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D1.6 An understanding of the shifts between microbial dormancy and activity and physico-chemical triggers at the snow-ice interface

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PREFACE

This document is intended to create an understanding about the microbial processes specifically related to the shifts between dormancy and activity in Alpine and Polar environments. The aim is to provide a general framework about the major physico-chemical triggers at the snow-ice interface and how it affects the microbial response between dormancy and activity. The information presented henceforth explains about the possible conditions where microbes have to trade-off their activity with temporary pause which enables them to coexist and promote the stability of the ecosystem. The information stated hereby is a deduction of microbial processes under identified parameters that is majorly found at the snow-ice interface.

1. Introduction

Dormancy is a reversible state of metabolic hiatus triggered by unfavourable environmental conditions which allows the microorganisms to conserve energy and prolong their chances of survival. When the natural habitat of the microorganism undergoes physico-chemical changes, it alters the equilibrium of several biotic and abiotic factors that induces a stress response among the microbial community and forces them to adapt to the new condition (Casanueva et al., 2010; De Maayer et al., 2014; Mocali et al., 2017). When they fail to adapt or lack the genomic plasticity that could support them in the new scenario, they enter the state of dormancy (Lennon & Jones, 2011). Dormancy can be carried out by complete change in cellular morphology such as sporulation and cyst formation which is an ability akin to very limited clade in the microbial kingdom (Ashok & Bauer, 2020; Berleman & Bauer, 2004; Malard et al., 2023; Stragier & Losick, 1996). Sporulating species are also reported to preplan their revival by attaching the RNA polymerase at promoter regions of genes with essential cellular function during the sporulation (Zhou et al., 2023). Hence, during re-activation the necessary genes are transcribed rapidly. However, the majority of microbial species are unable to form such complex bodies and have been reported to reduce their cell size (Guerra et al., 2015), downregulate growth-associated pathways, and rely on endogenous energy reserves (Bourassa & Camilli, 2009; Kadouri et al., 2005) to match the metabolic demands (Kaprelyants et al., 1993). While dormancy offers key advantages in terms of resilience (Philippot et al., 2021; Sorensen & Shade, 2020) and lineage preservation (Lennon & Jones, 2011), it also entails trade-offs, such as vulnerability to prolonged inhospitable conditions and eventually inactivation. Thus, it can be regarded as a last resort for survival, employed when continued metabolic activity is no longer viable (Kim et al., 2023). In **Figure. 1**, We aimed to demonstrate how the combined influence of physicochemical triggers and nutritional fluctuations significantly shapes the metabolic strategies of microorganisms, leading to an imbalance in energy allocation between growth and maintenance. This imbalance subsequently affects the transition between dormancy and activity, which is governed by genetic factors such as diverse metabolic and stress response genes within the stressed microbial community. The onset of dormancy establishes an ecological barrier between dormant microbes and their environment, leading to the natural selection of the fittest to drive the ecological processes.

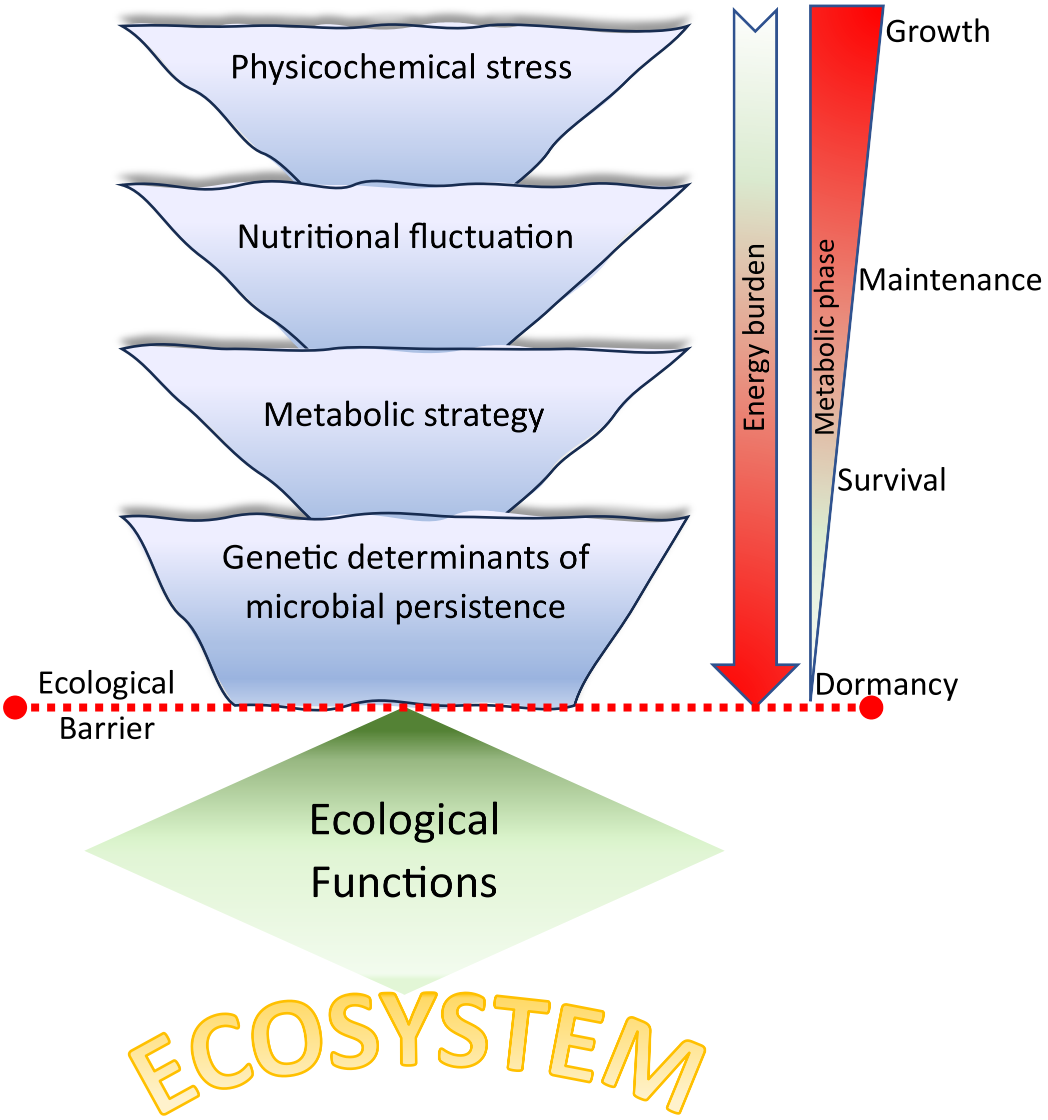

Fig. 1 Schematic representation of how the compounded effect of physico-chemical and nutritional stress alters the metabolic strategy and increases the energy burden of the cell. Genetic determinants associated with metabolic flexibility and stress adaptation are subjected to selective pressures, promoting the survival of optimally adapted phenotypes. The optimal species shifts its metabolic phase from dormancy to growth and the dormant species encounters ecological barrier as they are functionally incompatible to support the new functions of the ecosystem.

Dormancy enables microbial populations to coexist with reduced competition for resources and space thereby preserving the microbial diversity of a given habitat (Hibbing et al., 2010; Stolpovsky et al., 2016). As shown in **Figure. 2,** dormancy promotes species richness ($S_{dormancy} > S_{classical}$) but with slightly reduced rate of turnover ($T_{dormancy} < T_{classical}$) (Lennon & Jones, 2011; Locey, 2010). This dynamic promotes ecological resilience, allowing ecosystems to recover and stabilize following environmental disturbances by reactivating pre-existing microbial constituents (Chesson & Warner, 1981). Recovery trajectories following disturbance can vary, ranging from full compositional and functional restoration to partial or no recovery at all. Importantly, the reestablishment of microbial communities is often contingent upon the parallel recovery of abiotic parameters. It is therefore, difficult to regain the original diversity after a disturbance as many factors are involved in the change, such as immigration load, duration and intensity of disturbance to restoration and, microbial response time (Calderón et al., 2018; Jurburg et al., 2024; Philippot et al., 2021; Stolpovsky et al., 2016).

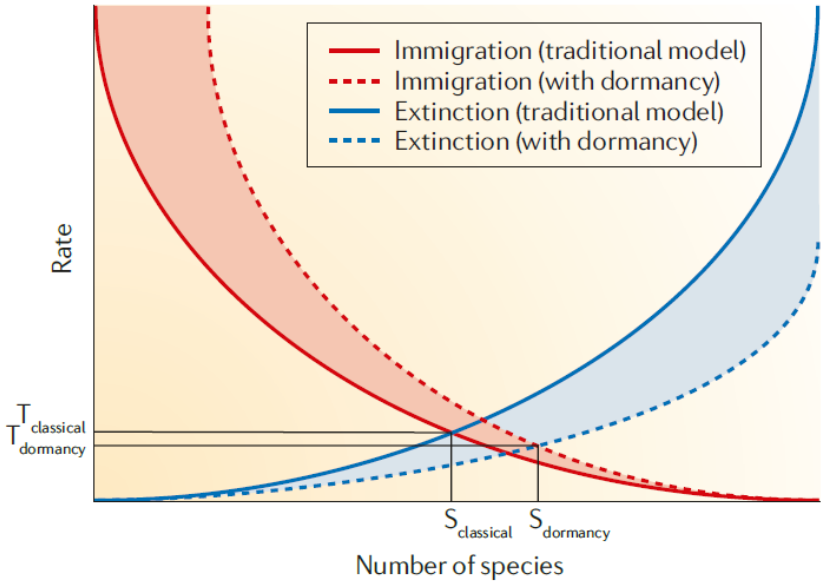

Fig. 2 Prediction of species diversity and turnover based on theory of island biogeography. Dormancy increases species richness (red dotted line) in habitat but with reduced turnover rate or at slow pace (blue dotted line). Adapted from (Lennon & Jones, 2011; Locey, 2010)

For instance, a short-term snowfall event over cryoconite hole was shown to disrupt microbial diversity, with rare taxa becoming temporarily dominant. This shift in community structure was majorly associated with cold adaptation of rare taxa and partly due to nitrogen limitation (melt runoff), which created an opportunity for dormant taxa to activate and increase in abundance (Y. Chen, Liu, Liu, Ji, et al., 2022). Such short disturbances can stimulate dormant members of the community, facilitating dynamic shifts in activity and maintaining ecosystem functions (Bradley et al., 2023).

Alternatively, gradual environmental changes—such as those driven by climate change—act as ecological filters, altering microbial composition over time. Seasonal algal blooms provide a clear example: long-term shifts in temperature, nutrient availability, and dissolved gas concentrations have led to shift in microbial communities within blooms (Wiltshire et al., 2008). Dormant species respond to gradual change through several successions and dominate the nutrient pool (REF?). Despite compositional changes, these systems often maintain their core functional attributes, demonstrating the role of dormancy in supporting ecological continuity through community turnover (Hoffmann et al., 2012; Wiltshire et al., 2008).

It is difficult to define and identify the process of dormancy, mostly owing to the multitude of biotic and abiotic stimuli that can initiate or sustain a metabolically inactive state for undefined duration (Lauritano et al., 2020). Microbes with streamlined genomes, can exhibit rapid and spontaneous metabolic downregulation for short time. The absence of multi-layer regulatory networks allows these species to rapidly adjust their metabolic state, facilitating faster reactivation upon restoration of favourable conditions (Carini et al., 2013; Noell et al., 2023).

It is important to distinguish dormancy from mere reductions in microbial activity due to mineral or trace metal limitations which reduces reaction kinetics of enzymes and may not involve a true dormancy response (Gray et al., 2019). Additionally, within microbial communities, species with overlapping metabolic pathways can suppress the activity of neighbouring cells by limiting the availability of metabolic byproducts (Amarnath et al., 2023; Kaprelyants et al., 2000; Morris et al., 2013). Such short-lived events are difficult to designate as dormancy but it still contributes to different phases of microbial life in different time points.

In oligotrophic environments, specifically at the snow-ice interface, dormancy is affected by several dynamic environmental exchanges, including snow cover and proximity to marine or other sources of lake, soil and vegetation which may modulate the physico-chemical components (Schüpbach et al., 2018). Microorganisms and associated nutrients can originate from the ocean and inland water bodies (Alsante et al., 2021; Mayol et al., 2014), or the atmosphere (Després et al., 2012; Mayol et al., 2017; D. J. Smith et al., 2013), and their availability varies with location and season. The physical and chemical properties of the snow–ice interface also play a crucial role in modulating microbial responses. Microorganisms introduced to these habitats via long-range atmospheric transport may already exist in a dormant state (Hara & Zhang, 2012; D. J. Smith et al., 2011), while others may transition into dormancy in response to local physico-chemical stressors. In addition to abiotic stress, microbial populations encounter biotic interactions—ranging from commensal to opportunistic—that can elicit the fight or flight response. To mitigate competitive pressures and ensure survival, microbes may deploy or sense signalling molecules such as autoinducers (Bespalov et al., 2000; Kolpakov et al., 2000; Xiong et al., 2024) or antibiotics (Medaney et al., 2015) to assess environmental capacity and interspecies competition. These cues facilitate strategic decisions such as niche relocation or entry into dormancy, thereby minimizing unnecessary conflict and promoting persistence under adverse conditions.

Our aim is to understand the environmental triggers and the ecological scenarios that influence microbial transitions between active and dormant states at the snow–ice interface. We address the major physico-chemical triggers and describe its individual or compounded effect on the microbial population. Through these stressors, we can deduce the response strategy of the microbes and how it decides to switch between active and dormant state at the snow-ice interface. Understanding these dynamics enables us to understand the survival strategies of microorganisms in cryospheric habitats and their roles in biogeochemical processes.

2. Physico-chemical triggers at the snow-ice interface and microbial response

Physico-chemical stressors in cryospheric environments are influenced by a range of environmental variables, including weather patterns or seasonal changes (Ai et al., 2024; Nawrot et al., 2016), precipitation (Kotowski et al., 2020; Sadro et al., 2018), vegetation cover, and other ecological factors that shape the availability of resources and the physico-chemical properties of microhabitats (Winkel et al., 2022). Microorganisms commonly encounter stressors such as ultraviolet radiation (Ariya et al., 2011; Q. Chen et al., 2025; Nevada & California, 1995; Sanchez-Cid et al., 2023a), freeze–thaw cycles (Keaney et al., 2022; Panikov et al., 2006; Walker et al., 2006), osmotic shock (Gostinčar & Gunde-Cimerman, 2023; Wilson et al., 2012), oxidative stress (Anastasio et al., 2007; Grannas et al., 2007), low temperatures (Bhakoo & Herbert, 1979; Nedwell, 1999; Russell, 1990) and, nutrient limitation(Antony et al., 2016; Y. Chen, Liu, Liu, Vick-Majors, et al., 2022; Darcy & Schmidt, 2016). The severity and duration of these stressors play a critical role in determining microbial survival outcomes, potentially causing mortality across entire populations or selectively affecting a subset of cells.

In this review, we aim to investigate the dominant stressors present at the snow–ice interface, their effect on the microbes and the mitigative responses to these environmental triggers. Particular focus is given to understand how these mechanisms could regulate transitions between dormancy and metabolic activity, thereby contributing to microbial persistence under extreme and fluctuating conditions.

2.1. Radiation and oxidative stress

The stress of radiation, especially ultraviolet radiation, is intense during the late spring and summer season (Bernhard et al., 2023; Sliney & Wengraitis, 2006). Especially in habitats with perennial snow cover such as the high alpine glaciers and polar regions (Cockell et al., 2002a). UV radiation (UVR) initiates the formation highly reactive species of oxygen that can react with micro or macromolecular structure and damage the microbial components (Kataria et al., 2014; Santos et al., 2012). The radiation itself causes damage to the DNA (Kciuk et al., 2020) and alters the expression patterns (Ellington et al., 2025; Matallana-Surget & Wattiez, 2013). However, the extent of damage depends on the intensity and duration of exposure to the radiation. The cloud cover, snow cover, ice cover and snow density can significantly reduce the radiative and reactive radical damage on the microbial community. For example, a snow with density of 0.65 g/cm3 was found to receive 27% and 10% of irradiance at a depth of 5 cm and 15 cm in contrast to the surface snow (Cockell et al., 2002b) This reduced the inactivation of Bacillus spores to 30% and <=10% as compared to the surface exposure. It was found that the ice with snow crust of 1 mm had a UV transmission of 56%, which means intense radiative damage. These findings suggest that the age of the snow affects the UV transmission where older ones have better transmittance at shallow depths (Cockell et al., 2002b). Even though the radiation is suppressed by the overlaying snow, the photoreactive species are energized by these UV rays and causes secondary damage to the cellular components in the lower layers of surface snow (Santos et al., 2012). Such events divert a significant proportion of microbial processes from growth to maintenance and survival strategies. But these reactive species are also beneficial in transforming the persistent and bioaccumulative organic and synthetic biomass into biodegradable form which might facilitate the microbial activity and add more energy into the system (Anesio et al., 2000, 2005; Q. Chen et al., 2025; Gonsior et al., 2014). Snow receives plant and soil biomass rich in recalcitrant compounds which might be converted to bioavailable carbon or volatiles for microbial activity (Anesio et al., 2005; Antony et al., 2018; Grannas et al., 2004). Hence, UVR has both negative and positive impact on microbial activity which correlates with the duration and intensity of exposure.

Microbial communities possess a suite of defence mechanisms to mitigate and repair damage caused by ultraviolet radiation (UVR) and the associated oxidative stress (Sanchez-Cid et al., 2023b; Seixas et al., 2022). High doses of UVR can directly damage DNA and disrupt fundamental cellular processes, thereby increasing reliance on DNA repair pathways, enhancing reactive oxygen species (ROS) detoxification responses, and occasionally inducing mutagenesis (Anastasio et al., 2007; Dolinová et al., 2006; Grannas et al., 2007). Protective pigments such as carotenoids (Reis-Mansur et al., 2019) serve as an initial barrier to UVR, while enzymes including catalase, superoxide dismutase, and glutathione contribute to the neutralization of ROS (Pérez et al., 2017).

Studies have reported increased expression of genes associated with antioxidant production and DNA repair in snow-inhabiting microbial communities exposed to UVR (Maccario et al., 2019; Sanchez-Cid et al., 2023c). During the prolonged exposure to UVR, the photosynthetic and the growth efficiency of the microbes were significantly affected. The photosynthetic process was inhibited by 25% in red algae and 85% in green algae when incubated with UVR (Nevada & California, 1995; Remias et al., 2010). This decline in productivity, compounded by sustained oxidative stress, can deplete metabolic reserves and shift microbial strategy toward energy conservation and survival.

Under such conditions, microorganisms may transition from an active state to dormancy, relying on internal energy stores for maintenance metabolism. However, during spring and summer, the snow–ice interface often supports a rich algal bloom that fuels bacterial activity through rapid consumption of algal products (Anesio et al., 2017; Winkel et al., 2022). This short-lived burst of productivity may temporarily sustain microbial activity until the resource is exhausted, at which point energy limitation and environmental stressors together may drive the transition into dormancy. The radiation itself might not suffice in inducing the dormancy if the microbe has sufficient resources to produce biofilm, pigments, antioxidants and DNA repair cascades. However, during the winter, the snow cover protects the snow-ice interface from radiation and its oxidative damage. And the microbial community is majorly affected by nutritional content and water availability at the snow-ice interface. And prolonged deficiency of nutrients induces starvation and dormancy in winter (Fowler & Winstanley, 2018; Sullivan et al., 2020; Winkel et al., 2022).

2.2. Temperature and Freeze-thaw

Low temperatures itself might not be lethal to cause mortality. However, it can significantly reduce the rate of microbial activity. As per the Arrhenius equation (Arrhenius, 1889),

$$k = Ae^{-\frac{Ea}{RT}}$$

where,

- **k** is the rate constant (frequency of collisions),
- **T** is the absolute temperature (in Kelvin),
- **A** is the pre-exponential factor or Arrhenius factor or frequency factor,
- **Ea** is the molar activation energy for the reaction,
- **R** is the universal gas constant

reaction kinetics is significantly reduced at lower temperatures. During winter, the snow–ice interface in alpine and polar regions typically experiences temperatures ranging from approximately −2°C to −8°C, depending on factors such as snow depth, snow density (Rosso, 2002), thermal contact resistance (Hammonds & Baker, 2016) and air temperature (Mott et al., 2018). Temperature variability within the snow and ice layers also arises from differences in their mean thermal conductivity, often resulting in relatively warmer snow compared to the underlying ice. Moreover, the insulating properties of a thick snowpack can shield deeper layers from surface wind exposure, producing a pronounced vertical temperature gradient—from as low as −30°C at the surface to around −10°C near the base (Hongwei et al., 2014; Kilic et al., 2019; Maggioni et al., 2009; Sobota, 2011).

The difference in temperature gradient results in freeze–thaw cycles which can be lethal to microorganisms, depending on the intensity and frequency (Lim et al., 2020; Morley et al., 1983). Melting enables water availability (Liu et al., 2025) and stimulates activity whereas refreezing reduces the rate of activity as a result of limited substrate diffusion (Price, 2009;

Rohde & Price, 2007a). The repeated exposure to freeze–thaw stress can also act as a selective pressure, promoting the survival of more resilient taxa and enhancing the overall fitness of the microbial community. For instance, repeated freeze–thaw events have been shown to enrich tolerant species within soil microbiomes, thereby reshaping community composition and increasing mortality among more sensitive populations (Walker et al., 2006). Remarkably, certain species such as *Deinococcus radiodurans* and *Paraburkholderia fungorum* have demonstrated the ability to withstand up to 20 cycles of freeze–thaw between −80°C and +30°C, and subsequently exhibited increased resistance to UV radiation under both stress (Keaney et al., 2022). Microbial activity under naturally frozen conditions is not completely halted and certain species remain active by utilizing more diffusive substrates such as CH_4, H_2, CO, and NH_4 (Rohde & Price, 2007a).

Microbial activity during thaw periods is modulated by environmental conditions such as nutrient concentration, salinity, and pH of the surrounding microhabitat (Rosinger et al., 2022). The thawed microbial cells might not have similar environment as when it froze and their resuscitation depends on the new environmental parameters and how stressful it is (Pastore et al., 2023a; Rohde & Price, 2007a). In simple, microbial survival under repeated freeze–thaw cycle is primarily governed by physico-chemical history (Pastore et al., 2023b) of microbe which would result in the development of intrinsic physiological traits (Choudhary et al., 2024; Pastore et al., 2023a).

Microorganisms have evolved a range of adaptive mechanisms to preserve cellular function under subfreezing conditions (Choudhary et al., 2024). These include maintaining membrane fluidity, stabilizing protein structures and enzymatic activity, and protecting nucleic acids from degradation (Choudhary et al., 2024; Pastore et al., 2023a; Seixas et al., 2022). Exposure to low temperatures induces a suite of regulatory responses (Potts et al., 2017), involving RNA- and protein-based cold shock and antifreeze elements that modulate gene expression and metabolic rates (Lee et al., 1994; Phadtare & Severinov, 2010; Pourciau et al., 2023). These responses are coordinated through complex intracellular signalling cascades that facilitate acclimation and survival in cryogenic environments. In general, microbial populations transition into dormancy under extremely low temperature, in accordance with the thermodynamic constraints imposed on proteins and enzymes (Kristjánsson & Kinsella, 1991;

More et al., 1995). However, some microorganisms remain metabolically active even below −10°C, albeit with significantly prolonged doubling times, representing notable exceptions to the typical dormancy response (Price & Sowers, 2004).

In addition to temperature, freezing significantly restricts substrate diffusion, further limiting metabolic activity. At sub-zero temperatures, the reduced mobility of nutrients (Ghesquière et al., 2015; Mispelaer et al., 2013) can lower substrate availability below the threshold required to sustain active metabolism, thereby inducing a transition to maintenance or dormancy states (Rohde & Price, 2007b). These limitations are secondary effects that occur at low temperature and high viscosity. Nonetheless, microorganisms have been shown to survive—and in some cases remain metabolically active—for millennia within microenvironments such as mineral grain boundaries and liquid veins in ice (Price, 2000). These micro-pockets, which retain unfrozen water and trace nutrients (Anderson & Tice, 1973), can exceptionally support microbial life over extended timescales. An ice core drilled from Greenland was dated to be 100,000 years old and the sediment layer of that core had active microbial communities with a live to dead ratio of 5:1 *(Sheridan et al., 2003)*. It shows how adhering surfaces, mineral layer and water pockets even at -10°C can prolong the survival of microbes over millenniums. Proving that temperature alone is not governing dormancy when there is sufficient resources and water available to grow (Anderson & Tice, 1973; Price, 2000).

In contrast, snow and ice matrices lacking such mineral inclusions pose considerable challenges for microbial persistence. The absence of stable surfaces for adhesion, coupled with minimal water retention, hinders environmental sensing and substrate acquisition. Rhode and Price proposed a theoretical model to estimate the maximum cellular size that can be supported solely by diffusion-driven nutrient supply under such extreme conditions. They show that microbes of several micrometer size can sustain metabolic activity given the diffusion rate of substrate is atleast: $D \approx 1 \times 10^{-15}\ \mathrm{m^2 s^{-1}}$ (Rohde & Price, 2007b). The expression— **D(T)Ce** —can be regarded as the supply of the habitat whereas the expression— μ(T) —is considered as the demand of the microbe.

$$R_{cell} = 1.35 \left[\frac{D(T)C_e}{\mu(T)}\right]^{1/2}$$

Where,

- **D(T)** is the diffusion coefficient of nutrient gas molecule
- **Ce** is the equilibrium concentration of a nutrient gas molecule
- $\boldsymbol{\mu(T)}$ is the metabolic rate at the absolute temperature
- **T** is the absolute temperature

And as per the Stokes-Einstein-Sutherland equation (Einstein & others, 2013; Perrin, 1908; Sutherland, 1905; von Smoluchowski, 1906), the diffusivity **(D)** of the particle or substrate of radius **(r)** is significantly affected by the viscosity **(η)** of the diffusive medium**.** When the temperature **(T)** is low, the interplay of radius **(r)** and the viscosity **(η)** decides the diffusion rate of the substrate particle.

$$D = \frac{K_B T}{6\pi\eta r}$$

Where,

- $\mathbf{k_B}$ is the Boltzmann constant,
- **T** is the absolute temperature,
- **η** is the dynamic viscosity,
- **r** is the Stokes radius of the spherical particle

Microorganism undergo a range of physiological adaptations, including cell size reduction (Guerra et al., 2015), mobilization of internal energy reserves (Bourassa & Camilli, 2009; Kadouri et al., 2005), bypassing non-essential metabolic pathways, and repurposing intracellular metabolites to meet minimal energetic demands (Cavaco et al., 2022; Kaprelyants et al., 1993; Makowka et al., 2020). The transition between active and dormant states is primarily driven by the combined effects of reduced molecular mobility, water unavailability due to freezing, decreased reaction kinetics and, increased fluid viscosity, all of which contribute to the overall decline in metabolic activity. And when the supply is lower than the demand, metabolic activity gets capped and forces the microbe to enter dormancy.

2.3. Resource limitation and dependent factors

One of the major factors that drives dormancy at the snow-ice interface stems from the limitation and competition for resources. The cryospheric habitat receives majority of its nutrient from the atmospheric deposit (Després et al., 2012; Mayol et al., 2017; D. J. Smith et al., 2013). The aerosols carry dust, minerals and microbes from local and distant regions that gets deposited on the snow (Barbaro et al., 2024; Feltracco et al., 2021; Kirpes et al., 2019; Rocchi et al., 2024; Udisti et al., 1999). However, prior to deposition the radiation and photooxidative damage alters the biochemical composition of the aerosol during the transport (Ellison et al., 1999; Malecha & Nizkorodov, 2016; Robinson et al., 2006). These deposits in snow are again affected by the radiation (Antony et al., 2018; Gonsior et al., 2014), oxidative damage (Anastasio et al., 2007; Dolinová et al., 2006), freeze-thaw (Rosinger et al., 2022) and, melt seepage (Ono & Takeuchi, 2024; Young et al., 2022) that changes the strength, composition and volume of biochemical components. During all these events, the microbial community goes through several successions. These shifts are governed by the metabolic capacity of the microbial community which is driven by substrate diversity, concentration and microbial immigration (Y. Chen, Liu, Liu, Vick-Majors, et al., 2022; Hoffman et al., 2022a; Ono & Takeuchi, 2024). A habitat under stress significantly affects the rate of substrate utilization (Fuggle et al., 2025) and selects for species with efficient stress tolerance and defence mechanism. Additionally, the ability to utilize complex nutrient pool is limited by the grazing pressure of predators (Frede Thingstad, 2022; Guillonneau et al., 2022; Jessup & Bohannan, 2008). Hence, microbes show stronger shift towards dormancy when the resources are limited as it reduces the ability to meet the demands for maintenance and mitigating biotic or abiotic stress (Lahtvee et al., 2016). The metabolic load faces energy crisis where the maintenance takes priority over spending energy for defence (primary vs secondary metabolite) which naturally triggers dormancy (Romero-Olivares et al., 2019).

Availability of resources and its biological transformation in all the habitats are dynamic. It is critical in sustaining biodiversity and differential activity at different timepoints (Hibbing et al., 2010; Muratore et al., 2022). As per the monod equation (Monod, 1949),

$$\mu = \mu_{max} \frac{S}{S + K_s}$$

Where,

- $\boldsymbol{\mu}$ is growth rate
- $\boldsymbol{\mu_{max}}$ is the maximum growth rate
- **S** is the substrate concentration
- **Ks** is the half saturation constant

The maximum growth **(μ_{max})** rate depends on the concentration of the limiting nutrient. This compromises the metabolic rate of the microbial species at the snow-ice interface where season and sources may create different types of limitations (Ai et al., 2024; Y. Chen, Liu, Liu, Vick-Majors, et al., 2022; Hoffman et al., 2022a; Nawrot et al., 2016; Ono & Takeuchi, 2024). However, the expression of V_{max}/K_m which is similar to μ_{max}/K_s is regarded as the substrate affinity of an enzyme in the Michaelis Menten equation (Johnson & Goody, 2011; Michaelis & Menten, 1913). This expression describes the sensitivity of enzymes towards the substrate concentration. It plays a major role in spatiotemporal activity of the microbial community.

Microbes from oligotrophic habitats such as the snow-ice interface often have enzymes with varying affinity (Aghajari et al., 1998; Feller et al., 1996; Q. Wang et al., 2020; X. Wang et al., 2018). Two different population with low and high affinity enzymes can coexists at different substrate concentration and at different timepoints. For example, the algal bloom on the snow-ice interface may enrich the organic matter content which might boost the growth of r-strategists (Campbell et al., 2018; McGrath Grossi et al., 1984; R. E. H. Smith et al., 1989). These species rely on low affinity enzymes which require high organic matter for stimulation and hence are found growing attached to the biomass particle (Hou et al., 2025)(McGrath Grossi et al., 1984). Similar patterns are observed in the microbes for major element utilization and uptake (Hoffman et al., 2022b; Hoffmann et al., 2012). Such distribution of microbial population (r and k strategists) based on enzyme kinetics allows the species to enter or exit dormancy at different timepoints based on substrate concentration (Hou et al., 2025). Remarkably, microbes with high substrate affinity enzymes are capable of metabolizing the trace atmospheric gases to sustain activity for survival (Greening & Grinter, 2022).

In natural environments, the continuous availability of any specific substrate within a niche is rare, precluding the formation of idealized, unbounded growth and predation networks. The inherently dynamic nature of habitats imposes persistent selective pressures on the stability of microbial communities. Consequently, temporal shifts in community composition are commonly observed, although certain ecological functions tend to remain stable. These shifts typically occur through transitional phases, during which microorganisms often attempt to buffer environmental disturbances by mobilizing internal energy reserves such as wax esters, polyhydroxyalkanoates, glycogen, lipids, and amino acids. These endogenous carbon and energy stores support microbial activity during periods of nutrient limitation or chemical perturbation in the environment. Such reserves enable the maintenance of essential cellular functions over extended periods—ranging from days to weeks—and may persist even longer under cryogenic conditions. However, sustained physico-chemical stress under nutrient-limited conditions inherently constrains the energy available for extensive cellular processes, leading to a prioritization of essential functions (Romero-Olivares et al., 2019). As shown in **Fig. 1**, the compounded stress affects the metabolic strategy and thus the energy gain is affected where priority tasks of maintaining cellular damage activates and the halted energy supply further triggers several physiological changes such as reduced ribosomal turnover, diminished protein synthesis, decreased transcriptional activity, and lowered enzymatic function, collectively resulting in a global decline in microbial metabolic activity and thus dormancy.

3. Implementation and findings of the ICEBIO project under DC2

In the course of this study, analyses were performed on winter samples collected from diverse habitats in Ny-Alesund, Svalbard. The primary objective was to investigate the biological processes of microbial communities inhabiting these environments, with a particular focus on variations in their metabolic requirements. Specifically, the study aimed to elucidate the mechanisms that support microbial survival and activity during the winter season. The working hypothesis claims that microbial activity in winter is primarily constrained by water availability. To test this, samples were obtained from a range of habitats including soil, snow, ice, lake water, and seawater. We even conducted one microcosm study where we simulated rain on snow.

Our findings for the winter samples indicate that microbial communities exhibited measurable activity across all sample types. In certain samples, a high dominance index was observed, suggesting that a few taxa were disproportionately active relative to the rest of the community. In contrast, other samples showed more even but generally low level of activity. Notably, rare taxa appeared to be more active during the winter, while the abundant community members displayed low rRNA read levels. This pattern reflects the presence of microbial populations originating from the spring season, when diatom and algal blooms typically promote the proliferation of bacterial scavengers. The reduced rRNA read ratios observed in these dominant taxa suggest the initiation of dormancy or other survival strategies in response to the resource- and water-limited conditions characteristic of the winter environment.

4. Conclusion

The objective of this deliverable was to review and investigate the physico-chemical stressors encountered by the microbial community at the snow-ice interface and to assess how these stressors influence microbial activity and dormancy. By addressing these environmental pressures, we aimed to identify potential mechanisms that microbes employ to cope with stress. Specifically, we explored how the tug of war between the external stress and the microbial response affects the cellular energy allocation, ultimately leading to dormancy when energy demand surpasses the supply under environmental disturbance.

The cryosphere is characterized by several stressful conditions that affects the physiology and the energetic feasibility of growth-supporting metabolic processes. Despite these limitations, these environments are teeming with microbial life where the stages of microbial activity vary from dormancy to cellular division. In this context, we examined the dominant physico-chemical stressors and their possible impact on the microbial population. We found that the stressors can be detrimental or beneficial, depending on the physiological tolerance of the microbial community. Detrimental effects occur when the environmental stress exceeds the adaptive capacity of a microbe where the elevated intensity and duration of the stress leads to cell damage, metabolic shutdowns and dormancy or death. In natural settings, multiple stressors often act simultaneously, leading to complex stress responses that redirect cellular energy from growth to maintenance or survival or dormancy.

This diversion of energy creates a trade-off, wherein some microbes enter dormancy due to insufficient resources for continued activity. Conversely, stress conditions unfavourable to one group may create ecological niches for more tolerant taxa, allowing them to dominate the community. The new key player begins to dominate the habitat which brings a shift in the microbial community over time. Importantly, these shifts are not solely driven by microbial fitness but also by the reduction in competition or stress, replenishment of new resources and, renewed carrying capacity. As conditions become less favourable for some populations, others can emerge from dormancy or low-activity states and contribute to ecological processes. This behaviour was previously hypothesized by Baas Becking that “Everything is everywhere, but the environment selects”. It also follows the concept of seed bank where the dormant microbes can be reactivated under favourable condition.

We suggest that dormancy at the snow–ice interface is primarily regulated by the availability of liquid water and bioavailable resources, acting as key ecological filters that determine microbial survival and activity. Over the geological timescales, microorganisms have adapted to wide array of environmental stressors from the prehistoric earth to present. With time, the microbial communities have undergone several genetic modifications which have evolved them to occupy every habitat on earth.

Environmental stressors such as desiccation, freeze–thaw cycles, and limited nutrient flux at cryospheric boundaries impose strong selective pressures, leading to community shifts through processes like species sorting, niche partitioning, and local extinction. It may be argued that such stressors can drive microbial dispersal or exclusion from inhospitable niches, facilitating migration into more permissive environments where resource abundance and reduced interspecific competition promote colonization and growth. These resource-enriched habitats may act as ecological refugia, supporting population persistence and diversification.

Conversely, when microbial taxa are transported into environments with minimal water activity and severely limited resources—such as the upper atmosphere or dry surface snow during winter—the absence of sufficient energy input may trigger dormancy as a survival strategy, or in extreme cases, result in cell death. These dynamics underscore the importance of both abiotic filtering and biotic interactions in shaping microbial biogeography and community assembly. Ultimately, the interplay between environmental constraints and microbial functional traits governs not only survival but also the long-term ecological and evolutionary trajectories of microbial communities.

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