2006, 2010; Laichmanová, 2020); 22 – (Zucconi et al., 2012); 23 – (Crous et al., 2019; Kochkina et al., 2012; Marfenina et al., 2016; Nikitin, 2018); 24 – (Knowlton et al., 2013); 25 – (Gonçalves et al., 2017); 26 – (Godinho et al., 2015); 27 – (Hughes and Lawley, 2003; Malosso et al., 2006); 28 – (Arenz and Blanchette, 2011; Bridge et al., 2005, 2008; Christie and Nicolson, 1983; Hughes et al., 2003, 2007; Jumpponen et al., 2003); 29 – (Arenz and Blanchette, 2009, 2011; Christie and Nicolson, 1983); 30 – (Arenz and Blanchette, 2011); 31 – (Christie and Nicolson, 1983; Gray et al., 1982; Gray and Lewis Smith, 1984); 32 – (Arenz and Blanchette, 2011); 33 – (Arenz and Blanchette, 2011; Coleine et al., 2017; Ogaki et al., 2020a); 34 – (Christie and Nicolson, 1983; de Menezes et al., 2019); 35 – (Abneuf et al., 2016); 36 – (Arenz et al., 2011); 37 – (Christie and Nicolson, 1983); 38 – (Brito Devoto et al., 2022); 39 – (Arenz and Blanchette, 2011); 40 – (Arenz and Blanchette, 2011; de Menezes et al., 2019); 41 – (Caretta and Piontelli, 1977); 42 – (de Menezes et al., 2019); 43 – (Abneuf et al., 2016; Alves et al., 2019; Arenz and Blanchette, 2011; da Silva et al., 2022; de Menezes et al., 2019; Gonçalves et al., 2012, 2015, Held and Blanchette, 2017; Lindsay, 1976; Rosa et al., 2020a); 44 – (da Silva et al., 2022); 45 – (Alves et al., 2019; Caretta and Piontelli, 1977; Kostadinova et al., 2009; Litova et al., 2014; Upson et al., 2007); 46 – (Alves et al., 2019; Houbraken et al., 2012; Lucini et al., 2022); 47 – (Abneuf et al., 2016; Alves et al., 2019; da Silva et al., 2022; de Menezes et al., 2017, 2019, Gomes et al., 2018); 48 – (Alves et al., 2019; Bridge and Worland, 2004; Caretta and Piontelli, 1977; Crous et al., 2021a, 2021b, Czarnecki and Biasiewicz, 1987; da Silva et al., 2022; de Carvalho et al., 2020; de Menezes et al., 2019; Ding et al., 2016; Gomes et al., 2018; Gonçalves et al., 2012, 2015, Kochkina et al., 2012, 2019, Krishnan et al., 2016; Lucini et al., 2022; Möller and Dreyfuss, 1996; Nikitin, 2018; Ogaki et al., 2020b; Schubert et al., 2007; Stchigel et al., 2001; Upson et al., 2007, 2003, Wang et al., 2015; Yu et al., 2014; Bertini et al., 2022); 49 – (Alves et al., 2019; Crous et al., 2013, 2017; Gomes et al., 2018); 50 – (Bailey and Wynn-Williams, 1982; Bridge and Denton, 2007; Christie and Nicolson, 1983; Duddington et al., 1973; Gaiser et al., 2021; Gray et al., 1982; Gray and Lewis Smith, 1984; Latter and Heal, 1971; Lindsay, 1976; Upson et al., 2007; Weinstein et al., 1997, 2000); 51 – (Bridge et al., 2008; Christie and Nicolson, 1983; Hurst et al., 1983; Lindsay, 1976; Smith, 1994; Upson et al., 2007); 52 – (Knowlton et al., 2013).

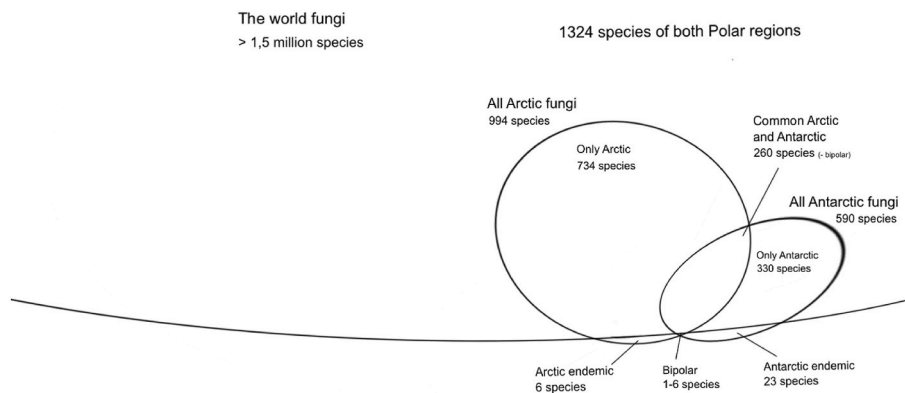


Fig. 3. Schematic illustration of the number of fungal species found in the polar regions.

Table 1
Substrates of fungal isolation.

Substrate	Arctic	Antarctica	Both poles	Only from this substrate (from either of the poles)
Dead material				
Plants (wood material, fallen leave and litter, fossil plants, peat)	193	37	37	86
Animals (corpses, skeleton remains, faeces, feathers)	13	28	6	8
Living material				
Plants (algae, mosses, wood, leaves, herbaceous plants, roots, lichens)	309	179	27	253
Animals (seals)	1	16	0	5
Substrates dominated by organic substances:				
soil, birds spots and nests, lake sediments, microbial mats	454	282	170	449
Substrates dominated by inorganic substances:				
rocks, ice and snow, cryoconites, water	117	38	11	22
Substrates with anthropogenic influence:				
settlements and different materials from its, soil with kerosene and oil, food, coal mine spoils	112	16	25	35
Airborne fungi	17	28	10	8

and disadvantages; for instance, the use of amplicon sequencing captured the diversity of environmental microbiota in deeper detail, but several black fungi that were successfully isolated were not detected by this approach” (Selbmann et al., 2021). Nikitin and Semenov (2022) explored the fungal diversity of the Franz Josef Land archipelago using the classical plating techniques and real-time PCR methods for samples from five islands of the archipelago. They estimated the abundance of fungal rRNA gene ITSs, the CFU numbers, and the taxonomic diversity of culturable micromycetes in cryosols of the islands. The number of copies of the fungal rRNA gene ITS significantly exceeded CFU/g of soil in the same samples (Nikitin and Semenov, 2022). Edwards et al. (2013) investigated the fungal community in Svalbard cryoconite holes with both traditional cultivation methods and multivariate analysis of terminal-restriction fragment length polymorphism (T-RFLP) profiles of rRNA ITS amplicons and showed differences in the results obtained by these different approaches (Edwards et al., 2013). All the authors of the aforementioned studies acknowledge the significance of employing diverse methodologies to attain the most comprehensive identification of the species diversity of fungi. Furthermore, these examples demonstrate that researchers, using different methods can achieve different

and almost incomparable results.

About a half of fungal cultures isolated from the material of the polar regions are sterile mycelium (e.g., Bölter et al., 2002; Kochkina et al., 2012), which limits the drawing of a taxonomic picture. Moreover, many species of fungi are characterized by significant variability in taxonomic characters, and hence their identification by morphology can be difficult (O.A. Grum-Grzhimaylo et al., 2016; Kaitera et al., 2019). These cases require isolation of DNA from the mycelium, followed by sequencing of the internal transcribed spacer (ITS) region, which has been used in the most studies on the diversity of fungi in the polar regions (Fig. A.1.6). However, other difficulties arise when using molecular identification methods. In some cases, the ITS region is not sufficient for identifying species, and other DNA regions require additional sequencing (Bölter et al., 2002). Furthermore, there is not enough information in the databases to identify all detected species with DNA data (Hyde et al., 2010). For these reasons, it is frequently feasible to identify samples based on DNA sequences up to higher taxonomic categories than the species (Tedersoo et al., 2020). It has been noted that it is useful to combine molecular techniques and morphological observations to identify many fungal species (Baturó-Cieśniewska et al., 2020). The limitation of combining these two identification methods is that it is only possible for fungi obtained through cultivation. Even when fungi were detected through cultivation in a very small number of polar studies, they were identified both by morphological features and by sequencing DNA regions (e.g., Grum-Grzhimaylo et al., 2018; O.A. Grum-Grzhimaylo et al., 2016; Kaitera et al., 2019; Kochkina et al., 2019).

It is therefore difficult to obtain an understanding of the biogeography and functioning of fungi living in the Arctic and Antarctic from the available data, obtained by various methods. Therefore, at present we still need to employ multiple methods to get a good picture. More research is needed to understand the relationship between different sampling methods, and particularly to distinguish active mycelia from spores.

Table 2
Abundance of fungal divisions in the polar regions.

Division	No of species		Common for both poles	Total
	Arctic	Antarctica		
Ascomycota	388	279	229	896
Basidiomycota	326	34	12	372
Mucoromycota	20	14	19	53
Glomeromycota	0	1	0	1
Entomophthoromycota	0	1	0	1
Zoopagomycota	0	1	0	1
Total	734	330	260	1324

5. Taxonomy and ecology of fungi in the polar regions

More fungal species have been detected in the Arctic region than in Antarctica (717 and 326 unique species, respectively) and the number of species common to both polar regions was 250 species (Fig. 3), corresponding to approximately 19%. Such differences can be attributed to both the geographical distance between polar regions and the unique ecological characteristics specific to these regions. In this section, we provide a brief comparative overview of the taxonomy of fungal communities in the Arctic and Antarctic, as well as their ecological associations. Additional information about the ecological significance of fungi from our list was taken from 358 articles and 16 Internet resources (Tables A.1).

Table 3

The list of reviews characterizing different groups of fungi and their ecology in polar regions and permafrost.

Titles	References
Microbial Life in Permafrost	Altshuler et al. (2017)
Microbial Life in Supraglacial Environments	Edwards and Cameron (2017)
Heterotrophic Microbes, Microbial and Enzymatic Activity in Antarctic Soils	Bölter et al. (2002)
Arctic soil microbial diversity in a changing world	Blaud et al. (2015)
Permafrost active layer	Dobiński (2020)
Fungi in cold ecosystems	Frisvad (2008)
Mycorrhizal diversity in arctic and alpine tundra: an open question	Gardes and Dahlberg (1996)
Psychrophilic and psychrotrophic fungi: a comprehensive review	Hassan et al. (2016)
How will thawing permafrost affect the microbial abundant and diversity in the Arctic?	Maria and Langvad (2020)
Decomposer Basidiomycota in Arctic and Antarctic ecosystems	Ludley and Robinson (2008)
Microbial diversity and functional capacity in polar soils	Makhalanyane et al. (2016)
Microbial diversity and biogeography in Arctic soils	Malard and Pearce (2018)
Root-associated fungi and carbon storage in Arctic ecosystems	Robinson et al. (2020)
Cold adaptation in Arctic and Antarctic fungi	Robinson (2001)
Snow moulds in polar environments	Tojo and Newsham (2012)
Adapting the changing environment: microbial way of life Trends in yeast diversity discovery	Aley et al. (2022)
Introduced and indigenous fungi of the Ross Island historic huts and pristine areas of Antarctica	Boekhout et al. (2021)
No need for speed: slow development of fungi in extreme environments	Farrell et al. (2011)
Structure and function of alpine and arctic soil microbial communities	Gostinčar et al. (2022)
Mycorrhizas and dark septate root endophytes in polar regions	Nemergut et al. (2005)
Antarctic microfungi	Newsham et al. (2009)
The Role of Ectomycorrhiza in Boreal Forest Ecosystem Biodiversity in the dark: root-associated fungi in the Arctic	Onofri (1999)
Fungi in Antarctica	Qu et al. (2010)
Fungi of Antarctica: Diversity, Ecology and Biotechnological Applications	Botnen (2020)
Resurrection of inactive microbes and resistome present in the natural frozen world: Reality or myth?	Ruisi et al. (2007)
Seasonal dynamics of previously unknown fungal lineages in tundra soils	Rosa et al. (2019)
Antarctic permafrost: An unexplored fungal microhabitat at the edge of life	Sajjad et al. (2020)
Fungi in hot and cold deserts with particular reference to microcolonial fungi	Schadt et al. (2003)
Global diversity and geography of soil fungi	da Silva et al. (2019)
Peeking through a frosty window: molecular insights into the ecology of Arctic soil fungi	(Sterflinger et al., 2012)
Natural products from polar organisms: Structural diversity, bioactivities and potential pharmaceutical applications	Tedersoo et al. (2014)
Microbial Communities and Processes in Arctic Permafrost Environment	Timling and Taylor (2012)
	Tripathi et al. (2018)
	Wagner (2008)

5.1. Taxonomic description and abundance of fungi in the polar regions

There is a large difference between the Arctic region and Antarctica in the distribution of different fungal divisions (Table 2). The highest number of species common to the two poles belongs to the divisions Mucoromycota and Ascomycota (~37% and ~25%, respectively), while shared Basidiomycota species account for only ~3%. According to our data only a few species are known to be endemic to Antarctica or Arctic, and there are 1–6 identified bipolar species, i.e. species occurring at both poles, but not at intermediate latitudes (Fig. 3). General information on the taxonomic composition of fungi found in the polar regions is given in Tables A.3. Ascomycota species represent the largest group of fungi reported from both polar regions. The discovered species belong to 12 classes, and 31 species have an unclear taxonomic position (incertae sedis; Tables A.3). Basidiomycota species are the second-largest taxonomic group of fungi in the polar regions mostly recorded in Antarctica and mainly represented by species belonging to the class *Agaricomycetes* (Tables A.3). The most species-rich were genera *Cortinarius* (Pers.) Gray (65 species), *Inocybe* (Fr.) Fr. (33 species), *Russula* Pers. (28 species), *Lactarius* Pers. (15 species) and *Mycena* (Pers.) Roussel (12 species; Tables A.1, A.3). The biggest part of Mucoromycetes belongs to *Mortierella* Coem. and *Mucor* P. Micheli genera, species of which were found in both polar regions, predominantly in Arctica (Tables A.3).

5.2. A brief sketch of the ecology of fungi in the polar regions

A significant cause of the difference between fungal communities in the Arctic and Antarctic regions, as described in section 5.1, may be the various ecological factors specific to these regions. Interesting reviews characterizing different groups of fungi and their ecology in polar regions and permafrost already exist in scientific literature (Table 3). We did not intend to provide a complete picture of the ecology of fungal communities in polar regions, partly due to the fact that certain ecologically important groups of fungi in polar regions, such as yeasts (Buzzini et al., 2017), snow mold (Hoshino et al., 2019; Tkachenko, 2013), lichenicolous fungi (Brackel, 2010; Brinker, 2020; Santiago et al., 2015), certain species associated with animals (Bridge and Worland, 2004), and many macrofungi (Denchev et al., 2020), were not considered because they were detected using methods that we did not take into account. Another complicating factor in data analysis was that many fungal species can perform multiple roles in ecosystems simultaneously (Tables A.1). To investigate certain patterns of fungal distribution in polar regions based on their ecological associations according to our data, we only included species whose role in ecosystems has been studied the most.

Approximately half of the polar fungal species are saprotrophs (Fig. A.1.7). It is among these species that the greatest number of species shared between both polar regions has been found. The second largest group in the Arctic consists of symbionts, dominated by mycorrhizal species associated with a much larger number of Arctic plant species than Antarctic ones. Pathogenic species for plants and animals follow (Fig. A.1.7). The ecological role of about 8.2% of the identified fungal species remains unknown. Interestingly, approximately 3.5% (47 species) of the identified fungi are known to be pathogenic, as well as potentially or conditionally pathogenic for humans and warm-blooded animals (Fig. A.1.7; da Silva et al., 2022). The list of these species, their frequency of occurrence in studies, and the substrate of detection are provided in Table A.4. It is impossible to determine with certainty how these species reached the polar regions, but it can be assumed that they were introduced by humans, animals, or migratory birds (Table A.4). It is also unknown whether pathogenic fungi are active in polar regions or remain in the form of spores. The presence of thermophilic species, such as *Acaulium caviariforme*, *Collariella gracilis*, *Mycothermus thermophilus*, *Thermomyces lanuginosus*, and *Thermothelomyces thermophiles* (Tables A.1), is intriguing. It can be confidently assumed that with global warming, the activity of both pathogenic species and

thermophilic and thermotolerant species will increase.

It is interesting to compare the fungal complexes of two polar regions isolated from similar substrates, such as drifting wooden material in the Arctic (Blanchette et al., 2016) and wooden structures in Antarctica (Arenz et al., 2006; Blanchette et al., 2004; Duncan et al., 2006; Gaiser et al., 2021), bird feathers from high Canada (Robicheau et al., 2019) and Svalbard (Singh et al., 2015) and Antarctica (Brito Devoto et al., 2022; Del Frate and Caretta, 1990), mosses, vascular plants, and lichens (e.g. (de Carvalho et al., 2020; Jumpponen et al., 2003; Kerry, 1990a; McRae and Seppelt, 1999; Möller and Dreyfuss, 1996; Osono et al., 2012; Park et al., 2015; Rosa et al., 2020b; Tosi et al., 2002; Zhang et al., 2015b), peat (Lapteva et al., 2017; Olga A. Grum-Grzhimaylo et al., 2016; Semenova et al., 2015; Yakushev et al., 2019), ice, snow, and cryoconites (Borzęcka et al., 2022; Christner et al., 2003; Edwards et al., 2013; Gilichinsky et al., 2005; Graciéle C.A. de Menezes et al., 2019; Gunde-Cimerman et al., 2003; Knowlton et al., 2013; Ozerskaya et al., 2008; Perini et al., 2019, 2021; Tsuji et al., 2022), aerial dispersal of fungi (Czarnecki and Bialasiewicz, 1987; Duncan, 2007; Duncan et al., 2010; Kirtsideli et al., 2011; Sun et al., 1978). Interesting comparative descriptions of fungi on plants and mosses in the Arctic and Antarctica are presented in the book by Tsuji and Hoshino (2019) and in the publication by de Carvalho et al. (2020), but they cover a limited number of studies. Separate interest is raised by studies of mycorrhizal fungi and their movement together with symbiotic plants, mainly characteristic of the Arctic (Bjorbækmo et al., 2010; Botnen et al., 2020; Chlebicki et al., 2005; Dunleavy and Mack, 2021; Geml et al., 2012; Kaitera et al., 2019; Lorberau et al., 2017; Miyamoto et al., 2022) and to a lesser extent for Antarctica, as there are only two species of vascular plants (*Colobanthus quitensis* (Kunth) Bartl. and *Deschampsia Antarctica Desv.*), but they also form mycorrhizae (Barbosa et al., 2017; Christie and Nicolson, 1983; Lucini et al., 2022; Upton et al., 2008). The results of studies on the biogeography of fungi along transects from temperate to cold latitudes (Timling et al., 2014), the adaptive features of fungi in polar regions, such as optimal temperature for growth (Alias et al., 2013; da Silva et al., 2022; Gaiser et al., 2021; Kerry, 1990b; Kostadinova et al., 2009; Krishnan et al., 2016; Latter and Heal, 1971; Litova et al., 2014; Lucini et al., 2022; Singh et al., 2006; Stakhov et al., 2008; Tosi et al., 2002; Wang et al., 2015; Weinstein et al., 1997, 2000; Zucconi et al., 1996, 2012), their enzymatic and antimicrobial activity (Abneuf et al., 2016; Ding et al., 2016; Duncan, 2007; Duncan et al., 2006; Krishnan et al., 2016; Lindsay, 1976; Mercantini et al., 1993; Montemartini Corte et al., 2000; Singh et al., 2012), resistance to extreme factors such as high UV radiation and radiation, freezing, dryness, oligotrophic conditions (Bergero et al., 1999; Fell et al., 2006; Gunde-Cimerman et al., 2003; Hughes et al., 2003; Sazanova et al., 2019; Selbmann et al., 2008, 2015; Singh et al., 2006; Tosi et al., 2005; Tsuji et al., 2013), their associations with vertebrates and invertebrates (Bridge and Denton, 2007; Bridge et al., 2005; Bridge and Worland, 2004; Brito Devoto et al., 2022; Meyling et al., 2012; Roddam and Rath, 1997), as well as the physiological response of fungi to global warming (Geml et al., 2015; Semenova et al., 2015; Tosi et al., 2005; Weinstein et al., 2000), changes in snow cover thickness (Morgado et al., 2016), succession dynamics (Juottonen et al., 2020; Kerry and Weste, 1985; Poosakkannu et al., 2017), changes in fungal communities due to anthropogenic influence (Blanchette et al., 2004, 2010; Czarnecki and Bialasiewicz, 1987; Gaiser et al., 2021; Kirtsideli et al., 2016; Korneykova et al., 2022; Line, 1988; Ogaki et al., 2020; Tsuji et al., 2022) undoubtedly deserve attention.

It is impossible not to mention the works relating to paleontological studies of fungi in polar regions. For example, we encountered such an interesting case: *Eucasphaeria capensis*, firstly obtained in South Africa in living leaves and leaf litter of *Eucalyptus* sp. and described by Crous et al. (2007), was detected by metabarcoding of DNA in ancient arctic permafrost a few years later (Bellemain et al., 2013). Analysis of paleontological studies can help understand the biogeography of fungi in polar regions hundreds and thousands of years ago (Bellemain et al.,

2013; Gilichinsky et al., 2007; Knowlton et al., 2013; Lydolph et al., 2005; Ma et al., 1999; Ozerskaya et al., 2008; Stakhov et al., 2008).

Thus, a more detailed description of the ecological role and adaptive features of fungi in polar regions deserves a separate research work.

6. Are these fungi endemic?

Some fungi in polar regions have not been recorded in other parts of our planet. Fungi that occur only in one of the polar regions, according to one definition of endemism (Shiple and McGuire, 2022), will be referred to as endemic species in this work. For the Arctic, this will be the area within the polar circle, and for Antarctica, it will be the continent itself and the islands of the Antarctic and sub-Antarctic seas. Species known in both polar regions but not recorded in other parts of the planet will be referred to as bipolar endemics (Cox et al., 2016).

When attempting to assess the presence and number of endemic species and bipolar endemics, we encountered several problems: 1) some species that were originally described as Antarctic fungi (e.g., *Penicillium antarcticum*, *Drechmeria coniospora*, *D. obovata*, *Phialophora dancoi*, *Sclerococcum dobrowolskii*, *Thelebolus mircosporus*) were later found in other regions, in certain instances including the Arctic (e.g., *Conidiobolus antarcticus*, *Drechmeria balanoides*, and *Thelebolus ellipsoideus*), or only in the Arctic, making them bipolar endemics (*Acrodontium antarcticum*, *Antarctomyces pellizariae*, *A. psychrotrophicus*, *Cadophora antarctica*, *Cladosporium antarcticum* and *Mortierella antarctica*); 2) species that were once considered boreal and only found in the circumpolar regions of the Arctic and subarctic zones have since been discovered in high mountainous areas (e.g., *Inocybe arctica*, *I. borealis*); (Cripps and Horak, 2006; Kokkonen and Vauras, 2012), or known from Antarctic and high alpine areas (e.g., *Psychrophila antarctica*, Wang et al., 2015); 3) there are species that were previously considered bipolar endemics but were later found in other places, such as *Penicillium amphipolaria*; 4) as the number of studies analyzed increased, the number of unique fungal species for the poles decreased, and more species became common to both the Arctic and Antarctic; 5) the later the species were described, the fewer regions they were recorded from, suggesting that over time, the unique fungal species presently found in polar regions may be discovered in other places. All of these issues are closely linked to researchers' noted incomplete understanding of fungal distribution worldwide (Tedersoo et al., 2021), and especially in polar regions (e.g., Bridge and Spooner, 2012; Cox et al., 2016; Newsham et al., 2016), so the concept of endemic fungal species has to be considered relative and tentative.

In this section, we have attempted to gather information about fungal species that are currently considered endemic to polar regions, or were believed to be so for a long time until they were found at the opposite pole or in inter-polar regions.

6.1. Characteristic Antarctic fungi

Antarctica, along with its surrounding islands, represents extreme and well-isolated regions on our planet that are challenging for survival. As a result, unique plant and animal communities have formed here. It would be logical to expect unique fungi in this area, many of which are parasitic and symbiotic species that are commonly found in association with plants and animals. The distribution of saprotrophic fungi, as heterotrophic organisms that feed on ready-made organic materials, is closely associated with the presence of suitable substrates, whose chemical composition is closely linked to the enzymatic apparatus of fungi capable of breaking down specific substances thus determining substrate specialization. Extreme sub-zero temperatures, dryness, and intense UV radiation also have a significant impact on the growth and metabolic activity of Antarctic fungi. The complex combination of these factors determines the species composition of fungi inhabiting this area.

Out of the more than 300 Antarctic fungi we have found in various studies, 23 species in the table are considered endemic until today. Part of these species are actively being studied, while others have only been

Table 4
Endemic fungal species of Antarctica; endolithics are in bold.

Species of fungi (modern names from the Index Fungorum)	Names of species from articles (archaic), if different	Substrate of detection	Ecology	References
<i>Acremonium psychrophilum</i>	–	Lichens	Lichenicolous, psychrophilic	(Etayo et al., 2023; Möller and Dreyfuss, 1996; Vishniac, 1996)
<i>Apenidiella antarctica</i>	–	Permafrost soil	n.i.	Crous et al. (2019)
<i>Arthroderma magnisporum</i>	<i>Chrysosporium magnisporum</i>	Bird pellet	Keratinolytic, psychrotolerant	Crous et al. (2013)
<i>Arthroderma oceanitis</i>	<i>Chrysosporium oceanitesii</i>	Dead bird, lake sediments	Keratinolytic, psychrotolerant	(Crous et al., 2013; Ogaki et al., 2020a)
<i>Chalara antarctica</i>	–	Rhizosphere of <i>Deschampsia antarctica</i> and <i>Colobanthus quitensis</i>	Vascular plant associated	(Newsham et al., 2020; Onofri, 1999; Vishniac, 1996)
<i>Cladosporium australitorale</i>	–	Coastal sea sand	Saprotrophic, psychrotolerant	Crous et al. (2021b)
<i>Comoclathris antarctica</i>	–	Soil	n.i.	Crous et al. (2021a)
<i>Cryomyces antarcticus</i>	–	Sandstone, soil, rocks	Endolithic, psychrophilic	(Nikitin, 2023; Selbmann et al., 2005)
<i>Cryomyces minteri</i>	–	Soil	Endolithic, psychrophilic	Selbmann et al. (2005)
<i>Drechmeria bactrospora</i>	<i>Acrostalagmus bactrosporus</i>	Soil with <i>Deschampsia antarctica</i>	Endoparasitic nematophagous	Gray and Lewis Smith (1984)
<i>Extremus antarcticus</i>	<i>Extremus antarcticus</i>	Rocks, sandstones	Endolithic	Selbmann et al. (2021)
<i>Friedmanniomyces endolithicus</i>	–	Granite or pegmatite, sandstone, rocks, soil	Endolithic, psychrophilic	(Nikitin, 2023; Onofri et al., 1999; Selbmann et al., 2005)
<i>Friedmanniomyces simplex</i>	–	Sandstone	Endolithic, psychrophilic	(Nikitin, 2023; Selbmann et al., 2005)
<i>Humicola marvinii</i>	–	Soil	Psychrophilic	(Weinstein et al., 1997, 2000)
<i>Jugulospora antarctica</i>	<i>Apiosordaria antarctica</i>	Soil, bird colonies	Bird associated	(Nikitin, 2023; Stchigel et al., 2003)
<i>Laetinaevia colobanthi</i>	–	Plant tissues	Plant associated	Onofri (1999)
<i>Paecilomyces antarcticus</i>	–	Invertebrate animals (springtail)	Entomogenous	(Bridge et al., 2005; Song et al., 2017)
<i>Psychronectria hyperantarctica</i>	<i>Thyronectria antarctica</i> var. <i>hyperantarctica</i>	Mosses	Bryophilous	(Hawksworth, 1973; Hoshino et al., 2019; Pawlowska et al., 2017; Rosa et al., 2020b, 2021)
<i>Rachicladosporium antarcticum</i>	–	Rocks	Endolithic	(Coleine et al., 2017; Laichmanová, 2020)
<i>Rachicladosporium mcmurdoi</i>	–	Rocks, sandstones	Endolithic	Selbmann et al. (2021)
<i>Rhizophagus antarcticus</i>	<i>Glomus antarcticum</i>	Plants roots	Endomycorrhizal	(Barbosa et al., 2017; Cabello et al., 1994)
<i>Sclerotinia antarctica</i>	<i>Sclerotium antarcticum</i>	Soil, <i>Deschampsia antarctica</i>	Plant associated	(Bridge et al., 2008; Hoshino et al., 2019; Onofri, 1999)
<i>Trichocladium antarcticum</i>	<i>Thielavia antarctica</i>	Lichens, birds spots, lake sediments	Lichen associated, bird associated, psychrotolerant	(Stchigel et al., 2003; Ogaki et al., 2020a; Nikitin, 2023; van den Brink et al., 2015)

found in Antarctic substrates, described and studied little. The characteristic Antarctic fungi identified in these studies were isolated from typical substrates in this region, such as plants, lichens, soil, lake sediments, bird and insect waste, nematodes, and rocks. Among the species with certain physiological characteristics, keratinophilic fungi have been identified, which can potentially degrade animal keratin structures, and psychrophilic and psychrotolerant fungi, capable of functioning at low temperatures (Table 4).

A separate group represents fungi associated with typical and endemic Antarctic plants. De Carvalho et al. (2020), studying the cultivable fungi in mosses, demonstrated that mosses provide a favorable habitat for survival, colonization and establishment of symbionts and decomposer fungi in various extreme Antarctic conditions. However, no endemic fungi were found in this study, except for the species *Antarctomyces psychrotrophicus*, but according to our data, the endemism of this species is disputable, which will be discussed below. The authors also note that the mycobiota of Antarctic mosses is poorly understood, and further research is likely to lead to the discovery of new fungal species (de Carvalho et al., 2020). Osono et al. (2019) investigated the mycobiota of mosses and dead tissues of introduced *Salix* spp. in Antarctica and compared it with the mycobiota of the same substrates in the Arctic. They identified several similarities and differences, but no endemic fungi were found in their study. There are studies of fungi causing diseases in Antarctic moss "fairy ring", among which the species *Psychronectria hyperantarctica* is noted, known only for Antarctica to date (Graciéle Cunha Alves de Menezes et al., 2019; Pawlowska et al., 2017; Rosa et al., 2020b). The parasitic species *Sclerotinia antarctica* and *Laetinaevia colobanthi* were isolated from the two known and endemic Antarctic vascular plants *Deschampsia antarctica* and *Colobanthus*

quietensis, respectively, and has not been reported elsewhere in the literature. However, Hoshino et al. (2019), noting *S. antarctica* morphological similarity to the Arctic species *S. borealis*, suggest that a comparative study of these two species is necessary.

The parasitic fungus *Paecilomyces antarcticus* was isolated from the Antarctic springtail *Cryptopygus antarcticus* and described by Bridge et al. (2005). We could not find mentions of this species elsewhere, but it is possible that this fungus associated with the Antarctic springtail inhabits only its habitats - Antarctica, subantarctic islands, and Australia. The genome study of *C. antarcticus* by Song et al. (2017) shows that *C. antarcticus* contains an endogenous fungal gene acquired through horizontal transfer from a fungal parasite to its host. The authors also demonstrated the potential for horizontal transfer of cellulase genes from fungal parasites to hosts at an early stage of evolution in distantly related species of Arctic (*Onychiurus arcticus*) and Antarctic (*C. antarcticus*) springtails. We were unable to find other studies of parasitic fungi in Arctic springtails to determine the species of these fungi. However, the studies by Song et al. (2017) indicate long-term coevolutionary relationships between fungi and springtails, suggesting that fungi associated with endemic springtail species (and other animals) may also be endemic. Overall, a very limited number of studies on fungi associated with Antarctic animals have been noted (Simões et al., 2019), although potentially new and endemic fungal species could exist in this niche.

The study of the physiology of cryptoendolithic fungi, isolated from rocks, has become a topic of significant interest among researchers. Cryptoendolithic microorganisms form a small community that has adapted to live inside rocks in the smallest pores of rocks up to 10 mm deep, where conditions are milder than outside. Cryptoendolithic fungi

have a melanized, thick-walled mycelium that protects against desiccation and intense UV radiation and have a highly reduced morphology with scarce differentiation. Exopolysaccharides secreted by hyphae may also protect them from desiccation and frost. As the living conditions of Antarctic cryptoendolithic fungi are believed to be similar to those on Mars, their physiological and genetic characteristics are actively studied. Selbmann et al. (2005) described four cryptoendolithic species (*Cryomyces antarcticus*, *C. minteri*, *Friedmanniomyces endolithicus*, *F. simplex*), among which *F. endolithicus*, noted as the most common and well adapted species to the harshest conditions of the Antarctic cryptoendolithic community (Selbmann et al., 2005), is studied the most intensively. *F. endolithicus* has been shown to be resistant to acute doses of gamma radiation, accompanied by an increase in metabolic activity (Pacelli et al., 2018). Coleine et al. (2020) sequenced the genome of *F. endolithicus* to study gene content and genomic patterns that can be associated with its specialization and found that some stress-resistance features, such as meristematic growth and cold tolerance, are enriched in *F. endolithicus*, which could be attributed to the adverse conditions of Antarctica. They also identified genomic features in response to salt, X-ray radiation, cold, and DNA damage, confirming the exceptional polyextremotolerance and ability to survive various stresses of this species.

The cryptoendolithic species *Cryomyces antarcticus* has been extensively studied for over a decade (Onofri et al., 2020). The genome project of *C. antarcticus* has been published (Sterflinger et al., 2014), and analysis of the genome did not reveal significant deviations from mesophilic fungi, but it suggests that the fungus possesses a unique set of previously unknown proteins that exhibit high stress resistance. The authors emphasize the need for a deep analysis of the *C. antarcticus* genome (Sterflinger et al., 2014). Selbmann et al. (2011) found that the DNA of *C. antarcticus* and *C. minteri* species exhibited high resistance to prolonged (up to 240 min) UV-B radiation compared to *Saccharomyces pastorianus*. Studies have been published on the radiation-protective pigments melanin of *C. antarcticus*, demonstrating its enhanced radioresistance (Pacelli et al., 2020). This fungus also maintained survival, DNA integrity, ultrastructure stability, and rapid recovery of metabolic activity after 18 months of exposure to space and Martian conditions in low-Earth orbit (Onofri et al., 2020). The authors of these studies note that their findings have astrobiological value and warrant reconsideration of the possibility of extraterrestrial life. *Rachicladosporium antarcticum*, *R. mcmurdoi* and *Extremus antarcticus* appears to be the least endolithic species studied for now (Table 4).

Table 5
Endemic fungal species of Arctic.

Species of fungi (modern names from the Index Fungorum)	Substrate of detection	Ecology	References
<i>Comoclathris arctica</i> ^a	Plants: <i>Festuca brachyphylla</i> , <i>Puccinellia angustata</i>	Plant parasitic	(Crous et al., 2021a; Shoemaker and Babcock, 1992)
<i>Monodictys arctica</i>	Roots of <i>Saxifraga oppositifolia</i> , lichens, plant tissues, soil, lake water	Endophytic, lichen associated, water	(Day et al., 2006; Timling et al., 2014; Zhang et al., 2015a, 2015b; Zhang and Yao, 2015)
<i>Penicillium arcticum</i> ^a	Ice, water	Saprotrophic	Gunde-Cimerman et al. (2003)
<i>Penicillium svalbardense</i>	Ice, water	Saprotrophic, psychrotolerant	Gunde-Cimerman et al. (2003)
<i>Penicillium groenlandense</i> ^a	Ice, water	Saprotrophic	Gunde-Cimerman et al. (2003)
<i>Psychromyces glacialis</i>	Ice, cryoconite	Psychrophilic	Perini et al. (2021)

^a these names are not on the Indexfungorum or are outdated.

Based on these findings, it can be summarized that the Antarctic region harbors scientifically intriguing fungal species, including those with potential biotechnological applications. However, further research is needed to explore the overall diversity of fungi in Antarctica, as well as in similar habitats, to ascertain the endemism of Antarctic species. Additionally, the physiology and genome of the fungi already described in Antarctica require further investigation.

6.2. Characteristic Arctic fungi

The identification of information about endemic fungi in the Arctic has proven to be more challenging than the search for Antarctic endemics. This may be due to the fact that the investigated Arctic regions are less isolated, except for islands, many of which have been sporadically or not studied at all for their mycota. Additionally, the Arctic region is inhabited by numerous mycorrhizal fungal species, the distribution of which is often studied by collecting fruiting bodies or direct microscopy, which was not included in this review. As a result of our study, only a few unique fungal species specific to the Arctic region were identified (Table 5), and there is practically no information about these species. The parasitic fungus *Comoclathris arctica*, which parasitizes herbaceous plants, is known from the high Arctic of Canada (Shoemaker and Babcock, 1992). The name of this species in Index Fungorum is marked as obsolete (<http://www.indexfungorum.org/Names/NamesRecord.asp?RecordID=360252>), and no DNA sequences or other studies of this fungus could be found. The species *Monodictys arctica* was found in the roots of *Saxifraga oppositifolia* in the high Arctic of Canada in 2006 and described by Day et al. (2006). It was later found in Alaska (Timling et al., 2014) and Svalbard (Zhang et al., 2015a, 2015b; Zhang and Yao, 2015), but we could not find any mentions of its distribution in other regions. Three species of the genus *Penicillium* (*P. arcticum*, *P. groenlandense*, *P. svalbardense*) were discovered and identified as potentially new to science by Gunde-Cimerman et al. (2003) in the ice and seawater of Svalbard. We could not find any further mentions of *P. arcticum*, including its name in Indexfungorum or DNA sequences in the GenBank. *P. svalbardense* was described as a new species a few years later and noted as psychrotolerant (Sonjak et al., 2007), but we could not find more information about its distribution and physiology. The dimorphic fungus *Psychromyces glacialis* was recently discovered in the ice and cryoconites of Svalbard and Greenland, and described and noted as psychrophilic by Perini et al. (2021). Arai et al. (2022) isolated and characterized proteins from *P. glacialis* that bind ice, which are necessary for the fungus to survive freezing temperatures.

6.3. Bipolar endemic fungi

Fungi that we refer to as putative bipolar endemics were identified by researchers exclusively in two polar regions. We were able to identify six such species of fungi (Table 6), while Cox et al. (2016), through the analysis of Antarctic fungal eDNA (ITS region) and comparison with similar data from other regions, discovered approximately 20 bipolar fungi identified to the genus or higher taxonomic category. In our study, all bipolar species were initially found in Antarctica, and then, usually after a significant time lapse, they were also observed in the Arctic (Table 6). In attempting to ascertain the complete identity of putative bipolar endemic species, we encountered a number of challenges: 1) for *Acrodontium antarcticum* and *Antarctomyces pellizariae*, only sequences from Antarctic cultures are known, and Arctic studies (Conery, 2021; Nikitin and Semenov, 2022) only mention the names of these species, with the DNA sequences themselves not deposited in GenBank; 2) the well-known endemic Antarctic species, *Antarctomyces psychrotrophicus*, was recorded in Arctic soil studies by Timling et al. (2014), but BLAST results show similarity of ITS regions of the Arctic fungus with the type strain at 96.21%, which is insufficient for species identification; 3) *Cladosporium antarcticum* was recorded in Arctic peat (Grum-Grzhimaylo et al., 2016, 2018) and on feathers of Arctic birds (Robicheau et al.,

Table 6
Presumably bipolar endemic species of fungi; proved bipolar species is in bold.

Species of fungi (modern names from the Index Fungorum)	Substrate of detection	Ecology	GenBank number of antarctic strains (ITS)	GenBank numbers of arctic strains (ITS)	Similarity	References of articles with sequences of Arctic strains	material of DNA isolation of Arctic fungi	Comments	References (Antarctica)	References (Arctic)
<i>Acrodontium antarcticum</i>	Rhizosphere, wood	Plant pathogenic	MH862213	–	>97%	Conery (2021)	eDNA	no sequences of Arctic strains in a GenBank	(Onofri, 1999; Vishniac, 1996)	Conery (2021)
<i>Antarctomyces pellizariae</i>	Soil, snow, rocks, lake sediments, anthropogenic substrates	Psychrophilic	NR_164245	–	–	Nikitin and Semenov (2022)	pure culture	no sequences of Arctic strains in a GenBank	(de Menezes et al., 2017, 2017, 2017; Gomes et al., 2018; Alves et al., 2019; Ogaki et al., 2020a, 2020b; Nikitin, 2023)	Nikitin and Semenov (2022)
<i>Antarctomyces psychrotrophicus</i>	Soil, anthropogenic substrates, moss, peat, lichens, gut of Eretmoptera murphyi, air, penguins feathers, animal seals, lake water and sediments, snow	Psychrophilic	MH874317	KC965756	96.21%	Timling et al. (2014)	eDNA	–	(Stchigel et al., 2001; Arenz et al., 2006, 2011; Bridge and Denton, 2007; Duncan et al., 2010; Arenz and Blanchette, 2011; Gonçalves et al., 2012; Yu et al., 2014; Kochkina et al., 2014; Abneuf et al., 2016; Ding et al., 2016; Krishnan et al., 2016; Nikitin, 2018, 2023; de Menezes et al., 2019; de Carvalho et al., 2020; Ogaki et al., 2020a; Brito Devoto et al., 2022)	(Kirtsideli et al., 2014, 2016; Nikitin et al., 2021; Timling et al., 2014)
<i>Cadophora antarctica</i>	Soil with diesel, coal mine spoil	Psychrotolerant	NR_156381	MN833351	99.21%	Iliushin (2020)	pure culture	similarity of LSU (MT362720) with a type material is 100%, morphological description is also provided	Crous et al. (2017)	(Iliushin et al., 2022a; Iliushin, 2020)
<i>Cladosporium antarcticum</i>	Permafrost sediments, peat, soil, feathers	n.i.	OR046553	MK049894	100%	Robicheau et al. (2019)	pure culture	similarity 100% with 5 or more species of <i>Cladosporium</i> including <i>C. antarcticum</i>	(Kochkina et al., 2012; Schubert et al., 2007)	(Grun-Grzhimaylo et al., 2016, 2018; Robicheau et al., 2019)
<i>Mortierella antarctica</i>	Soil, mosses, lake sediments, anthropogenic	Saprotrophic	MH859873	KC965343	99.45%	Timling et al. (2014)	eDNA	–	(Frate and Caretta, 1990; Onofri, 1999; Tosi et al., 2002; Ding et al., 2016; Ogaki et al., 2020a, 2020b; Nikitin, 2023; Gomes et al., 2018)	(Semenova et al., 2016; Timling et al., 2014; Tsuji et al., 2022)
				LC514998	99.69%	Tsuji et al. (2022)	pure culture	–		
				LC515021	99.69%		pure culture	–		
				LC515040	99.92%		pure culture	–		
				LC515137	99.85%		pure culture	–		
				–	98.5%	Semenova et al. (2016)	eDNA	number of the strain is among KX401620-KX404870		

2019), but in the first case, sequences were not deposited in GenBank, and in the second case, the BLAST results showed 100% identity of the ITS region of the Arctic fungus not only with *C. antarcticum*, but also with several other species of the genus *Cladosporium*; 4) for Arctic specimens of *Mortierella antarctica*, the similarity of the ITS region ranges from 98.5 to 99.92%, and no other evidence was found to suggest that they are the same species. As a result, only one species, *Cadophora antarctica*, initially found in Antarctica (Crous et al., 2017), was soon discovered in the Arctic (Svalbard) and described as a bipolar species based on the sequencing results of ITS and LSU rDNA sequences (99.21% and 100% similarity to the type material, respectively) and cultural-morphological characteristics (Iliushin, 2020). However, this species has been recently described and there is no guarantee that it will not be found later in other regions, especially given that both occurrences of this fungus are associated with anthropogenic substrates.

Thus, despite the available information on common fungal species in Antarctica and the Arctic, and attempts to hypothesize the influence of ecological selection and geographic distribution on fungal communities in geographically distant polar regions (Bridge and Spooner, 2012; Cox et al., 2016), there is currently very little evidence for fungi that are polar or bipolar endemics.

7. Conclusions

The Arctic and Antarctic regions are extreme environments to life in general, and fungi in particular, whether as saprotrophs or symbionts and parasites. Of the many studies that reported on fungi in the polar regions, only those that used cultivation and/or molecular characterisation of eDNA provide useful information for answering the main questions of whether there are fungi unique and endemic to the Arctic, Antarctica or both.

Based on available literature in which cultivation and isolation methods of eDNA were applied, 1324 species of fungi have been identified in polar regions, with the fungal biodiversity being higher in the Arctic compared to Antarctica. The difference in fungal species diversity between the two polar regions can largely be explained by variations in substrates specific to the Arctic and Antarctica. The methods employed for detecting fungi limit the detected biodiversity, thus a comprehensive approach is preferred. Most fungal species discovered are cosmopolitan, while the presence of endemic species in polar regions is mostly poorly supported, therefore caution should be exercised when claiming certain fungi as endemic to the polar regions or both poles. We believe that the statement made for microorganisms "Everything is everywhere, but the environment selects" (Baas Becking, 1934) may remain relevant for almost a century. However, for fungi, we would slightly rephrase this statement as: "Fungi are everywhere but the environment selects those that can become established".

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Declaration of competing interest

none.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fbr.2024.100382>.

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