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Review

Role of Microbes in the degradation of organic semivolatile compounds in polar ecosystems: A review

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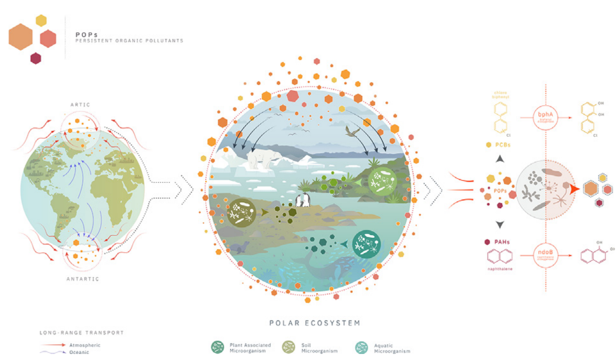
HIGHLIGHTS

- SVOCs present in terrestrial and aquatic polar regions are subject to bioaccumulation and biomagnification.
- Polar microbes can adapt to organic pollutants by expressing catabolic pathways able to degrade SVOCs.
- Bioremediation with native microorganisms can mitigate exposure of SVOCs in polar environments.

GRAPHICAL ABSTRACT



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ABSTRACT

The Arctic and the Antarctic Continent correspond to two eco-regions with extreme climatic conditions. These regions are exposed to the presence of contaminants resulting from human activity (local and global), which, in turn, represent a challenge for life forms in these environments. Anthropogenic pollution by semi-volatile organic compounds (SVOCs) in polar ecosystems has been documented since the 1960s. Currently, various studies have shown the presence of SVOCs and their bioaccumulation and biomagnification in the polar regions with negative effects on biodiversity and the ecosystem. Although the production and use of these compounds has been regulated, their persistence continues to threaten biodiversity and the ecosystem. Here, we summarize the current literature regarding microbes and SVOCs in polar regions and pose that bioremediation by native microorganisms is a feasible strategy to mitigate the presence of SVOCs. Our systematic review revealed that microbial communities in polar environments represent a wide reservoir of biodiversity adapted to extreme conditions, found both in terrestrial and aquatic environments, freely or in association with vegetation. Microorganisms adapted to these environments have the potential for biodegradation of SVOCs through a variety of genes encoding enzymes with the capacity to metabolize SVOCs. We suggest that a comprehensive approach at the molecular and ecological level is required to mitigate SVOCs presence in these regions. This is especially patent when considering that SVOCs degrade at slow rates and possess the ability to accumulate in polar ecosystems. The implications of SVOC degradation are relevant for the preservation of polar ecosystems with consequences at a global level.

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Contents

1. Introduction

The Arctic and the Antarctic continent are two eco-regions that exhibit extreme climatic conditions characterized by low temperature, strong winds, low water availability (mainly in Antarctica), and long periods of darkness in Winter and of light in Summer. Unfortunately, these polar ecosystems are under the added abiotic pressure of pollutants of human origin, which, in turn, represent a challenge to all lifeforms in these environments (Bengtson, 2011; Hung et al., 2010).

Anthropogenic activity and industrialization are responsible for the release of chemical substances to the environment, in turn, altering the global chemosphere. This has impacted not only diverse ecosystems but also human health (Tong et al., 2022). Anthropogenic pollution by semivolatile organic compounds (SVOCs) in Arctic and Antarctic ecosystems was first documented in the 1960s (Risebrough et al., 1967; Sladen et al., 1966). Then, Risebrough et al. (1976) addressed SVOC transport to Antarctica, especially transport of persistent organic pollutants (POPs). SVOCs can travel long distances and remain in the environment for long periods of time due to their low degradation rates, thus, accumulating in the ecosystems where they get deposited with the ensuing negative effects to both human and environmental health (Pennington, 2001).

Due to their long-range transport capacity, SVOCs exhibit a wide and dynamic global distribution with different SVOC species documented in polar environments (Ma et al., 2016). From a global perspective, Bartrons et al. (2016) state that SVOC accumulation in a certain ecosystem depends on the history of industrialization in the nearby continents and the distance to emission sources. Accordingly, emissions from the Northern and Southern Hemispheres have determined and continue to determine the presence of SVOCs in the Arctic and Antarctica, respectively. While the production and use of these compounds has diminished or has been regulated, new organic compounds are synthesized, making the study of SVOCs a current issue and a concrete worry for scientific polar programs and policy makers (AMAP, 2021; Protocol on Environmental Protection to the Antarctic Treaty, 1991).

While diverse strategies have been applied to remediate contamination by SVOCs, bioremediation of SVOCs remains key when considering the vulnerability of polar ecosystems to the exposition of these pollutants. An additional hurdle to the study and potential bioremediation of polar ecosystems is the limited access to these regions and the extremely low temperatures, both of which limit the development and deployment of bioremediation schemes (Bajaj and Singh, 2015; Lambo and Patel, 2006). This situation calls for the use of cold-adapted native microbes for the efficient treatment of polar environments polluted with SVOCs (Bajaj and Singh, 2015).

Microbial communities from polar environments represent an ample reservoir of biodiversity adapted to the taxing polar conditions. Several studies report the isolation and characterization of individual microbes and communities from nearly every habitat in the polar regions: aquatic and terrestrial, free-living, or associated to plant hosts (Guajardo-Leiva et al., 2022). Studies have shown polar microbes capable of degrading organic pollutants through their metabolic machineries, thus potentially mitigating the impact of anthropogenic activities globally (Aislabie et al., 2006).

2. Semivolatile organic compounds in polar ecosystems

SVOCs represent a group of organic compounds, being the persistent organic pollutants (POPs) and polycyclic aromatic hydrocarbons (PAHs) the most common. As their name suggest, SVOCs are semivolatile (Göktaş and MacLeod, 2016), have a high solubility in lipids, and a long half-life and persistence (Lohmann et al., 2007).

In particular, POPs are compounds with nitro-, sulfur-, and halogen functional groups (Cl, Br, F) associated with hydrocarbon rings or chains (Pennington, 2001). POPs have been used in agriculture, industry, and domestic applications and are often classified according to their origin as pesticides, industrial chemical products, and byproducts. For instance, organochloride pesticides such as hexachlorobenzene (HCB), hexachlorocyclohexane (HCH) and dichloro-diphenyl-trichloroethane (DDT) are POPs. Additionally, industrial products such as polychlorinated biphenyls (PCB), flame retardants as polybromo diphenyl ethers (PBDE), perfluorooctanoic acid (PFOA) and perfluoro octane sulfonic acid (PFOS); and byproducts of industrial processes and of combustion HCB, PCBs, dioxins, and furans (polychlorinated dibenzo-p-dioxins/furans, PCDD/Fs) all belong to POPs. All of these compounds are regulated by the Stockholm Convention (PreUNEP, 2001). In turn, Polycyclic Aromatic Hydrocarbons (PAHs) are characterized by having two or more aromatic rings, e.g., naphthalene, phenanthrene, anthracene, and pyrene. PAHs are originated by fossil fuel combustion, biomass burning including incomplete combustion, as well as biogenic sources. PAHs are regulated by the Convention on Long-Range Transboundary Air Pollution (Aarhus, 1998).

SVOCs are subjected to long-range transport (LRT) through the atmosphere, oceanic currents, and migratory species (e.g., birds, fish), which contribute to their global dynamics and distribution (Bengtson, 2011; Blais et al., 2005, 2007; Ma et al., 2016; Vilela et al., 2022). SVOCs also participate in progressive mobilization and deposition cycles from regions of origin (temperate and tropical regions) towards more remote regions (colder climates; Bengtson, 2011). Therefore, SVOCs are able to travel from higher primary emission regions (primary sources) to more distant polar regions where SVOCs have not been either produced or utilized (Fig. 1; AMAP, 2021; Bengtson, 2011; Bengtson et al., 2017; Brown and Wania, 2008; Cabrerizo et al., 2013). LRT would be related to cold condensation of SVOCs, or cold trapping, where low temperature prolongs their half-life and contribute to their persistence (Wania and Mackay, 1993, 1995).

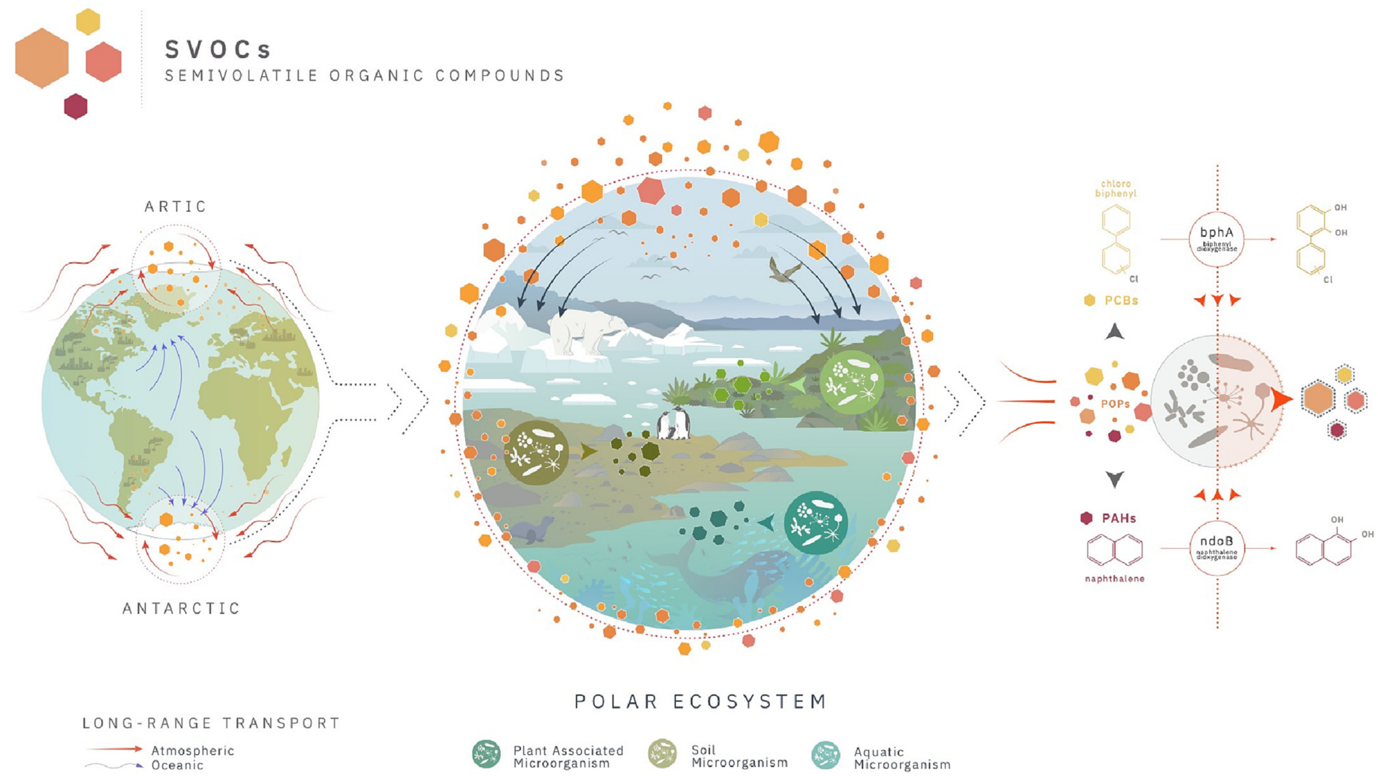


Fig. 1. SVOC transport from temperate and tropical regions in the northern and southern hemispheres to the Arctic and the Antarctic Continent. Cold-adapted microbes can degrade SVOCs whether in soil, water or plant-associated.

It is important to note that atmospheric transport is the main source of entry of SVOCs to polar systems (Bengtson, 2011; Cabrerizo et al., 2012). During transport and deposition, SVOCs are seamlessly exchanged between atmosphere and surface compartments, whereas less volatile compounds are predominantly associated with atmospheric aerosols and are then irreversibly deposited to surface compartments (Göktaş and MacLeod, 2016; Wania, 2006). Consequently, terrestrial and aquatic SVOC reservoirs are generated, i.e., bodies of water, sediments, soil, marine ice, and vegetation, where their concentrations are amplified by cold trapping (Wania and Mackay, 1995). These reservoirs then could act as secondary sources in the polar regions (Cabrerizo et al., 2013; Ma et al., 2011).

On the other hand, together with SVOCs from LRT, there is a sizeable contribution at the local level. Studies show that research stations and scientific activities, together with tourism imprint an anthropogenic pollution fingerprint originated from fossil fuel combustion and SVOCs with measurable local impacts (Gao et al., 2021; Grant et al., 2021; Law et al., 2017; Tin et al., 2009; Xie et al., 2022; Wu et al., 2023). Studies have demonstrated that Antarctic research stations are sources of PAHs and POPs. Then, Wild et al. (2015) established a direct distance relationship from a research station and the concentration of PDBEs and PFAS, showing decreasing concentrations as distance increased from the source. Additionally, the researchers demonstrated the presence of a novel POP (PFAS) in the polar regions.

Although the Arctic and Antarctica exhibit similarities in their climatic characteristics, there are differences regarding the origin of emission sources of organic compounds (Azcune et al., 2022). Exposure of SVOCs in the Arctic is influenced by historical industrial activity in the Northern Hemisphere. In addition, the Arctic Monitoring and Assessment Programme (AMAP), created in 1991, allowed continuous monitoring of POPs in the atmosphere for decision-making management (Hung et al., 2010; Wu et al., 2023). In the case of the Antarctica, local scientific activity and LRT influence the exposure of SVOCs in the continent. Although there are published studies on the presence of pollutants, a continuous monitoring network between countries with Antarctic presence would provide effective coordination and use of resource (Luarte et al., 2023). In relation to this, two working groups: the Input pathways of persistent organic pollutants to Antarctica (ImPACT) of the Scientific Committee on Antarctic Research (SCAR), and the Antarctic Monitoring and Assessment Programme (AnMAP) are promoting research and surveillance of POPs in the continent (Bengtson, 2022).

Despite the scarcity of recent studies with focus on SVOCs from polar regions (Bhardwaj et al., 2018; Wang et al., 2019), we have compiled a list of SVOCs from polar regions and from different reservoirs including terrestrial and aquatic ecosystems (Table I). We observe ample diversity of SVOCs, not only in presence but also in concentration, i.e., AHs, HCB, HCH, DDT, DDE, PCB, PFOS, PFOA, and PBDE. Xiong et al. (2021) found new flame-retardant compounds (NBFRs) in soil and vegetation samples. NBFRs are used as replacement for regulated bromine compounds (i.e., PBDE). Currently, NBFRs are not part of the list of regulated bromine compounds (UNEP, 2022) despite presenting adverse effects on the environment and human health (Xiong et al., 2021). Some studies have also reported novel POPs in sea water and lake systems such as perfluoroalkyl substances (PFAS), namely acid (PFOA) and Perfluorooctanoic sulfonic acid (PFOS). Although POPs are regulated so that their production, utilization, trade, and environmental emission are increasingly reduced (UNEP, 2022), novel pollutants are regularly being developed, emitted, transported, and deposited in polar regions.

In addition, to terrestrial studies, some reports address the fate and distribution of pollutants in polar oceans. In the Arctic, Zhang et al. (2023) and Liu et al. (2022) show PAH fluxes between the Arctic Ocean and Atlantic Ocean. Furthermore, Zhang et al. (2023) mention that PAH concentrations and composition profile varied for water mass structure, and it is potentially influenced by microbial degradation and the biological pump. Liu et al. (2022) indicated that PAHs present a "surface-enrichment and depth-depletion" profile in the water column, and the depletion mechanism is explained by microbial degradation for dissolved PAHs in the open ocean (González-Gaya et al., 2019). In the case of Antarctica, Zhang et al. (2021) reports PAHs air-seawater fluxes along a sampling transect from the northwestern Pacific to the Southern Ocean and they suggest that

Table I
Summary of studies reporting the presence and concentrations of SVOCs in polar ecosystems.

SVOCs	Environment (soil, vegetation, and water)			Study sites	References
Antarctica					
PCBs	Seawater sediment			Ross sea and Drake passage, Antarctica	Deng et al., 2020
PCBs	Sediment cores			Admiralty Bay, King George Island, Antarctica	Combi et al., 2017
PAHs	Soils y sediment			Admiralty Bay, King George Island, Antarctica.	Prus et al., 2015
PAHs			Seawater	Western Pacific and Southern Ocean	Cai et al., 2016
PAHs			Seawater (surface waters)	Northwestern Pacific to the Southern Ocean	Zhang et al., 2021
PAHs			Seawater (coastal waters)	South Shetland Islands, Antarctica.	Iriarte et al., 2023
PCBs, PCDD/Fs, PBDEs	Soils	Lichens		Chinese Station, King George Island, Antarctica	Mwangi et al., 2016
PBDEs and PCBs	Soils and freshwater sediment	Vegetation mat		Victoria Land, Antarctica	Corsolini et al., 2019
PCBs and PBDEs	Soils y sediment	Lichen and moss		Fildes Peninsula, King George Island, Antarctica.	Wang et al., 2012
NBFRs	Soils	Lichen and moss		Chinese Antarctic Station, King George Island, Antarctica	Xiong et al., 2021
PAHs, PCBs, HCB, DDE,	Soils	Lichen, moss and vascular plants		South Shetlands Islands, Antarctica	Cabrerizo et al., 2012, 2013, 2016
HCH, HCB, DDT, PCBs, PBDEs	Soils	Lichen, moss and vascular plants		King George Island, Antarctica.	Cipro et al., 2011, 2019
PCBS, HCH	Soils and sediment	Lichen and moss		Fildes Peninsula, King George Island, Antarctica.	Wang et al., 2015a, 2015b
OH-PBDEs, MeO-PBDEs	Soils	Lichen, moss and vascular plants		Fildes Peninsula, King George Island, Antarctica.	Sun et al., 2022
OCPs	Soils and sediment	Lichen and moss		Fildes Peninsula, King George Island, and Western Antarctic Peninsula, Antarctica.	Zhang et al., 2013; Zhang et al., 2015
PBDE		Lichen, moss and vascular plants		King George Island, Antarctica.	Yogui and Sericano, 2008; Yogui et al., 2011
PAHs, PCBs, HCB, PBDEs, DDTs, Drins		Mosses		Brazilian Antarctic Station, King George Island, Antarctica.	Colabuono et al., 2015
PBDEs, HBCDs		Lichen and moss		South Shetland Islands, Antarctica.	Kim et al., 2018
PFAS			Seawater samples	Livingston Island, South Shetland Islands, Antarctica.	Casas et al., 2020
PFAS			Surface waters (ice-melting lakes)	Larsemann Hills, East Antarctica	Shan et al., 2021
PCBs, HCB and HCH			Seawater	Southern Ocean, Antarctica	Galbán-Malagón et al., 2013b, 2013c, 2013d
OCPs			Seawater Sea-ice Snow	Southern Ocean and Davis Research Station, Antarctica	Bigot et al., 2016, 2017
OCPs			Seawater	Amundsen Sea and the Weddell Sea, Antarctica	Xuan et al., 2023
PCBs, HCB, HCH, PAHs			Seawater	Southern Ocean	Echeveste et al., 2016
PFRs, PAHs, PCBS, OCPs			Freshwater and seawater	Fildes Peninsula, King George Island, Antarctica.	Gao et al., 2018
ARCTIC					
PCBs	Soils			Lomonosovfonna glacial, Svalbard.	Bartlett et al., 2019
PAHs, PCBs and OCPs	Soils and Snow			Tromsø island, Norway, Artic	Casal et al., 2019
OPEs	Soils			Ny-Ålesund and London Island, Svalbard, Arctic	Han et al., 2020
PAHs	Soils			Pyramiden, Svalbard, Arctic	Marquès et al., 2017
PCBs	Soils and sediment	Moss and Plants		Ny-Ålesund, Svalbard, Arctic	Zhang et al., 2014
PCBS and PBDEs	Soils	Moss and Plants		Ny-Ålesund and London Island, Svalbard, Arctic	Zhu et al., 2015
PCBs, OCPs, PFASs	Soils	Lichen, moss and vascular plants		Canadian High Arctic	Cabrerizo et al., 2018
PCBs	Soils	Moss and plants		Ny-Ålesund and Adventdalen, Svalbard, Arctic	Aslam et al., 2019
OH-PBDEs, MeO-PBDEs	Soils	Moss and plants		Svalbard, Norway, Arctic	Sun et al., 2022
PAHs PBDEs	Soils	Moss		Ny-Ålesund, Svalbard, Arctic	Wang et al., 2009, 2015a, 2015b
OPEs	Sediment			Northeast Atlantic and Arctic Ocean	Ma et al., 2017
PCBs and HCB			Marine sediment	Arctic fjord system (Isfjorden, Svalbard)	Johansen et al., 2021
PCBs			Seawaters and sediments	Arctic Ocean	Sobek and Gustafsson, 2014
PCB, HCH and HCB			Seawater	North Atlantic and Arctic Ocean	Galbán-Malagón et al., 2012, 2013a
OPEs			Snow and seawater	Northeast Atlantic and Arctic Ocean	Li et al., 2017
OH-PBDEs, MeO-PBDEs			Seawater and sediment	Hudson Bay, Canadian Arctic	Kelly et al., 2008
DDTs			Seawaters	Arctic Ocean	Carrizo et al., 2017
PBDEs			Seawater	East Greenland Sea, Arctic	Möller et al., 2011
PFOS, PFOA			Seawater	Ny-Ålesund, Svalbard, Arctic	Choi et al., 2020
OCPs			Seawater Sea-ice Snow	Villum Research Station (VRS), Station Nord, North Greenland	Bigot et al., 2017
OCPs and PAHs			Seawater (surface water)	North Atlantic and Arctic Ocean	Lohmann et al., 2009
PCB, HCB and PAHs			Seawater	Arctic fjords	Pouch et al., 2021
PCB, PFASs and PAHs			Seawater (surface water)	Kongsfjorden, Svalbard, Arctic	Ademollo et al., 2021
PAHs	Surface sediment			Svalbard,Arctic	Lin et al., 2022
PAHs			Seawater	North Pacific and Arctic Ocean	Ke et al., 2017
PAHs			Seawater	North Pacific and Arctic Ocean	Zheng et al., 2021

Table I (*continued*)

SVOCs	Environment (soil, vegetation, and water)	Study sites	References
PAHs	Seawater	Subarctic and Arctic Ocean	Svavarsson et al., 2021
PAHs	Seawater	Arctic Ocean	Na et al., 2021
PAHs	Seawater	North Atlantic and Arctic Ocean	Liu et al., 2022
PAHs	Seawater	Arctic Ocean	Zhang et al., 2023
PAHs	Seawater	Northwest Pacific and Arctic Ocean	Fu et al., 2022

coastal outflows and ocean currents play an important role in spatial distribution trends for PAHs. Moreover, Cai et al. (2016) analyzed dissolved PAHs in the surface waters from the western Pacific to the Southern Ocean, which suggests, that the water masses as well as the phytoplankton were possible influencing factors on PAH surface-enrichment depth-depletion distribution (Cai et al., 2016). More recently, Iriarte et al. (2023) in coastal Livingston and Deception Islands in the South Shetlands Islands showed that biogeochemical cycling, including microbial degradation, was dependent on snow-derived inputs of organic matter on an annual basis. These examples allow us to glimpse about the fate of SVOCs, but further studies should consider oceanic modelling in both direct and indirect ways based on SVOCs data in multi-environments (Liu et al., 2022).

Most studies that evaluate SVOCs in polar vegetation have focused on lichens and mosses, however, vascular plants are also adapted and can thrive. In Antarctica, for instance, two vascular plants can thrive *Deschampsia antarctica* and *Colobanthus quitensis* (Convey, 2011; Convey et al., 2011); whereas in the Arctic more than 100 species have been described (CAFF, 2022). For instance, in Svalbard (high Arctic) 173 vascular plants have been described, of which 167 are native (Elvebakk and Prestrud, 1996). Importantly, a global study addressing SVOC concentration in vegetation found that HCB, HCH, and DDT concentrations in remote sites including the poles increased over time, suggesting a remobilization of SVOCs, i.e., reemission from primary sources or polar reservoirs (Bartrons et al., 2016; Cabrerizo et al., 2013).

Therefore, SVOCs as secondary sources are available for polar biodiversity, potentially affecting microbes, phytoplankton, krill, fish, vegetation, birds, and marine mammals, as well as contributing to the local burden of pollutants in these regions (Cabrerizo et al., 2012).

Native species from polar regions have shown potential for bioaccumulation and biomagnification of SVOCs, predominantly in adipose tissue. For instance, in the case of organophosphate esters (e.g., flame retardants, plasticizers, antifoaming agents), Fu et al. (2020) described both accumulation and magnification in sediments, algae, mollusks, fish, and birds of the Antarctic trophic web. Other studies have shown SVOCs negative impact on ecosystem functioning in these regions (Bates et al., 2017; Brown et al., 2018; Corsolini et al., 2017; Jara-Carrasco et al., 2015; Potapowicz et al., 2020; Rigét et al., 2019; Rotander et al., 2012; Verreault et al., 2005).

Altogether, the slow natural decay of SVOCs, coupled with new primary and secondary sources and their bioaccumulation and biomagnification properties, pose a complex problem for the scientific community to approach (Hung et al., 2016; Wang et al., 2019). In the context of current and future anthropogenic activity and Climate Change, new strategies for bioremediation to mitigate exposure of SVOCs in polar environments are sorely needed.

3. Degradation of SVOCs by polar microorganisms

Bioremediation by polar microorganisms is a viable strategy to mitigate the long-term exposure of polar biodiversity to SVOCs (Flocco et al., 2019). Bioremediation consists of biodegrading organic pollutants *in situ*, leveraging on the enzymatic activity and metabolic potential of microorganisms and other organisms (Gaur et al., 2018; Negrete-Bolagay et al., 2021; Sharma et al., 2018). Polar microbes, often times poly-extremophiles, are ideal for bioremediation (Orellana et al., 2018), including in polar environments polluted with SVOCs.

Biodegradation of pollutants in polar regions by native microbes through their metabolic potential is considered safe and cost-effective (Bamforth and Singleton, 2005). Although low temperatures tend to inhibit or reduce metabolic activity in microbes (Qi et al., 2007), studies demonstrate the capacity of cold-adapted bacteria and fungi to biodegrade SVOCs in low-temperature settings (Bajaj and Singh, 2015; Giovanella et al., 2020). Additionally, the introduction of non-native species is not allowed in polar regions (Crisafi et al., 2016; Gran-Scheuch et al., 2017; Okere et al., 2012), thus, the identification and characterization of native polar microbes becomes ever more relevant. To date, we have an incomplete picture of the distribution, taxonomic and phylogenetic diversity, and biogeography of naturally occurring polar microbes with potential for degrading SVOCs.

Aquatic and terrestrial microbes, as well as microbes from the rhizosphere of plants, in polar ecosystems show potential to biodegrade SVOCs (Table II). Most published studies have looked at PAH biodegradation (i.e., naphthalene, anthracene, phenanthrene, and pyrene), which are highly stable given their chemical structure.

Several studies show bacteria from soil and water bodies able to metabolize organic pollutants, which mainly belong to the following species: *Sphingobium xenophagum*, *Burkholderia glathei*, *Paeniglutamicibacter* sp., *Psychrobacter* spp., *Pseudomonas* sp., *Rhodococcus* sp., *Polaromonas*, and *Pseudoalteromonas*. Soil fungi also are able to degrade organic pollutants, e.g., *Penicillium* sp. y *Aspergillus* sp. Flocco et al., 2009 identified a rhizosphere bacterium from the *Pseudomonas* genus capable of biodegrading SVOCs (Flocco et al., 2009). These studies either based their assessments on microbial growth rates in polluted environments and/or SVOCs degradation rates (i.e., Gran-Scheuch et al., 2017); valuable information that might be used to parameterize *in situ* and *in vitro* assays for biotechnological development.

Microbes can rapidly adapt to abiotic stress including pollution by organic compounds (Chakraborty and Das, 2016). In the studies listed in Table II, researchers have identified enzyme encoding genes that subtend the catabolic pathways involved in biodegradation by polar microbes (Cerro-Gálvez et al., 2020; Ellis et al., 2022; Flocco et al., 2009; Gran-Scheuch et al., 2017; Jurelevicius et al., 2022; Martínez-Varela et al., 2021, 2022; Muangchinda et al., 2015; Panicker et al., 2010; Papale et al., 2017). However, to date, only one of these studies has conducted a global characterization of the degradation pathway for a PAH-degrading Antarctic microbe (Martínez-Varela et al., 2022). Evidently, more studies focusing on characterization and mechanisms of organic pollutant biodegradation are needed.

4. Mechanisms of mitigation of the effect of SVOCs in polar ecosystems

SVOCs are characterized by the presence of nitro-, sulfur-, and halogen functional groups (Cl, Br, F) and/or aromatic rings that makes them recalcitrant to degradation (Pennington, 2001). Water and soil dwelling, free living microbes and those associated with plants in polar regions exhibit a varied genetic and enzymatic machinery capable of performing key processes in the degradation of the complex chemical structure of SVOCs (Table III; Bajaj and Singh, 2015; Chakraborty and Das, 2016; Fester et al., 2014; Fuchs et al., 2011; Rolli et al., 2021). The molecular mechanisms responsible for metabolizing SVOCs correlate with the chemical structure and functional groups of these compounds and can be grouped into halogenated organic compounds (HOCs) and aromatic organic compounds (AOCs) (Gaur et al., 2018).

Bacteria can co-metabolize HOCs, be it anaerobically or aerobically, i.e., PCBs (Atashgahi et al., 2018; Jeon et al., 2016). In the absence of

Table II
Summary of studies identifying polar microbes able to biodegrade SVOCs.

Microorganism	SVOCs	Study sites	References
Antarctica			
Soil and plant bacterial community	PAHs	Argentina Station and Potter Peninsula, King George Island, South Shetland Islands, Antarctica	Flocco et al., 2009
Soil bacterial community and Pseudomonas sp	PAHs	Scott Base, the former Vanda Station and Marble Point, Antarctica	Panicker et al., 2010
Soil bacterial community	PAHs	Livingstone Island, South Shetlands Islands, Antarctica	Okere et al., 2012
Soil *Sphingobium xenophagum* D43FB	PAHs	King George Island, South Shetland Islands, Antarctic	Gran-Scheuch et al., 2017
Soil bacterial community bacterial	PAHs	Brazilian Station, King George Island, South Shetland Islands, Antarctica	Jurelevicius et al., 2012, 2022
Soil *Paeniglutamicibacter sp.*	PAHs	China Station, King George Island, Antarctica	Sakdapetsiri et al., 2021
Soil and sediment bacterial community	PAHs	Japan Station, Ongul Oriental Island, Antarctica	Muangchinda et al., 2015
Sea-Surface bacterial community	PAHs	Livingston Island, South Shetlands, Antarctica	Martínez-Varela et al., 2022
Soil fungus community	PAHs	Livingstone Island, South Shetlands Islands, Antarctica	Gerginova et al., 2013
Soil fungus community	PAHs	Bulgarian base, Livingston Island, Antarctica	Stoyanova et al., 2022
Marine sediment bacterial	PCBs	Terra Nova Bay, Ross Sea, Antarctica	Lo Giudice et al., 2013
Coastal bacterial community	PFOS	Port Foster Bay, Deception Island, South Shetland Islands, Antarctica	Cerro-Gálvez et al., 2020
Seawater bacterial community	PFOS	South Bay of Livingston Island, South Shetland, Antarctica	Martínez-Varela et al., 2020
Arctic			
Seawater bacterial community	PAHs	Kongsfjorden, Svalbard Islands, Arctic	Crisafi et al., 2016
Deep-sea sediments bacterial community	PAHs	High-latitude Arctic Ocean	Dong et al., 2015
Costal sediment bacterial community	PAHs	Polar and Subpolar Coastal	Espínola et al., 2018
Beach sediment bacterial community	PAHs	Canada's Northwest Passage, Arctic	Ellis et al., 2022
Seawater bacterial community	OPE and PAHs	Northeast Subarctic Pacific Ocean	Martínez-Varela et al., 2021
Freshwater and sediment bacterial	PCBs	Pasvik River and Varanger Fjord Norway, Arctic	Rappazzo et al., 2019
Seawater and sediment bacterial community	PCBs	Kongsfjorden, Svalbard Islands, Arctic	Papale et al., 2017

oxygen, bacteria carry out a reductive dehalogenation where HOCs act as electron acceptors, losing their halogen group and maintaining the biphenyl skeleton (e.g., PCBs; Pimviriyakul et al., 2019). For instance, Haruna (2019) isolated a *Bacillus* species from Antarctic soil (isolate IH1) and determined that it could release chlorine ions through the enzymatic action of dehalogenases acting upon HOCs.

On the contrary, aerobic biodegradation works for PCB congeners with low chloride content, where the biphenyl group can be either metabolized by a single microbe or a consortium (Pimviriyakul et al., 2019). This is a two-step process, the upper pathway that includes the oxidation of a biphenyl molecule forming chlorobenzoic acid that then goes into the benzoate degradation pathway (associated with aromatic compounds). The second step, called lower pathway, takes the biphenyl molecule (chlorobenzoic acid), and catabolizes it into intermediaries of the tricarboxylic acid cycle (TCA; Chen et al., 2021a, 2021b; Fuchs et al., 2011; Furukawa and Fujihara, 2008; Pieper, 2005; Pieper and Seeger, 2008). The key enzyme in the pathway is the biphenyl 2,3-dioxygenase (BphA) and the *bphA* gene has been identified in Arctic and Antarctic bacteria (Table III). This further suggests that bioremediation of polluted polar regions might be possible with native microorganisms.

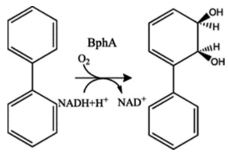
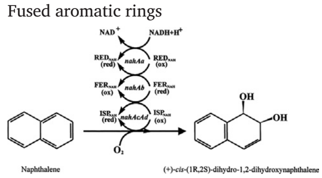
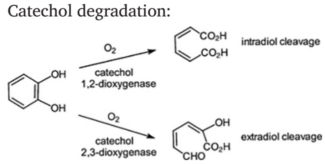
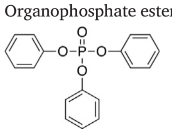
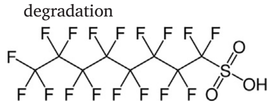
On the other hand, AOCs like PAHs can be degraded aerobically in a process that can be classified by two pathways. The first pathway is carried out by bacteria and produces intermediaries such as catechol or protocatechuate (the upstream pathway) that are then degraded down to less toxic compounds part of the TCA cycle (downstream pathway). In the latter pathway, aromatic-ring-hydroxylating dioxygenases (RHDs) catalyze the first step in PAH degradation, transferring two oxygen atoms to the substrate. The second degradation pathway is carried out by bacteria and fungi through the action of monooxygenases (e.g., CYP450) that transfer one oxygen atom to the substrate. Antarctic bacteria exhibit genes encoding the RHD protein complex and catechol dioxygenases (Table III). Using metagenomics, Jurelevicius et al. (2022) showed a higher abundance of genes associated with PAH degradation encoding CYP450 monooxygenases and benzoate dioxygenases. In another study, this time in Antarctic marine microbial communities, Martínez-Varela et al. (2022) found RHD overexpressed genes, as well as genes from the upper pathway, in communities exposed to PAHs. However, genes involved in downstream steps were not overexpressed. In marine communities of the Arctic, Martínez-Varela et al. (2022) also identified RHD genes, protocatechuate dioxygenase, catechol dioxygenase, and muconate cycloisomerase. These results show that marine and soil microbes from both polar regions have the potential to mitigate the impact of AOCs.

While we have limited information, degradation of organic compounds by fungi have been reported (Duarte et al., 2018). Ligninolytic fungi, as well as non-ligninolytic ones, degrade SVOCs through initial oxidation of substrates (Marco-Urrea et al., 2015; Pozdnyakova, 2012). Ligninolytic fungi produce extracellular enzymes such as manganese peroxidase, laccase, and lignin peroxidases, which in turn produce quinone intermediaries. Non-ligninolytic degradation uses intracellular enzymes, monooxygenases (CYP450) to produce non-stable arene oxides that are then converted into phenolic compounds or trans-dihydrodiols (Prenafeta-Boldú et al., 2018). For instance, Stoyanova et al. (2022) showed that soil Antarctic non-ligninolytic fungi were capable of degrading AOCs (naththalene and anthracene), identifying key intermediates and enzymatic activity through phenol 2-monooxygenase and catechol 1,2-dioxygenase. Currently, this study is the only one available on the degradation of AOCs by fungi.

The interaction between the plant host and its microbiome contribute to the structure and functioning of the holobiont (evolutionary unit composed of the plant and associated microorganisms), where SVOC degrading microbes contribute to mitigate the effects of this pollutants in the whole ecosystem (Arslan et al., 2017; Sánchez-Cañizares et al., 2017; Trivedi et al., 2020; Turkovskaya and Muratova, 2019; Uhlik et al., 2013). Moreover, plants might adapt a variety of strategies to facilitate microbial metabolism in the presence of organic compounds (Di Guardo et al., 2017; Fester et al., 2014). For instance, plants can release primary and secondary metabolites (sugars; aminoacids; organic acids) that might foster the growth of specific microbial taxa (Macek et al., 2000). Also, plants release root exudates that would have a role decreasing the concentration of organic pollutants in soils with vegetation cover (Chaudhry et al., 2005; Ionescu et al., 2009; Jha et al., 2015; Rohrbacher and St-Arnaud, 2016; Rolli et al., 2021).

Rhizosphere microbes associated with the Antarctic vascular plants *D. antarctica* and *C. quitensis* harbor genes able to metabolize organic pollutants, e.g., naphthalene dioxygenase (*ndo* and *nahAc*), though the abundance of these genes is equivalent to that of bulk contaminated Antarctic soils (Flocco et al., 2009). Plants carry out a slow and incomplete degradation of organic pollutants due to the lack of the necessary enzymes for complete mineralization, often times provided by microorganisms (Rolli et al., 2021; Schwitzguébel, 2017). However, plants possess other molecular mechanisms to metabolize SVOCs (Sandermann, 1994), such as the transformation to more soluble hydrophilic compounds, conjugation and

Table III
Genes associated with SVOCs degradation pathways reported in polar microbes.

SVOCs degradation pathway	Genes	References
Upstream PCBs degradation	Biphenyl dioxygenase, ***bphA***	Panicker et al., 2010
Biphenyl:		Papale et al., 2017
		Rappazzo et al., 2019
		Jurelevicius et al., 2022
	Biphenyl and dihydroxybiphenyl dioxygenase, ***bphA and bphC***	Martínez-Varela et al., 2021
Upstream PAHs degradation	Ring hydroxylating dioxygenases (RHD):	Flocco et al., 2009
Fused aromatic rings	-Naphthalene dioxygenase: ***ndoB, nahAc, nahA, phnAc, pdoA, nidA***	Panicker et al., 2010
		Muangchinda et al., 2015
		Martínez-Varela et al., 2021, 2022
	-Protocatechuate dioxygenase: ***pcaG and pcaH***	Martínez-Varela et al., 2021, 2022
	-Glyoxalase dioxygenase, ***nahC***	Martínez-Varela et al., 2022
	-2-hydroxychromene-2-carboxylate isomerase, ***nahD***	
	-Dihydrodipicolinate synthetase, ***nahE***	
	-Salicylaldehyde dehydrogenase, ***nahF***	
	-Salicylate hydroxylase, ***nahG***	
	-4,5-dihydroxyphthalate decarboxylase ***pht5***	
	-3,4-dihydroxyphthalate decarboxylase ***padC***	
	-1,6-dihydroxycyclohexa-2,4-diene-1-carboxylate dehydrogenase, ***benD***	
Downstream PAHs degradation	-Catechol 2,3-dioxygenase, ***C23DO***	Panicker et al., 2010
Catechol degradation:	-Catechol 1,2-dioxygenase, ***C12O/catA***	Stoyanova et al., 2022
		Martínez-Varela et al., 2021, 2022
	-Muconate cycloisomerase, ***catB***	Martínez-Varela et al., 2021, 2022
	-2-hydroxymuconate semialdehyde hydrolase, ***xylF***	Martínez-Varela et al., 2022
	-4-hydroxy-2-oxovalerate aldolase, ***xylK***	
	-Metapyrocatechase, ***xylE***	
	-Muconolactone Delta-isomerase, ***catC***	
PAHs degradation	Cytochromo P450 (CYP450) family: phenanthrene 1,2-monooxygenase and 1-methylnaphthalene hydroxylase	Jurelevicius et al., 2022
	-Benzoate-1,2- dioxygenase, ***Bdo/benA and benB***	Jurelevicius et al., 2022
		Martínez-Varela et al., 2021
	Predicted pathways of phenanthrene degradation	Gran-Scheuch et al., 2017
Organophosphate esters (PBDE) degradation	Phosphoesterases: ***PTE and PTE-LL, PDE, PMO***	Martínez-Varela et al., 2021
		
Perfluoroalkyl acids (PFOS, PFOA) degradation	-Sulfonate and alkanesulfonate monooxygenases	Cerro-Gálvez et al., 2020
	-DMSP degradation: DMSP lyases (dddP, dddD, etc.) and DMSP demethylase (dmdA)	
	-Sulfatase genes (sulfohydrolases).	

storage, and elimination (Labrou et al., 2015; Pang et al., 2012). Plant mechanisms involve cytochrome P450 enzymes for transformation and glutathione-S-transferases for conjugation. Transformed and conjugated compounds can be transported and stored in a vacuole mediated by ABC transporters, sequestered by cell wall polymers, or excreted out of the cell (Kvesitadze et al., 2009). While some studies have documented that rhizosphere microbes favor stress tolerance in Antarctic vascular plants (Molina-Montenegro et al., 2019; Znój et al., 2021), the role of these microbes in the presence of SVOCs remains to be elucidated.

In Antarctic marine bacteria, studies have identified three gene families associated with sulfur metabolism, such as sulphonate and alkanesulphonate monooxygenases, genes involved in the metabolism of Dimethylsulfoniopropionate (DMSP), and genes encoding sulfatases that would participate in PFOS degradation (Cerro-Gálvez et al., 2020). These results suggest Antarctic microbial communities in the ocean can metabolize PFOS in aerobic conditions and the role of organic sulfur compounds of anthropogenic origin in the biogeochemical cycle of reduced sulfur (Cerro-Gálvez et al., 2020). Moreover, in marine bacteria from the Artic, researchers have identified genes encoding phosphoesterases able to hydrolyze phosphate ester bonds such as those part of organophosphates (flame retardants and plasticizers) or pesticides (Martínez-Varela et al., 2021).

Interestingly, in the Mediterranean, organic pollutants can modulate extracellular enzymatic activity and bacterial growth depending on nutrient levels (Cerro-Gálvez et al., 2019). Moreover, researchers have shown that microbes and their trophic level are relevant variables to understand and predict *in situ* degradation of organic pollutants, as well as, evaluating the risk posed by synthetic chemicals in marine environments (Cerro-Gálvez et al., 2019). Altogether, studies reveal not only the importance of microbes in degrading organic pollutants but also the need to deepen our knowledge regarding metabolic pathways responsible for SVOC degradation in polar environments.

5. Conclusions and final remarks

Several studies have evidenced the presence of SVOCs and their bioaccumulation and biomagnification in polar regions, with negative effects on biodiversity and ecosystems. Despite that the production and use of SVOCs is now regulated, their presence remains a problem. Three situations call for a long-term look at how we deal with SVOCs: their slow degradation rate, their capacity to accumulate in polar regions, and the temporal projections of presence and concentration of these pollutants. The consequences of SVOCs in the polar regions go beyond the poles since polar ecosystems have a global ecological role.

5.1. Metabolic pathways exclusive in polar microbes and their application to bioremediation processes

Polar microbes are key to biodegrade aromatic and halogen organic compounds, in part, this is evidenced by the increasing interest in studying them. We now know of key genes required for metabolizing SVOCs; however, we still require a more in-depth understanding of the metabolic potential of polar-adapted microbes. Currently, few studies analyze the presence and expression of SVOC degrading genes and the metabolites that participate in the biodegradation process, i.e., Garrido-Sanz et al., 2018.

On the other hand, future studies must consider today's global changes, e.g., increase in temperature, ice-cover season, and nutrient concentrations. For instance, Jurelevicius et al. (2022) suggested that soil bioremediation might be carried out by nitrogen fixing bacteria able to degrade hydrocarbons *in situ*. This implies that evaluating carbon and nitrogen biogeochemical cycles would contribute to understanding degradative processes and the associated microbes' metabolic potential.

Cold-adapted microbes with a wide temperature tolerance could improve biodegradation rates. Their study would require field measurements and the feasibility of biotechnological tools on polluted environments.

5.2. SVOCs and Climate Change

Climate Change is relevant to the vulnerable polar environments since SVOCs exchange processes respond to air and ocean changes in temperature. Studies have documented the remobilization of organic pollutants to polar ecosystems as a result of Climate Change, which increases the availability of SVOCs linked to increasing temperatures (Hung et al., 2022; Ma et al., 2016). Moreover, Climate Change may affect plant cover in Antarctica, which in turn might have an antagonistic effect on remobilizing SVOCs (Cannone et al., 2022). Altogether, integrated long-term monitoring of SVOC concentrations and the fate of these pollutants is needed, both considering local and global sources, i.e., Kallenborn et al. (2012), as well as, developing ecosystem and Earth-level models to evaluate future Climate Change scenarios (Cavicchioli et al., 2019). Additionally, Kennicutt et al. (2015) stated the need to coordinate a network of researchers in interdisciplinary polar science that would strengthen our chances to solve looming problems.

Finally, the scientific community needs to strengthen research areas related to the vulnerability of polar environments polluted with SVOCs, produce long-term data and analyses, and make them available to citizens and policymakers alike. Participation of not only scientist but all parties is key and can contribute to the establishment of international public policy aimed at preventing the collapse of the polar eco-regions.

6. Future research

Despite harboring microbes and SVOC-degrading genes, bioremediation in the polar regions will not occur spontaneously. As new compounds are made and old ones are remobilized, natural attenuation will only have marginal effects on SVOCs in the polar regions. Instead, biostimulation of native microbial communities with attention to the heterogeneity in nutrient availability and physical properties of soils and coastal waters might be more effective and efficient in remediating polar environments. In turn, bioaugmentation with consortia developed from polar environments will facilitate pollutant degradation in critical areas, e.g., research bases, tourism camps and cruises, and fisheries associated polluted sites.

We pose that future research should be focused on two broad areas, namely, to further understand the landscape of SVOCs in both terrestrial and aquatic ecosystems and to fully understand molecular mechanisms underlying SVOC microbial degradation.

6.1. Understanding the landscape of SVOCs in both terrestrial and aquatic polar ecosystems

Polar ecosystems are diverse and are differentially affected by human activities and by pollution. Consequently, we do not currently have a proper understanding of the distribution and type of pollutants in polar regions. Naturally, research has focused nearby research stations and camps and to some extent on distant sites. Moreover, sampling designs are convenience-based instead of informed by pollutant dispersion or atmospheric models.

Future research would benefit from data derived from more permanent observatories, where meteorological, biological, and environmental data are collected over longer periods of time. This would allow researchers to jointly model disparate sources of data and develop new hypotheses regarding the impact of primary and secondary sources of SVOCs on wildlife and the environment. Likewise, long-term data would allow researchers to test seasonality of SVOC emissions (or re-emissions), as well as annual and decadal trends in the biotic and abiotic components of the polar regions.

Microbes are cosmopolitan though functionally diverse and thus it is not uncommon to find the same microbial species living under widely different conditions (Sunagawa et al., 2015; Bahram et al., 2018; Escalas et al., 2019). This fact stems from the highly fluid horizontal exchange of genetic material within both closely and distantly related species, in particular those species with large population sizes (McInerney et al., 2017). In turn, this has led to the realization that microbial genomes do not exist as a single representative but rather as a pangenome, i.e., large amounts of within-species variability in genome content. Microbial pangenomes, then, need to be accounted for when surveying polar regions. Microbial distribution alone, e.g., 16S rRNA gene surveys or equivalent, do not capture the functional capabilities of microbes and thus do not provide information on metabolic potential. Imputation methods perform well with microbial communities from more traditional study sites, e.g., human gut microbiome, but their performance remains unknown with microbial communities from extreme environments such as the polar regions (Sun et al., 2020). Future research will benefit from studies that employ the full power of high-throughput sequencing for surveying not only gene content (metagenomics) but also gene expression (metatranscriptomics). Together with a better understanding of the SVOC landscape in polar regions, understanding microbial distribution in light of metabolic capabilities will allow researchers to develop tailor-made formulas to biostimulate local communities for bioremediation.

6.2. Understanding molecular mechanisms underlying SVOC microbial degradation

While molecular mechanisms underlying the degradation of pollutants are partially known, their full consequences remain understudied. Specifically, two areas need attention: how genes involved in bioremediation are activated and what are the potential toxic byproducts of *in situ* pollutant degradation.

Future developments in bioremediation in the polar regions, especially in those protected by international treaties, e.g., Antarctica, forbid the introduction of exotic species, including microbes, which makes biostimulation a viable *in situ* bioremediation approach. Also, bioaugmentation by native microbes in the form of enriched cultures or the like could be applied in protected areas. Whereas many studies have reported the presence of SVOC-degrading microbial genes and metabolic pathways in aquatic or terrestrial polar ecosystems, the mere presence of these genes and pathways do not necessarily translate into active biodegradation of pollutants (Hua et al., 2015). As with other molecular complexes, e.g., biosynthetic gene clusters, microbes only turn on these genes and pathways under particular, and sometimes mysterious, circumstances (Libis et al., 2022). Enzyme cofactors and specific nutrients, aside from minute concentrations of pollutants, might be needed for microbes to express bioremediation genes and pathways (Iyer et al., 2013). For instance, Antarctic soils are relatively depleted of organic matter except for coastal areas where birds and marine mammals input carbon and nutrients to the system (including animal carcasses).

These soils might also contribute nutrients to distant sites by wind transport, which coupled with seasonal meltwater runoff, create a patchy landscape of organic matter and nutrients, some of which might be needed for activating SVOC degrading microbes (Cowan and Ah-Tow, 2004).

Microbial degradation of pollutants may not only lead to the production of more toxic compounds, but also more mobile. For instance, the microbial reductive dehalogenation of trichloroethene results in vinyl chloride, a known carcinogen and neurotoxic compound (Ennis et al., 2005). Better understanding the molecular mechanisms behind SVOC transformations might help ameliorate unwanted effects. In the case of trichloroethene transformation into vinyl chloride, researchers have identified bacteria belonging to the genera *Nocardioides* and *Mycobacterium* capable of utilizing and co-transforming vinyl chloride (Taylor et al., 2007).

6.3. Deploying specific solutions in a Climate Change scenario

Climate Change is a complex problem operating across disciplines and scales. Studies have pondered its effects globally and in the polar regions (Robinson, 2022). In the Arctic, warming is predicted to continue above the global average in both aquatic and terrestrial ecosystems, as well as in the Antarctic Peninsula and West Antarctica. In these environments, increasing temperatures imply more freshwater availability, more soil organic matter, and in some areas more vegetation cover. For POPs in Antarctica, researchers have found that an increase of 1 °C in ambient temperature would increase atmospheric inventories of PCBs by up to 45 %. At the same time, soil organic carbon would increase and counteract the influence of warming due to a reduced POP fugacity, turning soil and vegetation derived organic carbon into a net sink of POPs (Cabrerizo et al., 2013). In the Arctic, in turn, increased mobilization of pollutants such as POPs is expected, especially from more southernly latitudes (Hung et al., 2022).

The distribution and metabolic potential of microbes and the distribution of SVOCs in polar regions need to be considered when designing and deploying bioremediation solutions. Researchers need to consider Climate Change, which adds another layer of complexity since not only space, but also temporal heterogeneity will likely influence the success of any bioremediation attempt in the polar regions.

CRediT authorship contribution statement

CE, CGM, ECN and MAMM conceived the ideas; CE and MAMM compiled data; CE and MAMM generated figures; CE, CGM, ECN and MAMM wrote the draft manuscript, and all authors contributed to editing it.

Data availability

No data was used for the research described in the article.

Declaration of competing interest

No potential conflict of interest was reported by the authors.

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