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Fungi's contributions to people in glaciered environments

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Abstract

Climate change is driving ecosystem shifts worldwide, particularly impacting glaciers and the unique ecosystems they support. This paper investigates the often-overlooked role of fungi in glacial environments and their provision of ecosystem services. Despite their cryptic nature, fungi play critical roles in nutrient cycling, decomposition, and symbiotic relationships in these extreme environments. Through a systematic literature review that spans from 1950 to 2024, this study categorizes and evaluates 14 ecosystem services provided by psychrophilic fungi in glacial environments. These services encompass provisioning (e.g., food supply, medicinal resources), regulating (e.g., carbon storage and sequestration, mycoremediation), cultural (e.g., spiritual significance, recreational activities), and supporting (e.g., soil formation, nutrient cycling) functions. The analysis identifies climate change as a primary driver of change affecting fungal populations and their associated services, emphasizing the urgent need for enhanced research, conservation, and management strategies. Despite their ecological significance, fungi currently lack institutional recognition and protection in global conservation frameworks, highlighting a critical gap in conservation efforts. This paper underscores the importance of understanding and conserving cryospheric fungi for maintaining ecosystem stability and resilience in glacial environments. Moving forward, interdisciplinary collaborations and targeted research initiatives are essential for addressing knowledge gaps and promoting the conservation of fungi in these vital habitats.

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1. Introduction

Ecosystem shifts driven by climate change are shrinking glaciers, creating new terrestrial, marine, and freshwater ecosystems (Bosson et al., 2023). Biodiversity faces anthropogenic threats in every niche of the planet (Prakash et al., 2022), with pronounced impacts observed in the cryosphere (Center for Biological Diversity, n.d.; The Research Council of Norway, 2020). Areas of land once covered by glaciers face new opportunities and threats, such as commercial shipping (Anisimov et al., 2007), geopolitical interests (Bradley Intelligence Report, 2023), PFAS pollutants (Bossi et al., 2015; Kwok et al., 2013), and questions around conservation (Tollefson, 2023).

Growing evidence shows that fungi mediate links between organisms and ecosystems (Bahram et al., 2022), yet the kingdom remains understudied due to their cryptic form and late classification as a separate kingdom from *Plantae* and *Animalia*. Cryospheric fungi thrive in frigid environments and inhabit diverse ecological niches, from polar regions to alpine environments. Their ability to flourish in such harsh conditions offers unique insights into the limits of life on Earth and potential applications in various fields, including biotechnology, pharmaceuticals, and environmental remediation. However, with the continuous increase in global temperatures (IPCC, 2023), fungi accustomed to such extreme conditions might either evolve to cope with the shifting environment or face local extinction without detection (Joshi et al., 2021). This is particularly concerning considering the estimation that merely 33% of fungi in the Arctic have been formally documented (Meltofte et al., 2013), while globally, only about 2% have been identified (Taylor et al., 2014). As glaciers recede at unprecedented rates, understanding the roles and importance of fungi in glacial environments has become increasingly critical to comprehend and mitigate the cascading impacts of biodiversity loss, ecosystem disruptions, and the interconnectedness of global ecological systems. Expanded research on fungi's contributions to people will contribute to the understanding of how fungi underpin our ecosystem health and well-being (Castañón, 2023; Martínez-García et al., 2017).

The 2019 IPBES Global Assessment Report on Biodiversity and Ecosystem Services Summary for Policymakers states that there are knowledge gaps in both the arctic biome as well as within fungal taxonomy (IPBES, 2019). The latest IPBES report combined with peer-reviewed articles calls for a greater need for the global conservation of fungi and offers a launching point for further research on fungi. At present, environmental institutions, like CITES, IUCN, and CBD, do not consider fungi in their legal frameworks (Barron, 2023; Niskanen, 2023). Understanding the ecosystem services provided by fungi in glacial environments supports the conservation and management of these ecosystems. A consolidated list of ecosystem services could serve as an evaluation and integration model for decision-makers (TEEB, 2010) and is particularly relevant as the current emphasis on biodiversity as a provider of ecosystem services throws the spotlight on the vast diversity of fungi (Heilmann-Clausen et al., 2015).

The Millennium Ecosystem Assessment (MEA) (2005) revealed that two-thirds of the planet's ecosystem services were in decline, and the global assessment report by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES, 2019) highlights an acceleration of drivers of change contributing to ecosystem degradation. The ecosystem services framework provides an analytical approach to understanding the link between ecosystems and human well-being (MEA, 2005). The aim of this paper is to conduct a systematic literature review to synthesize state of the art knowledge on fungal ecosystem services in psychrophilic climates, specifically glacial environments. Through the ecosystem services framework, I will assess fungi ecosystem services in psychrophilic environments for the period of 1950 to 2024. The objective of this paper is to categorize ecosystem services of psychrophilic fungi in glacial environments. The research is guided by the question: What are the ecosystem services provided by fungi in glacial environments?

2. Background

2.1. Organism Description: Fungi

Fungi, a diverse kingdom encompassing more than just the conspicuous fruiting bodies commonly observed, play pivotal roles within ecosystems. This taxonomic group extends beyond mushrooms to include lichens, which form symbiotic associations with algae or cyanobacteria, particularly significant in psychrophilic environments. In such habitats, fungi offer critical ecosystem services, such as providing alternative sources of edible proteins and animal feed, facilitating industrial biotechnology for sustainable goods production, and carbon sequestration (Amara et al., 2023; Kržišnik et al., 2023; Niego et al., 2023). Fungi live in every habitat and span a wide range of sizes, from smaller than the naked eye can see to one of the largest organisms on Earth (Sipos et al., 2018), and their spores travel thousands of kilometers (Mims et al., 2004).

Ecologically, fungi serve as essential decomposers, symbiotic partners, and contributors to nutrient cycling (Lutzoni et al., 2018; Richard et al., 2004). They break down organic matter, recycling nutrients, and facilitating the decomposition of dead biomass. Mycorrhizal fungi engage in symbiotic relationships with approximately 90% of land plants, enhancing nutrient absorption and conferring resilience to environmental stresses such as drought, climate change, and nitrogen deposition (Willis, 2018; Margulis et al., 2009; Pickles et al., 2017; Martínez-García et al., 2017; Jia et al., 2021). Furthermore, certain fungi contribute to ecological processes such as mycofiltration and mycoremediation, effectively contributing to remediate environmental pollutants (Mnkandla and Otomo, 2021; Akhtar, 2020).

The fungal kingdom also holds significant importance in various spheres beyond ecology, including human health, agriculture, biodiversity, manufacturing, and biomedical research (Barzee et al., 2021; Case et al., 2022). Additionally, fungi may serve as indicators of ecosystem health, highlighting favorable or unfavorable trends in ecosystem functioning (Barron, 2023; Heilmann-Clausen et al., 2015). These functions underscore the indispensable role of fungi in maintaining ecological equilibrium and sustaining life in the environment.

2.2. Case study: Fungi in glacial environments

The choice to study fungi within glacial environments is motivated by their direct vulnerability to climate change and the subsequent urgent need to understand their ecological dynamics in response to rapidly shifting environmental conditions. Rising temperatures accelerate change in all parts of the cryosphere, including snow cover, freshwater ice in lakes and rivers, sea ice, glaciers, ice sheets, and ground ice or permafrost (MacCracken, 1985, Liu et al., 2020). Cryospheric fungi, or fungi inhabiting environments where water is in solid form, such as polar regions and high-altitude ecosystems, face unprecedented adaptation challenges as temperatures rise and glaciers retreat, although research suggests that some fungal communities are resilient to short-term climate change (Jiang et al., 2018). For a long time, glaciers and glacial waters were considered abiotic, but recent research has revealed their substantial contribution to global microbiological activity, garnering increased attention over the past two decades (Perini et al., 2019). To date, most assessments of the ecosystem services of fungi are species-specific case studies and less explored in the global perspective (Fang et al., 2023). Moreover, compared to other fungal communities, like those of forest soils, psychrophilic fungi (i.e., fungi that grow at or below 0 °C) remain understudied and an open frontier for ecosystem services research (Geml et al., 2015; Calvillo-Medina et al., 2020). Despite their ecological significance, frigid biomes remain relatively under-researched compared to other microbial communities. Therefore, investigating fungi in the cryosphere presents an opportunity to fill critical knowledge gaps, enhance our understanding of ecosystem responses to climate change, inform conservation efforts aimed at preserving these vulnerable habitats, and generate a starting point for further research.

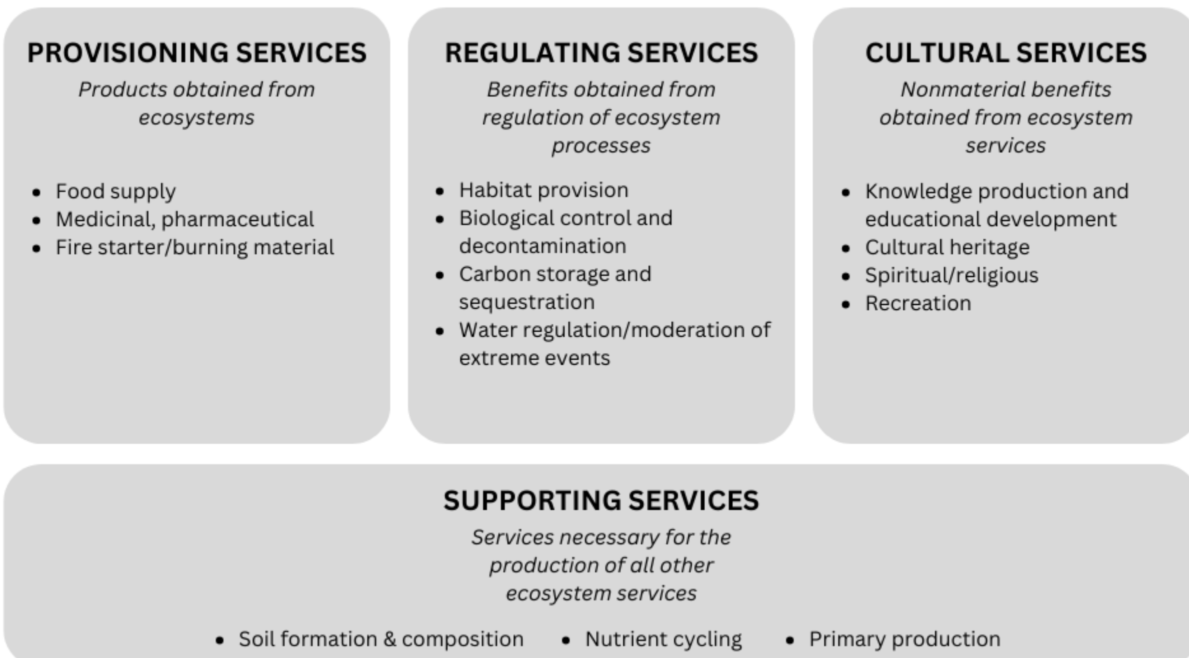
In cold environments, lichenized fungi, such as reindeer lichens (*Cladonia*), dominate the landscape, serving as keystone species and contributing to ecosystem stability (Meltofte et al., 2013; Hoffman, 2022). These fungi adorn substrate surfaces, adding vibrant hues to frozen ecosystems, particularly noticeable in the high Arctic and sub-Arctic regions. Despite the seemingly inhospitable conditions of glacial environments, fungi thrive at micro- and geomorphological levels in glacial ice and glaciers (Butinar et al., 2009). Spores and mycelial fragments of fungi have been trapped in ice matrices since the last glacial maximum 25,000 years ago (Gunde-Cimerman et al., 2003; D'Elia, 2008). Fungi exhibit remarkable diversity in the Arctic, with estimates suggesting a species richness that far exceeds current inventories (Meltofte et al., 2013). As advances in DNA sequencing enhance our understanding of fungal biology, diversity, distribution, and evolution (Niskanen et al., 2023), it becomes increasingly apparent that fungi constitute an indispensable component of ecosystems worldwide, including glacial environments.

3. Framework and Methods

3.1. Analytical framework: Ecosystem service assessment

Fungi contribute ecosystem services (ES) within all categories (regulating, supporting, provisioning, and cultural) proposed by the Millennium Ecosystem Assessment (MEA) at the beginning of the 21st century as well as within all related categories of the Nature's Contribution to People (NCP) proposed by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) (IPBES, 2019). Both concepts were developed to make the values of nature more visible and to underscore the imperative of recognizing and sustaining these services for long-term environmental and human health (Carpenter et al., 2006).

In line with the MEA, collected data was organized through the four main ES categories: provisioning, regulating, cultural, and supporting (MEA, 2005; TEEB, 2010) and subsequently subdivided by sub-categories from *Fungi in Ecosystem Processes* (Dighton, 2018).



3.2. Classification and categorization of ecosystem services

Data was collected through a systematic literature review. Material was considered relevant if it met the following criteria: 1) the study area was in glacial environments, i.e. polar regions or high alpine regions, 2) the study explicitly focused on fungi, including lichenized and non-lichenized fungi, macrofungi, and microfungi, 3) the quality of the sources was either peer-reviewed or from established institutions and reports, like the Arctic Biodiversity Assessment (Meltofte et al., 2013), and 4) the publishing date was from 1950 until 2024.

ES were divided into four main categories (provisioning, regulating, cultural, and supporting services) with several sub-categories. To identify and assess the ES provided specifically by fungi in glacial environments, I conducted a literature review of scientific papers, books, webpages of relevant institutions and organizations, master theses, Ph.D. dissertations, and media documents. Some of the published papers explicitly used an ecosystem services language, whereas in most cases the identification involved the translation of information into the language and framework of ecosystem services and indicators, like the correct spatial range (glacial environments) and organism (fungi).

The selected time frame chosen for relevant criteria was from 1950 until today because 1) fungi that live in near zero temperatures were scientifically neglected until the 1950s (Robinson, 2001) and 2) this time frame is consistent and comparable with the one adopted by various local to global ecosystem service assessments (i.e. MEA, 2005, IPBES 2019).

3.3. Literature review and data analysis

Articles were gathered from international databases, predominantly utilizing Google Scholar, with additional sources obtained from Oria.no. Grey literature, such as university websites and professional organizations, served as a starting point for additional research. Some of the keywords and terms that guided the search included *fungi*, *lichen*, *ecosystem services, regulating, supporting, provisioning, cultural, Arctic, North Pole*, *polar*, *glacier*, *glacial*. Combinations of these keywords varied and included a definition of spatial scale. For example, *Arctic* or *Arctic biome* was searched with *fungi*. Because not all papers explicitly labeled fungi functions with the term *ecosystem service* or with *regulating, supporting, provisioning,* or *cultural*, I expanded each search to using *fungi* or *lichen* and *Arctic* and categorized the ecosystem service from there. Sources with scientific articles related to fungi, lichen, and ecosystem services within defined spatial ranges were identified. Inclusion criteria, such as publication date (1950 until present), language (English), type of literature (peer-reviewed research articles, review papers), geographic location of study (glacial environments), and study design (systematic review), were formulated. The literature search was executed using predefined terms in selected databases, refined using Boolean operators, and records were collected and managed in a Google sheet. Articles were screened based on relevance to the research question, and a shortlist was created for full-text review. During the full-text review, relevant information was documented, findings were organized, and data were extracted. The synthesized findings were analyzed to identify patterns and gaps in the literature, particularly regarding the contribution of fungi in glacial environments to ecosystem services. Potential biases or limitations in the literature were addressed, and finally, the literature review was composed, integrating the findings into the broader research context.

4. Results

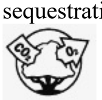
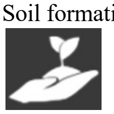
4.1. Classification of Fungi's Ecosystem Services in Glaciered Environments

A total of 14 ecosystem services were identified from the literature review. Table 1 provides a summary of the ecosystem services along with a description and references. In total, I identified and characterized four provisioning services, four cultural services, four supporting services, and three regulating services.

Table 1
Classification of important ecosystem services (ES) in glacial environments and underlying ecosystem functions and components

ES category	*Sub-category*	*Description*	*References*
Provisioning services		*Physical goods obtained from nature*	
Food supply 	Animal provisions	Lichens are a primary food source for reindeer. Animal mycophagy provides inoculum for diversifying mycorrhizal fungi populations for early successional plants	Elliott et al., 2022; Kater, 2022; Cázares et al., 1994
	Secondary production	Mammals consume fungi if/when mosses and other plants are not nearby	Elliott et al., 2022; Hågvar et al., 2015
	Human provisions	Yupik, Chukchi, and non-indigenous residents of Chukotka of the Bering Strait provision fungi. Ascomycetous yeasts used to make beer, bread, wine, and other fermented foods isolated from glaciers	Turner et al., 2022; Yamin-Pasternak, 2009; Meltofte et al., 2013; Cantrell et al., 2011
Medicinal 	Traditional medicinal practices	*Cladosporium*, *Aureobasidium*, and *Penicillium* hold medicinal properties. Doo'ii ahshii (*Lycoperdon spp.*) spores treat sores and infections. Indigenous knowledge recognizes the therapeutic potential of caribou lichen, boiled and administered during illness, resembling conventional cough syrup. Macrofungi (*Cordyceps sinensis*) are classified in Chinese Pharmacopoeia	Das et al., 2022; Johnstone, 2009; Meltofte et al., 2013; Dong et al., 2015; Sung et al., 2019

	Biotechnology	Bioactive molecules like polypeptides, polyketides, and terpenoids show antibacterial, antiviral, and anticancer properties	Hassan et al., 2016; Cantrell et al., 2011; Gonçalves et al., 2024; Wang et al., 2015; Ibrar et al., 2020; Das et al., 2022; Berde et al., 2021; Rogers et al., 2004; Peintner et al., 1998
Fire starter and burning material 	Fire tinder	Fungi used to start and maintain fire	Turner et al., 2022
	Mosquito repellant	Burnt fungi repel mosquitos	Turner et al., 2022
	Smoking material	Maintain smoking materials in tobacco pipes, smoke fish, and create emergency smoke signals	Cuerrier et al., 2019
Cultural services		*Immaterial benefits obtained from interaction with nature*	
Knowledge production and educational development 	Knowledge production and biotechnological potential	Reveal insights into fungal evolution, ecology, and the discovery of bioactive compounds and enhance knowledge of contemporary and ancient fungal diversity	Zhang et al., 2015; Wang et al., 2015; Ma et al., 2000; Rogers et al., 2004
	Educational development and environmental monitoring	Distribution patterns serve as indicators for ongoing climate change monitoring initiatives and aid in predicting biotic responses to climate change	Semenova-Nelson, 2016, Ortiz-Rivero et al., 2023; Peintner et al., 1998
Cultural heritage 		Fungi (e.g. Puffball, Frog's umbrella, and ghost's face powder) reflect varying cultural attitudes across different regions and are included in rituals and traditions surrounding their harvesting, utilization, and sharing for present and future provisions	Turner et al., 2022; Johnstone, 2009; Yamin-Pasternak, 2008; Yamin-Pasternak, 2009
Spiritual/Religious 		Historical connections between mushrooms and spirits play central role in rituals and beliefs and reflect ancient cultural practices	Yamin-Pasternak, 2009; Lincoff, 2010; Turner et al., 2022; Peintner et al., 1998
Recreation 	Mushroom gathering	Mushroom gathering serves as a recreational activity deeply intertwined with the cultural practices of indigenous communities like the Yupik, Chukchi, and Chipewyan peoples	Yamin-Pasternak, 2007; Yamin-Pasternak, 2009
	Toys	Chipewyan peoples use fungi to craft toys for children	Turner et al., 2022
Regulating services		*Benefits humans derive from ecological regulation processes*	
Habitat provision 		Mycorrhizal symbiosis is essential for over 90% of land plant species to support nutrient cycling, carbon regulation, and ecosystem resilience	Behie et al., 2013; Timling et al., 2012; Hobbie et al., 2006; Klarenberg, 2021

Carbon storage and sequestration 	Fungi maintain soil carbon loss, impacting soil-plant interactions, nutrient cycling, and carbon flow	Robinson, 2001; Semeova et al., 2015; Grau et al., 2017; Smith et al., 2017; Nikitin et al., 2020
Biological control/ Decontamination 	Mycoremediation remedies contaminated environments	Calvillo-Medina et al., 2020; Kumar et al., 2021; Marchetta, 2022; Semeova et al., 2015; Perini et al., 2023
Water Regulation/ Moderation of extreme events 	Psychrophilic fungi like *Penicillium anthracinoglaciei* and *Articulospora spp*. sustain glacier algal blooms and provide benefits such as physical shielding and modulation of microbial growth	Perini et al., 2023; Cantrell et al., 2011; Marchetta, 2022
Supporting services	*Services necessary for the production of all other ecosystem services*	
Soil formation 	Decomposition, symbiotic relationships with algae and cyanobacteria, and rock weathering are dependent on fungi	Kononova, 1966; Finlay et al., 2019; Koshila et al., 2019; Větrovský et al., 2020; Mugnai et al., 2020; Semenova et al., 2015; Ortiz-Rivero et al., 2023
Nutrient cycling 	Release essential nutrients back into the ecosystem. Species such as *Acremonium* and *Coniothyrium* produce extracellular enzymes, aiding in organic matter decomposition	Tsuji, 2023; Chen et al., 2023; Mundra et al., 2016; Zhang et al., 2016; Robinson, 2001; Grau et al., 2017; Semenova, 2016
Primary production 	Fungi generally act as initial colonizers in deglaciated areas, driving primary production	Hassett et al., 2017; Yoshitake et al., 2010; Zhang et al., 2016

Source: Own elaboration based on tables, categories, descriptions, and icons from Gomez-Baggethun et al. (2019) and Berglihn et al., 2021. Icons by Jan Sasse for TEEB (except icons for ‘science and education’ which is from Gomez-Baggethun et al., (2019); ‘Fire starter and burning material’ which is from Elyzzle (n.d.); ‘Cultural heritage’ which is from Ivanić et al. (2020); and ‘Biological control/Decontamination’, ‘Soil formation’, and ‘Primary production’ which are from NaturScot (2023)).

4.2.1. Food supply

Animal mycophagy, the consumption of fungi by vertebrates and invertebrates, is a significant, yet incompletely studied trophic interaction (Elliott et al., 2022). The ingestion of fungi by mammals holds ecological importance as it may influence the migration and reestablishment patterns of mycorrhizal fungi, particularly during substantial climate shifts such as glaciation, thereby potentially impacting the contemporary distribution of fungal species (Elliott et al., 2022).

Psychrophilic lichens are a primary food source for reindeer, caribou, and other herbivores, indirectly serving as important for the indigenous populations who rely on these non-human animals for their livelihood (Kater, 2022). Providing secondary production, fungal hyphae and spores have been found in the guts and feces of vertebrates and invertebrates. At a receding glacial site in Norway, fungal hyphae were recorded in 46% of the guts of the beetle *B. hortensis* (Hågvar et al., 2015). Fungi represent a valuable food source for these invertebrates when mosses, *B. hortensis* primary food, are not nearby. Studies of the fecal matter of chipmunks, marmots, pikas, mountain goats, and deer living on glacier forefronts have also shown fungal genera, indicating that animal mycophagy provides inoculum for diversifying mycorrhizal fungi populations for early successional plants (Cázares et al., 1994).

In addition to non-human animal provisions, humans in glacial areas also provision fungi for food, like Canadian Indigenous Peoples, the Yupik, Chukchi, and non-indigenous residents of Chukotka of the Bering Strait (Turner et al., 2022; Yamin-Pasternak, 2009). While historically, wild mushrooms had limited use among Arctic peoples, recent decades have seen growing interest in their edibility, particularly due to cultural exchanges and immigration influences (Meltofte et al., 2013). A story of retired Chukotka teacher illuminates the story of settlers well:

> "I had thought that this land would be completely barren, what else can one expect from permafrost? Imagine my joy when I saw that in Chukotka people harvest mushrooms and berries in quantities we could only dream about on the mainland. I remember I wrote to my sister that not only do mushrooms grow here, they rise above all the rest. "Chukotka," I wrote, "is a magical place where mushrooms are taller than trees" (recorded in Studenok, Ukraine, 2004) (Yamin-Pasternak, 2009).

Additionally, ascomycetous yeasts, used to make beer, bread, wine, and other fermented foods, have also been isolated from subglacial ice in Arctic coastal glaciers, Italian alpine glaciers, and Patagonian glaciers, indicating their adaptability to cold conditions (Cantrell et al., 2011).

4.2.2. Medicinal

Several genera of fungi found in psychrophilic environments, like *Cladosporium*, *Aureobasidium*, and *Penicullium* in Arctic permafrost, exhibit medicinal properties (Das et al., 2022). Notably, traditional remedies in remote Arctic communities include the utilization of Doo'ii ahshii (*Lycoperdon spp*.) spores, which are collected and applied to treat sores, burns, and infections (Johnstone, 2009). Traditional ecological knowledge (TEK) of indigenous Arctic communities includes the therapeutic potential of caribou lichen during times of illness within camps, when lichen is boiled and then administered for results akin to the efficacy of conventional cough syrups (Meltofte et al., 2013). Recent research suggests an expanding potential for leveraging psychrophilic fungi to medical benefits on a global human population (Gonçalves et al., 2024; Das et al., 2022; Berde et al., 2021; Hassan et al., 2016; Cantrell et al., 2011; Wang et al., 2015; Ibrar et al., 2020; Rogers et al., 2004; Peintner et al., 1998). Bioactive molecules derived from extremophilic fungi, including polypeptides, polyketides, and terpenoids demonstrate antibacterial, antiviral, and anticancer properties and present promising avenues for drug discovery and applications in environmental, industrial, and food technology (Das et al., 2022; Rogers et al., 2004). Moreover, these fungi exhibit a diverse range of bioactive compounds with potential applications across various industries, such as pharmaceuticals, biotechnology, and agriculture (Gonçalves et al., 2024; Wang et al., 2015). Additionally, exploration of extreme environments has unveiled novel metabolites with medicinal properties, including antimicrobial, antioxidant, and anti-inflammatory activities (Gonçalves et al., 2024; Ibrar et al. 2020; Das et al., 2022; Berde et al., 2021). Besides microfungi and lichens, macrofungi that grow in glacial environments also hold notable significance. Species such as *Cordyceps sinensis*, colloquially known as caterpillar fungus, has garnered substantial attention within traditional Chinese medicinal practices due to their purported therapeutic attributes (Dong et al., 2015). Additionally, *Ophiocordyceps sinensis* thrives within altitudinal ranges between 3,000 to 5,000 meters and is officially classified as a drug in the Chinese Pharmacopoeia (Sung et al., 2019).

4.2.3. Fire starter and burning material

In cold desert regions, fungi play crucial roles in various aspects related to fire among local communities. *Fomes fomentarius*, commonly known as hoof fungus, serves multiple purposes among Canadian Indigenous Peoples, including as tinder for fire, as a mosquito repellant when burned, and as an additive in smoking pipes alongside tobacco and red willow bark to maintain the smoking materials (Turner et al., 2022). Similarly, Inuit communities in the Subarctic utilize dry lichen as fire starters and for smoking fish and skins, as well as creating emergency smoke signals (Cuerrier et al., 2019). The utilization of fungi as fire resources highlights the intricate relationship between cold desert dwellers and macrofungi, showcasing the resourcefulness deeply embedded within indigenous societies.

4.2.4. Knowledge production and educational development

Psychrophilic fungi provide insights into evolutionary biology, biotechnological potential, ecosystem functioning, and environmental monitoring within psychrophilic environments. Lichen thalli, for example, serve as reservoirs of diverse fungi and contribute to our comprehension of fungal evolution and ecology in the Arctic (Zhang et al., 2015). Additionally, glacial fungi reveal novel bioactive compounds with applications in pharmaceutical and agrochemical research (Wang et al., 2015). Polar regions serve as expansive field laboratories for fundamental research with global implications, owing to their extreme climates, habitats, and biogeography. They provide valuable information on evolutionary processes, ancient biodiversity, and species previously considered extinct (Ma et al., 2000; Rogers et al., 2004; Ma et al., 2005). Moreover, psychrophilic fungi and lichen distribution patterns serve as crucial indicators and offer data for ongoing climate monitoring initiatives. They aid in predicting biotic responses to climate change and facilitate the monitoring of ecosystem disturbances in tundra ecosystems (Semenova-Nelson, 2016, Ortiz-Rivero et al., 2023). Fungus identification also opens a window to historical ecological data, for instance about the way prehistoric people lived (Peintner et al., 1998). Glacial fungi provide unique insight into both contemporary and ancient fungal diversity (Ma et al., 1999). In essence, psychrophilic fungi lichens enhance educational ecosystem services by illuminating past, present, and future ecosystems.

4.2.5. Cultural heritage

Fungi hold significant cultural value in psychrophilic environments among local populations. Notably, species such as the Puffball, Frog's umbrella, ghost's face powder, and approximately 40 other fungal species are of cultural importance to Canadian Indigenous Peoples (Turner et al., 2022). In the Vuntut Gwitchin Territory, Indigenous Peoples seek out the Puffball mushroom, known as the Doo'ii Ahshii, during the summertime, regarding it as "good for everything" (Johnstone, 2009, p. 38). Cultural attitudes toward fungi in glacial environments vary across national borders, as evidenced by differing views between communities inhabiting the Bering Strait regions of present-day Russia and Alaska (Yamin-Pasternak, 2008). Beginning in mid-July, various mushrooms, including *Lacterius*, *Russula*, and *Leccinum*, are harvested on the Chukchi Peninsula and are abundant in nearly every household for present and future provisions, enjoyed individually or shared as gifts (Yamin-Pasternak, 2009).

4.2.6. Spiritual/religious

Ethnomycological studies have revealed historical connections between mushrooms and various types of spirits, good and bad, especially prior to Russian influence (Yamin-Pasternak, 2009). *Amanita muscaria*, found in areas with receding glaciers like the Kamchatka Peninsula in Russia, are ingested by various minority peoples for their physical and spiritual powers (Lincoff, 2010, p. 150). In the traditions of Canadian Indigenous Peoples, fungi hold profound spiritual and sacred significance, playing integral roles in rituals, ceremonies, narratives, and belief systems. This reverence for fungi likely stems from ancient practices of Asian or European ancestors during the Pleistocene era, with similar cultural customs persisting among their descendants on these continents today (Turner et al., 2022). The discovery of the 'Iceman,' a Neolithic corpse found in September 1991 on an alpine glacier, revealed three distinct fungal objects carried by the individual, one of which is suggested to be a source of eternal strength or wisdom (Peintner et al., 1998). The intersection of ethnomycology, indigenous traditions, and archaeological discoveries underscores the enduring significance of fungi in human culture and spirituality across millennia.

4.2.7. Recreation

Macrofungi play diverse roles in recreational activities, including mushroom gathering. Mushroom-gathering exemplifies a symbiotic relationship between indigenous communities like the Yupik and Chukchi peoples and the natural environment they inhabit (Yamin-Pasternak, 2009; Yamin-Pasternak, 2007). Moreover, the recreational potential of mushrooms extends to childhood realms, where the Chipewyan peoples use fungi to craft toys for children (Turner et al., 2022). In this manner, mushrooms surpass their utilitarian value and serve as avenues for recreational expression and preservation of cultural heritage.

4.2.8. Habitat provision

Terricolous macrolichens, like *Cetraria islandica* and reindeer lichens, contribute to important ecosystem processes in sub-Arctic regions, like nitrogen fixation via their microbiome (Klarenberg, 2021). Symbiotic relationships with fungi, or mycorrhiza, are crucial for the survival of over 90% of terrestrial plant species (Behie et al., 2013). These associations persist even in cold environments, where mycorrhiza exhibit adaptation to low temperatures. They play a critical role in sustaining ecosystem functions essential for the resilience of extreme habitats, particularly amidst challenges posed by climate change (Timling et al., 2012).

Additionally, mycorrhiza aid plants in absorbing nutrients and water from the soil while obtaining carbon from the host plant in exchange. Their importance is heightened in Arctic ecosystems, where limited water and nutrients constrain plant growth and productivity (Timling et al., 2012). Research suggests that up to 86% of the nitrogen acquired by Arctic plants comes from mycorrhiza, particularly ectomycorrhizal (ECM) species (Hobbie et al., 2006). Understanding the distribution and activities of psychrophilic mycorrhiza is essential for predicting and managing ecosystem responses to climate change, as they influence vegetation patterns and ecosystem dynamics in these fragile environments. Mycorrhizal symbioses connect individual plants and allow for the exchange of nutrients and information needed for habitat provision.

4.2.9. Carbon storage and sequestration

The ability of mycorrhiza to thrive in cold temperatures ensures the continuity of soil-plant interactions, nutrient cycling, and carbon flow in low temperature regimes (Robinson, 2001). Moreover, as the Arctic stores approximately 50% of the Earth's soil carbon (Semenova et al., 2015), mycorrhiza significantly contribute to the carbon balance and regulation of warming-induced changes in Arctic ecosystems, mitigating positive feedback effects such as increased decomposition rates and carbon efflux (Semenova et al., 2015). Additionally, mycorrhiza aid plants in absorbing nutrients and water from the soil while obtaining carbon from the host plant in exchange.

The role of fungi in all ecosystems is crucial for carbon storage and sequestration, as evident through studies in the Arctic (Grau et al., 2017) and Antarctica (Smith et al., 2017). The discovery of substantial carbon reserves in soils of both the Arctic and Antarctic regions (Nikitin et al., 2020) validates the existence of fungal populations within these ecosystems. However, as carbon content increases with the age of soil (Bradley et al., 2014), the effectiveness of carbon storage and sequestration also depends on how long the land has been barren and the rate of glacial melt in that region.

4.2.10. Biological control/Decontamination

Fungi possess significant potential for remediating contaminated through the process of mycoremediation, where they absorb and transform pollutants. Comparative studies of fungal communities in Arctic and Antarctic lakes have demonstrated their capacity for environmental decontamination by tolerating and breaking down heavy metals (Calvillo-Medina et al., 2020; Kumar et al., 2021; Marchetta, 2022). Fungi emerge as crucial components in ecosystem services for biological control and decontamination in psychrophilic environments, particularly amidst warming-induced changes. These changes contribute to alterations in Arctic vegetation, such as increased leaf litter and reduced cover for shade-intolerant lichens, thereby reshaping habitat conditions (Semenova et al., 2015). Within the fungal community, psychrophilic species, like *Penicillium anthracinoglaciei* and *Articulospora spp*., play pivotal roles in sustaining ecosystem functions by contributing to the regulation of biological control by mobilizing organic and inorganic compounds, secreting secondary metabolites, and modulating the growth of other microorganisms, which in turn impacts disease-causing soil organisms (Perini et al., 2023).

4.2.11. Water Regulation/Moderation of extreme events

Psychrophilic fungi such as *Penicillium anthracinoglaciei* and *Articulospora spp*. are vital contributors to ecosystem dynamics in polar regions and high-altitude glaciers. These fungi contribute significantly to sustaining glacier algal blooms during both the ablation season and over-wintering periods. They provide various benefits including the physical shielding from light or water currents and modulation of the growth of other microorganisms (Perini et al., 2023). Fungal communities inhabiting poorly understood niches, such as Antarctic dry valleys, high Arctic glaciers, salt flats, hypersaline microbial mats, and plant trichomes, exhibit high diversity and functional redundancy. This diversity enhances ecosystem resilience to both natural and anthropogenic disturbances (Cantrell et al., 2011). Polar glaciers, despite being among the least sampled habitats for fungi, host filamentous fungi and yeasts in microbial cryoconite holes, ancient ice cores, and subglacial ice (Cantrell et al., 2011, Marchetta, 2022).

4.2.12. Soil formation

In glacial environments and beyond, fungi play pivotal roles in soil formation processes (Kononova, 1966; Finlay et al., 2019; Koshila et al., 2019; Větrovský et al., 2020). Specifically, psychrophilic fungi engage in vital ecological functions, including the decomposition of organic matter, establishment of symbiotic relationships with photosynthetic algae and nitrogen-fixing cyanobacteria to form lichens, and weathering of rocks, all of which contribute to soil stabilization and nutrient cycling (Mugnai et al., 2020). However, the warming-induced changes, such as shrub expansion and altered vegetation patterns, present challenges to these fungal roles (Semenova et al., 2015). The increased leaf litter resulting from changing vegetation patterns underscores the importance of fungi in nutrient cycling. Yet, the expansion of shrubs negatively impacts shade-tolerant lichens and disrupts symbiotic relationships and soil stabilization processes (Mugnai et al., 2020). Fungal communities are frequently the first visible colonizers of deglaciated areas and initiate the process of soil formation by breaking down rock and organic matter (Ortiz-Rivero et al., 2023).

4.2.13. Nutrient cycling

Psychrophilic fungi play indispensable roles in the nutrient cycle of the polar region ecosystems (Tsuji, 2023). Despite diminished enzyme activity at colder temperatures, psychrophilic fungi exhibit functionality in decomposing organic matter and release essential nutrients back into the ecosystem (Chen et al., 2023, Mundra et al., 2016). For instance, species like *Acremonium* and *Coniothyrium* produce extracellular enzymes, which indicates their potential role in litter degradation (Zhang et al., 2016). Further research is necessary to understand the intricacies of sporulation and other adaptations in these fungi. Nonetheless, their significance in nutrient cycling within Arctic and Antarctic ecosystems remains undeniable (Robinson, 2001, Grau et al., 2017). Elevated temperatures have shown changes in nutrient cycling within the low Arctic, exerting significant impacts on tundra vegetation (Semenova, 2016).

4.2.14. Primary production

In glacial environments, fungi are responsible for transforming organic matter, such as nitrogen, phosphorus, and carbon, into essential nutrients for plant growth (Hassett et al., 2017; Yoshitake et al., 2010). Studies conducted in the high Arctic have yielded varying results regarding the most significant primary producers in the region. One study suggests that lichens hold this distinction (Zhang et al., 2016), while another study indicates that vascular plants and mosses play a more substantial role in primary production (Uchida et al., 2006). Nonetheless, fungi typically serve as the initial colonizers in deglaciated areas, thereby assuming responsibility for the primary production of these regions.

5. Discussion

5.1 Fungi's contributions to people, drivers of change, and conservation

A total of 14 ecosystem services identified and described the most important services provided by fungi in glacial environments. They include three provisioning services, four cultural services, four regulating services, and three supporting services, each integral to the functioning and resilience in the cryosphere. Each service is intertwined and sometimes difficult to separate, showing the interconnectedness and complexity of fungal roles within these ecosystems.

The findings align with the overarching trends delineated in seminal assessments such as the Millennium Ecosystem Assessment (MEA, 2005) and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). These reports underscore climate change as a pivotal threat to biodiversity, as it reshapes vegetation patterns, alters habitat conditions, and accentuates bioaccumulation. Results are also consistent with other findings that underscore the multifaceted ecosystem functions of fungi across various ecosystems, such as freshwater bodies (Seena et al., 2023), forest soils (Li et al., 2022), and even within the global economy (Niego et al., 2023). Crucially, the ecosystem services in glacial environments are deemed equally vital, given the sustained sub-zero temperatures prevalent for most of the year. The indispensable role of fungi spans across all ecosystems.

The disturbance of fungi in glacial environments is attributed to both direct and indirect drivers of change. Climate change is a direct driver, followed by indirect drivers like developmental (Atlas et al., 1976), economic (Anisimov et al., 2007), geopolitical (Bradley Intelligence Report, 2023), cultural (Yamin-Pasternak, 2008), and contamination factors (Meltofte et al., 2013; Bossi et al., 2015; Kwok et al., 2013). Notably, the repercussions of warming temperatures are particularly pronounced in polar and glacial regions, manifesting in accelerated rates of ice melt (Arias et al., 2021; Hock et al., 2019). Consequently, shifts in water and surface temperatures, as well as precipitation patterns, are anticipated due to global climate change, creating new ecological niches ripe for colonization by various fungal species (Cantrell et al., 2021). This portends implications for profound and complex effects on native ecosystems and could lead to shifts in species composition, community structure, and ecosystem functioning.

Moreover, the delicate equilibrium of these ecosystems faces jeopardy from positive feedback loops, such as heightened greenhouse gas concentrations precipitating permafrost thawing and consequent carbon release (Semenova et al., 2015). The changing climate is anticipated to alter the richness and composition of taxonomic and functional groups of arctic fungi (Geml et al., 2020) and has already impaired species interactions and forced species adaptations, migration, and extinction in the Antarctic (Santos et al., 2020). Additionally, biogeochemical cycling and the functional dynamics of Arctic soil communities are expected to undergo transformations in response to climate change (Mundra et al., 2016). As fungi serve as linchpins for ecosystem services that support and regulate other functions, alterations in vegetation and fungal communities may disrupt carbon storage, nutrient cycling, and overall ecosystem functioning.

Despite their ecological significance, fungi lack institutional protection from entities like CITES, IUCN, and CBD (Barron, 2023; Niskanen, 2023). The nascent recognition of fungi in global sustainability initiatives is deemed imperative for a comprehensive acknowledgment and conservation of nature's contributions to people (Oyanedel et al., 2022). Historically, fungi have posed challenges for study due to their cryptic morphology, and relating the role of fungi to ecosystem processes has been challenging due to the vast difference in spatial scale over which ecosystem processes (centimeters to kilometers) and fungal hyphae work (micrometers to meters) (Dighton, 2018). Advances in phylogenomics and sequencing technologies, however, offer promising avenues for enhanced research into fungi and microorganisms (Niskanen et al., 2023; Marchetta, 2021). The growing institutional recognition of fungi's ecological roles is evident in initiatives such as the 2022 IPBES Sustainable Use Assessment (SUA), which underscores various ecosystem services provided by fungi.

From provisioning in indigenous communities to nutrient cycle regulation and soil formation, fungi in glacial environments play indispensable roles transcending their immediate ecological functions. Understanding the diverse ecosystem services furnished by these fungi is imperative for devising effective conservation and management strategies aimed at safeguarding the integrity and biodiversity of glacial environments amidst ongoing environmental transformations. For a comprehensive overview of the identified ecosystem services in glacial environments, refer to Table 1.

5.2. Limitations and Opportunities

There were two major limitations in this research that could be addressed in future research. Firstly, fungal taxonomic limitations hindered comprehensive studies. The cryptic form and inconspicuous nature of fungi often relegate them to obscurity, making them easy to forget. Moreover, the vast taxonomic diversity of fungi, coupled with challenges in accurate identification and classification due to morphological similarities and the requirement for resource-intensive molecular techniques, poses a significant obstacle to comprehensive taxonomic studies. Future researchers can address this by focusing on DNA-based typification and exploring other methodologies (Nilsson et al., 2023). This underscores the necessity for nuanced taxonomic analyses to capture the full variability in ecosystem services across different fungal taxa.

Secondly, the study area's limitation was notable. Despite their ecological significance, frigid environments have received comparatively less research attention than other microbial communities. This presents an opportunity for researchers to delve into these underexplored ecosystems and uncover the contributions of cyrospheric fungi to ecosystem services.

Additional limitations included seasonal variability in environmental sampling and the constraint of time, leaving potential avenues, such as biophysical assessments, unexplored. Lastly, uncovering cultural ecosystem services presents a knowledge gap due to the subjective and interdisciplinary nature of these services. Assessing the condition of cultural services heavily relies on direct or indirect human use and poses challenges in accurate evaluation. Addressing these knowledge gaps and limitations will contribute to a more comprehensive understanding of the role of cryospheric fungi in ecosystem dynamics and services.

6. Conclusion

Through this assessment of the ecosystem services of fungi, I identified 14 of the most significant ecosystem services of psychrophilic fungi in glacial environments. By employing an ecosystem services framework, the research identified and assessed the provisioning, regulating, cultural, and supporting services provided by fungi and highlighted the main drivers of change affecting these services.

These findings underscore the indispensable contributions of fungi to the functioning and resilience of glacial environments and their importance to people. From providing food sources for both humans and non-human animals to serving as medicinal resources, these fungi play pivotal roles in sustaining life in these harsh environments. Moreover, their significance extends to past, present, and future knowledge, and to spiritual and cultural realms, where they carry profound meanings and are integral to indigenous traditions. Furthermore, cryospheric fungi contribute to crucial ecological processes such as nutrient cycling, soil formation, and carbon storage and sequestration, highlighting their importance in maintaining ecosystem stability and resilience. However, glacial environments face threats from climate change and other anthropogenic pressures, including commercial shipping, geopolitical interests, pollution, and questions around conservation, which could disrupt fungal communities and their associated ecosystem services. Despite their ecological significance, fungi currently lack institutional protection and recognition in global conservation initiatives. Thus, there is a pressing need for enhanced research, conservation, and management strategies aimed at safeguarding these organisms and the vital ecosystem services they provide. In essence, understanding and appreciating the diverse ecosystem services provided by cryospheric fungi are essential for effective conservation and management of glaciered environments in the face of ongoing environmental transformations. This comprehensive overview of their roles serves as a foundation for future research and conservation efforts in these critical habitats. Overall, research on cryospheric fungi highlights their importance in providing valuable ecosystem services and underscores the need for continued exploration and conservation efforts in extreme environments.

In conclusion, this study highlights the importance of fungi in supporting ecosystem functioning and human well-being in glacial environments. By elucidating the diverse ecosystem services provided by these fungi and identifying key drivers of change affecting their populations, this thesis contributes to the broader understanding of fungal ecology and conservation efforts in the face of ongoing environmental changes. Moving forward, interdisciplinary collaborations and targeted research initiatives will be essential for addressing knowledge gaps, mitigating threats, and promoting the conservation of fungi in glacial environments and their invaluable contributions to ecosystem health and human societies.

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