Université du Québec en Abitibi-Témiscamingue

TRAITS FONCTIONNELS DES BRYOPHYTES ET LEUR RÔLE DANS L'ATTÉNUATION DES IMPACTS DU DÉCLIN DU COUVERT NIVAL INDUIT PAR LES CHANGEMENTS CLIMATIQUES SUR LES PROCESSUS DU CARBONE SOUTERRAIN DANS LES ÉCOSYSTÈMES FORESTIERS BORÉAUX

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FUNCTIONAL TRAITS OF BRYOPHYTES AND THEIR ROLE IN MITIGATING THE IMPACTS OF CLIMATE-CHANGE-INDUCED SNOW COVER DECLINE ON BELOW-GROUND CARBON PROCESSES IN BOREAL FOREST ECOSYSTEMS.

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PRESENTATION OF THE JURY

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dearest husband, Suman, who has stood beside me as a pillar of strength throughout this research, I owe gratitude for his patience, constant support, and unconditional love.

EPIGRAPH

What appears stable on the surface is often sustained by delicate processes beneath.

Bandana Subedi

FORWARD

This thesis represents the culmination of my Master's research journey in forest ecology and reflects both my academic growth and personal development over the course of this program. The motivation for this research stems from a recognition that understanding boreal forest resilience requires looking beyond the towering black spruce to the humble mosses beneath our feet.

Conducting this research involved extensive fieldwork under challenging climatic conditions, careful laboratory analyses, and rigorous data interpretation. These experiences strengthened my scientific skills, critical thinking, and resilience as a researcher. Beyond the technical aspects, his project reinforced the importance of interdisciplinary thinking, patience, and collaboration in ecological research.

This thesis is divided into three chapters: the first provides a general introduction to the study, the second presents the scientific article ready for submission to *Applied Soil Ecology*, and the third offers conclusions, implications, and direction for future research.

I am grateful for the academic environment, resources, and guidance provided throughout this program, which allowed me to explore complex ecological questions while developing confidence as an independent researcher. I hope that the findings presented here will contribute meaningfully to ongoing discussions on boreal forest resilience and inform future research on ecosystem responses to climate change.

Ultimately, this work reflects my commitment to advancing ecological knowledge and my aspiration to contribute to sustainable forest management and climate change mitigation through science.

RÉSUMÉ

Les forêts boréales constituent le deuxième plus grand biome terrestre et servent de réservoirs majeurs de carbone dans le sol. Cependant, les régions boréales subissent des changements climatiques considérables, entraînant des périodes chaudes plus fréquentes et une réduction du manteau neigeux. Cela diminue les propriétés isolantes de la couverture de neige et augmente les cycles de gel-dégel du sol. Les mousses, en particulier *Sphagnum* spp. et *Pleurozium schreberi*, dominent les sols des forêts boréales et contribuent à l'isolation du sol et à la rétention d'humidité. Malgré leur importance écologique, leur rôle dans l'atténuation des processus souterrains du carbone sous une couverture de neige réduite demeure mal compris.

Cette étude examine les traits fonctionnels de ces mousses et leur capacité à atténuer les effets de la perte de couverture neigeuse sur la composition de la biomasse racinaire, la biomasse microbienne du sol, ainsi que la diversité et la composition de la communauté microbienne du sol, tous étant liés aux processus souterrains. Trente-six parcelles expérimentales ont été établies dans trois peuplements matures d'épinette noire dans le Nord-du-Québec, Canada, avec des traitements variant selon la présence de mousse, le type de mousse et la couverture neigeuse. Les traitements comprenaient : *Sphagnum* spp. avec neige, *Sphagnum* spp. sans neige, *Pleurozium schreberi* avec neige, *Pleurozium schreberi* sans neige, sans mousse avec neige, et sans mousse sans neige, avec six répétitions par traitement. La température du sol a été surveillée à l'aide d'enregistreurs de données à une profondeur de 15 cm, et la neige a été retirée manuellement avec un minimum de perturbation. Des échantillons de sol ont été prélevés à la fin du printemps et en été pour mesurer la biomasse microbienne à l'aide de la méthode de fumigation au chloroforme. La PCR quantitative (qPCR) et le séquençage des gènes de l'ARNr 16S et *pmoA* ont été utilisés pour étudier l'activité et la diversité des champignons et des bactéries. La dynamique racinaire a été analysée avec WinRHIZO, et les traits fonctionnels des mousses tels que la rétention d'eau, la densité des colonies et la teneur en nutriments ont été évalués.

Les colonies de *Sphagnum* spp. sous la neige étaient plus denses et présentaient une capacité d'absorption d'eau plus élevée comparativement à celles sans neige. En revanche, *P. schreberi* ne différait pas significativement en termes de densité de colonie ou de capacité d'absorption d'eau entre les traitements avec ou sans neige. La biomasse racinaire totale sous *Sphagnum* spp. avec couverture neigeuse réduite était significativement plus faible comparativement à celle avec neige, tandis que la biomasse racinaire totale n'a pas changé sous *P. schreberi* et sans mousse. Bien que la diversité bactérienne du sol soit demeurée constante à travers les traitements, la composition de la communauté bactérienne a été modifiée. Plus précisément, les Actinobacteria étaient plus abondantes lorsque la neige était réduite dans les parcelles de *P. schreberi*, et l'abondance relative des Acidobacteriota était significativement plus élevée dans les parcelles de *Sphagnum* spp. avec neige comparativement à celles avec neige réduite. La diversité fongique du sol a significativement diminué lorsque la neige était réduite dans les parcelles de *P. schreberi*, mais est demeurée constante dans les parcelles de *Sphagnum* spp. La biomasse microbienne était stable au début de l'été, mais a augmenté dans les parcelles de *Sphagnum* spp. avec neige à la fin de l'été.

Alors que les changements climatiques s'accélèrent et que la couverture neigeuse diminue, les compromis entre les types de mousses deviennent critiques. Les sols forestiers dominés par *Sphagnum* spp. pourraient passer de systèmes stables et puits de carbone à des systèmes plus variables et sensibles aux perturbations, la réduction de la neige causant un déclin de la biomasse racinaire et des changements dans les communautés microbiennes. Les processus du sol étaient plus résistants sous la couverture de *P. schreberi*, mais cette résilience pourrait se faire au détriment d'une protection thermique réduite et d'une accumulation de carbone au sol à long terme.

Mots-clés **:** *Sphagnum* spp., *Pleurozium schreberi*, perte de neige, changements climatiques, biomasse microbienne, bactéries, champignons, capacité d'absorption d'eau, densité des colonies.

Keywords: *Sphagnum* spp., *Pleurozium schreberi*, snow loss, climate change, microbial biomass, bacteria, fungi, water absorption capacity, colony density.

ABSTRACT

Boreal forests are the second-largest terrestrial biome and serve as major soil carbon reservoirs. However, boreal regions are experiencing considerable climate change, leading to more frequent warm periods and reduced snowpack. This diminishes the insulating properties of snow cover and increases soil freeze-thaw cycles. Mosses, particularly *Sphagnum* spp. and *Pleurozium schreberi*, dominate boreal forest floors and contribute to soil insulation and moisture retention. Despite their ecological importance, their role in buffering belowground carbon processes under reduced snow cover remains poorly understood.

This study examines functional traits of these mosses and their ability to mitigate the effects of snow cover loss on root biomass, soil microbial biomass, and soil microbial diversity and their community composition, all of which are linked to belowground processes. Thirty-six experimental plots were established in three mature black spruce stands in Nord-du-Québec, Canada, with treatments varying in moss presence, moss type, and snow cover. Treatments included: *Sphagnum* spp. with snow, *Sphagnum* spp. without snow, *Pleurozium schreberi* with snow, *Pleurozium schreberi* without snow, no moss with snow, and no moss without snow, with six replicates per treatment. Soil temperature was monitored using data loggers at a 15cm depth, and snow was removed manually each month with minimal disturbance. Soil samples were collected in late spring and summer to measure microbial biomass using the Chloroform fumigation method. Quantitative PCR (qPCR) and sequencing of the 16S rRNA and pmoA genes to study the diversity of fungi and bacteria. Root dynamics were analyzed with WinRHIZO, and moss functional traits like water retention, colony density, and nutrient content were assessed.

Sphagnum spp. colonies under snow were denser and had higher water absorption capacity compared to those without snow. In contrast, *P. schreberi* did not differ significantly in either colony density or water absorption capacity across snow treatments. Total root biomass under *Sphagnum* spp. with reduced snow cover was significantly lower compared to that with snow, while total root biomass did not change under *P. schreberi,* and no moss. Although soil bacterial diversity remained constant across treatments, bacterial community composition was changed. Specifically, Actinobacteria were more abundant when snow was reduced in *P. schreberi* plots, and the relative abundance of Acidobacteriota was significantly greater in *Sphagnum* spp. plots with snow compared to reduced snow. Soil fungal diversity significantly decreased when snow was reduced in *P. schreberi* plots but remained constant in *Sphagnum* spp. plots. Microbial biomass was stable in early summer but increased in *Sphagnum* spp. plots with snow by late summer.

As climate change accelerates and snow cover decreases, the trade-offs between moss types become critical. Forest floors dominated by *Sphagnum* spp. may transition from stable, carbon sinks to more variable, disturbance-sensitive systems, with reduced snow causing root biomass decline and microbial community shifts. Soil processes were more resistant under *P.schreberi* cover, but this resilience may come at the cost of reduced thermal protection and long-term soil carbon accumulation.

Keywords: *Sphagnum* spp., *Pleurozium schreberi*, snow loss, climate change, microbial biomass, bacteria, fungi, water absorption capacity, colony density.

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LIST OF ABBREVIATIONS

ACIA	Arctic Climate Impact Assessment
ANOVA	Analysis of Variance
ASV	Amplicon Sequence Variant
DADA	Divisive Amplicon Denoising Algorithm
DNA	Deoxyribonucleic Acid
EMMs	Estimated Marginal Means
FUNGuild	Fungal Guild (database and tool)
HSD	Honestly Significant Difference
IPCC	Intergovernmental Panel on Climate Change
ITS	Internal Transcribed Spacer
LECO	Laboratory Equipment Corporation
LMMs	Linear Mixed-Effect Models
MBC	Microbial Biomass Carbon
N	Nitrogen
NMDS	Non-metric Multidimensional Scaling
PCR	Polymerase Chain Reaction
PERMANOVA	Permutational Multivariate Analysis of Variance
QIIME	Quantitative Insights into Microbial Ecology
rRNA	Ribosomal Ribonucleic Acid
SOC	Soil Organic Carbon
UNITE	Unified System for the Identification of Fungi

GENERAL INTRODUCTION

Context. Climate change is a pressing global issue, prompting widespread concern due to its profound and far-reaching impact on our planet. It is primarily driven by human activities, such as the burning of fossil fuels, deforestation, and various industrial processes that release greenhouse gases into the atmosphere, intensifying the natural greenhouse effect and thus altering Earth's climate (Hegerl et al., 2019). This human-induced climate change is currently causing warming of the atmosphere, oceans, and land, affecting weather and climate patterns worldwide and leading to unprecedented extremes in temperature and precipitation, with consequences spanning from centuries to thousands of years. Projections indicate that global surface temperatures may increase by 2.8° to 4.5° Celsius by 2090-2099, compared to 1980-1999, regardless of emissions scenarios (KELLY, 2014; IPCC, 2021).

During recent decades, the mid to high latitudes of the Northern Hemisphere have experienced significant warming, leading to significant ecological transformation worldwide (IPCC, 2014; Maxwell et al., 2012; Cao et al., 2023). One of the most vulnerable biomes is the boreal forest, which also represents one of the largest terrestrial carbon reservoirs. Boreal soils store large quantities of carbon in the organic horizons of moss-dominated forest floors, making these ecosystems critical for regulating the global climate (Gauthier et al., 2014; Bradshaw & Warkentin, 2015). Models forecast that temperatures across the boreal region will steadily rise between 1-2 degrees Celsius in the summer seasons and 2-3 degrees Celsius in the winter seasons from 1900 levels through the year 2050 (Price et al., 2013a; Albós, 2024). This changing climate has led to substantial changes in snow depth in the Northern Hemisphere, resulting from reduced snowfall and increased winter air temperatures (Bombonato & Gerdol, 2012; Gottlieb & Mankin, 2024; Hatami et al., 2025). Snow cover has decreased by an average of 10-17% over the past decades in Northern latitudes, and models project further declines, accelerating to 25-35% by 2100 throughout the boreal zone (Derksen & Brown, 2012; IPCC, 2024b). Snow acts as a thermal insulator for soils, which protects belowground biodiversity and ecological processes from freeze-thaw cycles. However, snow reduction will eventually expose soils to harsher temperature fluctuations, which impacts root dynamics, microbial activity and soil carbon processes (Tierney et al., 2001; Haugwitz et al., 2011, Zhao et al., 2022). Yet most existing studies have focused on short-term responses or on tundra and alpine systems, leaving uncertainity about how snow decline will influence below ground dynamics in boreal forest. In particular, the role of surface vegetation such as bryophytes in modulating these effects remains poorly understood.

In North American boreal forests, often characterized by extensive ground cover of moss and canopies dominated by black spruce (*Picea mariana)* or white spruce (*Picea glauca*), these changes threaten below-ground processes associated with carbon cycling derived from needles, bryophytes, and woody debris (Kurz et al., 2013; Bradshaw & Warkentin, 2015; Xu et al., 2023). The moss layer's influence on soil temperatures and belowground processes is greatest when snow cover is shallow or absent, since deep snowpack provides strong insulation. This is becoming increasingly important in northern regions where snow is predicted to decline (Young, 2023). Some past research has analyzed the water retention capacity, decomposition rate, desiccation tolerance, C/N ratios, and evapotranspiration rate of *Sphagnum* spp. and *Pleurozium schreberi* (Fenton and Bergeron, 2006; Gornall et al., 2011; Glime, 2024). However, these traits of the mosses in the broader context of climate change, particularly snow decline and its impact on belowground processes associated with boreal forest mosses, remain largely understudied (Cornelissen et al., 2007; Fenton et al., 2007; Glime, 2024).

As boreal forests are now projected to experience pronounced snow cover reductions, understanding how these changes affect belowground carbon-related processes has become critical. While boreal soils contain substantial organic carbon pools that develop over centuries through slow decomposition under cold, waterlogged conditions (Thiffault et al., 2013; Adamczyk, 2021a), this study does not directly quantify soil organic carbon stocks or measure carbon dioxide fluxes. Instead, we focus on key belowground processes and functional traits that regulate carbon inputs, turnover, and stabilization in these systems. This approach is based on the understanding that soil carbon stability in boreal forests depends not only on the size of existing carbon pools, but critically on the ongoing processes that regulate carbon inputs, carbon transformation, and the environmental conditions that govern these processes. Specifically, we examined (1) how snow removal affects key moss functional traits (colony density, water absorption capacity, and nutrient content) that control micoclimate buffering and organic matter inputs to soil, (2) the responses of fine root dynamics (biomass, mortality, and diameter) that determine belowground carbon allocation and turnover; and (3) the shifts in microbial communities (biomass, diversity, and composition) that mediate decomposition and nutrient cycling. These measurements provide mechanistic insights into how moss-mediated buffering may influence processes underlying soil carbon resilience under changing winter conditions.

Belowground carbon processes in boreal forest. The boreal biome is the second largest forested biome and is globally one of the most extensive reservoirs of Carbon (C) (Bradshaw & Warkentin, 2015b). It is characterized by cool temperatures, with long winters and short summers, resulting in low decomposition rates and accumulation of C (Hall et al., 2004). The widespread presence of coniferous trees [spruce (*Picea*), fir (*Abies*), pine (*Pinus*), larch (*Larix*)] and deciduous trees [birch (*Betula*), and aspen (*Populus*)], alongside dense ground cover of mosses, particularly *Sphagnum* spp., *Hylocomium splendens*, and *Pleurozium schreberi*, characterizes a significant aspect of the forest in the boreal region worldwide (Frolking, 1997; Larsen, 1980; Gower et al., 2001; Lafleur et al., 2011). Boreal forest soils represent one of the largest carbon reservoirs on Earth, storing approximately 471 Gt C, around 60% of the world’s soil organic carbon—primarily in thick organic horizons (Dixon et al., 1994; Pan et al., 2011).

All major vegetation zones are driven by mean annual temperature and precipitation (Gates, 1993). However, unlike other vegetation zones, the boreal forest zone is situated at latitudes undergoing great climatic stress, possibly altering its current role as a C sink (Bonan et al., 1995; Bradshaw & Warkentin, 2015c). Ongoing winter warming in this region has raised concern over the stability of mechanisms influencing soil carbon resilience, and their potential feedbacks to the global climate (IPCC, 2014).

Understanding the stability and future trajectory of boreal carbon stocks requires distinguishing between carbon pools and carbon processes. Carbon pool is a discrete reservoir of carbon that has the capacity to both take in and release carbon (e.g, moss tissue, root biomass, soil organic matter, microbial biomass), and carbon processes are mechanism that controls carbon flow between pools (Vallotton & Unc, 2024). Carbon inputs to boreal soils occur through multiple pathways, including aboveground inputs from moss and vascular plant litter, and belowground inputs from fine root production, mortality, and turnover (Dehlin et al., 2006; Ding et al., 2021). Moreover, soil microbial communities mediate carbon transformation and decomposition, whose activity depends on temperature, moisture, substrate quality, and community composition (Fang et al., 2022). Snow cover, soil temperature, and belowground processes.

The relationship between snow cover phenology, soil temperature dynamics, and belowground processes that influence carbon is an aspect of understanding boreal ecosystems. The physical structure of sufficient snowpack provides insulation, which plays a pivotal role in decoupling soil and air temperatures, while the depth and duration of snowpack strongly affect the timing and rate of soil warming/cooling in winter and spring (Mellander et al., 2007; Zhang et al., 2005). As a key regulator of cold region processes, a reduction in snow cover could compromise these insulating properties, resulting in more variable surface temperatures and deeper soil frost, since warming alone is insufficient to counter the reduced insulation (Henry, 2008; Halim & Thomas, 2018; Kosolapova & Altshuler, 2024a). These changes have cascading effects on processes critical to carbon cycling, potentially disrupting microbial activity, root vitality, and moss buffering capacity, thereby affecting ecosystem resilience in boreal forests.

Boreal forests, considered significant carbon sinks, sequestering 88 GtC in living biomass and 471 GtC in soils, face a precarious future in the wake of changing snow cover dynamics and rising temperatures (Dixon et al., 1994; Price et al., 2013). The exposure of roots and microbes to such temperature variability can result in cascading effects on belowground processes that regulate carbon inputs and decomposition. Damage to tree fine roots from soil freezing reduces belowground carbon inputs through decreased root production and increased mortality (Tierney et al., 2001; Cleavitt et al., 2008; Gaul et al., 2008). Conversely, changes in winter soil temperature might alter microbial biomass, activity, and decomposition rates, affecting C turnover from microbial decomposition.

Functional traits of *Sphagnum* spp. and *P. schreberi*. The functional trait approach goes beyond describing vegetation composition or biogeochemical cycling by explicitly linking measurable plant traits to underlying mechanisms that regulate ecosystem processes. By focusing on traits associated with resource use, stress tolerance, and environmental modification, this framework allows predictions of how climate change may alter ecosystem processes (Wright et al., 2005; Conti & Díaz, 2013).

In recent years, there has been a notable increase in research studying differences between species as to how their traits function in plant ecology. This approach helps to understand and predict ecosystem functions and their responses to environmental changes. However, little is known about the functional traits of non-vascular plants like bryophytes despite their crucial role in ecosystem processes. These organisms significantly impact aboveground and below-ground biomass production of boreal forest vegetation, contribute to nitrogen and carbon fixation, influence soil temperature, and affect belowground processes critical to the boreal carbon cycle (Cornelissen et al., 2007). Understanding functional traits aids in scaling from species traits to ecosystem functions and to ecosystem responses to environmental change (McIntyre et al., 1999; Garnier et al., 2004b; Díaz et al., 2013). Moss species (*Sphagnum* spp. and *P. schreberi*) are sensitive to environmental changes (Gignac, 2001) and shifts in snow cover directly influence microenvironmental conditions affecting moss functional traits (Ladrón De Guevara & Maestre, 2022).

Colony structure and water retention of mosses. The bryophyte genus *Sphagnum*, consisting of approximately 300 different species, is distributed worldwide and forms the dominant component of peat bog vegetation (Daniel and Eddy, 1985). Beyond peatlands, *Sphagnum* spp. also occur in boreal forest habitats in moist, open microsites that are more humid and illuminated than the surrounding forest (Fenton & Bergeron, 2006; Pacé et al., 2017). They form dense colonies of vertically arranged shoots composed of living photosynthetic cells interspersed with large, dead hyaline cells capable of storing water over a longer period. This sponge-like structure allows *Sphagnum* spp. to retain water up to 20 times its dry weight, enabling tissues to remain hydrated even during dry periods (Williams & Flanagan, 1996; Bisbee et al., 2001; Wang et al., 2014). This exceptional moisture-retaining capacity, in turn, helps maintain a moist microenvironment around the moss, buffering against temperature fluctuations and desiccation, while influencing decomposition rates and nutrient availability (Lavoie et al., 2005; Simard et al., 2007; Thiffault et al., 2013).

P. schreberi is one of the most widespread moss species across northern latitudes. This moss is characterized by its feathery and branching structure, dominating low-light, well-drained sites that are covered by dense coniferous stands like black spruce, white spruce, and jack pine (Harden et al., 1997; Kangas et al., 2014). However, it can also grow in more open habitats, such as forested peatlands. It forms a thick, continuous layer between the soil and the atmosphere, which influences soil temperature and biogeochemical cycling (Brown & Bates, 1990; Turetsky, 2003; Gornall et al., 2007). Specifically, *P. schreberi* lacks the specialized water transport system and capillary structure of *Sphagnum* spp. It is an ectohydric moss, relying on external capillary water movement or atmospheric moisture rather than internal storage. Unlike *Sphagnum* spp., which possess large hyaline cells that retain water internally, *P. schreberi* depends on surface moisture and therefore dries out more quickly when conditions become dry (Proctor, 2000; Longton, 1988). *P. schreberi's* low moisture retention capacity compared to *Sphagnum* spp. results in higher soil temperatures underneath, subsequently increasing decomposition rates of organic material (Williams & Flanagan, 1996; Lavoie et al., 2005; Fenton et al., 2010; Kangas et al., 2014).

Bryophytes and nitrogen fixation: In high latitudes and cold ecosystems such as the boreal forest, there is relatively high N_2 fixation activity in mosses (Zackrisson et al., 2004; Rousk, 2022). The diazotrophic bacteria associated with such mosses are important nitrogen fixers (Kreyling et al., 2012; Rousk et al., 2013; Augusto et al., 2015; Ramm et al., 2022) and can fix considerable amounts of nitrogen even under snow cover (DeLuca et al., 2002; Solheim et al., 2002; Forsum et al., 2008). When comparing the nitrogen-fixing capacity among moss species, nitrogen fixation associated with *Sphagnum* spp. is several times higher than in other mosses, facilitated by the presence of diazotrophic bacteria, primarily cyanobacteria, located within their water-filled cells. However, *P. schreberi* and *Hylocomium splendens* have cyanobacteria solely positioned on the leaf surface, resulting in lower nitrogen fixation rates (Bisbee et al., 2001; Houle et al., 2006; Kostka et al., 2016; Jean et al., 2020; Ramm et al., 2022).

However, changes in abiotic factors, such as climate, can impact the nitrogen fixation activity in mosses growing in different habitats (Calabria et al., 2020; Jean et al., 2020;

Stuart et al., 2021). Several studies have demonstrated that while an increase in temperature can potentially enhance N_2 fixation activity in mosses, this effect is contingent upon a simultaneous rise in moss moisture content (Rousk et al., 2017; Rousk et al., 2018). This sensitivity to temperature change underscores the susceptibility of non-vascular mosses to drying out and subsequent reductions in N_2 fixation when moisture levels decrease (Rousk et al., 2015).

Bryophytes and carbon sequestration. Mosses, including *Sphagnum* spp. and *P. schreberi*, play an important role in ecosystem carbon-related processes through their metabolism, growth, and litter production (Turetsky, 2003; Slate et al., 2024). These non-vascular cryptogams are foundational components of many ecosystems, influencing biogeochemical cycles, water retention, and biodiversity. They have recalcitrant cell walls and tissues that decompose more slowly than vascular plant litter, allowing carbon fixed through photosynthesis to remain sequestered for extended periods (Turetsky, 2003; Hájek & Adamec, 2010). In addition, traits such as high water-holding capacity, insulating properties, and the promotion of localized anoxic conditions can suppress microbial decomposition (Belyea, 1996; Robroek et al., 2015). Mosses are also capable of maintaining positive net photosynthesis at relatively low temperatures (down to -1.5 °C) via the C_3 photosynthetic pathway, enabling continued carbon fixation under cold conditions (Proctor, 2008).

Sphagnum spp. are renowned for their exceptional ability to retain water and slow decomposition rate, making them key contributors to carbon sequestration in these habitats through sustained photosynthetic activity (Jonsson et al., 2015). *Sphagnum* spp. exhibit much higher net primary productivity than *P. schreberi*, averaging about 228 g C m^{-2} yr^{-1} compared to 80 g C m^{-2} yr^{-1}, reflecting their greater contribution to carbon accumulation in forest floors (Bisbee et al., 2001; Swanson & Flanagan, 2001). Both *Sphagnum* spp. and *P. schreberi* produce chemically recalcitrant litter rich in phenolic compounds, and the acidic conditions created by them can further slow decomposition processes. Up to 20% of carbon fixed by these mosses can be retained in long-term storage pools (Dorrepaal et al., 2005). However, repeated freeze and thaw cycles due to climate change-induced snow reduction exposes plants to damaging temperature fluctuations, impairing their photosynthetic capacity more than consistent freezing. This reduced photosynthesis leads to a loss of carbon as plants are unable to effectively fix carbon through photosynthesis while respiring and consuming their stored carbon reserves (Kennedy, 1993). Therefore, understanding how moss functional traits respond to altered winter conditions provide important mechanistic insight into ecosystem processes influencing soil carbon resilience, rather than direct quantification of soil carbon pools or fluxes.

Root dynamics. Tree roots play a pivotal role in forest carbon cycling. The production, mortality, decomposition of roots, and rhizodeposition collectively represent important pathways influencing carbon inputs and turnover between soils and the atmosphere (Pregitzer et al., 2000; Prescott & Grayston, 2023). Tree root systems in northern forests are highly dynamic across temporal and spatial scales and are responsive to changes in environmental conditions. Roots are differentiated into two types, i.e., fine and coarse. Fine roots (<2mm diameter), small with a short life span, are more susceptible to freezing injury, and are primarily responsible for water and nutrient absorption, as well as contributing to belowground biogeochemical processes linked to carbon cycling. On the other hand, large coarse roots provide structural support and play a role in nutrient storage and transport (Lavigne & Krasowski, 2007; Vesterdal et al., 2013; Ostonen et al., 2005; Li et al., 2022). Although fine roots constitute a relatively small proportion of total biomass in boreal forests, they represent approximately 20 to 30% of the annual net primary production through their growth and turnover, whereas only a minor fraction of annual production is allocated to coarse roots (Kalyn & Van Rees, 2006; Sah et al., 2011; Lehtonen et al., 2016; Prescott & Grayston, 2023).

Fine root mortality during winter is lower compared to other seasons (Hendrick & Pregitzer, 1992; Fahey & Hughes, 1994). However, reduced snow cover increases soil exposure to freezing despite overall warming of air temperatures. More frequent or severe freeze-thaw cycles can damage fine roots through direct cellular injury, leading to increased mortality (Tierney et al., 2001; Cleavitt et al., 2008; Gaul et al., 2008). Because boreal forest soils receive substantial organic inputs from root turnover and rhizodeposition, reductions in fine-root growth and survival may alter belowground carbon inputs and associated soil processes (Schaberg et al., 2008; Adamczyk, 2021). In addition, accelerated root decomposition following freeze injury can stimulate microbial activity through priming effects, potentially enhancing the decomposition of existing soil organic matter (Högberg et al., 2001; Werth & Kuzyakov, 2008; M. Xu & Shang, 2016). Together, these processes suggest that increased root mortality may influence mechanisms linked to soil carbon persistence under repeated freeze-thaw cycles.

The thick bryophyte layer, characteristic of boreal forest, acts as a thermal buffer, reducing heat exchange between air and soil and maintaining more stable soil temperatures despite fluctuations in air temperature or snow cover (Gornall, Jónsdóttir, Woodin, & Wal, 2007). This buffering effect can protect shallow fine roots from desiccation and thermal stress, thereby supporting root survival in black spruce forests where fine roots are concentrated near the soil surface. By moderating microclimatic conditions, bryophyte cover can influence root dynamics and associated carbon-related processes (Brooker & van der Wal, 2003). Quantifying the interactive effects of snow cover decline and moss-mediated buffering on root health is therefore essential for understanding ecosystem processes underlying boreal forest resilience to climate change, given the central role of root productivity and turnover in belowground carbon cycling (Clemmensen et al., 2013).

Microbial biomass and diversity. Microbial communities play a pivotal role in soil functioning by driving nutrient mineralization, organic matter decomposition, and other biogeochemical processes essential for boreal forest ecosystems (Uroz et al., 2016; Deluca & Boisvenue, 2012; Gao et al., 2024). Through these activities, soil microbes influence carbon-related processes and contribute to ecosystem stability. Given their central role in ecosystem functioning, understanding microbial community dynamics and their responses to changing climatic conditions has become a major research focus over the past decade.

The processing of soil organic matter is regulated by multiple interacting environmental factors, including soil temperature, moisture content, pH, and substrate quality. In boreal conifer forests, decomposition rates are generally higher near the surface (5 to 10 cm depth), where fresh organic inputs from litterfall dominate, whereas deeper layers receive proportionally greater inputs from root turnover (Reichstein et al., 2005; Cornwell et al., 2008; Powlson et al., 2013; Prescott & Vesterdal, 2021). Boreal forest soils tend to have high microbial biomass, including both bacterial and fungal components, compared to temperate soils, with fungi often playing a dominant role in decomposition under cool, acidic conditions.(Trettin et al., 1996; Vanhala et al., 2008; Ziegler et al., 2013; Kimble et al., 2018).

Snow cover acts as a regulator of soil temperature and biochemical processes in boreal ecosystems (Kosolapova & Altshuler, 2024b). Under deep and persistent snow, soil temperature remains close to 0 °C throughout the winter, allowing microbial activity to continue at low but ecologically significant levels. However, reductions in snow cover due to climate warming expose soils to colder air temperatures and more pronounced freeze-thaw fluctuations, which can disrupt nutrient cycling and alter carbon-related processes (Wardle et al., 2004; Van der Heijden et al., 2008; Haugwitz et al., 2011). Freeze-thaw cycles can physically damage soil aggregates and microbial cells, leading to cell lysis and release of labile substrates that temporarily stimulate surviving microbial populations (Skogland et al., 1988; Schimel & Clein, 1996). This transient response may enhance microbial respiration during thaw periods, while prolonged soil freezing can suppress microbial activity or alter oxygen availability, ultimately reshaping microbial community structure and function (Das et al., 2023; Xu et al., 2023b).

Bacteria and fungi are key decomposers of soil organic matter, and their community composition is shaped by a combination of abiotic (edaphic) and biotic factors, such as dominant tree species and understory vegetation that influence mycorrhizal associations (Lladó et al., 2018; van der Heijden et al., 2015). Empirical studies from boreal coniferous forests and alpine forests suggest that short-term snow cover changes have relatively weak effects on bacterial diversity and community composition (Männistö et al., 2018a; Zhao et al., 2022b; Ren et al., 2020b; Liu et al., 2023) whereas fungal communities, particularly symbiotic and saprotrophic groups, tend to exhibit stronger and more consistent responses to snow reduction (Semenova et al., 2016). Notably, most studies have focused solely on snow-soil interactions, with limited consideration of understory vegetation such as bryophytes, despite their dominance in boreal forest floors and potential role in mediating microbial responses.

Problem statement. Despite their ecological significance, the functional role of mosses in mediating belowground carbon processes linked to soil carbon resilience under changing snow regimes remains poorly understood. While *Sphagnum* spp. are well known for their exceptional water retention and insulating capacity, and *P. schreberi* for its dominance in dry to mesic coniferous stands (Wang et al., 2014b; Lavoie et al., 2005; Gornall, 2007), little is known about how their contrasting functional traits influence soil temperature stability and below-ground carbon dynamics. Most studies of boreal carbon dynamics have either focused on snow cover (accumulation or reduction) effects alone (Ren et al., 2020; Hui et al., 2022; Hua et al., 2024) or on moss functional ecology in isolation (Bjerke et al., 2017; Zhang &

Zhang, 2020; Yin et al., 2024), but rarely on the interactive effects of moss, their traits, and snow reduction. This knowledge gap limits our ability to predict how boreal soils, which play a key role in global carbon cycling, will respond to ongoing climate change in regions where forest floors are extensively moss-covered. If unaddressed, this gap hinders our capacity to forecast forest resilience and soil process responses in northern ecosystems that are warming faster than the global average. Therefore, here we pose an important broad-scale question: How do functional traits differ between *Sphagnum* spp. and *P. schreberi* under varying snow cover? How do the interactions between moss type and snow cover affect soil temperature, microbial biomass, microbial diversity and composition, and fine-root dynamics?

Hypotheses. Our experimental design tests three hierarchical hypotheses addressing the effects of snow reduction on boreal forest ecosystems and the mitigation measures by different moss species (see Conceptual Framework, Figure 1).

H1. Snow reduction will decrease soil insulation, leading to colder and more variable winter soil temperatures, with effects moderated by moss presence and type.

H2. Altered soil temperature from snow reduction will increase root mortality and reduce microbial biomass and diversity, while shifting microbial community composition, with the greatest impacts in plots without moss cover.

H3. *Sphagnum* spp. will provide superior buffering of temperature extremes and maintenance of C and N cycling compared to *P. schreberi* and no moss plots, due to its higher colony density and moisture retention.

Conceptual Framework. An obvious characteristic of boreal forests of North America is a dominant canopy of black spruce and nearly continuous ground cover of a moss layer, composed mainly of feathermosses and *Sphagnum* spp., that play key roles in regulating soil microclimate (Lafleur & Schreader, 1994; Turetsky et al., 2012b; Williams & Flanagan, 1998; Zhu et al., 2019). In the face of the increasing temperature of northern latitudes and the decreasing rate of snowfall, we propose a conceptual framework quantifying how moss communities interact with changing snow cover regimes to influence interrelated belowground carbon properties within a boreal forest ecosystem. The unique functional traits of moss communities related to thermal buffering, hydrological regulation, and nutrient (carbon/nitrogen) processing may modulate soil biogeochemical responses to snow cover changes. By measuring subsurface temperature, root dynamics, microbial diversity, and their biomass across controlled moss and snow manipulations, we can clarify complex climate-ecosystem feedback. This also offers valuable insights into the resilience mechanisms that may safeguard below-ground carbon processes due to shifting climatic conditions. Ultimately, our research seeks to contribute essential knowledge to mitigate the ecological consequences of climate change and sustain the vital carbon dynamics in the forest ecosystem at current levels.

Independent variables:

- Moss cover
- Snow cover changes (ambient vs. experimentally reduced)

Dependent variable:

- Soil temperature
- Microbial biomass
- Microbial diversity (bacterial and fungal) and their composition
- Total root biomass and dead root ratio
- Moss functional traits related to structural attributes (colony density), hydrological regulation, and carbon and nitrogen content.

Co-variable:

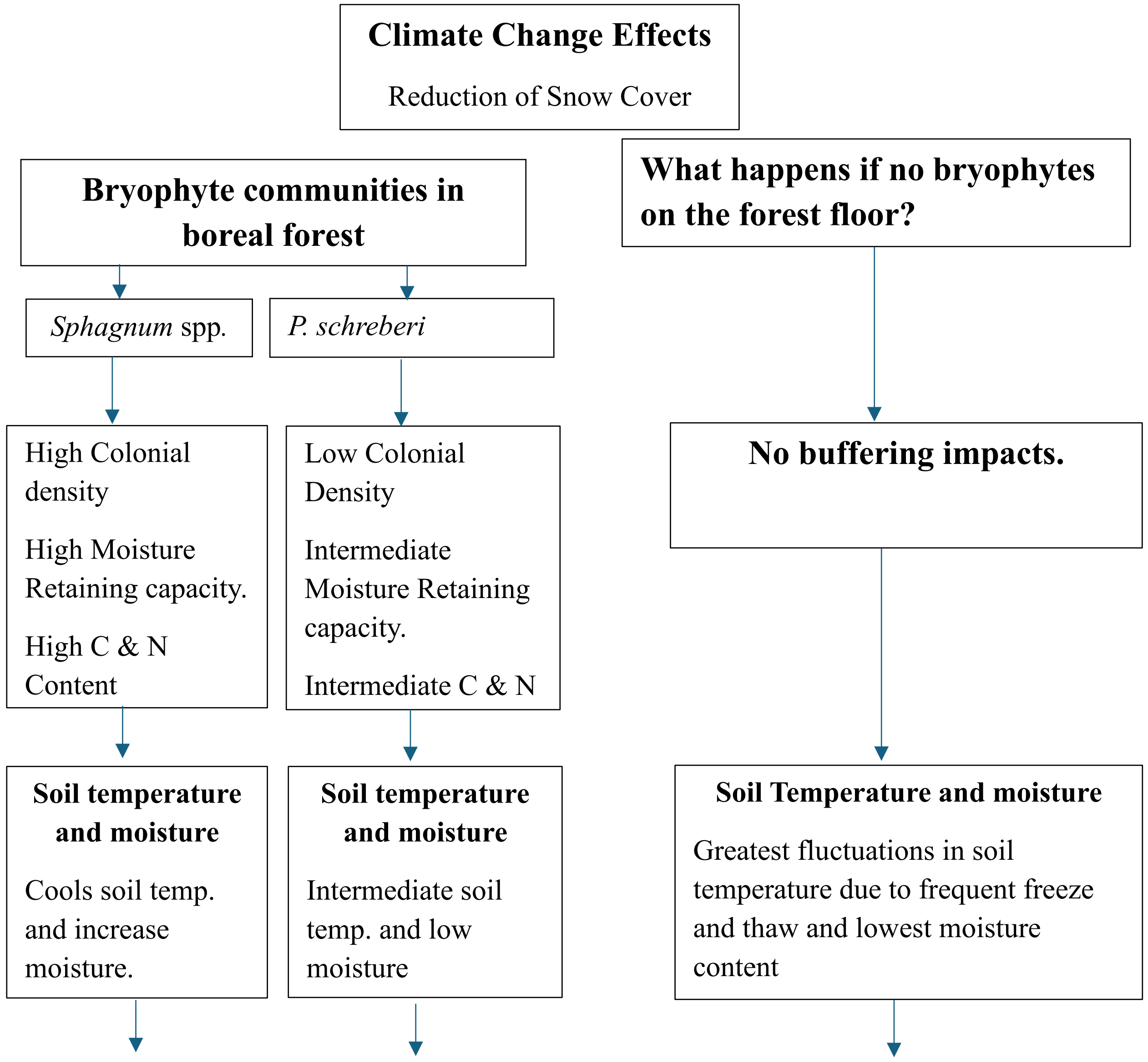
- Canopy cover

- Soil texture
- Soil pH

Potential mediating factors:

- Soil freeze and thaw cycle
- Deep freeze throughout the soil profile

How are they related?



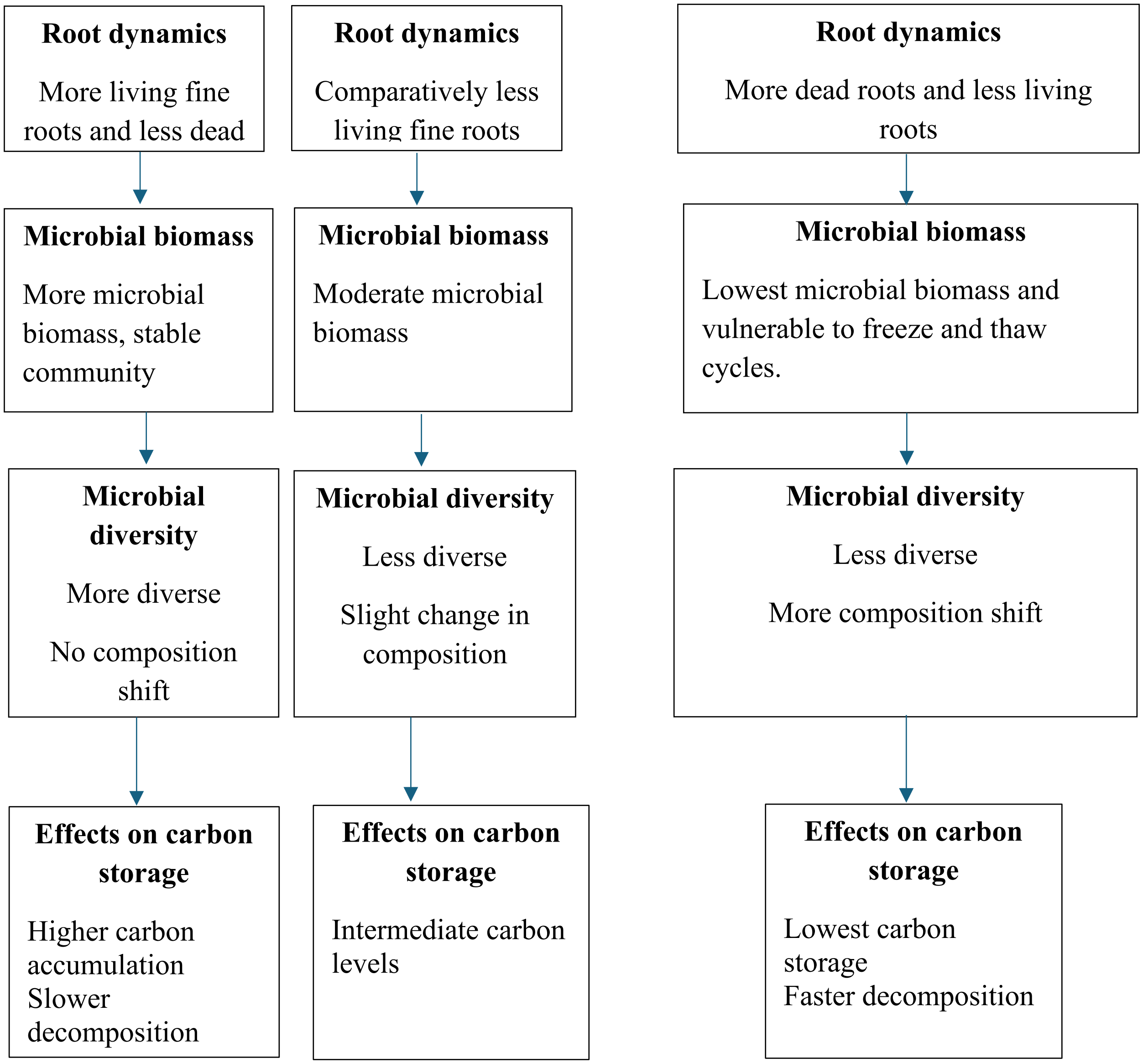


Figure 1

Conceptual framework illustrating the pathways through which bryophyte functional traits mediate the effects of snow cover decline on below-ground carbon processes in boreal black spruce forests.

1. MITIGATION OF THE IMPACTS OF SNOW COVER DECLINE ON BELOWGROUND CARBON PROCESSES BY BRYOPHYTES

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1.1. Introduction

Boreal forests are the second-largest terrestrial biome on Earth, storing nearly 60% of global soil organic carbon (Pan et al., 2011; Bradshaw & Warkentin, 2015). These ecosystems are strongly shaped by distinct seasons with persistent winter snow cover, making winter conditions a critical driver of ecological processes (Kreyling, 2020). However, carbon (C) storage in the boreal forest is highly sensitive to climate change. Climate models project that temperatures across the boreal region will continue to rise by 1-2 °C in summer and 2-3 °C in the winter relative to 1900 levels by 2050 (Price et al., 2013c). Rising winter temperatures are expected to shorten in duration, and the depth of snow is expected to decrease across northern regions (Bombonato & Gerdol, 2012; Mikkonen et al., 2015; Masson-Delmotte et al., 2021). Observations already show that snow cover has declined by an average of 10-17% over recent decades in northern latitudes, with projections indicating a further 25-35% reduction by 2100 throughout the boreal zone (Derksen & Brown, 2012; IPCC, 2021b). Snow cover serves as a thermal insulator, protecting soils from cold air and maintaining a relatively warm soil microclimate (Brooks et al., 2011; Wilson et al., 2020). It therefore represents one of the most important factors shaping belowground biodiversity and ecological processes by regulating soil temperature, moisture, nutrient availability, and microbial and enzymatic activities. Boreal forest soils generally have higher microbial biomass than temperate soils, likely due to the accumulation of organic carbon under cool, acidic conditions that slow decomposition (Trettin et al., 1996; Vanhala et al., 2008; Ziegler et al., 2013; Kimble et al., 2018). Evidence suggests that the loss of insulating snow cover increases soil freezing intensity and frequency, which, in turn, alters soil biogeochemical functioning (Groffman et al., 2001a). Reported effects include reduced soil moisture and altered enzymatic activities due to limited liquid water availability under sub-zero conditions (Campbell et al., 2014; Tan et al., 2014; Liu et al., 2023). Repeated freeze-thaw cycles can physically damage soil aggregates and microbial cells, leading to cell lysis and a temporary pulse of labile carbon substrates that stimulate surviving microbes (Skogland et al., 1988; Schimel & Clein, 1996). This transient increase in microbial respiration and carbon mineralization may accelerate CO_2 release during thaw periods (Das et al., 2023). Conversely, prolonged soil freezing may limit microbial respiration, while ice-encased conditions can deplete oxygen and accumulate CO_2, altering microbial community structure and function (Xu et al., 2023b).

Bacteria and fungi are key decomposers of soil organic matter, and their community composition is shaped by a combination of both abiotic (edaphic) and biotic factors, such as dominant tree species and understory vegetation that determine mycorrhizal associations (Lladó et al., 2018; van der Heijden et al., 2015). Studies in boreal and alpine forests suggest that short-term changes in snow cover have relatively weak effects on bacterial diversity and community composition (Männistö et al., 2018a; Zhao et al., 2022b; Liu et al., 2023; Ren et al., 2020a). In contrast, fungal communities, particularly those involved in symbiotic or saprotrophic processes, tend to respond more strongly and consistently to snow reduction (Semenova et al., 2016; Xu et al., 2022a; Ylänne et al., 2025).

Snow removal experiments also show that reduced snowpack intensifies soil freeze-thaw cycles, causing direct cellular damage to roots and increasing root mortality, even under overall warming conditions (Tierney et al., 2001; Cleavitt et al., 2008; Gaul et al., 2008). Since boreal forest soils store much of their carbon in roots and organic matter derived from root turnover, this reduction may disrupt a major input of carbon to the soil (Schaberg et al., 2008; Adamczyk, 2021). Reduced fine root growth and viability limit carbon inputs from root exudates, while accelerated root decomposition may trigger priming effects that release additional stored carbon (Högberg et al., 2001; Werth & Kuzyakov, 2008; Xu & Shang, 2016). Consequently, increased root mortality could progressively erode belowground carbon pools through successive freeze-thaw cycles.

However, most existing studies have focused on short-term snow-soil responses in tundra or alpine systems, largely overlooking the role of understory vegetation, particularly bryophytes, which dominate the coniferous boreal forest floor. In North American boreal forests, characterized by dense moss layers and *Picea*-dominated canopies, these changes threaten important belowground processes associated with carbon cycling derived from needles, bryophytes, and woody debris (Larsen, 1980; ; Kurz et al., 2013; Bradshaw & Warkentin, 2015; Xu et al., 2023). Given the strong insulating properties of both snow and moss, the influence of the moss layer on soil temperature and carbon dynamics is likely greatest under conditions of shallow or absent snow. This interaction is expected to become increasingly important as snow cover continues to decline across northern regions (Young, 2023).

Although previous research has explored traits such as water retention, decomposition rate, and nutrient content of *Sphagnum* spp. and *Pleurozium schreberi* (Silvola & Aaltonen, 1984; Fenton and Bergeron, 2006; Gornall et al., 2011), their functional roles in buffering snow-related soil changes remain poorly understood (Beringer et al., 2005; Cornelissen et al., 2007; Fenton et al., 2007). As boreal regions face pronounced snow decline, understanding how moss functional traits mediate belowground carbon-related processes is increasingly urgent.

We designed an experiment to evaluate how reduced snow cover influences key belowground processes by integrating snow manipulation with moss functional traits, root dynamics, and soil microbial responses. Specifically, we examined how snow removal and moss type affect (1) key moss functional traits (colony density, water absorption capacity, and nutrient content) that control microclimate buffering and organic matter inputs to soil, (2) fine-roots (biomass, mortality and diameter) that determine belowground carbon allocation and turnover; and (3) the shift in soil microbial communities (biomass, diversity, and composition) that mediate decomposition and nutrient cycling. We hypothesized that (H1) snow reduction would decrease soil temperatures across all the treatments, with the magnitude of temperature decline varying by moss type: greatest in no moss plots, intermediate under *P. schreberi*, and least under *Sphagnum* spp. We further predicted that (H2) declining snow cover will negatively affect colony density, water absorption capacity, and carbon and nitrogen fixation rates of mosses, and that these effects would be lower for *Sphagnum* spp. than for *P. schreberi*. For fine-root responses, we expected that (H3) reduced snow would result in lower fine-root biomass and high mortality in plots without moss cover, with intermediate values under *P. schreberi* and most favourable conditions under *Sphagnum* spp. Finally, we hypothesized that (H4) snow cover decline would result in higher microbial biomass and diversity under *Sphagnum* spp. compared to *P. schreberi* and no moss treatments. By linking plant functional traits to belowground carbon inputs, this study provides mechanistic insights into how bryophyte communities shape belowground processes under changing snow regimes.

1.2. Methods and materials

1.2.1. Study area

The study was conducted in northern Quebec, Canada (49°09′N, 78°47′W), approximately 10-30 km north of the villages of Authier-Nord and Villebois, within the black spruce-feather moss bioclimatic domain (Saucier et al. 2009). The region has a subpolar continental climate with a short growing season, with a mean annual temperature of approximately 0 °C, and 900-1000 mm of annual precipitation, with 40-45% falling as snow, or approximately 400-450 cm of snow accumulation (Environment Canada, 2021). Soils are Grey Luvisols with well-developed organic horizons over glaciolacustrine clays (Soil Classification Working Group, 1998).

1.2.2. Experimental design and treatments

In October 2023, a full-factorial experiment was established to test the effects of moss type (*S. capillifolium*, *P. schreberi*, and a no-moss control) and snow cover (present or absent), resulting in six treatments: (1) *Sphagnum* spp. with snow (SS), (2) *Sphagnum* spp. without snow (SNS), (3) *Pleurozium schreberi* with snow (PS), (4) *Pleurozium schreberi* without snow (PNS), (5) No moss with snow (NMS), and (6) No moss without snow (NMNS). The experimental design comprised three sites, with two replicated blocks per site, and the six treatments were randomly distributed within each block (Figure 2). In total, the experiment consisted of 36 plots of 1.5 m^2 (3 sites × 2 blocks × 6 treatments).

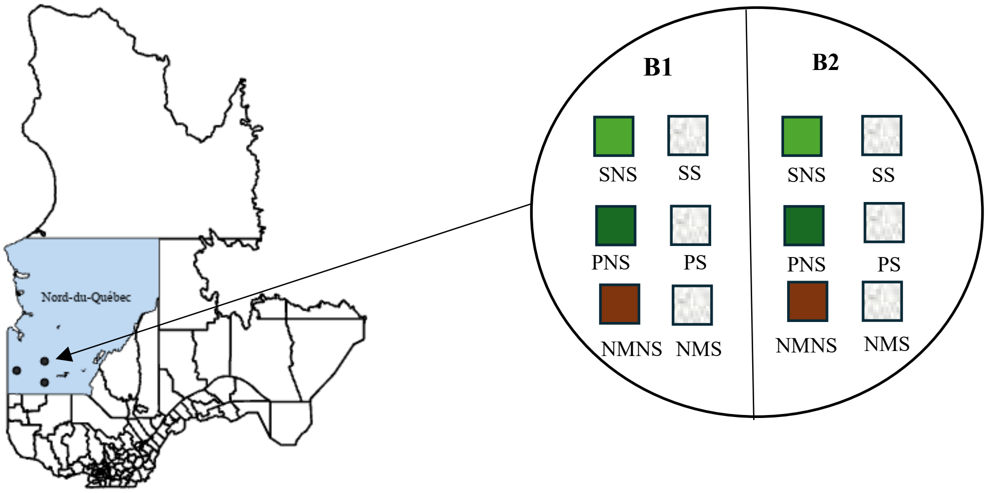


Figure 2
(a) Map of the study area showing the three sites—two near the village of Authier-Nord and one near the village of Villebois — within the Nord-du-Quebec region, Canada (b) Schematic representation of the experimental design, illustrating the division of each site into blocks, with each block further subdivided into plots assigned to six treatments, i.e., SS = *Sphagnum* spp with snow, SNS = *Sphagnum* spp. without snow, PS = *P. schreberi* with snow, PNS = *P. schreberi* without snow, NMS = No moss with snow, NMNS = No moss without snow.

Plots assigned to moss treatments consisted of visually dominant monospecific moss covers, where either *Sphagnum* spp. or *Pleurozium schreberi* comprised >95% of the ground bryophyte layer. In no moss treatments, all living bryophyte biomass was manually removed regardless of species identity, fully exposing the soil surface in the fall before snowfall while minimizing disturbance to the underlying soil and root systems. In no-snow plots, snow was manually removed monthly using a plastic shovel to minimize underlying vegetation disturbance.

1.2.2.1. Site and soil characterization

Baseline environmental conditions were characterized across all experimental plots to account for their potential influence on belowground processes (microbes, root dynamics) and moss trait responses. Canopy openness was measured at 0.3 m height above each plot using a Spherical Crown densiometer (Forestry Suppliers Inc., Jackson, MS, USA) in four directions. Measurements were averaged to estimate the proportion of open sky visible from the plot centre, providing an index of light availability, and to verify that differences in overstory structure did not confound observed treatment effects. 112 cm^3 mineral soil samples at 15-25 cm depth were collected in August 2024 from each plot and stored at 4 °C until further analysis. The samples were oven-dried at 60 °C for 48 hours, then finely ground using a Mixer Mill MM200 (Retsch GmbH, Haan, Germany). Soil pH was measured in a 0.01 M $CaCl_2$ using a 1:2.5 soil-to-solution ratio, following standard procedures as described by Pansu & Gautheyrou (2006). Soil texture was measured using the hydrometer method (Beretta et al., 2014). Mineral soil C and N concentrations were measured on air-dried, sieved (2mm), and ground samples using the LECO CNS 928 analyzer (LECO Corporation, St. Joseph, MI, USA) based on high-temperature combustion (McGeehan & Naylor, 1988). Those concentrations were measured to characterize background soil conditions across treatments.

1.2.2.2. Temperature monitoring

To monitor soil temperature, 24 dataloggers (HOBO, Onset U23 Pro v2, Bourne, Massachusetts, USA) were installed at 15 cm depth from the surface, across 36 experimental plots. The data loggers were distributed in a stratified manner within each site and block to ensure that all six treatment combinations were proportionally represented, avoiding repetition within blocks. Temperature loggers, protected by waterproof plastic covers, were also placed 2 cm above the ground for measurements of air temperature within the canopy in each of the three sites.

1.2.2.3. Bryophyte sampling

Moss samples (6 cm diameter) were collected from each moss-covered plot using a sharp-edged corer, including both photosynthetic and non-photosynthetic layers. In the lab, samples were rehydrated for 12 h to measure colony density (mass per unit volume via the water displacement method) and water absorption capacity (difference between saturated and drained weights). Subsamples were dried, ground, and analyzed for C and N concentrations using the LECO CNS 928 analyzer (LECO Corporation, St. Joseph, MI, USA).

1.2.2.4. Root Sampling

Intact soil cores (5 cm × 20 cm) were collected from each plot in June 2024. The soil samples were then soaked in water to facilitate root separation, followed by gentle washing over a sieve to eliminate coarse roots (>2 mm in diameter), rocks, and debris. The remaining fine roots (<2 mm in diameter) were manually sorted under a dissecting microscope based on viability (live or dead), following the morphological characteristics described by Lyford (1980). Live roots were identified as resilient, translucent, and white to tan in color, whereas dead roots were brittle, easily fragmented, and displayed a dull gray-to-black coloration (Rabearison et al., 2024). Following separation, roots were evenly spread in a 20 * 25 cm transparent tray filled with deionized water to minimize overlap. We determined average root diameter (mm) using a scanner at 400 dpi resolution (Epson Perfection V800; Epson, Ontario, Canada) and WinRhizo Pro 2019 software (Regent Instruments, Quebec, Canada). Finally, the roots were weighed and then oven-dried to a constant mass at 60°C. The dead-to-total root biomass ratio and the total root biomass were determined for each treatment group.

1.2.2.5. Microbial diversity and composition

Organic soil samples for DNA-based assessment of microbial diversity and community composition were collected from each plot in early May 2024 using a 5 cm diameter soil core to a depth of 20 cm. The samples were stored in a freezer at - 80 °C until further processing. Analyses were conducted by the Environmental Genomics Laboratory of the Laurentian Forestry Centre following previously described procedures (Nagati et al., 2024).

Briefly, subsamples of 250 mg of sieved soil were weighed in PowerBead tubes of the QIAGEN DNeasy Powersoil Pro kit for DNA extractions with the QIAcube system (QIAGEN, Valencia, CA, USA) following the manufacturer's instructions. The concentration of all DNA extracts was measured with the Qubit™ dsDNA HS (or BR if concentration was too high) Assay Kit (Thermo Fisher) on the Qubit 3.0 fluorometer device (QIAGEN). Soil bacterial and fungal communities were characterized by amplifying and sequencing the V4-V5 regions of the 16S rRNA gene with the primer pair 515F-Y (5'-GTGYCAGCMGCCGCGGTAA-3') / 926R (5'-CCGYCAATTYMTTTRAGTTT-3') (Parada et al., 2016) and the ITS2 region with the primer pair ITS9 (5'-GAACGCAGCRAAIIGYGA-3') (Menkis et al., 2012) / ITS4 (5'-TCCTCCGCTTATTGATATGC-3') (Innis et al., 2012), respectively. Library preparation for Illumina sequencing was performed according to the manufacturer’s instructions for user-defined primers (Illumina, 2013). Sequencing was performed on an Illumina MiSeq platform with a MiSeq Reagent Kit v3 (600 cycles) at the Next Generation Sequencing Platform of the Centre Hospitalier Universitaire de Québec-Université Laval Research Centre.

Bioinformatic analysis of Illumina sequences was performed using QIIME2 (Bolyen et al., 2019) within the Q2Pipe bioinformatic pipeline (Nagati et al., 2024). Briefly, sequence reads were truncated at their 5’ and 3’ ends based on 1) the length of the primer (16S) or the specific primer sequence (ITS) and 2) per base sequence quality score. The QIIME2 plugin DADA2 (Callahan et al., 2016) was then used for filtering, dereplication, merging of paired-end reads, and chimera identification. This process resulted in the inference of amplicon sequence variants (ASVs). Rare ASVs (frequency less than 0.05% of the mean ASV frequency) were filtered out. The taxonomic assignment of ASVs was done using the SILVA 138 database (Quast et al., 2012) for the 16S rRNA gene and the UNITE database (version 9.0) (Abarenkov et al., 2010) for the ITS2 region. For the 16S rRNA gene, ASVs not assigned at the kingdom level or assigned to Eukaryota, mitochondria, and chloroplasts were filtered out. For the fungal ITS2 region, only ASVs assigned to the kingdom Fungi were retained in the analysis. Data were rarefied prior to further analyses to control for uneven sequencing effort (Schloss, 2024), with 14056 and 24278 sequences retained per sample for the 16S rRNA gene and ITS2 region, respectively. Filtered ASV tables of the fungal ITS2 region were further analyzed with FUNGuild to infer the ecological guilds of fungi based on their taxonomy (Nguyen et al., 2016).

1.2.2.6. Microbial biomass

Microbial biomass (C) was analyzed using the chloroform fumigation-extraction method (Brookes et al., 1985). Organic soil samples (5 cm × 20 cm) were collected in May and September 2024 to account for seasonal variability in microbial biomass associated with post-snowmelt and late-growing-season conditions. The samples were fumigated for 24h with $CHCl_3$, extracted with 0.5M K_2SO_4, and analyzed for organic C using a Dohrman DC 80 analyzer. Biomass C was calculated as (C_fumigated - C_unfumigated)/k_EC, where k_EC = 0.35.

We used the following equation [1] to calculate the Soil Water Content (WS) based on the study of Topp (2003).

$$\mathrm{WS}(\%) = \frac{soil\ wet\ weight\ (g) - soil\ ovendry\ weight (g)}{soil\ ovendry\ weight\ (g)} \times 100 \qquad \text{(Eq. 1)}$$

We measured the oven-dry equivalent mass of soil (MS) used for microbial biomass measurements by the equation [2]. Since fresh soil was weighed wet, this correction standardizes results to dry weight.

$$\text{MS (g)} = \frac{soil\ wet\ weight\ (g) \times 100}{(100 + WS\ (\%))} \qquad \text{(Eq. 2)}$$

WS % was calculated previously in equation [2].

We calculated the total liquid volume for extraction (VS) after mixing soil and extractant by using equation [3].

VS (mL) = soil wet weight (g) – soil oven-dry weight (g) + extractant volume (mL) (Eq. 3)

The difference between wet and dry weights gives the water present in the soil originally, which is then added to the extractant volume to obtain total volume of the solution.

We estimated the total extractable carbon in the fumigated and unfumigated soil extracts using equation [4]. This is expressed per gram of soil.

$$OC_F,\ OC_{UF}\ (\mu g/g\ \text{soil}) = \text{extractable C}\ (\mu g/mL) \times \frac{VS(ml)}{MS(g)} \qquad \text{(Eq. 4)}$$

VS and MS in the equation are the total volume of solution and oven-dry equivalent mass of soil, respectively.

Finally, we measured C in living microbial biomass by using equation [5].

$$\text{MB-C}\ (\mu g/g\ \text{soil}) = (OC_F - OC_{UF})/k_{EC} \qquad \text{(Eq. 5)}$$

The difference between fumigated and unfumigated samples is corrected by an extraction efficiency coefficient $k_{EC} = 0.35$. OC_F and OC_{UF} are calculated in equation [5].

1.2.3. Statistical analysis

All analyses were done in the RStudio software (Team, 2016). Preliminary analyses using scatter plots and ANOVA tested for relationships between environmental variables (canopy openness, soil pH, soil texture, mineral soil C and N content) and response variables. No significant relationships were detected ($P > 0.05$), indicating that baseline site conditions did not confound treatment effects.

1.2.3.1. Temperature

The complicated logistics of temperature measurements and loss of some sensors in the field resulted in multiple sampling gaps in the no moss no snow plots. We were only able to extract data from a single probe in this treatment. Therefore, we restricted our temperature analysis to the general buffering effect of moss. For each replicate of each measurement series, we calculated average daily temperature amplitudes. The winter temperature was the temperature from December to April. Variations in winter soil temperature across the treatments were compared by two-way ANOVA with Moss type and Snow cover as factors. Line plots were used to illustrate the temporal trends of soil temperature across different treatments compared to air temperature.

1.2.3.2. Bryophyte functional traits analysis

Treatment effects on bryophyte functional traits (colony density, water absorption capacity, nitrogen content, carbon content), each treated as a continuous dependent variable, were tested using linear mixed-effects models (LMMs) fitted with the "*lme4*" package (Bates et al., 2015). In these models, moss type (*Sphagnum* spp., *P. schreberi,* and no moss) and snow cover (with vs without snow) were included as fixed effects, while block nested within site was a random factor. Model assumptions of normality and homoscedasticity were checked using diagnostic plots (residual vs. fitted, Q-Q plots), and the data were transformed when the assumptions were not met. The *emmeans* package in R was used as a post hoc method (Tukey's Honest Significant

Difference (HSD) test) to make pairwise comparisons when a significant main effect or interaction was found (Lenth et al., 2023).

1.2.3.3. Root analysis

Furthermore, root responses (root diameter, dead-to-total root biomass, and total root biomass) were analyzed using LMMs following the procedure described above. The total dry root biomass was square root transformed before analysis to meet model assumptions.

1.2.3.4. Soil bacterial and fungal diversity and composition

Soil microbial community data (i.e., rarefied ASV tables) were processed using the phyloseq package in R (McMurdie & Holmes, 2013), creating a unified data set from ASV counts, taxonomic classifications, and sample metadata (vegetation type and snow treatment). Alpha diversity (i.e., Shannon index) was calculated using the "estimate_richness" function of the phyloseq package and was tested using LMMs following the procedure described above. Beta diversity was assessed on rarefied ASV tables using Bray-Curtis dissimilarity matrices ("vegdist" function) and permutational multivariate analysis of variance (PERMANOVA, "adonis" function) with 999 permutations using the vegan package. Microbial community composition was visualized using non-metric multidimensional scaling (NMDS) ("metaMDS" function, *vegan* package). The relative abundance of major bacterial and fungal phyla (>2%), top-20 genera, and fungal functional groups was modeled using zero-inflated beta regression (*glmmTMB* package; Brooks et al., 2017) and was visualized with stacked barplots (*ggplot2*). Post-hoc comparisons were performed where appropriate as described above.

1.2.3.5. Microbial biomass

Microbial biomass carbon was tested using LMMs at two time points (start vs. end of the growing season). End-of-season data were log-transformed to meet the model assumptions. Post-hoc pairwise comparisons were performed as described above.

1.3. Results

1.3.1. Winter soil temperature

Winter soil temperatures showed a clear thermal buffering compared to ambient air across all treatments. While air temperature fluctuated sharply, dropping below -30 °C during extreme cold and rising above 5 °C on mild days, soil temperatures remained comparatively warmer and more stable (Fig. 3). Snow-covered treatments (SS, PS, NMS) showed the highest insulation capacity, with an average of daily minimum temperatures remaining near or above 0 °C (0.32 ± 0.19 °C, 0.23 ± 0.25 °C, and 0.41 ± 0.24 °C, respectively). In contrast, snow reduced treatments (NMNS, PNS, SNS) experienced deeper frost penetration, with PNS showing the coldest mean minimum (– 4.45 ± 4.04) °C, although this is still warmer than the air temperature (Fig. 3; Tab.1).

Statistically, soil under *Sphagnum* spp. with snow was on average 2.17 °C warmer than under the no-snow treatment ($P < 0.01$), while *Pleurozium schreberi* plots with snow were 4.68 °C warmer than their snow-reduced counterparts ($P < 0.01$) (Tab.2).

Table 1
Winter (December – April) soil and air temperature characteristics across moss and snow cover treatments. Values represent the average of daily mean temperatures per plot, calculated across the winter period and then averaged over six replicate plots per treatment.

Treatment	Snow	Mean_Minimum (°C)
AIR		-12.25 ± 9.15

No moss	No	-0.25 ± 0.51
No moss	Yes	0.32 ± 0.19
Pleurozium	No	-4.45 ± 4.04
Pleurozium	Yes	0.23 ± 0.25
Sphagnum	No	-1.75 ± 2.13
Sphagnum	Yes	0.41 ± 0.24

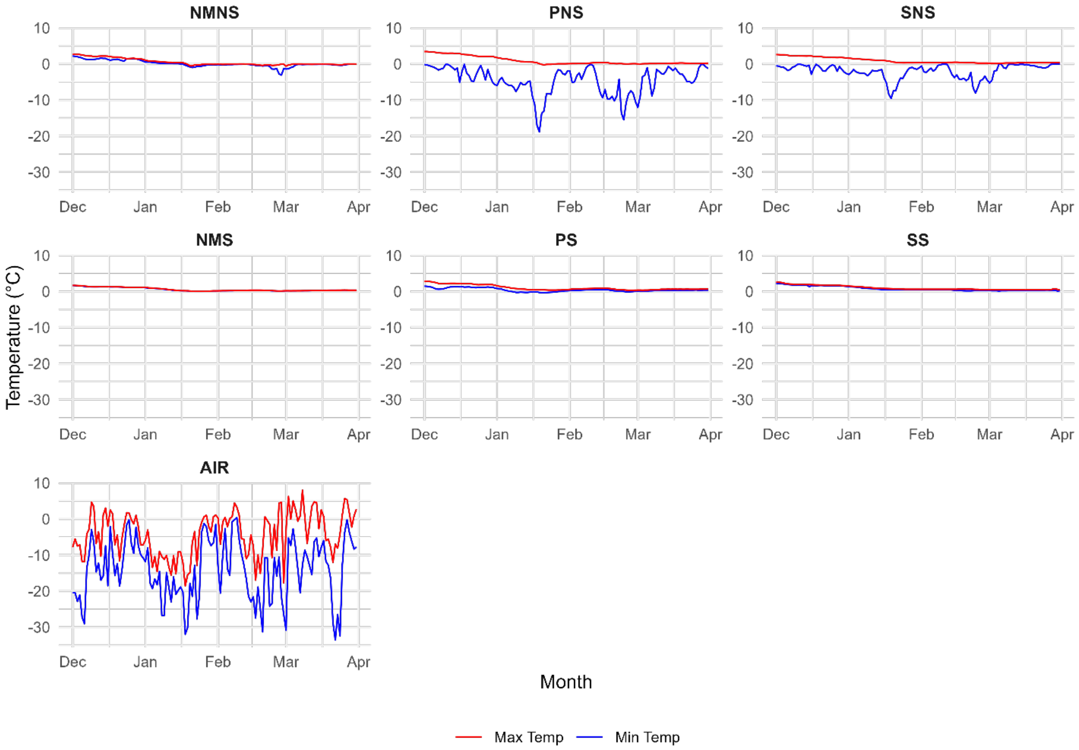


Figure 3

Seasonal trends of daily maximum (red) and minimum (blue) temperatures (°C) from December to April across treatments differing in moss type and snow cover. Each panel represents the average of six replicate plots per treatment. Treatments include: AIR (ambient air), NMNS (no moss, no snow), NMS (no moss, snow), PNS (*Pleurozium schreberi*, no snow), PS (*Pleurozium schreberi*, snow), SNS (*Sphagnum* spp. no snow), SS (*Sphagnum* spp. snow).

Table 2
Pairwise comparisons of minimum soil temperatures (°C) among treatments based on Tukey HSD post-hoc test following two-way ANOVA. Significant differences are indicated in bold.

Treatments	**Mean Difference (°C)**	**Lower CI**	**Upper CI**	***p*-value**
Sphagnum with snow – *Sphagnum* without snow	2.17	0.70	3.65	**<0.001**
Pleurozium with snow – *Pleurozium* without snow	4.68	3.21	6.15	**<0.001**
Sphagnum with snow-No moss with snow	0.09	-1.38	1.56	0.99
Pleurozium with snow-No moss with snow	-0.09	-1.56	1.37	0.99
Sphagnum with snow-*Pleurozium* with snow	0.18	-1.28	1.66	0.999
Sphagnum without snow-*Pleurozium* without snow	2.69	1.21	4.16	**<0.001**

1.3.5. Bryophyte functional traits

1.3.5.1. Colony density

The colony density of mosses was primarily driven by moss species ($P = 0.001$), and the interaction with snow cover ($P = 0.005$). Overall, *Sphagnum* spp. maintained higher colony density than *P. schreberi* (Fig. 4a, Tab.3). Snow removal reduced colony density in *Sphagnum* plots ($P = 0.02$), whereas *P. schreberi* did not show any response to changes in snow cover ($P = 0.95$). Despite this decline, *Sphagnum* spp. colonies under snow removal conditions remained denser than *P.schreberi* under either snow treatment (*P* < 0.001).

1.3.5.2. Water absorption capacity

Sphagnum's water absorption capacity decreased when snow cover was reduced (P < 0.001), whereas *P. schreberi* showed no change in water absorption capacity between snow conditions (P = 0.99). Although snow removal decreased Sphagnum's water absorption capacity, it remained higher than *P. schreberi* even under reduced snow conditions (P = 0.004) (Fig. 4, Tab. 3).

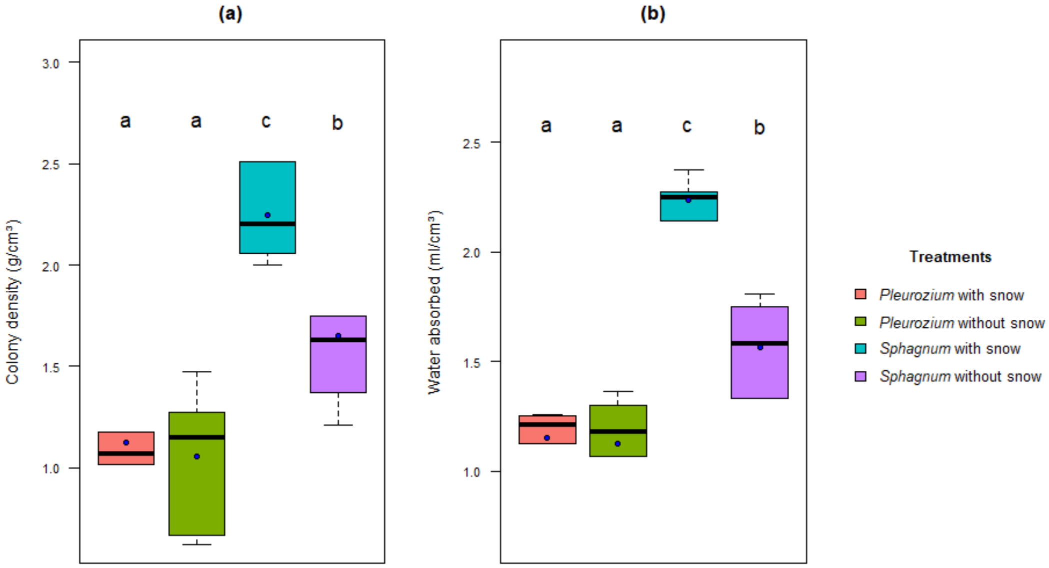


Figure 4
Functional traits of bryophytes across moss and snow treatments.
(a) Colony density (g/cm³) and (b) water absorption capacity (ml/cm³) for four experimental treatments combining moss species (*P. schreberi* and *Sphagnum* spp.) with normal and declined snow conditions. Different letters denote statistically significant differences among treatments based on Tukey-adjusted comparisons (p < 0.05).

Table 3

Summary table of linear mixed-effects models testing the effects of snow cover on colony density (A) and water absorption capacity (B) of different mosses. Values represent model-estimated mean effects ± standard error (SE), with associated t-values and p-values. Statistically significant effects ($p<0.05$) are indicated in bold.

Variable	Mean effect ± SE	t-value	p-value
A			
Moss (*Sphagnum* vs *Pleurozium*)	0.636 ± 0.159	3.99	**0.001**
Snow (Normal vs Reduced)	0.0772 ± 0.155	0.49	0.62
Canopy cover (%)	-0.0124 ± 0.011	-1.13	0.27
Moss × Snow interaction	0.4754 ± 0.223	2.12	**0.005**
B			
Moss (*Sphagnum* vs *Pleurozium*)	0.420 ± 0.108	3.91	**0.001**
Snow (Normal vs Declined)	0.020 ± 0.107	0.19	0.85
Canopy cover (%)	0.005 ± 0.005	1.10	0.29
Moss × Snow interaction	0.672 ± 0.005	4.43	**0.0006**

1.3.5.3. Carbon and Nitrogen Content

P. schreberi had significantly higher carbon contents than *Sphagnum* spp. under both snow and no-snow conditions ($P < 0.05$). However, there was no effect of snow presence, and it did not interact with moss type ($P > 0.05$).

In contrast, nitrogen content (Fig. 5b) did not show any differences between treatments ($P > 0.05$), although *Sphagnum* spp. without snow tended to show higher variability and slightly lower mean nitrogen levels.

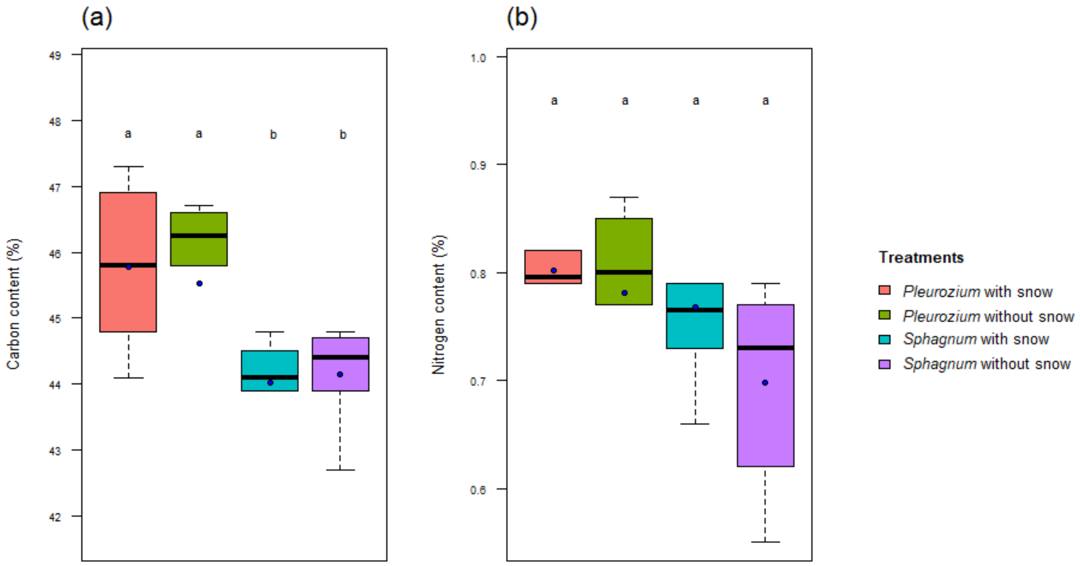


Figure 5
Carbon and Nitrogen content (% dry weight) in moss tissues under different moss and snow treatments. Different letters denote statistically significant differences based on Tukey-adjusted pairwise comparisons; blue dots indicate means.

Table 4
Summary table of linear mixed-effects models testing the effects of snow cover on carbon content (A) and Nitrogen content (B) of different mosses. Values represent model-estimated mean effects ± standard error (SE), with associated t-values and p-values. Statistically significant effects (p < 0.05) are indicated in bold.

Variable	Mean effect ± SE	t-value	p-value
A			
Moss (*Sphagnum* vs *Pleurozium*)	-1.528 ± 0.478	-3.19	**0.006**
Snow (Normal vs Reduced)	0.223 ± 0.462	0.48	0.63
Canopy cover (%)	0.043 ± 0.038	1.12	0.27
Moss × Snow interaction	-0.206 ± 0.671	-0.30	0.76
B			
Moss (*Sphagnum* vs *Pleurozium*)	-0.082 ± 0.048	-1.72	0.10
Snow (Normal vs Reduced)	0.020 ± 0.047	0.43	0.67
Canopy cover (%)	-0.0004 ± 0.002	-0.15	0.87
Moss × Snow interaction	0.048 ± 0.067	0.71	0.48

1.3.6. Root dynamics

1.3.6.1. Treatment effects on total root biomass and dead root

Total fine root biomass was significantly influenced by moss type (*P* = 0.001) and its interaction with snow cover (*P* = 0.01). Snow removal had no effect on root biomass under *P. schreberi* or with no moss, while it decreased root biomass under *Sphagnum* spp (Fig.6a, Tab. 4A).

Soils under *Sphagnum* spp. plots tended to have lower dead root ratios compared to no moss and *P. schreberi* plots (*P* = 0.05). The dead root ratios did not differ significantly between snow and no-snow conditions within any moss type (*Sphagnum* spp. ($P = 0.9$), *P. schreberi* ($P = 0.2$), and no moss plots ($P = 0.5$) (Figure 6b).

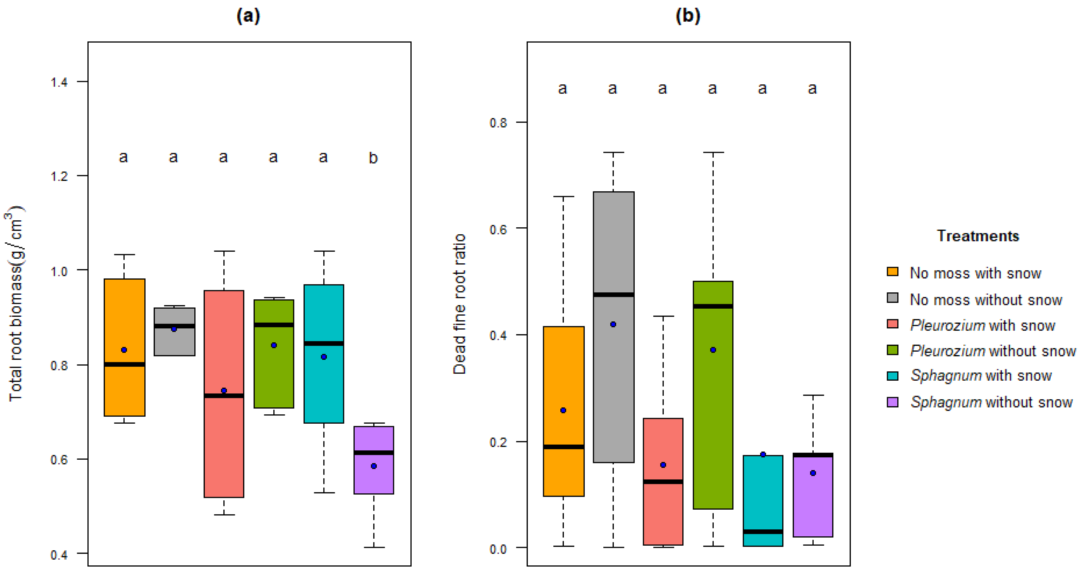


Figure 6
Boxplots showing the effects of bryophyte and snow cover treatments on belowground root dynamics across two metrics: Total Root Biomass (left)and Dead Root Ratio (right). Treatments include: SS (*Sphagnum* spp. with snow), SNS (*Sphagnum* spp. without snow), PS (*P. schreberi* with snow), PNS (*P. schreberi* without snow), NMS (No moss with snow), and NMNS (No moss without snow).

Table 5
Summary table of linear mixed-effects models testing the effects of moss type, snow cover, and their interactions on total fine root biomass (A) and dead fine root ratio (B). Values represent model-estimated mean effects ± standard error (SE), with associated t-values and p-values. Statistically significant effects (p < 0.05) are indicated in bold.

Variable	Mean effect ± SE	t-value	p-value
A			
Moss (*Sphagnum* vs No moss)	-0.290 ± 0.078	-3.73	**0.001**
Moss (*Pleurozium* vs No moss)	-0.033 ± 0.078	- 0.42	0.67
Snow (Normal vs Reduced)	-0.044 ± 0.078	- 0.57	0.57
Sphagnum × Snow	0.276 ± 0.110	2.51	**0.01**
Pleurozium × Snow	-0.053 ± 0.110	-0.49	0.63
B			
Moss (*Sphagnum* vs No moss)	-0.281 ± 0.137	-2.04	0.05
Moss (*Pleurozium* vs No moss)	-0.049 ± 0.137	-0.35	0.72
Snow (Normal vs Reduced)	-0.161 ± 0.137	-1.17	0.25
Sphagnum × Snow	0.197 ± 0.194	1.01	0.32
Pleurozium × Snow	-0.054 ± 0.194	-0.27	0.78

1.3.6.2. Treatment effect on Root diameter

Root diameter (Live/dead) was influenced by moss type (P = 0.02) the interaction with snow removal showed a marginal trend (*P* = 0.07). Live roots in *Sphagnum* spp. plots were thinner than dead roots in most snow/moss combinations (*P* = 0.02). Specifically, they were thinner than dead roots in no moss with snow ($P = 0.0002$) and *Sphagnum* spp. with snow ($P = 0.04$). Relative to live roots in *Sphagnum* spp. without snow, dead roots were also thicker in No moss without snow ($P = 0.0001$) and *P. schreberi* without snow ($P < 0.0001$). The within-*Sphagnum* spp. contrast under no snow (dead vs live) was marginally significant ($P = 0.09$), showing a trend of thicker roots dying under snow removal conditions.

1.3.7. Soil bacterial and fungal diversity and composition

1.3.7.1. Soil bacterial and fungal diversity

Shannon bacterial diversity was not significantly affected by moss type, snow cover, and their interaction with snow cover (Tab. 5A, Fig. 7a). Shannon fungal diversity was not significantly affected by moss type or snow cover, but their interaction had significant effects. The soil fungal Shannon diversity decreased significantly when snow was reduced in *P. schreberi* plots (Fig. 7, $P < 0.05$). The diversity was slightly higher in the *Sphagnum* spp. plots with snow than with no snow, but these differences were only marginally significant (Fig. 7b, $P = 0.08$).

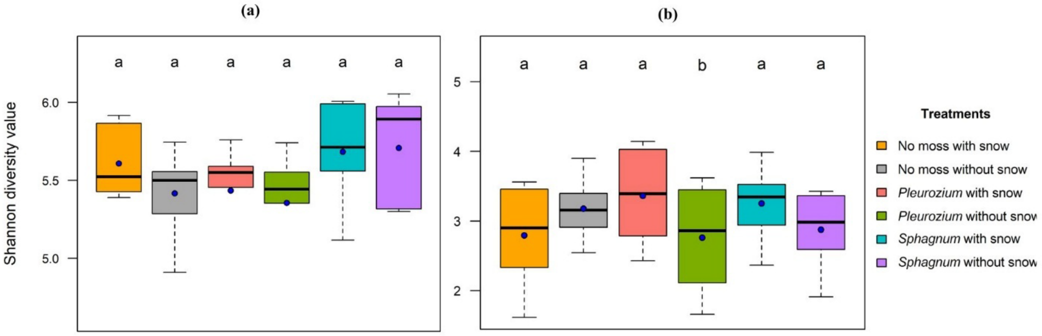


Figure 7
Boxplots showing Shannon diversity index of bacteria (a) and fungi (b) across treatments with varying moss types (No moss, *P. schreberi*, and *Sphagnum* spp.) and snow presence (with snow and without snow). Different lowercase letters indicate significant differences between treatments.

Table 6

Summary table of linear mixed model testing the effects of moss type, snow cover, and their interactions on bacterial diversity (A) and fungal diversity (B). Statistically significant effects ($p < 0.05$) are indicated in bold.

Variable	Mean effect ± SE	t-value	p-value
A			
Moss (*Sphagnum* vs No moss)	0.301 ± 0.171	1.75	0.08
Moss (*Pleurozium* vs No moss)	-0.06 ± 0.162	- 0.37	0.71
Snow (Normal vs Reduced)	0.191± 0.162	1.18	0.24
Sphagnum × Snow	-0.226 ± 0.236	-0.95	0.34
Pleurozium × Snow	-0.112 ± 0.22	-0.49	0.62
B			
Moss (*Sphagnum* vs No moss)	-0.302 ± 0.30	-0.99	0.32
Moss (*Pleurozium* vs No moss)	-0.427 ± 0.30	-1.37	0.17
Snow (Normal vs Reduced)	-0.38 ± 0.30	-1.27	0.21
Sphagnum × Snow	0.75 ± 0.42	1.77	0.08
Pleurozium × Snow	0.98 ± 0.42	2.30	**0.02**

1.3.7.2. Soil bacterial and fungal community composition

Soil bacterial community composition differed significantly among moss types (*P* = 0.03) but was not driven by snow removal alone nor its interaction with moss type. Pairwise comparisons showed that soil bacterial composition associated with *Sphagnum* spp. plots was significantly different from those in no moss (*P* = 0.042) and *P. schreberi* plots (*P* = 0.042), patterns supported by NMDS (Fig. 8). In contrast, no significant difference was found between no moss and *P. schreberi* plots. (*P* = 0.293). Moreover, there were no differences on soil bacterial composition between snow and no snow conditions within any moss type (*P* = 0.02).

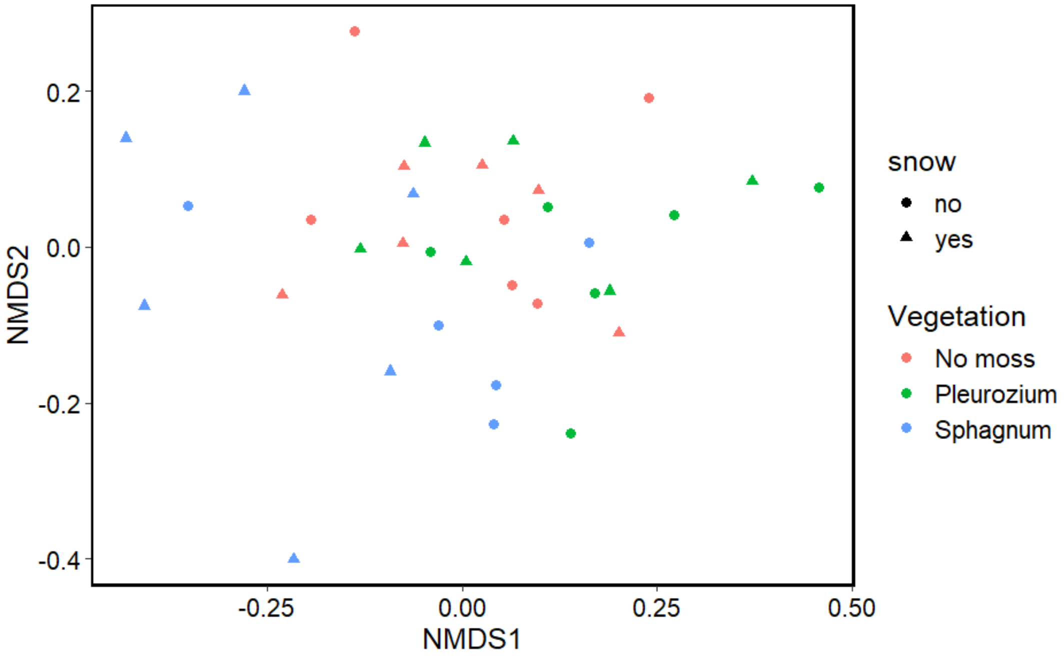


Figure 8
Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarity of bacterial community composition across vegetation types and snow treatments. Points represent individual samples, colored by vegetation type (No moss, *P. schreberi*, *Sphagnum* spp.) and shaped by snow cover (circle = no snow, triangle = snow).

Snow cover influenced the relative abundance of soil Acidobacteriota and Actinobacteriota differently across vegetation types. In *Sphagnum* spp. plots, snow removal decreased the relative abundance of Acidobacteriota (*P* <0.05), whereas only a quasi-significant effect was detected in *P. schreberi* plots (*P* = 0.064) and no significant effect in no-moss plots (*P* = 0.574). In contrast, the relative abundance of Actinobacteria showed a significant increase when snow was reduced in *P. schreberi* plots (*P*< 0.05), while snow did not affect Actinobacteriota's relative abundance in *Sphagnum* spp. plots (*P* = 0.198) or no-moss plots (*P* = 0.929; Fig. 9).

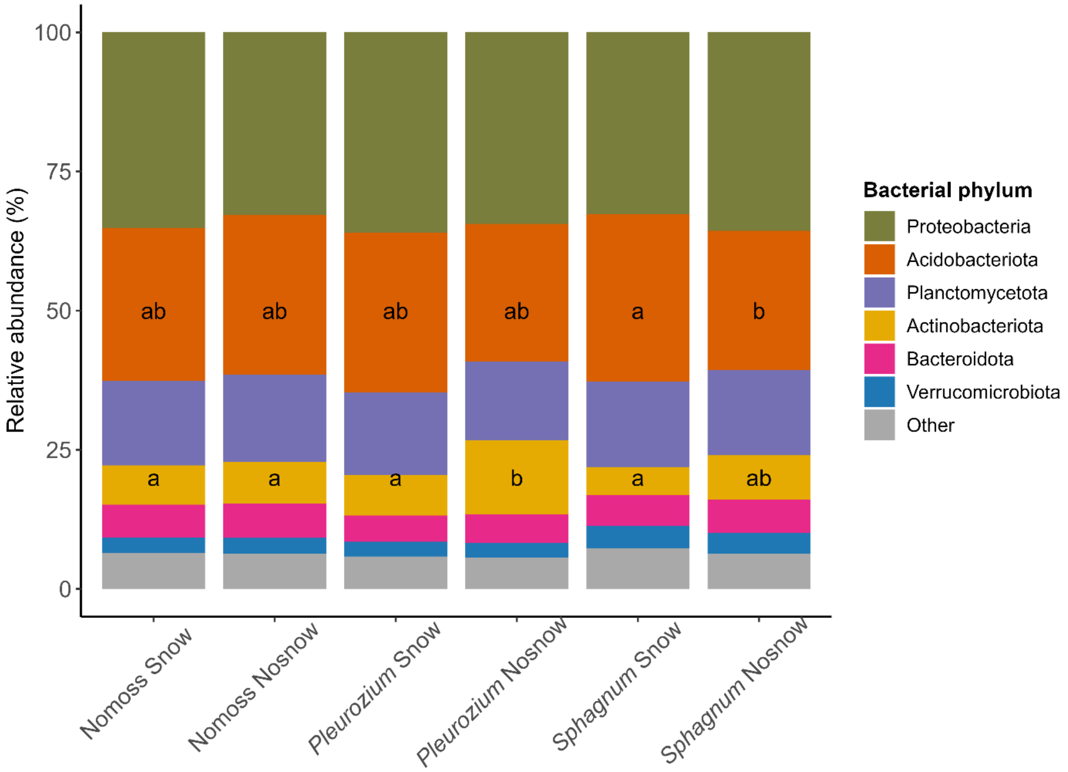


Figure 9
Relative abundance of dominant soil bacterial phyla across vegetation types (*Sphagnum* spp., *P. schreberi*, No moss) under snow and no snow conditions. Bars represent the mean relative abundance (%) of each phylum, with phyla contributing < 2% grouped as "Other." Different letters indicate significant differences between treatments within each phylum.

Soil fungal community composition was not influenced by moss type, snow cover, or their interaction (P = 0.18), (Figure 10). There was no significant difference in the relative abundance of any soil fungal phyla across moss type, snow cover alone, or their interaction. However, for soil fungal guilds, the relative abundance of ectomycorrhizal fungi (ECM) in *Sphagnum* spp. plots were slightly higher when snow was reduced (P = 0.09), and the relative abundance of pathogens in no moss plots also increased slightly when snow was reduced (P = 0.06). In addition, the composition of soil ectomycorrhizal communities appeared to vary among treatments (Fig. 11). Snow reduction significantly reduced the relative abundance of *Cortinarius* in no moss plots ($P < 0.01$) and increased *Cenococcum* in *Sphagnum* plots ($P < 0.05$).

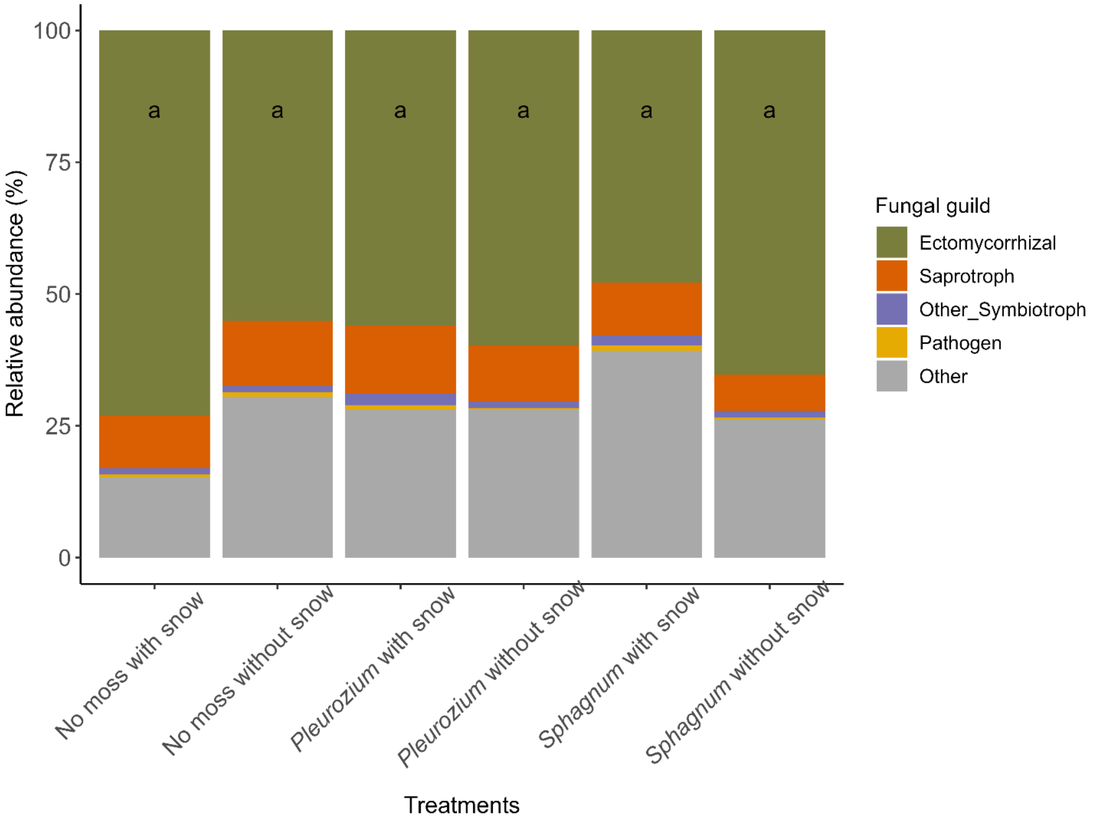


Figure 10

Relative abundance of fungal guilds across different moss types. Bars represent the mean relative abundance (%) of each phylum within samples, grouped by

vegetation type (*Sphagnum* spp., *Pleurozium schreberi*, and no moss). Different lowercase letters indicate significant differences between treatments.

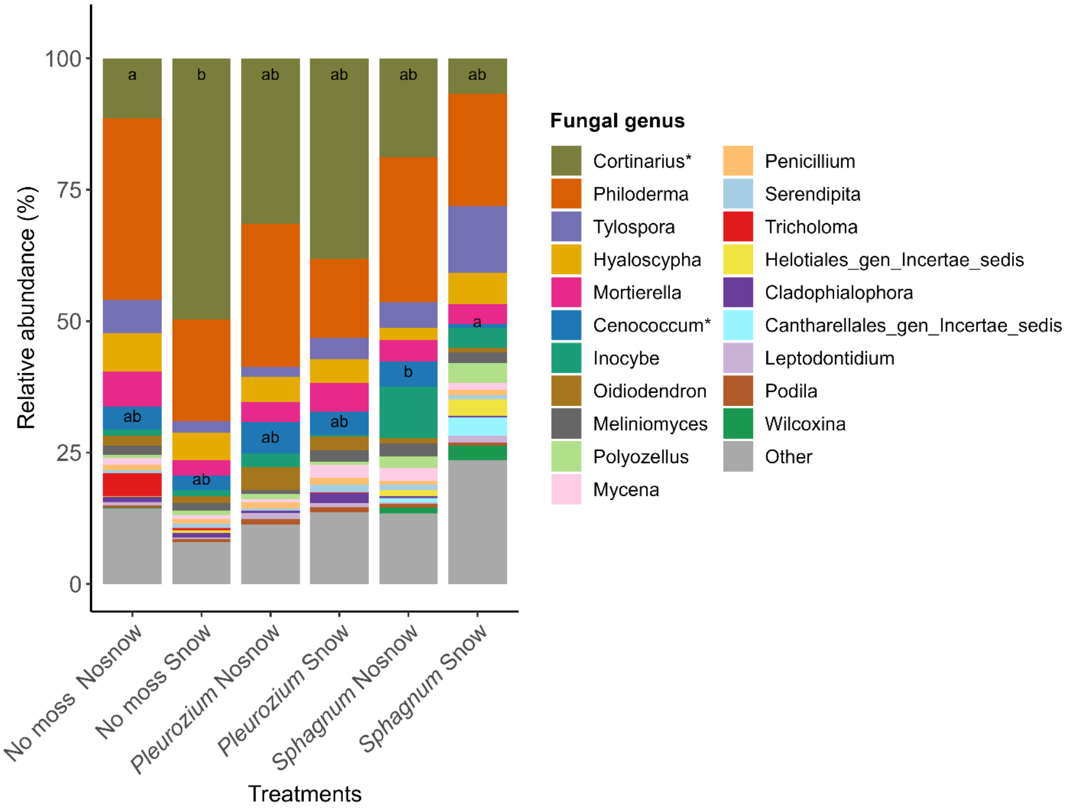


Figure 11 Relative abundance of dominant soil fungal genera across moss–snow treatments. Genera marked with an asterisk (*) indicate ectomycorrhizal (ECM) fungi.

1.3.8. Microbial biomass

During the early growing season, microbial biomass carbon (MBC) didn't change significantly across any of the treatments (*P* > 0.49). However, the snow removal in *Sphagnum* spp. plots decreased the MBC during the late growing season (*P* = 0.0021; Fig. 12). The presence and absence of snow didn't show any significant difference in MBC of no moss and *P. schreberi* plots.

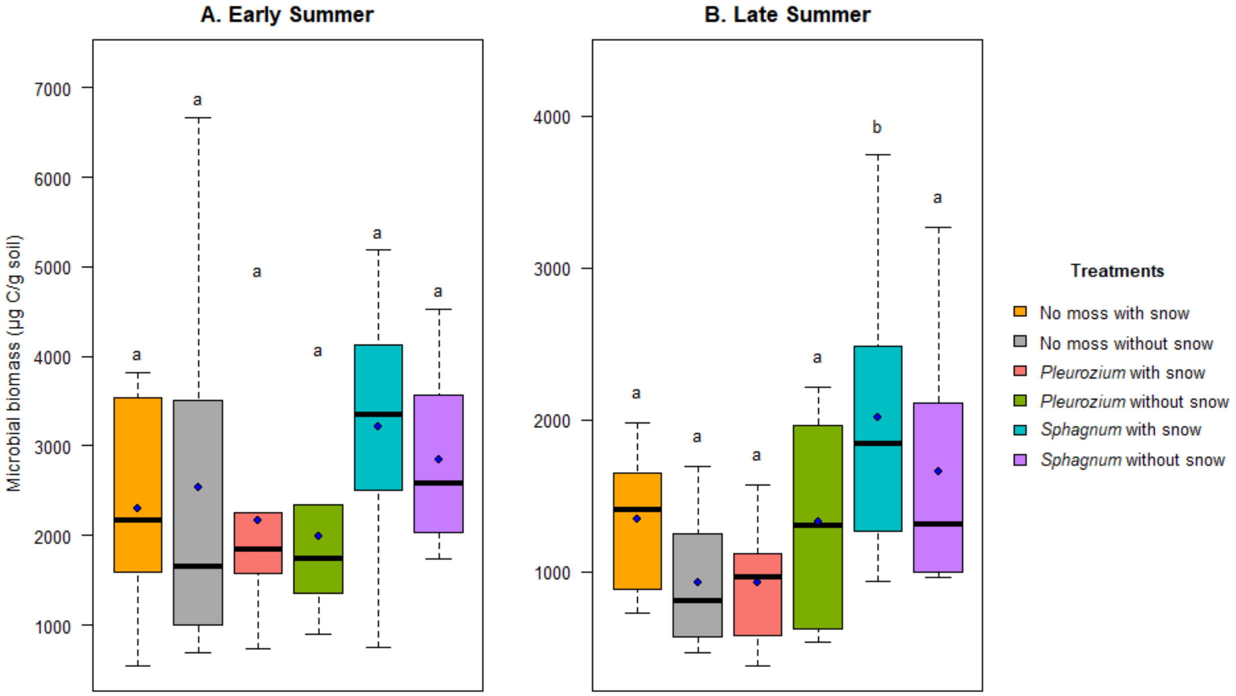


Figure 12

Microbial biomass of early growing season and late growing season across treatments, categorized by moss type (*Sphagnum* spp., *P. schreberi*, no moss) and snow presence (with snow and without snow). Different lowercase letters indicate significant differences between treatments.

1.4. Discussion

1.4.1 Differential snow effects on functional traits of mosses

1.4.1.1. Colony density and water absorption capacity

Contrary to H2, *Sphagnum* spp. colonies maintained higher density under snow cover, while snow removal reduced their colonial density. This unexpected pattern reflects a critical vulnerability in *Sphagnum's* buffering strategy. Under snow cover, *Sphagnum* spp. maintained denser colonies due to the insulating role of snow: under snow, capitula remain close to 0 °C throughout winter, enhancing a favorable environment for denser colonies (Dyukarev et al., 2009). However, snow removal exposes colonies to extreme temperature fluctuations and desiccation, leading to shoot mortality and sparser growth. Previous comparative studies confirmed that *Sphagnum* spp. are among the least frost-tolerant mosses (Segreto et al., 2010; Vitt et al., 2014; van Zuijlen et al., 2024). However, it is important to note that even under snow removal, *Sphagnum* spp. maintained higher colony density than *P. schreberi*.

The stability of *P. schreberi* colony density across treatments was unexpected, given our hypothesis (H2). This resilience may reflect its adaptation to environments with reduced snow cover and greater exposure to temperature fluctuations. Furthermore, its structurally stable, horizontally spreading growth form, which relies less on vertical capitula development than *Sphagnum* spp., likely contributes to greater tolerance to harsh winter exposure (Kangas et al., 2014; Rice et al., 2011). This morphological strategy may enable *P.schreberi* to maintain colony integrity even under variable thermal regimes induced by snow reduction.

Structural differences between *Sphagnum* spp. and *P. schreberi* directly influence the water absorption capacity by altering their ability to retain and distribute moisture within the colony (Grau-Andrés et al., 2021; van de Koot et al., 2024). Dense *Sphagnum* spp. colonies under snow retain water in capillary spaces, allowing high extracellular storage (Rice et al., 2008; Ruiliang, 2022), with spreading branches capturing atmospheric moisture and snowmelt, while pendant branches wick water upwards to the capitula. In our study, this structural advantage likely contributed to *Sphagnum's* superior thermal buffering under ambient snow conditions. However, when snow was reduced, *Sphagnum* spp. become highly sensitive to freezing, which contradicts H2 (Schipperges & Rydin, 1998; Wang & Bader, 2018), as shown in Fig. 2 . This vulnerability occurs because growing ice crystals outside the cell withdraw water from adjacent unfrozen cell contents due to an osmotic gradient created by the lower water potential of ice, causing desiccation and structural damage (Lenné et al., 2010). Our observation of reduced water absorption in *Sphagnum* spp. under snow removal supports this mechanism and suggests that while *Sphagnum* may employ adaptation measures such as rapidly reducing cellular water potential during desiccation to pause metabolic activity and limit intercellular ice crystal damage. However, these adaptations were insufficient to fully protect against the freeze-thaw cycles imposed by our snow removal treatment.

Despite the freezing-induced desiccation stress described above. *Sphagnum* consistently absorbed more water than *P. schreberi* in our experiment, supporting H2. This species-specific difference is explained by their contrasting water economies (Michel et al., 2013). *P. schreberi,* an ectohydric moss with loosely arranged shoots, lacks hyaline cells and capillary architecture depends on surface films, dew, and precipitation for hydration, resulting in low and stable water absorption (Longton & Greene, 1979; Rice et al., 2011). Moreover, the slow metabolic recovery and weak responsiveness of *Pleurozium* to microclimate shifts likely explain the absence of snow-driven changes in its water absorption observed in our study (Bjerke et al., 2013). However, long-term reduction in snow cover can still stress *P. schreberi*, as shown by Bjerke et al. (2017), indicating that while immediate responses are weak, continuous exposure to reduced snow cover may ultimately reduce segment growth and photosynthetic performance.

Taken together, these results show that snow cover amplified the functional differences between the two mosses: *Sphagnum* spp. rely on snow insulation to maintain dense, water-saturated colonies, but this same water retention may increase its vulnerability to frost damage during repeated freeze-thaw cycles after snowmelt. However, *P. schreberi* follows a desiccation-tolerant strategy that readily loses water during dry or freezing conditions but can rapidly resume metabolism upon rehydration, thereby better withstanding fluctuating winter microclimates.

1.4.1.2. Carbon and Nitrogen content

The carbon and nitrogen cycling component of H2 received stronger support than the colony density and water absorption components. Snow reduction did not affect the carbon and nitrogen content of either moss species. Instead, species-specific functional traits were the primary drivers of carbon content differences in moss tissue. *P. schreberi* consistently showed higher carbon content per unit dry mass than *Sphagnum* spp. under both snow-covered and snow reduction conditions. However, as *Sphagnum* spp. forms much denser colonies with greater shoot biomass, it likely contributes larger overall organic carbon inputs to the forest floor, despite lower tissue-level carbon concentrations (Clymo & Hayward, 1982a; Gerdol et al., 1996; Campeau & Rochefort, 1996). In contrast, *P. schreberi's* higher tissue carbon content, combined with its stable colony structure across snow treatments, suggests a more conservative but resilient carbon input strategy—lower but constant carbon inputs under variable conditions.

1.4.2. Modulation of soil temperature by moss species under snow and no-snow conditions

Consistent with H1, snow decline promoted colder soil microclimates in winter for *Sphagnum* spp. and *P. schreberi* plots, whereas snow cover maintained warmer soils across all treatments, confirming its insulating effect. While the role of bryophyte layers in soil temperature regulation is well known (Gornall, Jónsdóttir, Woodin, & Van der Wal, 2007; Jaroszynska et al., 2023), our study is the first to compare soil thermodynamics across different bryophyte layers under varying snow conditions in a boreal ecosystem. This pattern likely exists because snow is a poor heat conductor with high thermal capacity, reducing freeze-thaw cycles and maintaining a relatively higher temperature compared with the free air temperature (Zhang, 2005; Li et al., 2017). Mosses further enhanced this buffering by retaining snow at the forest floor, and by promoting a thicker and more stable snowpack. Snow removal in our study decreased the soil temperature beneath both moss species, consistent with findings from permafrost areas where moss mats reduced the soil temperature (Guglielmin et al., 2008; Guglielmin et al., 2012). When the snow was reduced, the water retained within a moss mat froze, which increased thermal conductivity and decreased its insulation effect.

The moderation of temperature effects by moss type, as predicted in H1, was clearly seen in our results. Comparing moss species, *Sphagnum* spp. had stronger thermal buffering than *P. schreberi* in line with our hypothesis. Despite *Sphagnum's* higher thermal conductivity (O'Donnell et al., 2009; Jaroszynska et al., 2023b; Soudzilovskaia et al., 2013), its denser structure and greater water absorption capacity likely enhanced its ability to stabilize soil temperatures (Clymo & Hayward, 1982; Taylor & Price, 2015). Interspecific differences in habitat preferences may also contribute to these observed differences between species. Contrary to H1 and general knowledge, reduced snow cover causes colder soils (Groffman et al., 2001b), our experiment showed warmer soils in the no moss plots under snow removal compared to moss-covered plots, a pattern also observed by Robroek et al. (2013). The insulating properties of snow, however, strongly depend on snow depth and snow density (Stieglitz et al., 2001; Zhang et al., 2008), factors which should be considered in future studies. However, this finding contrasts with several studies showing that snow removal increases frost depth and makes soils more responsive to air temperature fluctuations (Friesen et al., 2021; Xu et al., 2022). This discrepancy may be linked to methodological factors. Snow in our experiment was removed manually only once per month, which may not have been sufficient to maintain persistently colder conditions, and there may have been some time before the snow was removed, i.e., when the snow was still present (Brin et al., 2018). Finally, data loss in the no-moss/no snow treatment limits the robustness of these results.

1.4.3. Effect of snow removal on fine roots

Consistent with our H3, in *Sphagnum* plots, the insulating effect of snow, combined with the high water-holding capacity of dense colonies (Rice, 2009), created a favorable microclimate for root survival. Soil temperatures remained close to 0 °C, supporting longer root lifespans and low mortality (Soudzilovskaia et al., 2013), which contributed to higher fine-root biomass. Similar patterns have been observed in Norway spruce, where greater root longevity under cold soils was linked to higher fine-root biomass accumulation (Helmisaari et al., 2009). Following snow removal, the decline in total root biomass was expected, as snow loss exposes soils to freezing temperatures and accelerates frost penetration, with a decrease in belowground carbon allocation (Keel et al., 2012).

Interestingly, roots did not undergo widespread mortality despite snow reduction in *Sphagnum* plots but appeared to adopt a conservative survival strategy. In these colder plots, growth was minimized, likely through morphological adjustments such as reduced root diameter. Such a strategy aligns with the physiological constraints imposed by frozen soils, where low temperatures restrict water uptake and delay thawing, leading to prolonged stress or even cellular damage (Alvarez-Uria & Körner, 2007; Park et al., 2018; Cleavitt et al., 2008). The soil temperature recorded in our snow-removal plots (-10 °C at 15 cm depth) approached the cold tolerance threshold of fine roots (Bigras et al., 2001), explaining why roots entered dormancy rather than undergoing mortality.

Another factor contributing to lower mortality in *Sphagnum* plots with reduced snow may be the higher abundance of ectomycorrhizal fungi observed in these treatments. Ectomycorrhizae can tolerate freezing and protect root tips by improving water balance and buffering against temperature extremes (Lehto et al., 2008; Kilpeläinen et al., 2016). This pattern contrasts with earlier studies, where snow removal and deeper frost induced compensatory root growth (Tierney et al., 2001; Cleavitt et al., 2008). Such a difference may reflect species-specific traits: unlike feather moss or no moss, denser *Sphagnum* mats remain wetter and slower to thaw, leading to colder soil conditions that suppress compensatory root responses. Beyond reductions in structural root biomass, constrained root growth under snow reduction also reduced rhizodeposition, including the release of root exudates and sloughed root tissues that constitute an important pathway of carbon transfer from plants to soils (Tariq et al., 2024). Root-derived carbon inputs mediated through rhizodeposition and ectomycorrhizal associations have been identified as key controls on soil carbon accumulation (Gundale et al., 2024). Together, these findings suggest that snow-induced constraints on root production in *Sphagnum* plots may weaken soil carbon resilience by limiting both structural and rhizosphere-mediated carbon inputs.

1.4.4. Effect of snow removal on soil bacterial diversity and their community composition

Snow removal had weak effects on soil bacterial diversity during spring snowmelt, contrasting with H4 (Fig.6). This result is somewhat surprising, considering the reported deeper frost in snow reduction plots in winter, and contrasts with findings from tundra, alpine, and temperate ecosystems (Ricketts et al., 2016; Ade et al., 2018; Wang et al., 2020). The maintained diversity despite compositional shifts suggests that snow removal induced turnover in bacterial taxa, with some cold-sensitive groups declining while cold-tolerant groups increased, rather than net losses in diversity. This taxonomic reshuffling, while maintaining overall diversity levels, has been observed in other boreal coniferous forests (Männistö et al., 2018a; Zhao et al., 2022b), permafrost regions (Liu et al., 2023), Tibetan alpine forests (Ren et al., 2020c), and meadow steppes (Xu et al., 2022b). The functional redundancy among bacterial taxa in boreal soils may allow for compositional shifts without diversity loss, contributing to ecosystem-level resilience even as specific taxa respond to altered snow conditions (Chen et al., 2022; Stres et al., 2010) Additionally, the bacterial communities under *Sphagnum* spp. and *P. schreberi* were compositionally distinct from one another, and these inherently different communities may respond differently to the lower and less stable temperatures induced by snow reduction. It is important to note, however, that our assessment was based on DNA amplicon data, and soil DNA can persist for long periods. Relic DNA from inactive or dead cells can mask short-lived shifts in the living community (Burkert et al., 2019). Therefore, changes could have occurred but remained undetected at the time of sampling, or they might have become evident later in the growing season as soils warmed and nutrient conditions changed. Studies that reported clearer snow effects often focused on activity-linked signals (cDNA, metatranscriptomics, lipid biomarkers, enzyme activities, CO_2 fluxes), sampled weeks to months after snow melt (mid to late season), and applied long-term manipulations lasting several years. This suggests that our early-season sampling may have been too soon to capture slower community turnover following snow reduction.

Across all treatments, the dominant phyla were Proteobacteria, Actinobacteriota, Planctomycetota, and Acidobacteriota, similar to patterns from the boreal forest soils (Gao et al., 2024b), permafrost regions (Liu et al., 2023), the Arctic (Belov et al., 2020), and Antarctica (Waschulin et al., 2022). Bacteroidetes and Verrucomicrobia — commonly observed in cold ecosystems (Ricketts et al., 2016) were also present. These findings suggest that high-latitude and high-altitude soils share a core set of dominant bacterial taxa.

Snow effects on the relative abundance of soil bacterial phyla, however, differed by moss type. In *Sphagnum* spp. plots, the relative abundance of soil Acidobacteriota was lower in the snow reduction treatment. Responses of this group appear to be context-dependent: they increased with reduced snowpack in an alpine meadow (Ade et al., 2018), tolerated experimental freeze-thaw cycles (Kielak et al., 2016), and also increased under greater snow accumulation in the Arctic tundra (Männistö et al., 2013). Given that Acidobacteria are strongly structured by soil organic carbon, moisture, nutrients, and soil temperature (Naether et al., 2012; Ramirez et al., 2012). This pattern likely reflects indirect, moss-mediated changes in the microenvironment rather than a uniform response to snow loss. Because *Sphagnum spp.* strongly regulates water balance and nutrient cycling (Slate et al., 2024) snow removal altered the hydrological buffering capacity of the moss layer, thereby creating conditions less favorable for Acidobacteriota. They are key decomposers of complex organic matter in boreal soils and are associated with processing recalcitrant carbon compounds (Deng et al., 2018; Naether et al., 2012). The decrease in relative abundance in *Sphagnum* spp. plots under snow decline suggest a potential reduction in the microbial capacity to process complex organic substrates, which could alter decomposition rates and carbon turnover in the organic horizon. Given that *Sphagnum* litter is already slow to decompose due to its phenolic-rich, recalcitrant chemistry (Turetsky, 2003b), a shift away from bacteria specialized in degrading such compounds may further slow carbon cycling.

Conversely, the relative abundance of Actinobacteriota was higher in *P. schreberi* plots exposed to snow reduction treatment, consistent with previous observations (Liu et al., 2023). This group has specialized traits, such as mycelial growth, spore forming, gram-positive, and metabolic flexibility, which are capable of surviving under extreme conditions (Zhang et al., 2016; Wagner et al., 2009). Their higher relative abundance may simply reflect that Actinobacteriota resisted the colder, drier, and more variable conditions created in *P. schreberi* plots under reduced snow cover better than other taxa. Additionally, *P. schreberi* tissues tend to have higher carbon concentrations than *Sphagnum* spp., providing an environment enriched in recalcitrant or C-rich compounds. While snow reduction created harsher conditions, Actinobacteriota may have maintained their decomposition activity in this C-rich environment through their capacity to produce extracellular enzymes capable of degrading complex organic matter (Větrovský et al., 2014; Buresova et al., 2021), potentially decreasing carbon residence time in surface organic layers. These compositional shifts, occurring without major changes in bacterial diversity, show how functional capacity for carbon processing can change even when overall community structure appears stable.

1.4.5 Effect of snow removal on the diversity and composition of the soil fungal community

Although soil fungal community composition remained broadly similar across treatments, snow reduction significantly reduced fungal diversity in *P. schreberi* plots, while no such effect was observed in other treatments. As with bacterial communities, the fungal communities under *Sphagnum* spp. and *P. schreberi* were compositionally distinct, and these inherently different communities may respond differently to the lower and less stable temperatures induced by snow reduction. This shift in soil fungal diversity corresponds with the lower soil temperatures recorded in those plots, suggesting that increased cold exposure and freeze-thaw stress may have constrained fungal survival or activity. The decline in soil fungal diversity without major compositional changes contrasts with earlier findings (Semenova et al., 2016; Xu et al., 2022a; Ylänne et al., 2025), indicating that cold filtering rather than turnover of dominant taxa drove this response. Our results suggest that fungi are more sensitive to snow reduction than bacteria, and that the moss cover influences this sensitivity. The weaker insulating capacity of *P. schreberi* compared to *Sphagnum spp.* led to much lower soil temperatures under snow reduction treatment and likely exposes soils to earlier thawing under snow-reduced conditions, enhancing freeze-thaw cycles and nutrient leaching(Liasjø, 2016; Rousk et al., 2021). The observed decline in soil fungal diversity in *P.schreberi* plots under snow reduction occurred without significant shifts in overall fungal community composition, suggesting compositional reorganization rather than broad-scale turnover. Under more variable thermal and nutrient conditions, frost-tolerant taxa may have become dominant (Edwards et al., 2007), while cold-sensitive taxa may have been suppressed or eliminated by the lower soil temperatures in the *P. schreberi* plots, further declining the diversity. Such shifts may have implications for belowground carbon processes, as fungi typically dominate decomposition of recalcitrant substrates like lignin and complex polysaccharides in boreal soils (Lindahl & Clemmensen, 2016; Abrashev et al., 2025).

At the phylum level, relative abundances of soil fungal communities remained stable across treatments, with Ascomycota and Basidiomycota dominating all plots. This stability is consistent with patterns reported from boreal forests, alpine meadows, and moss-associated fungal communities (Gao & Yang, 2016; Zhang et al., 2021; Davey et al., 2012). This apparent stability at higher taxonomic levels likely reflects their broad ecological diversity, where different members can adjust functionally without altering overall phylum representation (Allison & Martiny, 2008). Indeed, our fungal functional guild analysis revealed a shift in functional composition, despite this phylum-level stability.

In *Sphagnum* plots, soil ectomycorrhizal (ECM) fungi increased slightly under snow reduction, with *Cenococcum* being particularly abundant. This genus produces heavily melanized hyphae that enhance protection against desiccation, freezing, and oxidative stress (Wang et al., 2025). Its mycelium can remain viable even after exposure to −80 °C and thrives at temperatures below 1 °C, likely linked to its high rate of cryoprotectant mannitol synthesis, showing exceptional resistance to extreme cold (Visser, 1995; Weinstein et al., 1997). The increased abundance of soil *Cenococcum* under reduced snow insulation, therefore, reflects its exceptional ability to maintain symbiotic activity under repeated freeze-thaw stress. These interactions are consistent with our field observations of *Sphagnum* spp. plots, where fine-root mortality remained low as roots stayed entangled within moist moss layers and in close contact with soil ECM fungi, likely benefiting from improved nutrient exchange and physical protection under stress (Clemmensen et al., 2013). In contrast, soil *Cortinarius* under snow-reduced conditions in no moss plots shows its sensitivity to soil thermal and moisture instability following loss of snow insulation (Ma et al., 2011). As a medium-distance ectomycorrhizal explorer with extensive extrametrical mycelium, soil *Cortinarius* appears particularly vulnerable to hyphal damage induced by snow decline, especially without a protective moss layer (Morgado et al., 2016).

We also observed an increase in soil pathogenic fungi in no moss no snow plots. This agrees with studies showing that soil pathogens are more responsive to snow reduction than other fungal guilds (Xu et al., 2022; Li et al., 2025). Snow cover buffers the soil against extreme temperature fluctuations, creating stable thermal and moisture conditions that can suppress stress-tolerant taxa. (Zhao et al., 2022c). When this insulating layer is lost, the resulting colder and more variable microclimate may favor soil pathogenic fungi capable of exploiting plant or microbial stress, leading to their increased relative abundance (Loiko & Islam, 2024). It can further suppress vegetation establishment and reduce carbon inputs to soil through diminished plant productivity. It is worth noting that soil pathogenic fungi relative abundance did not change in *Sphagnum* spp. or *P. schreberi* plots, suggesting that moss cover may mitigate the negative effects of snow loss by providing a protective function beyond thermal buffering. However, in bare soils, future declines in snowpack may elevate the risk of soil diseases. These functionally distinct responses underscore how moss type mediates not only magnitude but also the mechanisms through which snow decline affects soil carbon processes.

1.4.6 Effect of snow removal on soil microbial biomass

We measured soil microbial biomass carbon (MBC) in two seasons: immediately after winter (early growing season) and at the end of the growing season. In the later season, MBC was significantly higher in *Sphagnum* spp. plots with snow. The snowpack with the higher water absorption capacity of *Sphagnum* spp. not only maintained the optimal temperature but also enhanced the soil moisture regime, creating favorable conditions for microbial activity. In addition, energy-rich carbon inputs through root exudates during peak growth may have further stimulated microbial growth, contributing to the higher MBC observed (Griffin, 1963; Zhao et al., 2021). Microbial biomass serves dual roles in carbon cycling: microbes decompose organic matter (releasing CO_2), but they also transform plant-derived carbon into microbial-derived soil organic matter; a pathway increasingly recognized as critical for forming stable carbon pools (Prommer et al., 2020). The higher MBC in snow-covered *Sphagnum* plots, therefore, indicates not only greater decomposition capacity but also enhanced potential for stabilizing plant-derived carbon into longer-term soil organic matter pools through microbial biomass turnover and necromass formation. Conversely, the reduced fine root biomass observed under *Sphagnum* spp. plots without snow (SNS) may have limited the supply of labile carbon to the soil microbial community, resulting in lower MBC, which indicates a compounded negative effect on soil carbon resilience. This combination of diminished carbon inputs (through roots) and reduced transformation capacity (through microbial processing) suggests that *Sphagnum*-dominated forest floors may experience weakened soil carbon accumulation under sustained snow reduction.

No significant effect of snow manipulation on soil MBC was found in the early growing season. Even though some differences in diversity and community composition were detected, MBC remained unchanged in the spring. This is likely because variations in microbial diversity or composition do not necessarily correspond to changes in total biomass, as relative abundance data from sequencing reflect proportions rather than absolute microbial quantities (Hua et al., 2024b). At this stage, microbial communities may likely be just emerging from dormancy, carbon inputs from roots are minimal, and biomass recovery may require detectable time differences.

The relationship between microbial biomass changes and community composition shifts shows moss-specific pathways affecting carbon processing. In *Sphagnum* plots, reduced snow decreased both Acidobacteriota abundance and MBC, indicating a quantitative reduction in decomposition capacity; less microbial biomass means less potential for carbon processing and stabilization. In *P.schreberi* plots, increased Actinobacteriota and decreased fungal diversity occurred without changes in MBC, suggesting a qualitative shift in carbon processing, different decomposer taxa with potentially altered carbon use efficiency and substrate preferences, but maintained overall processing capacity. Therefore, *P.schreberi's* resilience in maintaining key carbon cycling processes under variable snow regimes suggests these systems may be better buffered against climate-induced disruptions to soil carbon dynamics.

Additionally, we found that studies on soil microbial communities, including bacterial and fungal abundance and their composition, remain relatively scarce in snow manipulation research. Such data would strengthen our understanding of whether compositional changes reflect shifts in functional capacity or simply reorganization of existing biomass. Additionally, analyzing microbial DNA later in the season (mid to late summer) could have provided stronger insights, as treatment effects on community composition and biomass are likely to become more pronounced once microbial activity and root carbon inputs peak.

1.5. Implications for forest management

Management strategies should recognize the functional trade-offs between moss types and tailor approaches to site-specific conditions and management goals. (1) Preserve snow-moss coupling in *Sphagnum*-dominated areas. Retain snow cover where *Sphagnum* is present by maintaining partial canopy closure, conserving woody debris, and minimizing winter soil disturbances that could reduce snow accumulation. Forest management activities (e.g., thinning, harvesting) should be planned to avoid creating large canopy gaps in *Sphagnum*-dominated areas where reduced snow interception could expose moss to desiccation and freezing. Under favourable conditions (adequate snow cover), *Sphagnum* supports high carbon sequestration potential, though at the cost of reduced tree productivity due to nutrient limitation (Pacé et al., 2018). (2) *Sphagnum* dominance indicates high carbon storage capacity, but creates nutrient-poor conditions that limit tree growth, regeneration, and above-ground biomass (Pacé et al., 2017; Lecomte et al., 2006). However, *P. schreberi* supports more productive soils with better nutrient availability, enabling greater tree biomass accumulation despite lower overall carbon stocks. Management objectives must therefore weigh carbon sequestration (favouring *Sphagnum* cover under stable snow) against timber production and forest regeneration (favouring *P. schreberi*). In areas projected for significant snow decline, promoting *P. schreberi* may preserve baseline belowground processes and maintain forest productivity, albeit with reduced total carbon accumulation rates. (3) Fine-root biomass, microbial biomass carbon, moss functional traits, and microbial composition respond more rapidly to environmental change than total carbon stocks. These process-level measurements can serve as early indicators of ecosystem trajectories before changes in soil carbon pools become detectable, enabling adaptive management responses. (4) Current forest carbon models often treat ground vegetation generically or ignore it entirely. Incorporating moss-type-specific effects on soil microclimate, root dynamics, and microbial communities would improve predictions of how boreal carbon cycling may respond to changing winter conditions. Our findings suggest that models assuming uniform moss buffering capacity will overestimate carbon stability in *Sphagnum*-dominated areas under snow decline, while potentially underestimating stability in *P.schreberi* systems. Therefore, by tailoring management strategies to dominant moss types and their specific climate vulnerabilities, it may be possible to better maintain the belowground processes that support soil carbon resilience and mitigate some cascading impacts of changing winter regimes on boreal forest carbon dynamics.

1.6. Conclusion

This study provides an integrated understanding of how moss functional traits modulate belowground carbon processes underclimate-induced snow decline in the boreal black spruce forest. Contrary to our expectations that *Sphagnum's* superior water holding capacity and insulating properties would buffer belowground processes against snow loss, *Sphagnum* spp. proved more vulnerable than *P. schreberi* across all measured variables. This sensitivity likely reflects *Sphagnum's* evolutionary adaptation to reliable snow cover. When snow was reduced, *Sphagnum* colonies dried, reducing their thermal and hydrological buffering capacity, which affected the system: soil experienced deeper frost penetration, declined fine root biomass, and both microbial biomass and community composition shifted. These concurrent changes indicate disruption of multiple pathways regulating carbon inputs (root production), transformation (microbial processing), and environmental buffering (moss microclimate regulation), suggesting that the *Sphagnum*-dominated forest floor depends on combined moss-snow insulation. However, *P. schreberi* maintained stable root and microbial responses under the same snow reduction despite experiencing the coldest soil temperatures. This stability indicates greater physiological resilience to snow decline, but this resilience may come at the cost of reduced thermal protection and long-term carbon accumulation, storing substantially less carbon than *Sphagnum* under stable conditions. Together, these findings demonstrated that the resilience of belowground processes influencing soil carbon dynamics in boreal forest depends not only on snow persistence but also on the dominant moss type and its associated soil microbial community.

GENERAL CONCLUSION

Conclusion. This study provides an integrated understanding of how moss functional traits modulate below-ground carbon processes under climate-induced snow decline in the boreal black spruce forest. Contrary to our expectation that *Sphagnum's* superior water-holding capacity and insulating properties would buffer below-ground processes against snow loss, *Sphagnum* spp. proved more vulnerable than *P. schreberi* across all measured variables—moss traits, root dynamics, microbial biomass, and community composition. This higher sensitivity likely reflects *Sphagnum's* evolutionary adaptation to habitats with reliable snow cover. When snow was experimentally reduced, *Sphagnum* colonies dried substantially, diminishing their thermal and hydrological buffering capacity. Consequently, soil under *Sphagnum* experienced deeper frost penetration, reduced fine root biomass, and marked shifts in both microbial biomass and community composition. These changes indicate disruption of multiple interconnected pathways regulating carbon input processes through root production, carbon transformation through microbial processing, and environmental buffering through moss microclimate regulation. Together, these results suggest that *Sphagnum*-dominated forest floors depend on the combined insulation of moss and snow layers; disrupting this dual protection fundamentally alters the belowground processes that underpin soil carbon resilience.

P. schreberi, which naturally occupies drier, more shaded microhabitats with thinner snowpacks, maintained relatively stable root and microbial responses under snow reduction despite experiencing the coldest soil temperatures. This stability indicates greater physiological resilience to abrupt changes in winter conditions, though this resilience appears to come at the cost of reduced thermal protection and lower overall carbon accumulation compared to *Sphagnum* under favourable conditions. This study thus reveals a fundamental functional asymmetry between moss types: the very traits that make *Sphagnum* an exceptional carbon accumulator under stable snow conditions, high productivity, dense water-saturated colonies, and moisture-dependent microbial assemblages also render it more vulnerable when winter conditions shift. While we didn't directly measure soil organic carbon stocks, our process-based measurements indicate that *Sphagnum* systems may transition from high carbon sequestration potential under favourable conditions toward reduced carbon accumulation capacity under snow decline. Conversely, *P.schreberi's* more aerated and less moisture-dependent system demonstrates adaptive tolerance to fluctuating winter conditions, albeit with lower baseline productivity.

These findings have important implications for understanding boreal forest carbon dynamics under ongoing climate change. As snow cover continues to decline across northern regions, the resilience of belowground processes influencing soil carbon storage will depend not only on snow persistence but also on the dominant moss type and its associated microbial community. Forest areas dominated by *Sphagnum* spp. may be particularly vulnerable to shifts in carbon cycling under reduced snowpack, while *P. schreberi* dominated systems may prove more resistant to winter climate variability. Future research should examine whether these moss-mediated responses translate into measurable changes in long-term soil carbon stocks and whether management strategies could enhance the resilience of vulnerable *Sphagnum*-dominated ecosystems. Understanding these moss-microbe-snow interactions is essential for predicting and mitigating potential carbon losses from boreal forests as winter climate regimes continue to shift.

Implication for forest management. As northern winters continue to be shortened and snow cover declines, forest floors dominated by Sphagnum spp. may transition from stable, high productivity carbon sinks to more variable, disturbance -sensitive systems with reduced carbon accumulation capacity. The simultaneous reduction in moss functional capacity (colony density, water absorption capacity), root carbon inputs (40% biomass decline), and microbial processing capacity (reduced biomass carbon) observed in Sphagnum plots under snow decline shows multiple pathways through which snow decline may compromise processes underlying soil carbon resilience. While these process-level changes occurred within a single winter season, sustained snow reduction could lead to long-term effects on soil carbon stocks as reduced annual inputs compound over decades.

Management strategies should therefore aim to preserve the ecological functions of moss mats and sustain soil microclimate stability, particularly in *Sphagnum*-dominated areas. (1) Retain snow cover where *Sphagnum* is present by maintaining partial canopy closure, conserving woody debris, and minimizing winter soil disturbances that could reduce snow accumulation. Forest management activities (e.g., thinning, harvesting) should be planned to avoid creating large canopy gaps in *Sphagnum*-dominated areas where reduced snow interception could expose moss to desiccation and freezing. (2) Recognize that *Sphagnum* and *P.schreberi* provide different ecosystem services: *Sphagnum* offers high carbon sequestration potential but requires stable snow cover, while *P. schreberi* provides lower soil carbon productivity but greater stability under variable conditions. In areas projected to experience significant snow decline, maintaining or promoting *P.schreberi* may preserve baseline carbon cycling processes even as total soil accumulation rates decrease. (3) Fine-root biomass, microbial biomass carbon, moss functional traits, and microbial composition respond more rapidly to environmental change than total soil carbon stocks. These process-level measurements can serve as early indicators of ecosystem trajectories before changes in soil carbon pools become detectable, enabling adaptive management responses. (3)

Current forest carbon models often treat ground vegetation generically or ignore it entirely. Incorporating moss-type-specific effects on soil microclimate, root dynamics, and microbial communities would improve predictions of how boreal carbon cycling may respond to changing winter conditions. Our findings suggest that models assuming uniform moss buffering capacity will overestimate carbon stability in *Sphagnum*-dominated areas under snow decline, while potentially underestimating stability in *P.schreberi* systems. Therefore, by tailoring management strategies to dominant moss types and their specific vulnerabilities, it may be possible to better maintain the belowground processes that support soil carbon resilience and mitigate some cascading impacts of changing winter regimes on boreal forest carbon dynamics.

Study limitations. This study provides new insights into how bryophytes mediate the effect of snow cover loss on belowground carbon inputs through a novel experimental approach. By combining field snow cover manipulation with measurements of moss traits, root dynamics, microbial diversity, and their biomass across replicated boreal forest plots, it established a robust framework to explore fine-scale ecological interactions with greater accuracy. However, certain constraints remain.

The experiment was limited to a short timescale and a small number of sites (i.e., few replications), which may not fully capture the spatial and interannual variability in boreal ecosystems. In addition, the relatively small size of the experimental plots may have constrained the representation of natural heterogeneity and edge effects, potentially influencing belowground processes and contributing to differences between our results and those reported in large-scale or observational studies. Another limitation arose from data loss in the No Moss No Snow plots, where most of the soil temperature data loggers were destroyed, likely by wildlife. This limited the precision of temperature comparisons among treatments. Installing multiple loggers per plot, or implementing protective measures such as mesh covers, could have minimized such losses and ensured consistent data collection across treatments.

Although this study focused primarily on snow depth as the main driver of belowground responses, other important physical characteristics of snow were not examined. Factors such as snow temperature, density, and compaction, as well as the process of destructive metamorphism, can impact the insulating properties of snow and thereby influence soil temperature, moisture, and other edaphic factors (Zhang et al., 2008a). Future research incorporating these additional snow attributes would provide a clear understanding of how snow cover interacts with moss cover to regulate belowground ecosystem functions.

Another limitation concerns the timing of microbial community analysis. DNA sequencing was done only on the early summer soil samples, while the late-summer samples, in which microbial biomass was found to be increased in *Sphagnum* spp. plots were not analyzed. However, analysing microbial DNA later in the season could have provided stronger insights, as treatment effects on community composition and biomass are likely to become more pronounced once microbial activity and root carbon inputs peak.

Finally, snow removal may have influenced the timing and length of the growing season by altering post-winter soil warming dynamics. Root growth typically starts above a threshold soil temperature (often around 4 °C), and reduced snow cover can accelerate spring soil warming (Pregitzer et al., 2000b). However, because root sampling was conducted immediately after snow melt to quantify winter-induced mortality, this study was not designed to capture cumulative root growth later in the growing season. As a result, potential treatment effects on growing season length and total root production may not have been fully detected.

While these limitations constrain the generalization of some findings, they also highlight important directions for future research.

Future directions. Results from this project will serve as a building block for an extensive framework in boreal ecology, enabling scientists to ask a broad spectrum of biological, ecological, and other questions about the role of bryophytes in carbon inputs. A number of key questions still need to be answered. First, what can be the long-term impact of reduced snow cover on moss traits, microbial biomass, and root dynamics? The current study provides insights into how moss functional traits, microbial biomass, and root dynamics respond to short-term snow cover reduction; however, it represents only a single-year experiment. In boreal ecosystems, many below-ground processes like microbial community succession and fine root turnover operate on multi-year timescales (Solly et al., 2018); (Porter et al., 2023) .Short-term experiments capture immediate physiological and microclimatic responses, but may not reflect the adaptive effects that unfold over several freeze-thaw seasons. So, long-term experimental designs should be adopted to know whether initial changes persist, amplify, or stabilize through time. Tracking these factors over time is also essential to be able to predict whether boreal soils will shift from stable carbon sinks to potential carbon sources under continued climate warming.

Second, what are the potential effects of increased snowfall? While most of the current research, including this study, focuses on the consequences of reduced snow cover, it is equally important to consider the opposite scenario— years with unusually heavy snowfall. Some climate models predict that global warming may increase precipitation intensity at high latitudes despite overall warming trends (Danco et al., 2016). An increased snow depth could alter the soil thermal regime by insulating the ground, thereby maintaining stable near-zero soil temperatures for longer periods. This may protect roots, microbial communities from extreme freezing events, bringing changes in nutrient cycling, carbon mineralization, and root growth. More protection may make the moss colony denser, absorbing more water within it, which can change the whole scenario in the boreal ecosystem. Therefore, future studies should study the bi-directional responses of moss functional traits and microbial dynamics to both reduced and enhanced snow regimes, ideally through controlled snow addition and snow removal experiments within the same ecosystem framework. Monitoring these contrasting treatments could also reveal whether enhanced snow cover fosters more resilient below-ground systems by stabilizing microclimatic conditions, or whether prolonged insulation suppresses microbial and root turnover and alters carbon balance.

Third, whether the effects observed in this study would remain consistent across different moss types and even among the species like the *Sphagnum* genus (eg, *S. capillifolium*, *S. magellanicum*, *S. fuscum*). Mosses vary widely in their morphology, physiology, and ecological strategies, which in turn influence their capacity to buffer soil temperature, retain water, and regulate microbial communities. Future studies should therefore incorporate a broader range of moss species to evaluate how trait variability modulates ecosystem responses to changing snow regimes.

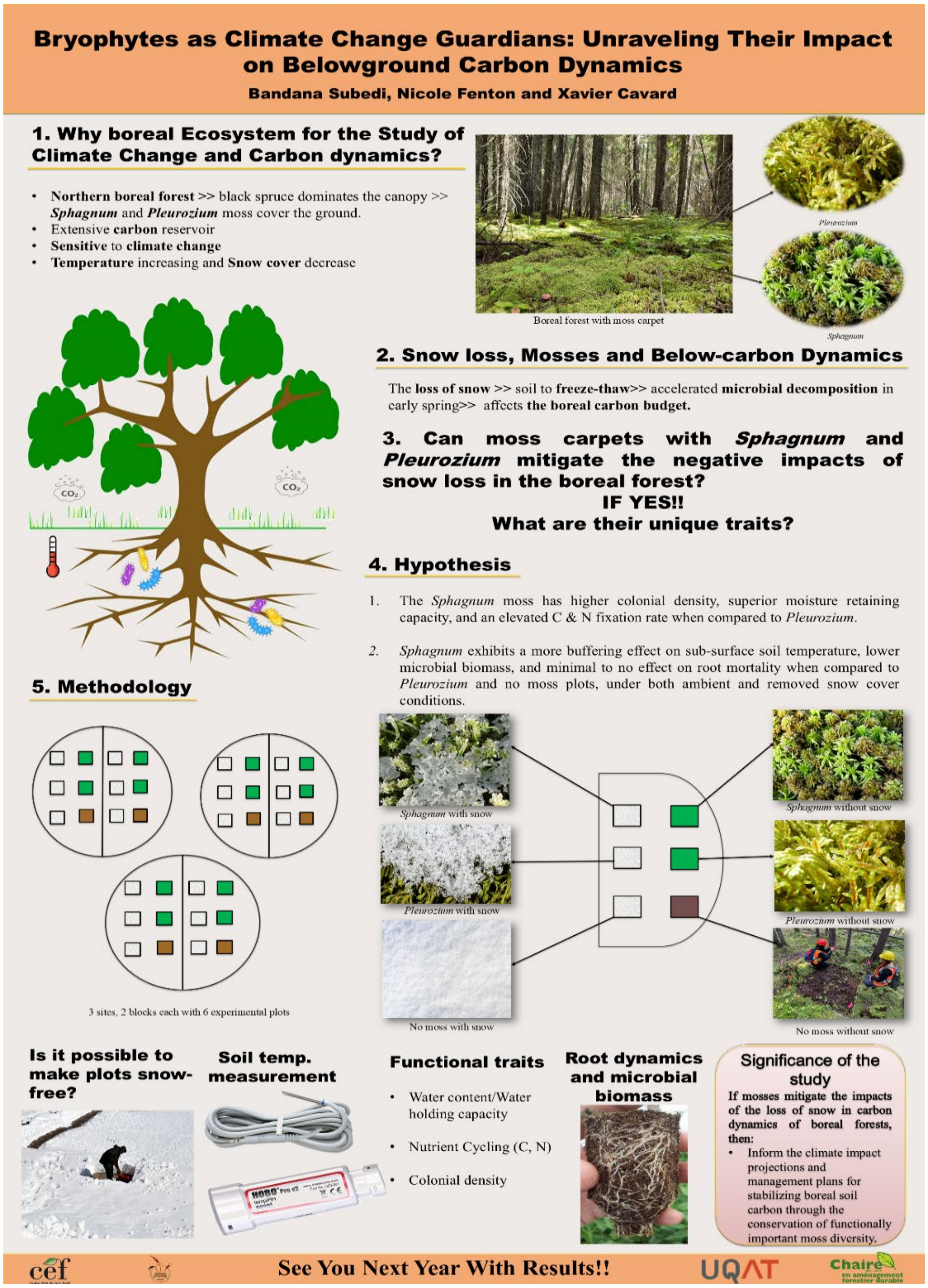
Fourth, do moss-snow-soil interactions operate through similar mechanisms across boreal, arctic, alpine, and temperate ecosystems, or are these relationships shaped by regional climatic and edaphic contexts? Mosses dominate not only boreal forests but also tundra, alpine, and temperate ecosystems, where snow regimes, soil thermal dynamics, and moisture conditions differ substantially. For instance, in Arctic tundra ecosystems, where snow persists longer and soils are underlain by permafrost, moss insulation can influence active layer thickness and methane emissions. In alpine systems, steep temperature gradients and variable snowpack can create strong microclimatic contrasts over short distances, affecting root and microbial activity differently from boreal sites. Conversely, in temperate forests, where snow cover is thinner and intermittent, mosses may contribute more to moisture regulation than to thermal buffering. Therefore, similar moss-snow manipulation experiments across these climatic gradients would help us to generalize the role of bryophytes in global carbon models.

Fifth, how do mosses influence the functional potential and activity of microbial communities (eg., through enzyme production, carbon use efficiency, or metabolic pathways)? Our present study looked at biomass and diversity, but not microbial functionality. Future research could include metagenomic, metatranscriptomic, or metabolomics analyses to identify genes involved in decomposition, nitrogen fixation, and stress tolerance under varying snow and moss conditions. This could connect community structure directly to ecosystem processes.

Sixth, is it possible to scale it up from plot-level findings to the landscape level by integrating field measurements with remote sensing and ecosystem modelling approaches? High-resolution satellite imagery, UAV–based vegetation mapping, and spectral indices could be used to quantify moss cover distribution across boreal regions. Coupling these spatial datasets with soil carbon and temperature models would allow estimation of the broader contribution of moss-dominated forest floors to regional carbon budgets. Such integration would help bridge the gap between local ecological processes and large-scale carbon-climate feedbacks, enhancing the predictive accuracy of boreal carbon models under changing snow cover.

Seventh, how can we use it as a forest management-focused trial? Experimental trials that test different interventions, such as partial harvesting and prescribed burning, could explain how these practices change microclimatic conditions and moss regeneration potential. Understanding these aspects will support the development of management strategies that preserve or restore moss layers, thereby promoting soil insulation, microbial resilience, and long-term carbon sequestration.

APPENDIX A – POSTER PRESENTATION: UNRAVELING THEIR IMPACT ON BELOWGROUND CARBON DYNAMICS AT THE 25TH AFD CHAIR CONFERENCE IN THE UNIVERSITY OF QUEBEC IN ABITIBI-TÉMISCAMINGUE, ROUYN-NORANDA, QUEBEC, NOVEMBER 2023



Bryophytes as Climate Change Guardians: Unraveling Their Impact on Belowground Carbon Dynamics

Bandana Subedi, Nicole Fenton and Xavier Cavard

1. Why boreal Ecosystem for the Study of Climate Change and Carbon dynamics?

- **Northern boreal forest** >> black spruce dominates the canopy >> ***Sphagnum*** and ***Pleurozium*** moss cover the ground.
- Extensive **carbon** reservoir
- **Sensitive** to **climate change**
- **Temperature** increasing and **Snow cover** decrease

Boreal forest with moss carpet

Pleurozium

Sphagnum

2. Snow loss, Mosses and Below-carbon Dynamics

The **loss of snow** >> soil to **freeze-thaw**>> accelerated **microbial decomposition** in early spring>> affects **the boreal carbon budget.**

3. Can moss carpets with *Sphagnum* and *Pleurozium* mitigate the negative impacts of snow loss in the boreal forest?

IF YES!!

What are their unique traits?

4. Hypothesis

1. The *Sphagnum* moss has higher colonial density, superior moisture retaining capacity, and an elevated C & N fixation rate when compared to *Pleurozium*.
2. *Sphagnum* exhibits a more buffering effect on sub-surface soil temperature, lower microbial biomass, and minimal to no effect on root mortality when compared to *Pleurozium* and no moss plots, under both ambient and removed snow cover conditions.

5. Methodology

3 sites, 2 blocks each with 6 experimental plots

Sphagnum with snow

Pleurozium with snow

No moss with snow

Sphagnum without snow

Pleurozium without snow

No moss without snow

Is it possible to make plots snow-free?

Soil temp. measurement

Functional traits

- Water content/Water holding capacity
- Nutrient Cycling (C, N)
- Colonial density

Root dynamics and microbial biomass

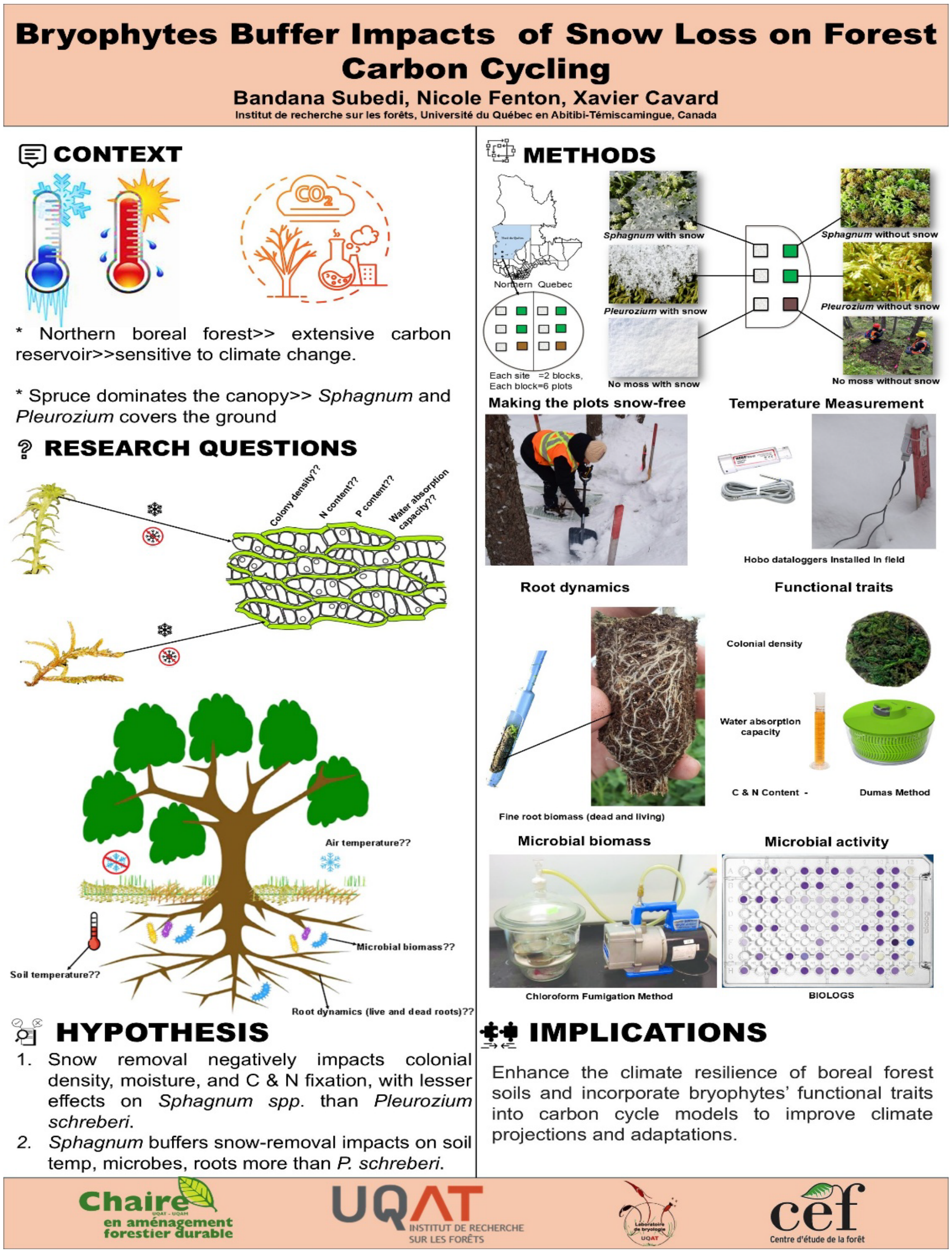
Significance of the study

If mosses mitigate the impacts of the loss of snow in carbon dynamics of boreal forests, then:

- Inform the climate impact projections and management plans for stabilizing boreal soil carbon through the conservation of functionally important moss diversity.

See You Next Year With Results!!

APPENDIX B – POSTER PRESENTATION: BRYOPHYTES BUFFER IMPACTS OF SNOW LOSS ON FOREST CARBON CYCLING AT 17E COLLOQUE CEF IN THE UNIVERSITY OF QUEBEC IN OUTAOUAIS, MAY 2024



Bryophytes Buffer Impacts of Snow Loss on Forest Carbon Cycling

Bandana Subedi, Nicole Fenton, Xavier Cavard

Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue, Canada

CONTEXT

* Northern boreal forest>> extensive carbon reservoir>>sensitive to climate change.

* Spruce dominates the canopy>> *Sphagnum* and *Pleurozium* covers the ground

RESEARCH QUESTIONS

HYPOTHESIS

1. Snow removal negatively impacts colonial density, moisture, and C & N fixation, with lesser effects on *Sphagnum spp*. than *Pleurozium schreberi*.
2. *Sphagnum* buffers snow-removal impacts on soil temp, microbes, roots more than *P. schreberi*.

METHODS

Making the plots snow-free

Temperature Measurement

Hobo dataloggers installed in field

Root dynamics

Fine root biomass (dead and living)

Functional traits

Microbial biomass

Chloroform Fumigation Method

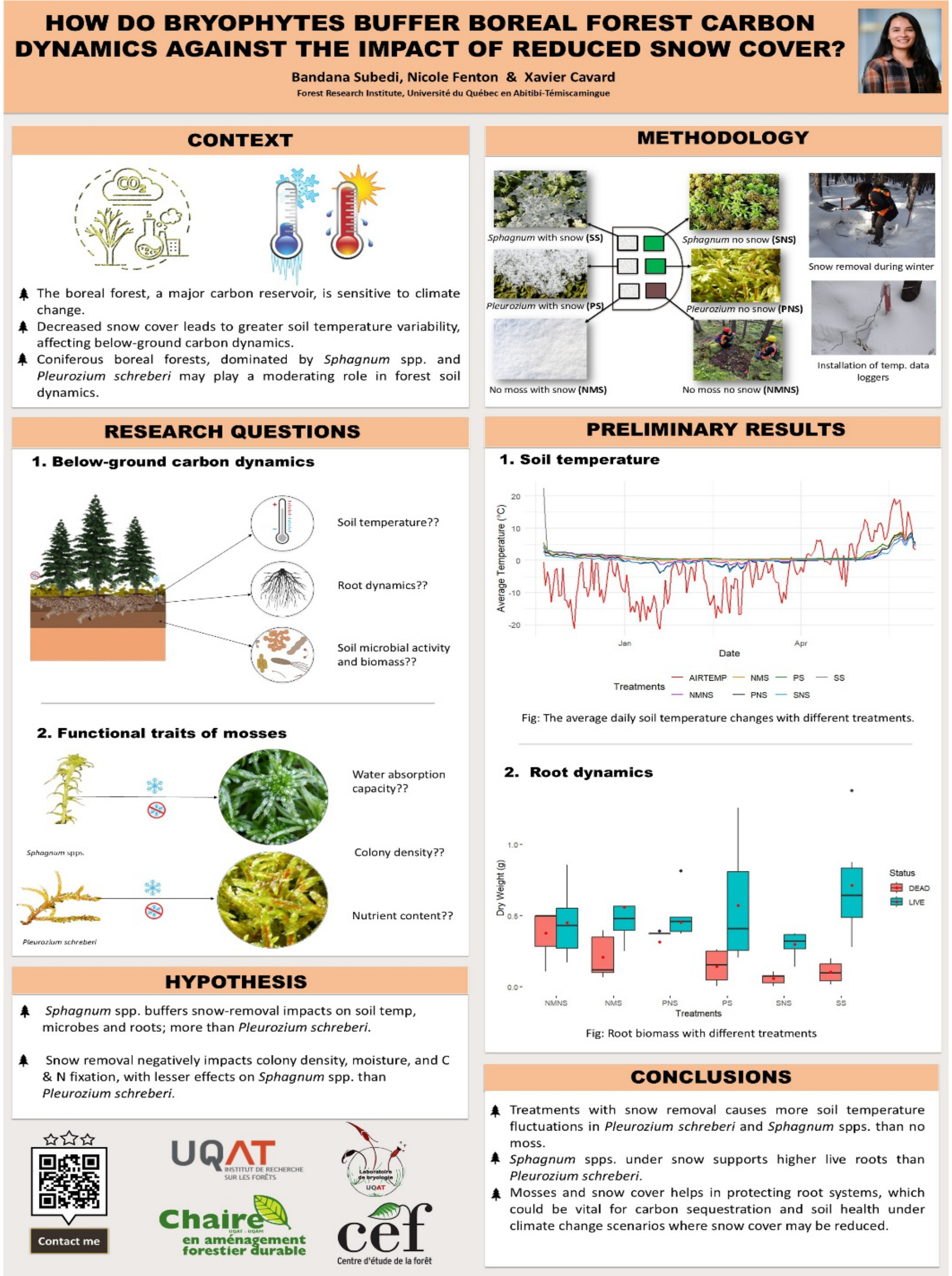
Microbial activity

BIOLOGS

IMPLICATIONS

Enhance the climate resilience of boreal forest soils and incorporate bryophytes' functional traits into carbon cycle models to improve climate projections and adaptations.

APPENDIX C – POSTER PRESENTATION: HOW DO BRYOPHYTES BUFFER BOREAL FOREST CARBON DYNAMICS AGAINST THE IMPACT OF REDUCED SNOW COVER? AT 26TH AFD CHAIR CONFERENCE IN HOTEL FORESTEL, VAL-D'OR, QUEBEC, NOVEMBER 2024



HOW DO BRYOPHYTES BUFFER BOREAL FOREST CARBON DYNAMICS AGAINST THE IMPACT OF REDUCED SNOW COVER?

Bandana Subedi, Nicole Fenton & Xavier Cavard

Forest Research Institute, Université du Québec en Abitibi-Témiscamingue

CONTEXT

- The boreal forest, a major carbon reservoir, is sensitive to climate change.
- Decreased snow cover leads to greater soil temperature variability, affecting below-ground carbon dynamics.
- Coniferous boreal forests, dominated by *Sphagnum* spp. and *Pleurozium schreberi* may play a moderating role in forest soil dynamics.

RESEARCH QUESTIONS

1. Below-ground carbon dynamics

Soil temperature??

Root dynamics??

Soil microbial activity and biomass??

2. Functional traits of mosses

Sphagnum spps.

Pleurozium schreberi

Water absorption capacity??

Colony density??

Nutrient content??

HYPOTHESIS

- *Sphagnum* spp. buffers snow-removal impacts on soil temp, microbes and roots; more than *Pleurozium schreberi*.
- Snow removal negatively impacts colony density, moisture, and C & N fixation, with lesser effects on *Sphagnum* spp. than *Pleurozium schreberi*.

Contact me

UQAT INSTITUT DE RECHERCHE SUR LES FORÊTS

Chaire UQAT – UQAM en aménagement forestier durable

Laboratoire de bryologie UQAT

cef Centre d'étude de la forêt

METHODOLOGY

Sphagnum with snow **(SS)**

Sphagnum no snow **(SNS)**

Pleurozium with snow **(PS)**

Pleurozium no snow **(PNS)**

No moss with snow **(NMS)**

No moss no snow **(NMNS)**

Snow removal during winter

Installation of temp. data loggers

PRELIMINARY RESULTS

1. Soil temperature

Fig: The average daily soil temperature changes with different treatments.

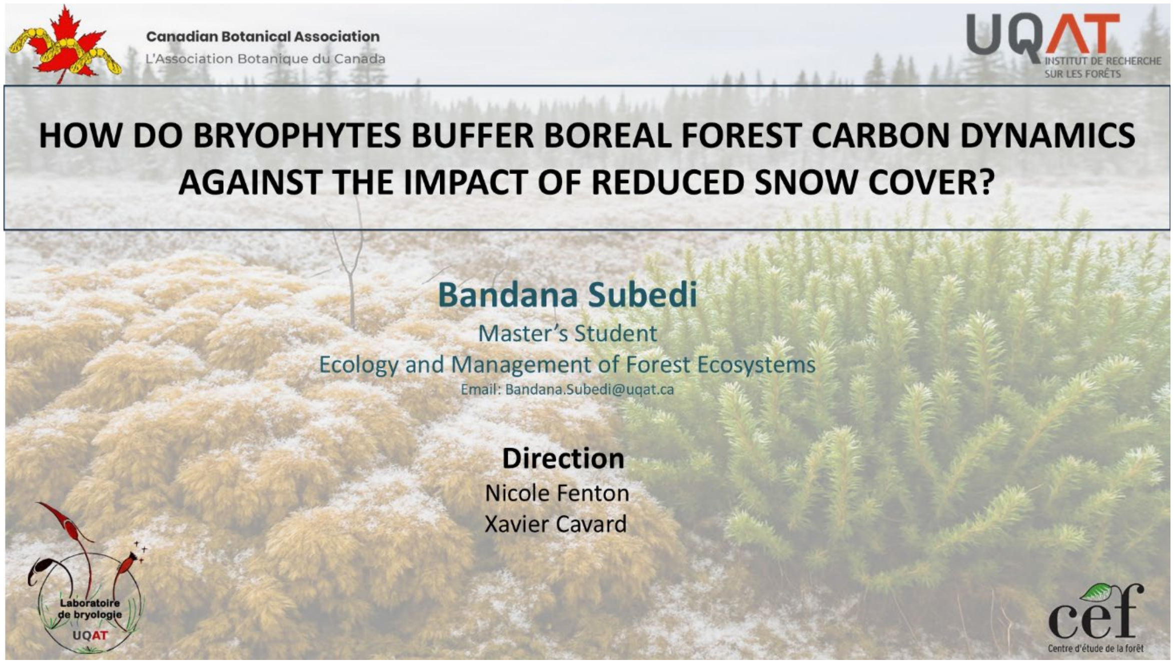
2. Root dynamics

Fig: Root biomass with different treatments

CONCLUSIONS

- Treatments with snow removal causes more soil temperature fluctuations in *Pleurozium schreberi* and *Sphagnum* spps. than no moss.
- *Sphagnum* spps. under snow supports higher live roots than *Pleurozium schreberi*.
- Mosses and snow cover helps in protecting root systems, which could be vital for carbon sequestration and soil health under climate change scenarios where snow cover may be reduced.

APPENDIX D – ORAL PRESENTATION: HOW DO BRYOPHYTES BUFFER BOREAL FOREST CARBON DYNAMICS AGAINST THE IMPACT OF REDUCED SNOW COVER? AT THE 61ST ANNUAL MEETING OF THE CANADIAN BOTANICAL ASSOCIATION IN MEMORIAL UNIVERSITY, ST.JOHN, NEW FOUNDLAND, JUNE 2025



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HOW DO BRYOPHYTES BUFFER BOREAL FOREST CARBON DYNAMICS AGAINST THE IMPACT OF REDUCED SNOW COVER?

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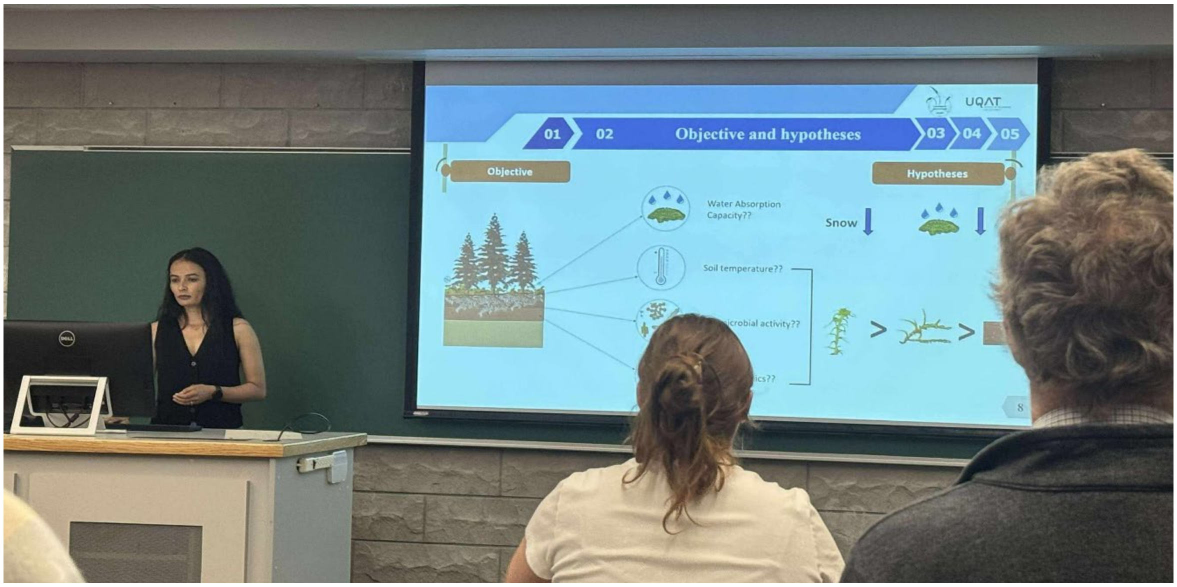

APPENDIX E – ORAL PRESENTATION: FUNCTIONAL TRAITS OF BRYOPHYTES AND THEIR ROLE IN BUFFERING THE IMPACTS OF CLIMATE CHANGE-INDUCED SNOW LOSS ON BELOWGROUND CARBON INPUTS IN THE BOREAL FOREST ECOSYSTEM AT THE RESEARCH SEMINAR OF SCIENTIFIC COMMUNICATION COURSE IN UNIVERSITÉ DU QUÉBEC EN ABITIBI-TÉMISCAMINGUE, AUGUST 2025

UQAT INSTITUT DE RECHERCHE SUR LES FORÊTS

Laboratoire de bryologie UQAT

Functional traits of bryophytes and their role in buffering the impacts of climate change-induced snow loss on belowground carbon inputs in the boreal forest ecosystem

Final Seminar

Bandana Subedi, Nicole Fenton, Christine Martineau, Xavier Cavard


01
02
03
Methodology
04
05
Microbial biomass
Chloroform Fumigation Extraction method
0.5M K2SO4
16
UQ


THANK YOU!!
UQ

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