Trophic interactions in the tundra

Impacts of large mammal herbivory on carbon processes and fungal communities

Cole Brachmann

Department of Earth Sciences

Faculty of Science

UNIVERSITY OF GOTHENBURG

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cole.brachmann@gu.se

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Cole Brachmann

Department of Earth Sciences, Faculty of Science
University of Gothenburg
Gothenburg, Sweden

ABSTRACT

Plant productivity is generally increasing in the Arctic as a consequence of accelerated climate change. The change in plant communities may coincide with a loss of carbon from Arctic soils due to increased decomposition and respiration. Herbivores can mediate these changes through preferential foraging on highly productive plant species, trampling, and waste deposition. Soil fungi are also a major component in these interactions and are controlled by plant community and soil conditions. Soil fungi have large impacts on the cycling of carbon in soil and its subsequent release to the atmosphere. Understanding of the effects of large mammalian herbivores on carbon processes, such as respiration and decomposition, and fungal communities is important for understanding the context of future changes in carbon storage in tundra soils.

I investigated the effect of herbivory on trace gas fluxes, decomposition and stabilization of organic matter, and soil fungal communities through the use of herbivore exclusion fences in tundra communities. Herbivory reduced ecosystem respiration in a meadow community, reduced stabilization under a deciduous shrub in a heath community, reduced arbuscular mycorrhizal fungi across the Arctic, and reduced ectomycorrhizal fungi locally in Swedish tundra. The presence of herbivores on the landscape can have complex effects on carbon in tundra habitats by reducing respiration rates and limiting fast cycling arbuscular mycorrhizal fungi, while simultaneously reducing the stability of organic matter as it decomposes and locally limiting slower cycling ectomycorrhizal fungi. The relative contribution of each of these processes to carbon cycling will determine the net effect of herbivores on tundra soils.

Herbivory impacts are context dependent and the net effect on soil carbon is likely related to the proportion of different tundra community types on the landscape.

Keywords: Herbivory, Arctic, Fungi, Trace Gas Fluxes, Decomposition, Biogenic Volatile Organic Compounds, Mycorrhiza, Tundra, Reindeer

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SAMMANFATTNING PÅ SVENSKA

Växtproduktiviteten ökar generellt i Arktis som en följd av den accelererade klimatförändringen. Förändringen i vegetationen kan också leda till en förlust av markkol från arktis på grund av ökad nedbrytning och respiration. Betesdjur kan motverka dessa förändringar genom att beta på högproduktiva växtarter, trampa och spillning. Marklevande svampar är också en viktig komponent i dessa interaktioner och styrs av växtsamhällen och markförhållanden. Marklevande svampar har stor inverkan på kolets kretslopp i marken och dess efterföljande utsläpp i atmosfären. Förståelsen av de stora däggdjurens effekter på kolprocesser, såsom respiration och nedbrytning, och svampsamhällen är viktig för att förstå framtida förändringar i kolinlagringen i tundrajordar.

Jag har undersökt effekten av betesdjurs på flöden av spårgaser, nedbrytning och stabilisering av organiskt material samt svampsamhällen i marken genom att använda hägn som utestänger betesdjur från tundraområden. Betesdjuren minskade ekosystemets respiration av kol i ängsvegetation, minskade stabiliseringen under lövfällande buskar i tundrahed, minskade arbuskulära mykorrhizasvampar i hela Arktis och minskade ektomykorrhizasvampar lokalt i svensk tundra. Förekomsten av växtätare i landskapet kan ha komplexa effekter på kolet i tundrahabitat genom att minska respirationshastigheten och begränsa arbuskulära mykorrhizasvampar som omsätter kol snabbt, samtidigt som det minskar stabiliteten hos organiskt material när det bryts ned och begränsar ektomykorrhizasvampar som omsätter kol långsammare. Det relativa bidraget från var och en av dessa processer till kolcykeln kommer att avgöra nettoeffekten betesdjur har på tundrajordar.

Effekterna av växtätare är i hög grad beroende av sammanhanget och nettoeffekten på markkol är sannolikt relaterad till andelen av olika tundrasamhällstyper i landskapet.

LIST OF PAPERS

This thesis is based on the following studies, referred to in the text by their Roman numerals.

I. **Brachmann, C. G.,** Vowles, T., Rinnan, R., Björkman, M. P., Ekberg, A., and Björk, R. G. 2023. Herbivore-shrub interactions influence ecosystem respiration and BVOC composition in the subarctic. Biogeosciences, 20, 4069-4086. https://doi.org/10.5194/bg-20-4069-2023.

II. **Brachmann, C. G.,** Bjorkman, A. D., Ekblad, A., and Björk, R. G. 2023. Shrub type influences herbivory effects on soil organic matter stabilization in tundra heaths. [Manuscript].

III. **Brachmann, C. G.,** Ryberg, M., Furneaux, B. R., Rosling, A., Ou, T., Ekblad, A., Autto, H. T., Barrio, I. C., Bret-Harte M. S., Fritze, H., Gough, L., Hollister, R. D., Jónsdóttir, I. S., Lindén E., Mäkiranta, P., Olofsson, J., Partanen, R., Reid, K. A., Sokolov, A., Sokovnina, S., Sujala, M. S., Sundqvist, M. K., Suominen, O., Tweedie, C. E., Young, A., and Björk, R. G. 2023. Herbivore-driven impacts on mycorrhizal fungi composition across the Arctic. [Submitted to New Phytologist].

IV. **Brachmann, C. G.,** Ekblad, A., Rousk, J., Ryberg, M., Rosling, A., Lopes Ramos, D. J., and Björk, R. G. 2023. Fungal species composition rather than abundance impacted by herbivory in the tundra. [Manuscript].

Author contributions

Paper I CGB analyzed the data and wrote the original manuscript.
Papers II-IV CGB helped design experiment, led a portion of the field campaigns, processed samples, analyzed data, wrote original manuscript, and contributed to edits and writing equally thereafter.

Other publications not included in this dissertation.

1. Scharn, R., **Brachmann, C. G.,** Patchett, A., Reese, H., Bjorkman, A., Alatalo, J., Björk, R. G., Jägerbrand, A. K., Molau, U., and Björkman, M. P. 2021. Vegetation responses to 26 years of warming at Latnjajaure Field Station, northern Sweden. Arctic Science 1-20.

CONTENTS

1 INTRODUCTION

The Arctic region has experienced approximately four times the rate of warming compared to the global average (Rantanen *et al.*, 2022). This warming trend has led to vegetation shifts (Myers-Smith *et al.*, 2011; Elmendorf *et al.*, 2012a,b; Bjorkman *et al.*, 2015, 2020), which have resulted in aboveground productivity increases and a general greening trend over much of the Arctic (Myers-Smith *et al.*, 2020). The predominant vegetation increasing in the Arctic are shrub and graminoid species, which are highly productive. These high productivity plant types consequently have strong repercussions on soil carbon stores via trace gas fluxes, litter input quality, decomposition rates, carbon turnover, and nutrient cycling as microbial communities shift concomitantly (Hobbie *et al.*, 2000; Read & Perez-Moreno, 2003; Averill *et al.*, 2014; Bjorkman *et al.*, 2018). These processes are essential as Arctic soils currently account for nearly 50% of global terrestrial belowground carbon (Hugelius *et al.*, 2013, 2014; Sistla *et al.*, 2013; Crowther *et al.*, 2016; Van Gestel *et al.*, 2018; Mishra *et al.*, 2021). Herbivores can act to either amplify or reduce changes in soil carbon via their effect on structuring plant communities (Olofsson *et al.*, 2009; Vowles *et al.*, 2017a; Sundqvist *et al.*, 2019; Lindén *et al.*, 2021). By shifting the proportion of different plant functional groups in a community herbivores can indirectly influence carbon and nutrient cycling in the Arctic (Ylänne *et al.*, 2015). Therefore, understanding the role of herbivores on carbon relevant processes, such as respiration and decomposition, through their effects on the plant community, and subsequently the microbial community, is essential to understanding future soil carbon stocks in the tundra.

1.1 TRACE GAS FLUXES

Trace gas emissions are the primary pathway by which terrestrial ecosystems can directly impact climate warming. Plant communities largely determine the production and consumption of trace gases through photosynthesis, respiration, production of secondary compounds, and regulation of the microbial community (Ward *et al.*, 2013). Trace gas emissions includes both CO_2 through ecosystem respiration (ER) and Biogenic Volatile Organic Compound (BVOC) emissions. BVOCs are chemicals produced by plants for a variety of purposes including reproductive signalling, communication, and herbivore deterrence (Peñuelas & Staudt, 2010). BVOCs

play a role in climate warming primarily through their interaction with ozone, effects on the lifetime of methane in the atmosphere, and the formation of secondary organic aerosols (Peñuelas & Staudt, 2010; Calfapietra *et al.*, 2013; Boy *et al.*, 2022). Secondary organic aerosols may have an overall cooling effect by scattering light and leading to cloud formation (Spracklen *et al.*, 2008; Shrivastava *et al.*, 2017); therefore, understanding the magnitude and identity of BVOC emissions is critical to future climate projections as they can act to both enhance or mediate climate change effects. ER is one of the largest contributors to CO_2 emissions globally (Sharkhuu *et al.*, 2016; Liu *et al.*, 2022) and is predicted to be increasingly vital to the CO_2 balance of northern regions as it is driven by vegetation change, productivity, and microbial activity (Parker *et al.*, 2015; Liu *et al.*, 2022). Thus, influences of vegetation changes on BVOC emissions and ER can impact the feedback effects on climate change, potentially exacerbating or mediating its effects, with implications regionally and globally (Heimann & Reichstein, 2008; Peñuelas & Staudt, 2010).

The magnitude of ER differs between plant communities within the forest-tundra ecotone (Treat *et al.*, 2018). These community types include birch forest, shrub heaths, and meadows. Subarctic birch forest, composed of mountain birch trees and deciduous shrubs primarily, have larger ER compared to tundra heath and meadow communities due to the high contribution from woody deciduous vegetation and stimulation of microbial communities through litter and mycorrhizal inputs to the soil (Parker *et al.*, 2015; Strimbeck *et al.*, 2019; Virkkala *et al.*, 2021). Heath communities have been found to have the lowest ER from these community types attributed to the relatively slow decomposition of organic matter in the soil (Parker *et al.*, 2015; Sørensen *et al.*, 2018). Concomitantly, the shift to ectomycorrhiza-dominated communities coincides with increased ER as they more effectively scavenge organic carbon and contribute to higher productivity (Parker *et al.*, 2015). Shifts in plant community composition due to climate change have been well documented in tundra ecosystems (Elmendorf *et al.*, 2012a; Bjorkman *et al.*, 2020), and have subsequent effects on ER (Virkkala *et al.*, 2018). Increases in vegetation biomass in tundra could also increase the magnitude of BVOC fluxes (Rinnan *et al.*, 2011), however, vegetation community composition changes will likely have a stronger effect on the composition of BVOCs emitted as these are plant species-specific (Peñuelas & Staudt, 2010). Therefore, changes in plant communities most likely will have a large effect on ER and BVOC emissions.

Herbivory may influence trace gas fluxes indirectly by altering the trajectory of vegetation community changes (Cahoon *et al.*, 2012; Metcalfe & Olofsson, 2015; Vowles & Björk, 2019). However, studies assessing the consequences of large herbivore grazing on BVOC fluxes and ER are lacking in tundra ecosystems and are important for a broader understanding of feedback mechanisms in the Arctic (Cahoon *et al.*, 2012; Metcalfe & Olofsson, 2015; Ylänne *et al.*, 2015; Köster *et al.*, 2018; Vowles & Björk, 2019).

1.2 DECOMPOSITION

Decomposition, carbon turnover, and nutrient cycling are major processes determining the balance of stored carbon in soils and all are impacted by plant abundance and community composition (Hobbie *et al.*, 2000). Vegetation impacts these processes primarily through functional traits that determine litter quality and root exudates (Fanin *et al.*, 2020). For instance, the quality of litter inputs, the proportion of easily extractable nutrients from the organic material, can vary dramatically between shrub types (Cornwell *et al.*, 2008). Thus, the relative shift toward deciduous or evergreen shrubs could influence carbon storage through altered decomposition rates (Freschet *et al.*, 2012; Vowles & Björk, 2019). Furthermore, different shrub types also have different root traits and mycorrhizal fungi associations which directly affect carbon quality and microbial activity and community in the soil (Finlay, 2008; Sulman *et al.*, 2017; See *et al.*, 2019). Similarly, stabilization of organic compounds, i.e., the proportion of labile organic material that is transformed into recalcitrant material during the decomposition process (Prescott & Vesterdal, 2021), can be altered by vegetation and microbial communities (Fernandez *et al.*, 2016; Prescott & Vesterdal, 2021). Further understanding of these processes and their drivers is important due to the large amount of carbon stored in tundra soils.

Herbivory can impact these processes through the plant community by changing the proportion of different shrub species (Olofsson *et al.*, 2004b; Kaarlejärvi *et al.*, 2017; Vowles *et al.*, 2017a,b; Lindén *et al.*, 2021; Ylänne *et al.*, 2021). Specifically, herbivores may increase the proportion of evergreen shrubs in the tundra by preferentially consuming deciduous shrubs (Vowles & Björk, 2019; Ylänne *et al.*, 2021), which can subsequently decrease decomposition and consequently shift the microbial community towards ericoid mycorrhiza dominant, which have slow decomposition rates (Parker *et al.*, 2021; Fanin *et al.*, 2022; Ward *et al.*, 2022). Community level differences in litter quality due to relative values of plant traits, such as nitrogen content

or leaf area, would also be affected by herbivory altering the proportion of shrub types on the landscape (Cornwell *et al.*, 2008; Burghardt *et al.*, 2018; Ridgeway *et al.*, 2022). For example, herbivory can indirectly increase the nitrogen content of plant leaves, and subsequent litter quality, by making plants mobilize nutrients to replace tissues that were consumed (Väisänen *et al.*, 2014; Koltz *et al.*, 2022), which increases the decomposability of the leaves. Simultaneously, plants may also respond to herbivory by changing the allocation of carbon between aboveground and belowground structures (Bardgett *et al.*, 1998; Lindwall *et al.*, 2013; Hicks *et al.*, 2022), which can change the modality of how carbon is returned to soils; either through leaf or root litter. Herbivores can therefore have a large impact on decomposition by altering plant community composition and trait space. However, the effects may also act antagonistically producing a weaker net effect, the strength of which is poorly known.

Herbivores can affect nutrient dynamics and microclimate properties at a site through waste deposition and trampling (Wang *et al.*, 2018, 2023). Faeces can directly increase nitrogen content in the soil (Hobbs, 1996; Sjögersten *et al.*, 2010), and promote plant and microbial growth (Barthelemy *et al.*, 2015). Trampling can increase soil temperature and moisture through compaction and by altering snow dynamics (Zimov *et al.*, 2009; Olofsson & Post, 2018; Egelkraut *et al.*, 2020). Soil temperature and moisture dynamics alter decomposition rates both physically (Moinet *et al.*, 2020) and through the microbial community (Christiansen *et al.*, 2017). Plant and microbial communities concomitantly interact with soil properties and microclimate which further impact decomposition and stabilization (Davidson & Janssens, 2006; Moinet *et al.*, 2020; de Godoy Fernandes *et al.*, 2021). By altering the dominance of focal shrub species, changing the nutrient load in soil by waste deposition, and impacting microclimate through trampling herbivores can play an important role in controlling decomposition rates in tundra.

1.3 MYCORRHIZAL FUNGI

As shrub species are expanding and becoming more prevalent in the Arctic (Myers-Smith *et al.*, 2011), soil fungal communities are expected to also change. Saprotrophic and mycorrhizal fungi both contribute to the cycling of carbon, nitrogen, and phosphorus in soils (Högberg & Read, 2006; Orwin *et al.*, 2011). However, as mycorrhizal fungi access recent plant photosynthates they are less carbon limited and can increase the storage of organic carbon in

the soil (Högberg & Read, 2006; Giesler *et al.*, 2007; Orwin *et al.*, 2011; Clemmensen *et al.*, 2021; Prescott & Vesterdal, 2021). Mycorrhizal fungi contribute to organic carbon storage by acting as a sink for recent carbon through plant photosynthates, outcompeting free living microbes for organic nitrogen, and through the recalcitrance of their own tissues (Giesler *et al.*, 2007; Averill *et al.*, 2014; Prescott & Vesterdal, 2021; Hicks *et al.*, 2022). Mycorrhizal fungi can therefore alter the rate of decomposition which impacts ER and BVOC fluxes, and plant productivity (van der Heijden *et al.*, 2014). Different plant types generally form different types of mycorrhizal associations, where deciduous shrubs primarily form ectomycorrhiza (EcM), ericaceous shrubs (which are primarily evergreen) form ericoid mycorrhiza (ErM), and grass and forbs form arbuscular mycorrhiza (AM), all of which may increase due to climate warming (Walker *et al.*, 2006; Vowles *et al.*, 2018; Vowles & Björk, 2019; Berner *et al.*, 2020; Clemmensen *et al.*, 2021; Betway-May *et al.*, 2022; Parker *et al.*, 2022). These mycorrhizal fungi types are linked to different degrees of recalcitrance of organic material, due to for example the enzymes used to degrade organic matter or the melanization of their tissues. Shifts in mycorrhizal dominance along a gradient from AM-EcM-ErM corresponds to slower carbon turnover and subsequently higher carbon storage in the soil (Phillips *et al.*, 2013; Clemmensen *et al.*, 2015, 2021; Parker *et al.*, 2021; Fanin *et al.*, 2022).

Although AM fungi form associations with almost 80% of terrestrial plant species globally (Smith & Read, 2008), AM fungi are generally limited in distribution in the Arctic due to their low tolerance to cold (Wang *et al.*, 2002; Ruotsalainen & Kytöviita, 2004; Kytöviita, 2005). However, their abundance may increase in grass and forb dominated communities if their host-species become more prevalent as climate conditions change (Olsson *et al.*, 2004; Hollister & Flaherty, 2010; Gao *et al.*, 2016; Newsham *et al.*, 2017). AM species may therefore respond quickly as climate warming continues (Bennett & Classen, 2020).

Factors that shift the prevalence of one plant functional type over another should concomitantly affect the proportion of mycorrhiza types in the soil (Martínez-García *et al.*, 2015; Grau *et al.*, 2017; Dahlberg & Bültmann 2013). However, fungal community composition is primarily influenced by the climate and edaphic properties of a site which may drive large scale community patterns. Herbivory may therefore act predominantly at local scale by altering vegetation abundance and competitive interactions. These multi-trophic level interactions have been previously indicated as important for Arctic ecosystems

(Vowles & Björk, 2019; Ylänne *et al.*, 2021), however, they have not been evaluated across the whole Arctic.

The combined indirect effects on mycorrhizae, decomposition, and soil gaseous fluxes through vegetation changes makes herbivores a potential keystone component in understanding the future of carbon in Arctic soils.

1.4 AIMS

The objective of this thesis is to determine the effect of large mammalian herbivores on carbon processes and mycorrhizal fungi in subarctic tundra. The aims of the manuscripts are to 1) Determine how vegetation shifts indirectly caused by large herbivore exclusion affect the magnitude of ER and composition of BVOC fluxes. 2) Evaluate the consistency of these effects among different vegetation communities. 3) Investigate how herbivory affects decomposition rates and stabilization under two focal shrub species. 4) Determine how intraspecific shrub traits influence decomposition and stabilization rates. 5) Determine how herbivory impacts mycorrhizal fungi community composition across the Arctic. 6) Elucidate how local edaphic and regional climate properties impact mycorrhizal fungi composition. 7) Determine the local effect of herbivory on soil fungal communities and diversity in two different tundra community types. 8) Evaluate fungal mycelial biomass in these communities and investigate the effect of herbivores. Altogether, these aims will provide a holistic understanding of the indirect effects of large mammalian herbivores on carbon release and cycling in soils, and fungal communities in the tundra.

2 METHODS

2.1 STUDY SITES

The sites studied in **Paper I** include four locations in the Swedish Scandinavian Mountains (LORI, LOMB, RIRI, and RIGA; Fig. 1), two of which were also used for **Paper II** (LORI and RIRI), and two for **Paper IV** (LORI and RIGA) alongside an additional southern heath site (SON). Each of the sites contained three (25 x 25 m) herbivore fences and three equal sized ambient plots. These sites encompassed three distinct community types: birch forest, shrub heath, and low-herb meadow. The southern sites for **Paper I** are referred to as: Långfjället mountain birch forest (LOMB hereafter; 62°03'59"N, 12°14'56"E; 809 m a.s.l.) and Långfjället shrub heath (LORI hereafter; 62°06'53"N, 12°16'30"E; 853 m a.s.l.), located approximately 5 km apart near Grövelsjön, Dalarna. The Northern sites are referred to as: Ritsem shrub heath (RIRI hereafter; 67°46'33"N, 17°32'22"E; 847 m a.s.l.) and Ritsem low herb meadow (RIGA hereafter; 67°49'35"N, 17°43'02"E; 719 m a.s.l.), located approximately 10 km apart near Ritsem, Norrbotten County. In RIGA only two of the three originally established ambient plots could be located and so a new ambient plot was established in 2012 (Vowles *et al.*, 2017b). The additional site for **Paper IV** is referred to as Sonfjället shrub heath (SON hereafter; 62° 16’ 65”N, 13° 28’ 21”E; 940 m a.s.l), located within Sonfjället National Park in Jämtland County.

The primary large mammalian herbivore at these sites is reindeer (*Rangifer tarandus*) which had tentative density estimates of 2.8 reindeer per km^2 near Långfjället and 2.2 reindeer per km^2 near RIGA and 1.4 reindeer per km^2 near RIRI previously reported for the three Sami herding villages nearest these sites (Vowles *et al.*, 2017a,b). Moose (*Alces alces*) are another large herbivore that could be present at the study sites and their populations are similar between the management areas in which our sites are located. Both areas have a density of approximately 0.1 – 0.2 moose per km^2 over the study period according to county board hunting statistics (SCAB Statistik Älgdata accessed 2022). Reindeer density index was also calculated previously for the sites in **Paper IV**, using fecal pellet counts along 50 m x 1 m transects (Sundqvist *et al.*, 2019).

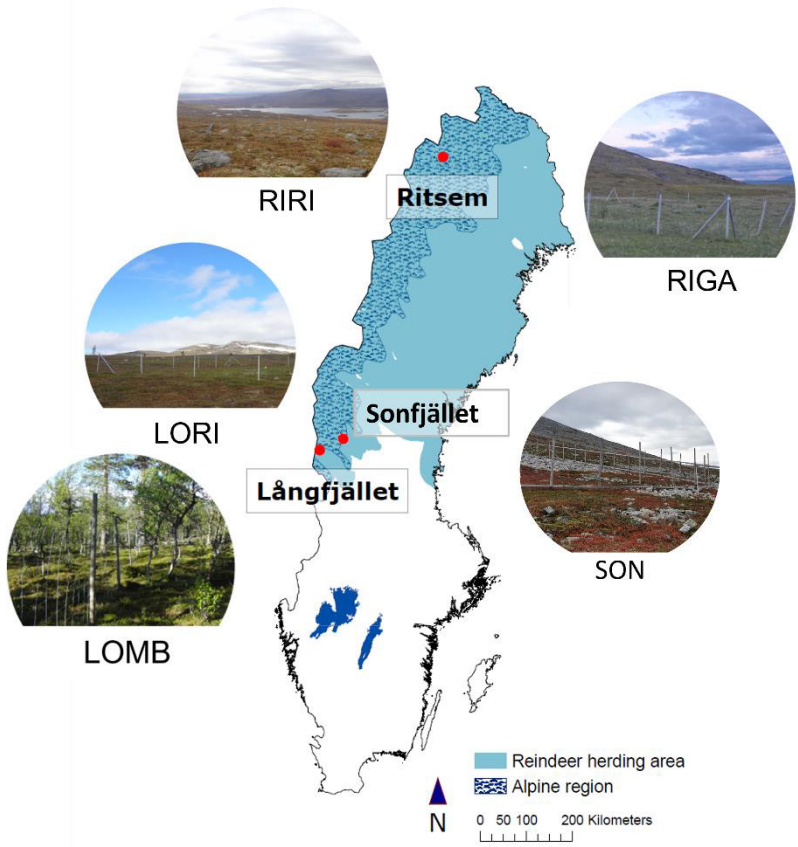

Fig. 1 *Map of study sites and communities in Papers I, II, and IV with overlay of reindeer herding area and alpine regions in Sweden. Photo credits: Tage Vowles.*

For **Paper III**, the influence of herbivory on mycorrhizal fungi community composition was determined using established herbivore exclosure fences at 13 sites across the subarctic (Fig. 2). The study sites included five sites in Sweden, three in Finland, two in USA, one in Iceland, one in Russia, and one in Canada (Fig. 2; Table. 1). The site designations listed in Table 1 will be used to refer to those sites within the context of **Paper III**. Most of the sites had three herbivore exclosure fences paired with three ambient plots of equal size, except for SAP1 and 2 (which had one large fence and ambient plot for each), ERK (which had 15 0.25 m^2 fences and 15 ambient plots), UTQ (which had 12 1 m^2 fences and 12 ambient plots), and YUK1 and 2 (which had three replicate 1 m^2 fences and three ambient subplots each). Sites with large fences and ambient plots had five subplots within each plot, while sites with small fences treated each fence as a plot.

Table 1. *Description of each site contributing to Paper III. Two of the KLP fences covered an area of 1994 m^2, while the third fence covered an area of 562 m^2. Soil moisture class is an approximation of moisture conditions at each site.*

Country	Site name	ID	Coordinates	# Fence and ambient plots	Fence area (m^2)	# Soil cores	# Composite soil samples	Year fences established	Experiment duration (years)	Vegetation surveyed	MAT (°C)	MAP (mm)	Soil moisture class	Dominant plants	Dominant large mammal herbivore	References
Sweden	Abisko	ABI	68° 19' 23" N, 18° 51' 57" E	3+3	64	25 / plot	6	1998	22	Yes	-1.6	637	Dry	*Empetrum nigrum, Betula nana*	*Rangifer tarandus*	Lindén et al. 2021
Sweden	Långfjället	LAN	62° 06' 53" N, 12° 16' 30" E	3+3	625	25 / plot	6	1995	25	Yes	0.0	840	Dry	*Empetrum nigrum , Vaccinium myrtillus , V. vitis-idaea , Calluna vulgaris , Betula nana*	*Rangifer tarandus*	Vowles et al. 2017b, Sundqvist et al. 2019
Sweden	Ritsem meadow	RIG	67° 49' 35" N, 17°43'02" E	3+3	625	25 / plot	6	1995	25	Yes	-3.4	719	Wet	*Deschampsia cespitosa , D. flexuosa , Carex aquatilis, Betula nana, Empetrum nigrum*	*Rangifer tarandus*	Vowles et al. 2017a, Sundqvist et al. 2019
Sweden	Ritsem shrub heath	RIR	67° 46' 33" N, 17° 32' 22" E	3+3	625	25 / plot	6	1995	25	Yes	-3.5	847	Dry	*Empetrum nigrum, Betula nana*	*Rangifer tarandus*	Vowles et al. 2017b, Sundqvist et al. 2019
Sweden	Sonfjället	SON	62° 16' 55" N, 13° 28' 21" E	3+3	625	25 / plot	6	1995	25	Yes	-1.5	773	Dry	*Empetrum nigrum, Deschampsia flexuosa*	*Rangifer tarandus*	Sundqvist et al. 2019
Finland	Kevo	KEV	69° 42' 28" N, 27° 04' 55" E	3+3	400	25 / plot	6	1970	50	Yes	-2.0	481		*Empetrum nigrum , Deschampsia flexuousa , Vaccinium myrtillus , and V. vitis-idaea*	*Rangifer tarandus*	Lehtonen and Heikkinen 1995
Finland	Kilpisjärvi	KLP	69° 02' 35" N, 20° 48' 22" E	3+3	1994/562	25 / plot	6	2020	0	No	-2.3	553	Dry	*Betula nana , Empetrum nigrum , Vaccinium myrtillus* and *V. vitis-idaea*	*Rangifer tarandus*	*N/A*
Finland	Sodankylä	SAP1	67° 22' 02" N, 26° 39' 02" E	1+1	5000	25 / plot	2	2001	19	No	0.4	567	Wet	Eriophorum vaginatum, Carex sp. Andromeda polifolia, Vaccinium oxycoccos, Betula nana	*Rangifer tarandus*	Meinander et al. 2020
Finland	Pallas	SAP2	67° 59' 49" N, 24° 12' 42" E	1+1	2000	25 / plot	2	2017	3	No	-0.9	592	Wet	Carex rostrata, Menyanthes trifoliata, Comarum palustre, Betula nana.	*Rangifer tarandus*	Meinander et al. 2020
USA	Toolik lake	TOO	68° 37' 27" N, 149° 36' 36" W	3+3	100	25 / plot	6	1996	24	Yes	-8.8	245	Moist	*Eriophorum vaginatum , Betula nana , Rubus chamaemorous*	*Rangifer tarandus*	Lindén et al. 2021
USA	Utqiaġvik	UTQ	71° 18' 49" N, 156° 36' 11" W	12+12	1	5 / plot	24	1959	61	No	-11.1	211	Dry-Wet	Deciduous shrubs and graminoids	*Rangifer tarandus*	Johnson et al. 2011
Iceland	Auðkúluheiði	AUD	65° 12' 0" N, 19° 42' 0" W	3+3	144	25 / plot	6	2016	4	Yes	2.8	708	Dry	*Betula nana*	*Ovis aries*	Mulloy et al. 2021
Russia	Erkuta	ERK	66° 39' 34"N, 66° 24' 33" E	15+15	0.25	5 / plot	30	2014	6	Yes	-6.1	561		Dwarf shrubs and sedges	*Rangifer tarandus*	Baubin et al. 2016
Canada	Yukon sites - North	YUK1	66° 36' 12" N, 136° 17' 13.2" W	3+3	1	5 / plot	2	2019	1	Yes	-16.8	207		*Betula nana, Eriophorum vaginatum, and Empetrum nigrum*	*Rangifer tarandus*	N/A
Canada	Yukon sites - south	YUK2	64° 55' 49" N, 138° 16' 23" W	3+3	1	5 / plot	2	2019	1	Yes	-6.36	326		*Betula nana, Eriophorum vaginatum, and Empetrum nigrum*	*Rangifer tarandus*	*N/A*

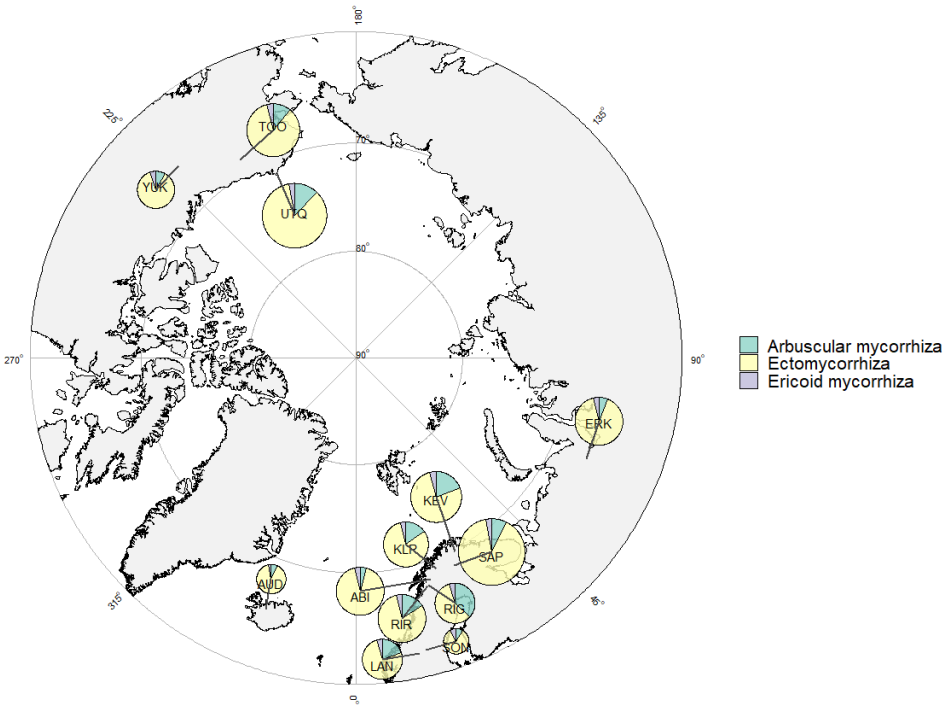

Fig. 2. *Map of site locations in Paper III with pie charts showing proportion of mycorrhiza types with the size of the pie charts scaled to the number of mycorrhizal species within sites.*

2.2 SOIL AND FUNGI SAMPLING

2.2.1 SOIL COLLECTION

Soils were collected for **Paper III** near the beginning of the growing season for each site. Sites that had large fence and ambient plots had five subplots within each plot, ERK, UTQ, and YUK1 and 2 treated each fence/ambient plot as subplots. In total there were 58 fences with paired control plot totaling 116 plots. Soils were collected from each site in summer 2020, except for UTQ which collected in summer of 2021, using a 2 cm diameter soil corer to a depth of 10 cm. Five cores were retrieved per subplot, which for large fences meant 25 soil cores were composited into a single plot sample, while for small fences 5 cores were composited. Soil samples were frozen and

stored as soon as possible at -20 °C until they could be processed. Each soil sample was sieved at 2 mm and freeze-dried for 24 hours to be dry stored until DNA extraction and soil physicochemical measurements.

Soils were also collected for **Paper II** in Summer 2021 from 10 subplots at each fence and ambient plot, 5 centered on the EcM shrub *Betula nana* and 5 centered on the ErM shrub *Empetrum nigrum*. Five soil cores were collected from each of these subplots and pooled at the plot level to form one composite sample focusing on EcM and ErM per plot. Soils were collected from each site using a 2 cm diameter soil corer to a depth of 10 cm from each plot. Soil samples from all subplots associated with one shrub type per plot were homogenized into a single composite soil sample in the field (12 soil samples total per site; one per shrub type at each plot). Soil samples were kept cold in the field and then stored at -20 °C. Each soil sample was sieved at 2 mm and freeze-dried for 24 hours to be dry stored until further analyses.

All soils were tested for various soil physicochemical parameters. pH was measured after adding 50 ml water to 10 g soil and allowing it to settle overnight before measuring with a pH meter (Metrohm 691 pH meter). pH was measured a second time after adding 0.5 ml 2M KCl to reach a final concentration of 0.02 M KCl to remove any potential effect of soil electrolyte concentration on the measurements (Kome et al., 2018). Soil organic matter was measured using Loss-on-Ignition method where the soil was heated at 550 °C for 8 hours with mass loss approximating the mass of organic material in the sample. Total carbon, $\delta^{13}C$, total nitrogen and $\delta^{15}N$ were analyzed on an elemental analyzer (GSL, Sercon Ltd., Crewe, UK) coupled to an isotope ratio mass spectrometer (20-22, Sercon Ltd., Crewe, UK).

2.2.2 MESH BAG PROTOCOL

Paper IV utilized fungal in-growth mesh bags to collect data on extramatrical mycelia (referred to as simply mycelia hereafter) in the soil. Mesh bags with a 2 cm diameter and 10 cm length were installed in the holes left by soil collection. The mesh bags are made from 50 μm nylon mesh to allow fungi to penetrate but preventing root growth and are filled with sand that has been burned at 550 °C for 8 hours to ensure there is no added carbon in the bag which encourages growth of mycorrhizal fungi mycelia preferentially. **Paper IV** utilized a sequential harvest scheme for the mesh bags arrayed at each plot where A bags were installed over the growing season (approx. late June - early September), B bags were installed for 1 year (June –

June), C1 bags were installed for 1 year + 1 growing season, C2 bags were installed for 2 years, and D bags were installed for 2 years + 1 growing season (full project length). A and B bags were sampled with replacement so in total there are three sets of A bags per plot (installed 2020, 2021, 2022) and 2 sets of B bags (2020-2021 and 2021-2022). The varying burial length of the mesh bags allows for estimation of biomass and biomass + necromass seasonally and between years. Upon retrieval the mesh bags were cut open in field and homogenized into a single sample (5 bags per sample). All mesh bags were frozen and stored as soon as possible at -20 °C. Mesh bag samples were freeze-dried prior to analyses.

2.3 TRACE GAS FLUXES

2.3.1 ECOSYSTEM RESPIRATION

For **Paper I**, ER during the growing season was measured using a closed-chamber technique (Björkman *et al.*, 2010a). An opaque chamber was sealed onto the collar during measurements where air from the headspace was circulated into 20 ml sample vials over 30 s using an electric pump (flow rate 0.5 L/min). Samples were obtained at 3, 6, 10, 30, and 50 minutes after the chamber was sealed onto the collar. The samples were analyzed for CO_2 concentration using gas chromatography (Agilent 7890A GC coupled to an Isoprime GC 5 interface and an Isoprime 100 IRMS, Aglient Technologies, Santa Clara, U.S.) and fluxes estimated as a linear change in CO_2 concentration over time. Growing season fluxes were measured from late June – early October in the southern sites and late June – early September in the northern sites, and again in early June the following year for all sites.

Winter ER was estimated during the snow-covered period at the LORI and LOMB sites based on Fick´s first law on diffusion (Sommerfeld *et al.*, 1993; Björkman *et al.*, 2010b; Pirk *et al.*, 2016). Air samples were withdrawn from the snowpack (at every 10 cm) using a gas-tight syringe fitted to 1/6" stainless steel tubing attached to an avalanche probe inserted into the snow above each flux collar. The air samples were then transferred to headspace vials for storage until analysed by gas chromatography. Snow density, temperature and profile characteristics were collected from adjacent snowpack to be used in the flux calculations (see Björkman *et al.*, 2010b for further details).

Q_{10}-values for each of the collars for the growing season (RIRI and RIGA) and for the full year (LORI and LOMB) were estimated based on the Arrhenius equation, by plotting the natural logarithm of the CO_2 emissions against the measured soil temperature (in 1000/K) as outlined in Davidson and Janssens (2006). To enable a direct comparison between the sites, an interpolation approach (Björkman *et al.*, 2010a) was used for the growing season data where data was first interpolated between two conjuncting measurements to generate a flux per day and summed up as cumulative count of emissions during July 02 - September 02, 2013.

2.3.2 BVOC EMISSIONS

For **Paper I**, BVOC fluxes were measured twice for each site during the growing season, in early July and again in late July/ early August (Table A1). Three permanent PVC soil collars (10 cm diameter) were inserted at random locations within the central area of each plot, at least 1 m from the edge a day prior to the first measurement. BVOC fluxes were measured using transparent teflon chambers fitted onto these soil collars just prior to measurement with a temperature logger connected to the chamber to record temperature throughout the measurement interval. A pump was used to circulate air from the chamber through stainless steel adsorbent cartridges containing 150 mg Tenax TA and 200 mg Carbograph 1TD (Markes International Limited) at 200 ml min^{-1} and then back into the chamber for a through-flow measurement of BVOCs over 20 minutes. At the end of the measurement, the collected air sample volume was recorded to calculate the BVOC flux. The adsorbent cartridges were analyzed using gas chromatography-mass spectrometry following thermal desorption (Clarus 500, PerkinElmer, Waltham, MA, USA; Ekberg et al., 2009). The obtained chromatograms were analyzed using PARADISe software (Johnsen *et al.*, 2017) and the compounds identified by matching with the NIST mass spectral library. Terpene compounds were quantified by comparing to pure standards for identification and quantification of α-pinene, β-pinene, 3-carene, limonene, eucalyptol and caryophyllene, while for all other monoterpenes and sesquiterpenes, α -pinene and caryophyllene were used for quantification, respectively. BVOC emission rates were calculated for monoterpenes (MT) and sesquiterpenes (SQT), while the NIST-identified dataset with peak areas of all other compounds was used to describe the chemical composition of the emitted BVOC blend.

2.4 VEGETATION

2.4.1 SURVEYS

Vegetation was surveyed for **Paper I** in each plot using twenty 1 m^2 subplots within which cover of each species was visually estimated (Vowles *et al.*, 2017a). All identified species were grouped into growth form categories for further analyses. The growth forms are deciduous prostrate dwarf shrub, deciduous semi-prostrate dwarf shrub, deciduous tall shrub, evergreen prostrate dwarf shrub, evergreen semi-prostrate dwarf shrub, evergreen tall shrub, forb, graminoid, non-vascular species, and other which encompasses the percent ground cover attributable to abiotic and bare ground components.

Vegetation was also surveyed from LORI, SON, RIRI and RIGA during summer 2022 with five 0.25 m^2 subplots, for use in **Papers II and IV**. Vegetation data for the other sites involved in **Paper III** was collected from the last known survey completed at each site individually. These plant surveys were also ordered into growth forms, but these were grasses, sedges, forbs, evergreen and deciduous dwarf shrubs, and tall deciduous shrubs.

2.4.2 TRAITS

Plant functional traits were collected for **Paper II**, where within each plot 2 individual shrubs of each focal species, *B. nana* and *E. nigrum*, were selected to evaluate intraspecific plant traits. Leaves from *B. nana* and *E. nigrum* individuals were collected in July 2022 for leaf trait measurements and plant height was also recorded. Leaves were analyzed for dry matter content, leaf area, specific leaf area, total carbon, total nitrogen, $\delta^{13}C$, and $\delta^{15}N$. Leaf dry matter content was determined as the mass difference between field moist and dried leaves (at 70 °C for 6 hours). Leaf area was measured by scanning field moist leaves and determining area of each individual leaf with petiole attached with imageJ software (Schneider *et al.*, 2012). Specific leaf area is calculated as the leaf area divided by the leaf dry matter content. Five *B. nana* leaves and 10-15 *E. nigrum* leaves were fine ground and total carbon, $\delta^{13}C$, total nitrogen and $\delta^{15}N$ determined using an elemental analyzer (vario PYRO cube EA; Elementar, Manchester, UK) coupled online to a continuous flow Isoprime precisION isotope ratio mass spectrometer (Elementar, Manchester, UK) as described by Rijk *et al.*, 2023).

2.5 ABIOTIC CONDITIONS

For **Paper I**, temperature loggers (Tinytag plus 2 TGP-4020; Gemini Data Loggers, Chichester, UK) were placed in the centre of each plot which measured hourly soil temperatures at 2 cm depth for the duration of the experiment. From the temperature data, thawing degree-days (TDD), which is the sum of all mean daily temperatures above 0°C, were calculated from the soil temperature data according to Molau and Mølgaard (1996) for the period that the chambers were in the ground. Air temperature was also recorded hourly by one logger (Tinytag plus 2 TGP-4500; Gemini Data Loggers, Chichester, UK) at each site, at a height of approximately 2 m (Table S3). Mean temperatures were calculated from the loggers at each site for the experimental period. In order to obtain a mean temperature for a whole year, site means were calculated from June 12, 2013 – June 11, 2014, at the Långfjället sites and from June 27, 2013 – June 26, 2014, at the Ritsem sites. Minor gaps in the temperature series caused by malfunctioning loggers were filled in using linear regression against the logger which gave the highest R^2-value. Soil moisture was measured from the top 6 cm on the same sampling dates as ER using a Delta ML2x Theta probe (Delta-T Devices Ltd, Cambridge, U.K.). Moisture was measured as % water content in the soil (Fig. A1).

Plant Root Simulator (PRS®) Probes (Western Ag Innovations, Inc., Saskatoon, Canada), which contain ion exchange resin membranes, were used to measure soil NO_3^- and NH_4^+ availability *in situ* at each plot. Four cation and four anion probes were installed to 10 cm depth, close to the centre of each plot, at the beginning of the experimental period. Before the winter season, the probes were replaced which then measured NO_3^- and NH_4^+ availability until the end of the experiment. After removal, the probes were cleaned and sent to Western Ag Innovations in Saskatoon, Canada, for ion extraction and analysis.

In **Paper II**, soil temperature and moisture was measured in the field using TMS-4 loggers (TOMST Ltd. Czech Republic; Wild *et al.*, 2019) for the 2022 growing season. Two TMS-4 loggers were installed in each plot which measured soil temperature at 6 cm depth, +2 cm surface temperature, and air temperature at 15 cm above ground surface, as well as soil moisture at a frequency of 15 minutes. These data were used to determine daily, monthly, and seasonal average, maximum and minimum values for soil, surface and air temperature and soil moisture.

For **Papers III** and **IV**, air temperature and precipitation data were retrieved from CHELSA downscaled climate data for the period 1979-2016 for each site. This data was used to determine mean annual temperature, maximum annual temperature, minimum annual temperature, mean growing season temperature, maximum growing season temperature, minimum growing season temperature, mean annual precipitation, and mean growing season precipitation across the sites.

2.6 LIPID ANALYSES

For **Paper IV** ergosterol was extracted from each sand sample according to Bahr *et al.* (2013). Where lipids were extracted from 10 g of sand with 5 ml of 10% KOH followed by 15 minutes sonication and one hour at 70 °C. Phase-separation of the hydrophobic fraction was achieved using cyclohexane and centrifuging, with the upper aqueous phase containing ergosterol then transferred to a new sample, this step was repeated to ensure all ergosterol was collected. The sample was then dried under N_2 and 200 µL methanol added prior to heating the sample to 40 °C for 15 minutes. The sample was filtered through a 0.45 µm Teflon syringe and loaded into the HPLC. Ergosterol is used to estimate biomass of mycelia in the plots and over time (Wallander *et al.*, 2013; Ekblad *et al.*, 2016).

2.7 AMPLICON SEQUENCING

2.7.1 DNA EXTRACTION AND SEQUENCING

For **Papers III** and **IV**, DNA extraction was performed using Qiagen DNeasy PowerSoil Pro extraction kits following the manufacturers protocol to isolate environmental DNA from the soil samples in **Paper III** and the harvest scheme D mesh bags from **Paper IV**. The DNA is extracted from approximately 250 mg of soil or sand from each sample. For **Paper IV**, an extra wash step was included in the extraction protocol to help remove potential interfering humic compounds. The samples were then checked using Qubit dsDNA High Sensitivity Assays for the presence and concentration of DNA in the sample prior to PCR and stored in -20 °C until further analyses.

Two sets of PCR were performed using two pairs of primers targeting different regions of the fungal genome; an ITS1m–LR5 pair for amplifying

general fungal groups and an SSU515Fngs–AML2 pair to target arbuscular mycorrhizal fungi (AM) specifically. A reaction volume of 50 µL was used for PCR with 5 µL each of template DNA, forward and reverse primer and 0.5 µL of Phusion High-Fidelity DNA polymerase. Two reactions using the same ratios between each component but with a volume of 25 µL was used for **Paper III**. Thermocycling conditions for the ITS1m–LR5 region were an initial denaturation at 98 °C for 30 s followed by 25 cycles of denaturation at 98 °C for 10 s, annealing at 59 °C for 45 s and extension at 72 °C for 45 s, with a final extension for 10 minutes after the final cycle. Thermocycling conditions for the SSU515Fngs–AML2 primer pair were an initial denaturation at 98 °C for 30 s followed by 30 cycles of denaturation for 10 s, annealing at 58 °C for 30 s and extension at 72 °C for 30 s and a final extension for 7 minutes after the final cycle. A total of 232 PCR products were cleaned using Agencourt AMpure XP magbeads (Beckman Coulter, Brea, CA, USA) and quantified using Qubit dsDNA High Sensitivity Assays prior to pooling for equimolar concentrations. A maximum volume of 48 µL was used for samples with too low concentration. For **Paper IV** samples were pooled after Qubit but prior to cleaning which was done on the total sample afterward using the same magbead method. Samples were then sequenced by SciLife laboratories at the National Genomics Infrastructure in Uppsala, Sweden using two SMRT cells on the Sequel platform (Pacific Biosciences, Menlo Park, CA, USA).

2.7.2 BIOINFORMATICS

For **Papers III** and **IV**, Circular Consensus Sequence (CCS) reads were demultiplexed and primers removed for the ITS1m-LR5 samples using cutadapt v4.4 (Martin, 2011). Reads were checked in both directions and any reads where primers were detected in the reverse direction were reverse complemented prior to downstream filtering. The SSU515Fngs–AML2 samples were returned demultiplexed from Uppsala Genome Center, so only primers had to be removed. The samples were analyzed with the DADA2 pipeline (version 1.26.0). Amplicons were filtered using the filterAndTrim function with default parameters except for maxEE = 2, minLen = 50, and rm.Phix = TRUE, denoised with DADA2 function using default parameters, and chimeras removed using the removeBimera function. Denoised ASVs for the ITS1m–LR5 primer sequences were taxonomically assigned with PlutoF SH matching v2.0.0 (Abarenkov *et al.*, 2010) which performs open-reference clustering with the UNITE database (v9.0; Nilsson *et al.*, 2019) at thresholds from 97% - 99% sequence similarity. The 97% threshold was selected for

downstream statistics as it limited duplication of species assignments for species hypotheses (although duplication was still high; approximately 70%). After taxonomic assignment, species hypotheses that were identified to family level were sorted into functional guilds using FUNGuild (Nguyen *et al.*, 2016). Mycorrhizal fungi were selected for analysis in **Paper III**, while both total fungi and mycorrhizal fungi were selected in **Paper IV**. Taxonomy was assigned for the SSU515Fngs–AML2 ASVs using the assignTaxonomy function from DADA2, using a local download of the MaarjAM database as the reference (Öpik *et al.*, 2010). SSU515Fngs–AML2 ASVs which could not be assigned to order were removed. Additionally, all ASVs assigned were compared to the ITS1m–LR5 assignments and any ASVs overlapping in assignment at species level were removed from the AM fungal sequence dataset. All identified species from the SSU515ngs–AML2 dataset were AM species.

2.8 STATISTICAL ANALYSES

All statistical analyses were carried out with R statistical software version 4.2.1 (R Core Team, 2022). All statistics use an alpha of 0.05 for significance, with alpha of 0.1 referred to as marginally significant.

For **Paper I,** a mixed effects model with a rational quadratic correlation structure was used to explore differences in CO_2 flux between exclosures and ambient plots, with treatment, date, site and soil temperature as fixed factors and plot as random factor using the nlme package (Pinheiro *et al.*, 2023). The lsmeans package (Lenth, 2016) was used to test for treatment effects at individual sites, using pairwise t-tests with Bonferroni P-value adjustments. Model parameters were evaluated with a mixed model analysis of variance (ANOVA) for significance.

The differences in MT and SQT emissions from each site and treatment were evaluated using linear mixed effects models using the lme4 package (Bates *et al.*, 2015) on log transformed data, where the best performing model for MT data included site and treatment as fixed effects with plot and date as random effects, and the best performing model for SQT data included site, treatment and soil temperature as fixed effects with plot and date included as random effects. A linear mixed model was used to follow up on β-pinene differences using site and treatment as fixed effects, and plot and date as random effects. The differences in BVOC composition from each

measurement was evaluated using a redundancy analysis (RDA) ordination using the vegan package (Oksanen *et al.*, 2022) on Hellinger transformed total BVOC compound data. The interaction between herbivory and the shrub types was also evaluated through RDA and subsequent ANOVA. 85% Confidence ellipses were drawn for each group within the RDA as they have been shown to have a good fit with data without being too conservative as estimates (Payton *et al.*, 2000, 2003).

For **Paper II,** ANOVA was used to determine the effects of site, treatment, and focal shrub type on decomposition (k) and stabilization (S) prior to adding other explanatory variables. A follow-up Tukey HSD post-hoc test was used to determine the difference between any significant predictors in the ANOVAs. A factor analysis was used to reduce the dimensionality of the total dataset (including all explanatory variables) by determining composite factors composed of individual variables of soil properties and plant traits separately. The models were fit for three factors for both the plant traits and soil property data. For the plant traits, factor 2 (leaf dry matter content, $\delta^{15}N$ of the leaf, and plant height) was retained for use in the models. Factor 1 (leaf total nitrogen, specific leaf area, leaf $\delta^{13}C$, carbon:nitrogen ratio of the leaf, and leaf area) was replaced by specific leaf area alone to reduce multicollinearity after checking with variance inflation factors. Factor 3 was primarily composed of leaf total carbon and so leaf total carbon was retained in the final models. For the soil properties factor 2 (carbon:nitrogen ratio, $\delta^{13}C$, and $\delta^{15}N$) was retained for use in the models. Factor 1 (Total nitrogen and carbon, and soil organic matter) was replaced with soil organic matter alone after reducing multicollinearity. Factor 3 was primarily composed of pH and so pH itself was retained in the final models. These factors were then used for linear models for k and S, as well as a path analysis using a subset of parameters. The explanatory variables for the linear decomposition model were site, treatment, focal shrub type, factor 2 for soil, pH, factor 2 for traits, and soil moisture. The explanatory variables for the linear stabilization model were site, treatment, focal shrub type, soil organic matter, factor 2 for soil, pH, specific leaf area, factor 2 for traits, leaf total carbon, soil temperature, soil moisture, and treatment*shrub interaction. The explanatory variables used in the path analysis were site, treatment, shrub type, pH, factor 2 for soil, specific leaf area, factor 2 for traits, soil temperature and soil moisture.

RDA was used to ordinate the vegetation cover data at each site against all explanatory variables. A follow up ANOVA was used to find the effect of the explanatory variables on the vegetation composition.

For **Papers III and IV**. The phyloseq package (McMurdie & Holmes, 2013) was used for handling bioinformatic data, and relevant functions from the vegan and ecodist packages (Goslee & Urban, 2007; Oksanen *et al.*, 2022) were used for community dissimilarity ordinations. In **Paper III**, the mycorrhiza communities were split into three main datasets: EcM/ErM species (from the ITS1m–LR5 primer pair sequences), AM species (from the SSU515Fngs–AML2 primer pair sequences), and total mycorrhizal community (both datasets merged).

Canonical Correspondence Analysis (CCA) was used as a constrained ordination for both **Paper III** and **IV** to evaluate species dissimilarity between plots, using Bray-Curtis distances, against soil properties and climate variables. Variable selection was performed with correlation matrix and variance inflation factor tests to reduce multicollinearity in between independent variables. Species presence/absence (P/A) data was used for **Paper III**, where the final model for the plot level soil property data included the community dissimilarity matrix against site, treatment, pH, total carbon, carbon:nitrogen ratio, $\delta^{13}C$, and $\delta^{15}N$. The final model for the site level climate data included community dissimilarity matrix against site, treatment, mean air temperature, and precipitation. Follow-up ANOVAs were performed to evaluate the effect of the independent variables on the mycorrhizal fungi community. Permutational Analysis of Variance (PERMANOVA) was performed for all mycorrhizal communities using the ordiR2step function from vegan for forward model selection as the models were overfit with the full parameters. For the EcM/ErM community, site and total nitrogen were selected; for the AM community, site, treatment, carbon:nitrogen ratio, and precipitation were selected; and for the total community, site and total nitrogen were selected. Treatment was added to all models regardless of selection as it is the parameter of interest. A separate CCA was performed to evaluate community dissimilarity influence by vascular plant functional types as vegetation community is expected to be a major driver of mycorrhizal community composition. Differences in soil properties between treatment conditions were calculated using student's t-test for each site individually.

Rarefied abundance data was used for the CCA in **Paper IV** to evaluate differences in total fungal community and mycorrhizal fungal community composition between sites and treatment conditions, as well as soil properties and percent cover of plant functional types. Analysis of Variance (ANOVA) was performed to evaluate the effect of the independent variables on the fungal communities following the CCA. PERMANOVA was used to follow up on the

constrained ordination comparing the total fungi and mycorrhizal fungi communities to pH, total nitrogen, and $\delta^{15}N$. A second PERMANOVA was also performed to evaluate the influence of soil organic matter, total carbon, and $\delta^{13}C$ as they vary between sites but were not selected by variance inflation factor testing. Linear models were used to determine the effects of reindeer density index from the three sites (Sundqvist et al., 2019) on total and mycorrhizal fungi richness and diversity in the ambient plots.

Species richness and Shannon diversity were calculated for each site and treatment condition for both total fungal species and mycorrhizal fungi species only. Shannon diversity includes a measure of community evenness whereas species richness is solely the observed number of species between each site and treatment condition. ANOVA were used to evaluate the effect of site and treatment on species richness and Shannon diversity.

Fungal biomass carbon was calculated for the full mesh bags (40 g sand in 3.14 cm^2 area) from the extracted ergosterol after applying a correction factor of 1/0.62 to account for partial extraction of ergosterol from the sample (Montgomery *et al.*, 2000) and using a ratio of 0.3% ergosterol in fungal biomass (Ekblad *et al.*, 2016; Hagenbo *et al.*, 2017). Biomass was converted to biomass carbon using a ratio of 45% of biomass made up of carbon (Ekblad *et al.*, 2016; Hagenbo *et al.*, 2017). Fungal biomass + necromass was calculated from the LOI measurements assuming the vast majority of the material in the mesh bags was fungal mycelia. Changes in fungal biomass over time were evaluated with a linear model, and differences between harvests was evaluated with ANOVA. Similarly, differences between harvests in biomass + necromass was evaluated with an ANOVA.

3 RESULTS AND DISCUSSION

3.1 TRACE GAS FLUXES

3.1.1 BVOC EMISSIONS

Herbivory had a significant impact on the composition of BVOCs emitted, seemingly through the composition of shrub species at each site (Fig. 3). The four sites investigated were separated based on BVOC composition, and this coincided with differences in the dominant shrub growth forms at these sites. In general, removing herbivores tended to shift BVOC composition towards one more similar to the mountain birch community LOMB. Additionally, of the interactions between treatment and shrub types that were investigated, only deciduous prostrate shrubs were significant drivers of BVOC composition. These shrubs likely contribute disproportionately to BVOC composition, or are more sensitive to changes in herbivory (Vowles *et al.*, 2017a,b). Shifts in shrub and graminoid abundance can have a large effect on certain types of BVOC emissions (Rinnan *et al.*, 2020; Wester-Larsen *et al.*, 2020; Männistö *et al.*, 2023). However, we did not observe any effect of herbivory on the emission rates of BVOC compounds, although they did vary by site and showed a potential relationship with soil temperature.

Two specific compounds had a large correlation with the dissimilarity of BVOC composition between measurements, which were β-pinene and 2-ethylfuran. These compounds showed a close trajectory to the treatment effect (Fig. 3) which may indicate that these compounds become more prevalent when herbivores are excluded. β-pinene is a monoterpene commonly produced by many species and is generally associated with defensive and antimicrobial properties, in particular it has been shown to affect bacteria, fungi and insect larvae (Mercier *et al.*, 2009; Silva *et al.*, 2012). 2-ethylfuran is predominantly a plant defensive chemical with antimicrobial properties shown to be effective against fungi, nematodes and can also inhibit seed germination in some species (Bradow & Connick, 1990; Aissani *et al.*, 2015; Lazazzara *et al.*, 2018). It has also been found to be emitted in BVOC samples from mountain birch and tundra ecosystems (Wester-Larsen *et al.*, 2020; Ryde *et al.*, 2021), although in low amounts.

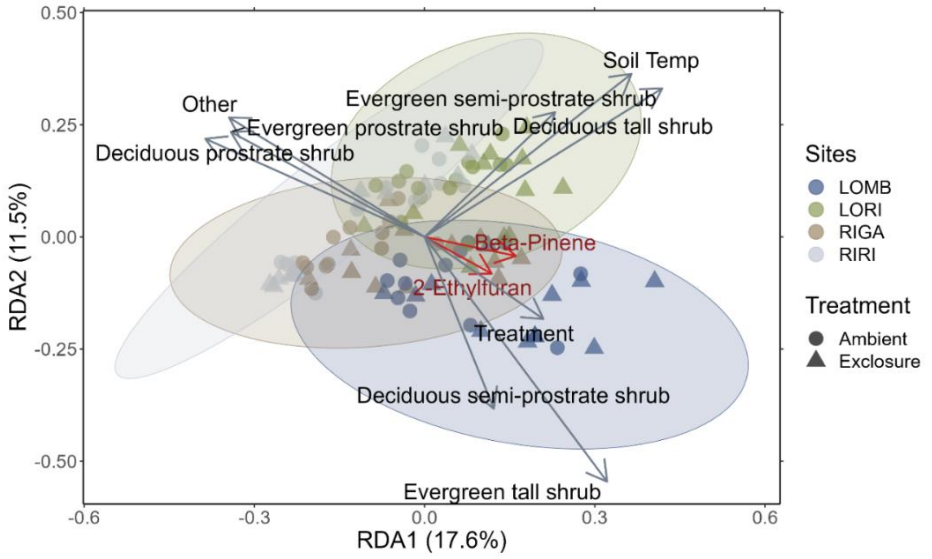

Fig. 3. *Redundancy analysis of BVOC compounds emitted from each site constrained by environmental properties. Circles represent ambient and triangles exclosure plots. Vectors correspond to significant environmental variables with the length of the vector representing the strength of the relationship. The treatment vector points towards the exclosure condition where herbivores are excluded. Ellipses are 85% confidence ellipses that correspond to the standard deviation of the plotted points for each site separately. The red vectors correspond to the BVOC compounds with correlation values greater than 0.7. Treatment, soil temperature, percent cover of abiotic components and all shrub categories were significantly related to the composition of BVOCs emitted from each measurement (sites scores).*

3.1.2 ECOSYSTEM RESPIRATION

Herbivory reduced growing season ecosystem respiration, but only in the meadow site RIGA (Fig. 4). RIGA also has the highest ER out of the four sites, which makes sense as it has the highest plant productivity (Vowles *et al.*, 2017a; Treat *et al.*, 2018). The higher productivity may make observation of a herbivory effect more likely at RIGA compared to the other sites. In general, ER was more strongly affected by site than herbivory. Soil temperature was also a significant driver for ER and coincided with the difference between the treatment conditions at RIGA. Thus, herbivory may indirectly affect soil temperature through trampling (Heggenes *et al.*, 2017), modifying the vegetation community (Myers-smith *et al.*, 2011; Kropp *et al.*, 2021), and/or by modifying microbial communities (Stark & Grellmann, 2002; Koltz *et al.*, 2022).

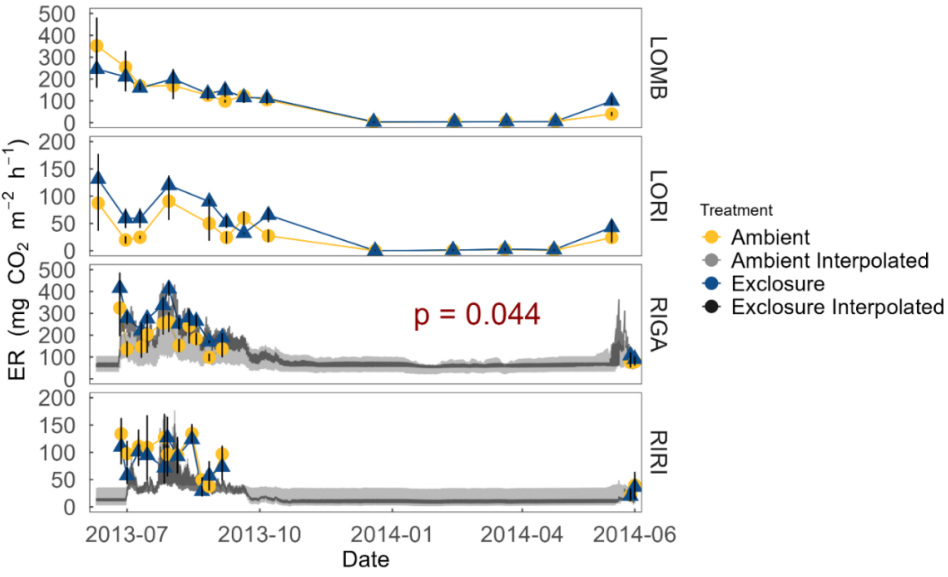

Fig. 4. *ER at each site measured year-round from July 2013 to July 2014. ER was not measured over-winter in the Ritsem sites. Interpolated ER using associated Q_{10}-values is also plotted for sites with a significant growing season Arrhenius relationship (α = 0.05) as an estimate of ER on a shorter temporal scale. Exclosure and ambient treatments were not significantly different, except in RIGA where exclosure plots consistently had higher ER during the growing season. Error bars denote standard error of the mean.*

3.2 DECOMPOSITION

3.2.1 DECOMPOSITION AND STABILIZATION

The changes observed in trace gas fluxes, due in part to herbivory, are related to changes in the cycling of carbon in the soil, such as the decomposition rate and stabilization of organic material. We found that herbivory had an indirect effect on stabilization under *Betula* shrubs in LORI but was otherwise not significant for decomposition or stabilization (Fig. 5). However, there were significant differences between the shrub heath sites in their decomposition rate and stabilization, generally due to differences in the deciduous and evergreen shrubs. LORI had an overall 31% lower decomposition rate and 6% higher stabilization than RIRI. The difference in decomposition rate was primarily due to slow decomposition under LORI *Betula* shrubs, whereas the *Empetrum* and exclosure *Betula* had higher stabilization.

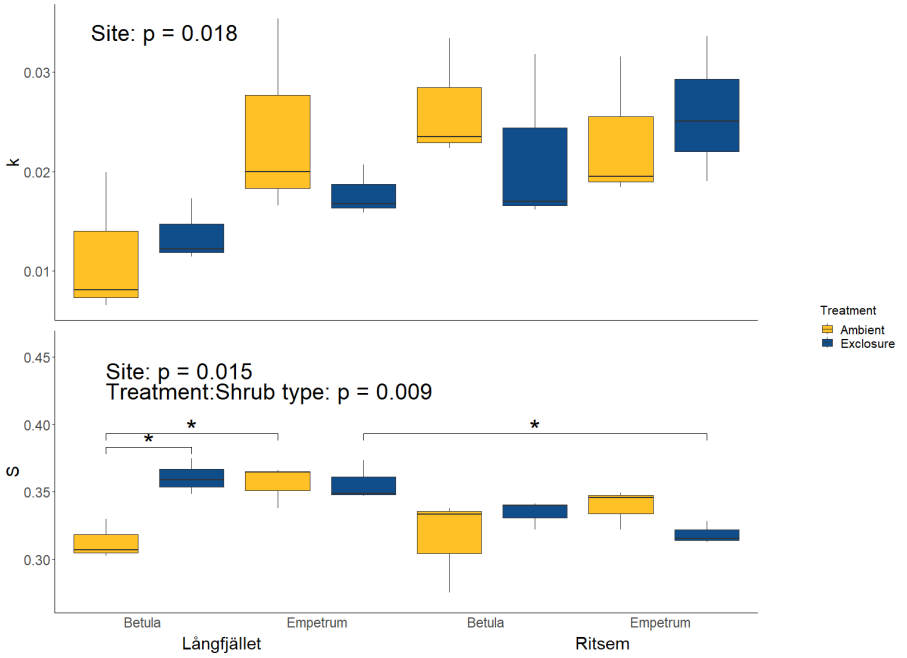

Fig. 5. *Decomposition (k) and Stabilization (S) rates at each site and treatment condition under each shrub type. The square brackets denote significance between pairwise comparisons. Significant differences between factors (Site, Treatment, Shrub type, or their interactions) are annotated on the panel directly.*

The variance in the decomposition rates was partially explained by negative relationships with carbon:nitrogen ratio, $\delta^{13}C$, and $\delta^{15}N$. Carbon:nitrogen ratio differences could be due to litter from Ritsem *Betula* having a higher amount of nitrogen relative to carbon, which selects for microbial communities better acclimatized to quickly decompose new labile carbon and nitrogen sources in the soil (Hicks *et al.*, 2022; Yan *et al.*, 2023). $\delta^{13}C$ is affected by decomposition due to preferential substrate use and fractionation (Drollinger *et al.*, 2019), which drives this relationship. Lower $\delta^{15}N$ in at the soil surface can result from litter addition that is depleted in ^{15}N, which will contribute to the buildup of organic matter (Högberg, 1997). ^{15}N depleted vascular plant litter can occur as a consequence of mycorrhizal fungi derived nitrogen, where the nitrogen taken up by the fungi is at a $\delta^{15}N$ signature similar to the bulk soil but the transfer compounds produced by the fungi and passed to the plant are depleted in ^{15}N, consequently enriching the fungi and depleting the plant (Hobbie & Hobbie, 2008; Hobbie *et al.*, 2009). Soil $\delta^{15}N$ signature can indicate prevalence of mycorrhiza types where low values indicate ErM fungi, medium values EcM fungi, and high values AM fungi or

non-mycorrhizal (Michelsen *et al.*, 1996, 1998; Read & Perez-Moreno, 2003; Barthelemy *et al.*, 2017). The patterns of $\delta^{15}N$ could also be related to the overall composition of different plant types (Fig. 6), especially the difference in cryptogamic species.

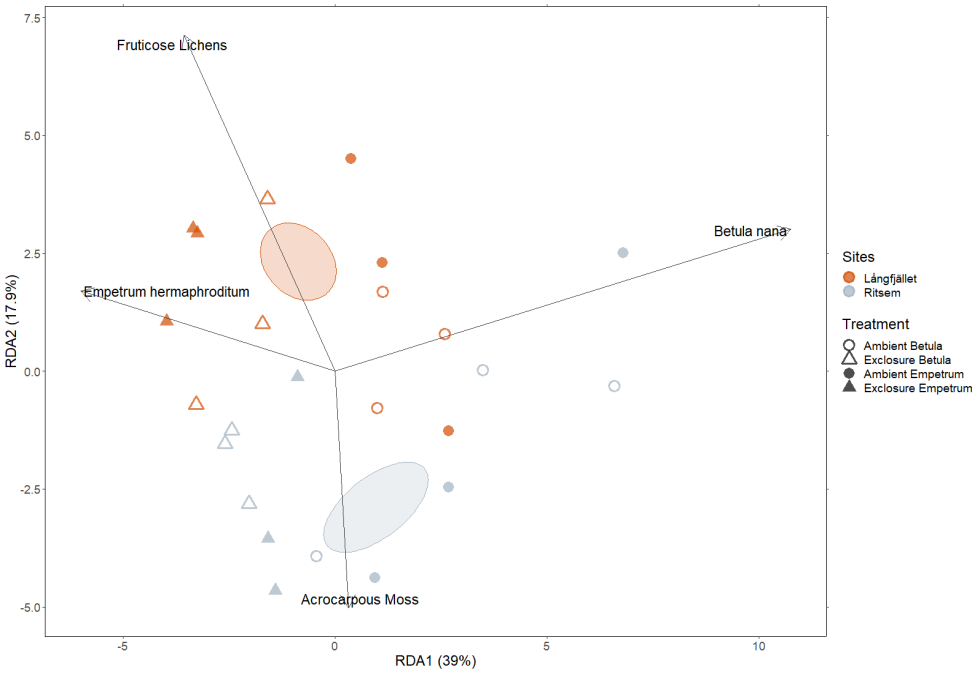

Fig. 6. *Vegetation RDA between sites and treatments. Vectors show significant species or functional groupings that distinguish between the sites, ellipses are the standard error of centroid for each site. The sites are primarily distinguished by non-vascular plants and the two focal shrub species of our study.*

The differences in stabilization between sites may also be due to differences in the microbial community as the enzymes microbe species use to break down organic material, and the composition of the microbe's tissues contribute to differences in stabilization (Fernandez *et al.*, 2016; See *et al.*, 2019; Prescott & Vesterdal, 2021). For example, EcM associated with deciduous shrubs like *Betula* and ErM that are associated with ericoid shrubs like *Empetrum*, play a prominent role in stabilization by forming stable organic residues during decomposition (Fernandez *et al.*, 2016). Herbivory has previously been shown to shift the dominance of these mycorrhizal types in tundra communities (Vowles *et al.*, 2018; Ylänne *et al.*, 2021). The low stabilization under ambient *Betula* in LORI could be due to herbivory

promoting a microbial community that differ in the modality of decomposition, where fewer stable residues are formed under these conditions; potentially a community shift towards more EcM compared to ErM, or a dominance of saprotroph or bacterial decomposers.

3.3 MYCORRHIZAL FUNGI

3.3.1 ARCTIC WIDE

Three major types of mycorrhizal fungi were captured by the data: EcM, ErM, and AM (Fig. 2, Fig. 7). The samples contained 150 mycorrhizal species within 3 phyla, 6 classes and 13 orders (Fig. 7). Of these species, EcM accounted for 82%, while ErM made up 2% and AM contained the remaining 14%.

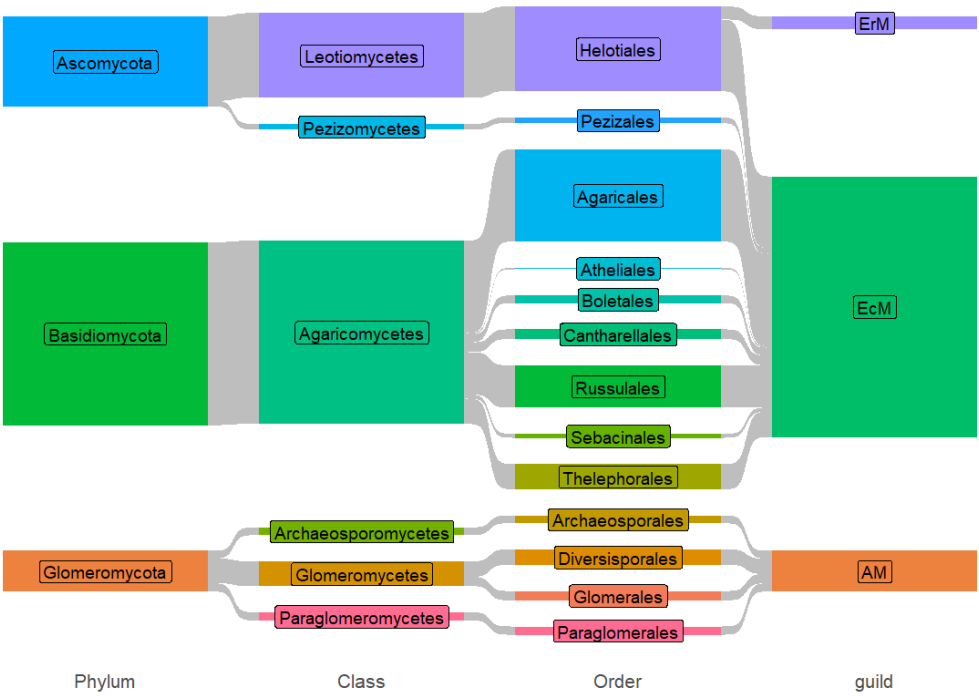

Fig. 7. *Overall proportion of unique mycorrhizal species separated into phylum, class, order, and guild. The height of each rectangle represents the number of unique species belonging to that group, and connections between columns indicate the proportion which belongs to both groups. EcM refers to ectomycorrhiza, ErM to ericoid mycorrhiza, and AM to arbuscular mycorrhiza.*

Herbivory had a weak effect on AM fungal species found across our sites (Fig. 8), where *Ambispora* spp. was most positively influenced by herbivory across the Arctic. AM species were not found to vary strongly with herbivory previously (Ruotsalainen & Eskelinen, 2011; Kytöviita & Olofsson, 2021). However under certain site conditions, i.e. low pH, high fertility soils, herbivory did increase AM colonization of plant root tips (Ruotsalainen & Eskelinen, 2011). The difference in the response of AM fungi to herbivory could therefore be tied to local plant and soil conditions, as AM fungi were also impacted by pH in our study. High grazing pressure can shift a site towards more meadow-like vegetation (Olofsson *et al.*, 2001, 2004a; van der Wal, 2006; Barthelemy *et al.*, 2017; Vowles *et al.*, 2017b), which coincides with increased AM and saprotrophic fungi (Ahonen *et al.*, 2021). Sedges were significant for explaining the dissimilarity in mycorrhizal species (Fig. 9), although they are generally non-mycorrhizal they can also form AM (Muthukumar *et al.*, 2004; Smith & Read, 2008), and increased towards the meadow site RIGA. High grazing pressure also includes increased trampling and snow compaction of a site which can warm the soil during the growing season potentially releasing AM fungi from their cold limitation, although it also makes winter soil temperatures colder (Yan *et al.*, 2018; Ylänne *et al.*, 2018; Fischer *et al.*, 2022). Changes in conditions suitable for AM fungi, such as warmer temperatures and meadow vegetation, may increase their prevalence in the Arctic.

The mycorrhizal fungi communities differed between sites, where the Russian, North American and Icelandic sites (UTQ, ERK, YUK, TOO and AUD) were generally separated from the Fennoscandian sites (Fig. 8). This also coincided with a gradient in total carbon which increased towards the coldest sites (ERK, TOO, UTQ and YUK). These sites were distinguished by EcM species with an increased abundance of *Oidiodendron* spp. (*O. majus*, *O. periconoides*, and *O. pilicola*) and *Fayodia gracilipes,* as well as a decreased abundance of *Lactarius* spp. (*L. trivalis*) and *Polyozellus umbrinus*. Herbivory was previously being identified as an important driver for Arctic EcM and ErM mycorrhizal community composition (Timling *et al.*, 2012; Santalahti *et al.*, 2018; Vowles & Björk, 2019; Botnen *et al.*, 2020; Van Geel *et al.*, 2020; Ahonen *et al.*, 2021). There was no overall effect in our data, however when evaluating single sites, we did see an impact of herbivory at ERK, LAN (LORI), RIG (RIGA), and UTQ. The impact of herbivory may be primarily local scale, except in the case of AM where it may also coincide with a large-scale reduction in temperature limitation for these fungi.

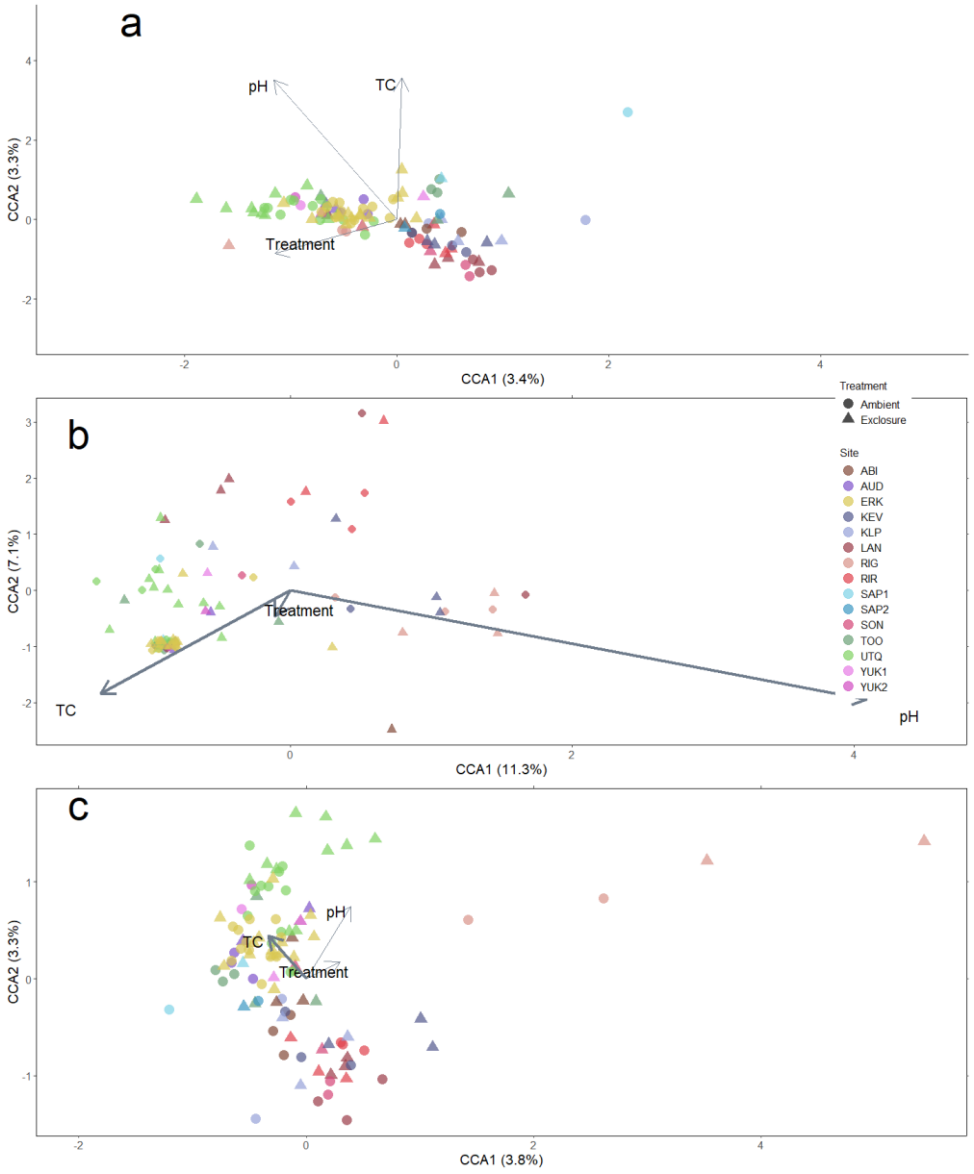

Fig. 8. *Canonical Correspondence Analysis (CCA) plot of Bray-Curtis dissimilarity matrix based on the presence of mycorrhizal species for:* ***A)*** *the EcM/ErM community composition,* ***B)*** *the AM community composition (note that no AM species was found in SON and AUD), and* ***C)*** *the total community composition. Each point corresponds to a plot's mycorrhizal community ordinated relative to other plots by their dissimilarity in community composition. Vectors belong to soil property predictors (TC = total carbon; pH) significant in at least one of the mycorrhizal communities, with thicker vectors indicating the property is significant at an alpha of 0.1 for that specific community. Altogether the graphs account for 7% - 18% of variance in mycorrhizal species composition between sites.*

The mycorrhizal fungi communities were also affected by soil conditions, where the total mycorrhizal fungi community varied along a total carbon gradient, and the AM fungi community varied with total carbon and pH. *Cortinarius* and *Inocybe*, two EcM genera, tended to increase alongside total carbon in our data. Increases in soil carbon have been linked to higher cover of EcM forming plants and relative abundance of EcM fungi corresponding to heath communities (Clemmensen *et al.*, 2021). Conversely, AM plants reduced soil carbon relative to non-mycorrhizal controls while EcM did not (Wurzburger & Brookshire, 2017). Soil pH is a strong driver of fungal community composition as some fungi are sensitive to pH differences (Yamanaka, 2003; Fujimura & Egger, 2012; Timling & Taylor, 2012; Zhang *et al.*, 2016; Tedersoo *et al.*, 2020). The AM genera *Acaulospora*, *Diversispora*, *Glomus*, and *Claroideoglomus* increased along the pH gradient, generally coinciding with the RIGA communities.

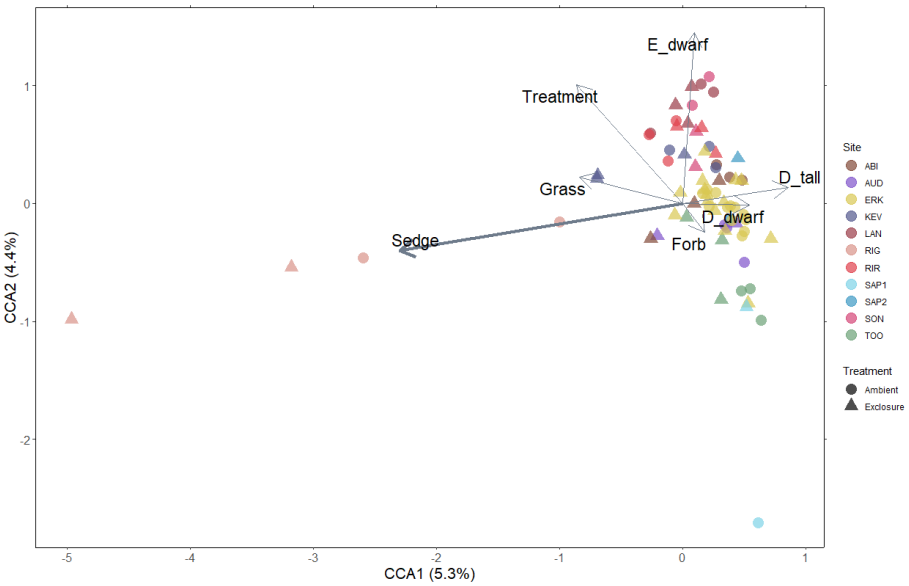

Fig. 9. *CCA analysis comparing mycorrhizal communities between sites based on percent cover of Plant Functional Types (PFT) at each site with available data. Each point corresponds to a plot's mycorrhizal community ordinated relative to other plots by their dissimilarity in community composition. Triangles are exclosure plots while circles are ambient plots. Vectors belong to percent cover of PFT predictors with thicker vectors indicating the property is significant at an alpha of 0.1. D_tall = Deciduous tall shrub, D_dwarf = deciduous dwarf shrub, E_dwarf = evergreen dwarf shrub. Sedges were the only PFT that showed a significant correlation with the mycorrhizal fungi data. Altogether the PFTs account for 9.7% of the variance in the mycorrhizal fungi community composition.*

3.3.2 WITHIN SWEDEN

Mycorrhizal fungi made up nearly 1/3 of the total fungi identified in the mesh bags. Of the mycorrhizal fungi species identified, EcM fungi comprised approximately 63%, ErM fungi were 7%, and AM fungi were 31%. Herbivory significantly affected the total and mycorrhizal fungi community composition (Fig. 10), predominantly through EcM fungi. The direction of the herbivore exclusion condition was close to the vector for the EcM genus *Helotiales*, indicating these species may be more common in the total fungi community when herbivores are removed. Similarly, *Tomentella* and *Seredipita* species were closely aligned to herbivore exclusion in the mycorrhizal fungi community. This more closely aligns with previous research (Santalahti *et al.*, 2018; Vowles *et al.*, 2018; Ylänne *et al.*, 2021), than the Arctic wide survey which may reinforce the idea that herbivory drives differences in EcM at a local scale. The herbivory effect is likely due to changes in vegetation as all the functional types were significant for fungal community composition.

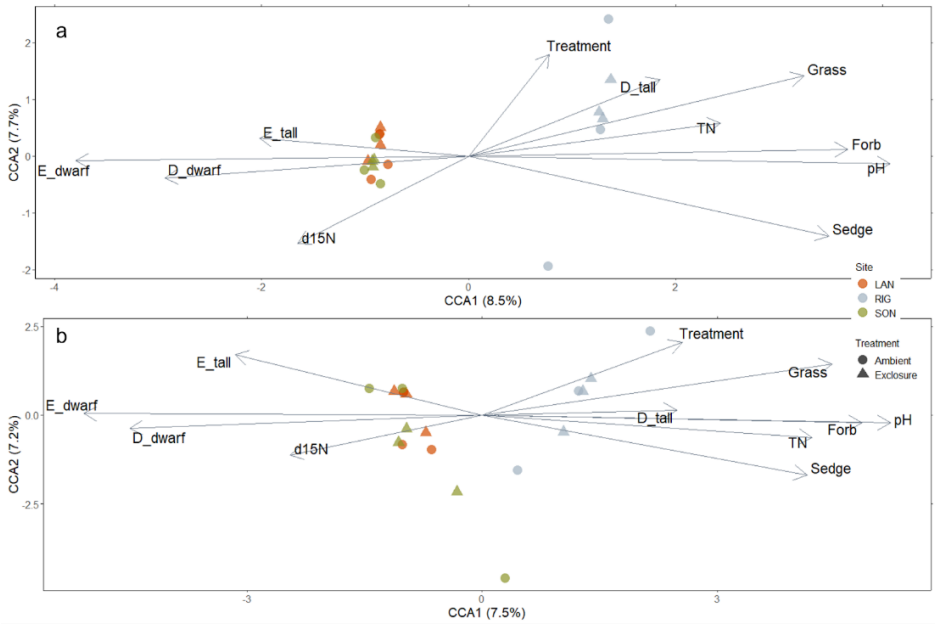

Fig. 11. *CCA ordination of* **a)** *total fungi composition and* **b)** *mycorrhizal fungi composition differences between sites and treatment conditions for rarefied sequence data. Triangles are exclosure plots and circles ambient. Grey vectors indicate significant environmental properties correlated with the dissimilarity between sites. In both cases treatment, total nitrogen (TN) and pH point towards RIG (RIGA) while* $\delta^{15}N$ *(d15N) points towards the southern heath sites.*

The heath sites coincided with increased abundance of the EcM species *Oidiodendron tenuissimum* and *Leccinum rotundifoliae*, whereas the meadow site was related to several other EcM species and AM species. Herbivory did not affect ErM fungi composition which may be due to herbivory not affecting evergreen shrub cover at our sites (Vowles *et al.*, 2017a,b). The meadow site, with high cover of graminoids and forbs (Vowles *et al.*, 2017b; Sundqvist *et al.*, 2019), coincided with an increased abundance of AM and some EcM fungi species, potentially using tall deciduous shrubs as hosts, and consequently high fungal species richness.

Herbivory had a negative impact on species richness in RIGA which was the site with the highest species richness and diversity of mycorrhizal fungi. Fungal species richness and diversity varied by site, likely due to differences in plant species richness and composition in the different habitat types (Timling *et al.*, 2012; Yang *et al.*, 2017; Masumoto *et al.*, 2021). The diversity of total fungal species was low in the meadow (RIGA) compared to a heath site indicating higher dominance of taxa in the meadow. SON had the lowest species richness, but highest diversity of total soil fungi. The low richness may be related to low plant species richness, as host plant diversity can coincide with low fungal diversity in some sites (Yang *et al.*, 2017), however, plant species richness was also low in LORI which had higher fungal species richness. Variation in abiotic conditions can be a stronger determinant of fungal composition and diversity than vegetation alone (Tedersoo *et al.*, 2012; Grau *et al.*, 2017; Collins *et al.*, 2018), which may correspond to the differences between the heath sites.

Total fungal and mycorrhizal fungi composition dissimilarity between the Swedish sites was related to gradients in soil pH and $\delta^{13}C$. Soil pH was indicated previously as important determinant of mycorrhizal fungi communities (Ruotsalainen & Eskelinen, 2011; Timling & Taylor, 2012; Zhang *et al.*, 2016; **Paper III**). Fungal composition may be related to soil $\delta^{13}C$ as they impact the isotope signature in the soil through preferential substrate use and fractionation during respiration (Hobbie *et al.*, 1999; Godbold *et al.*, 2006; Drollinger *et al.*, 2019). Differences in carbon input into the soil between fungi and plants (Hobbie *et al.*, 2004; Godbold *et al.*, 2006), and even different fungal types (Hobbie *et al.*, 1999, 2004) will affect the $\delta^{13}C$. Changes in the soil conditions will select for different communities of soil fungi which will have reciprocal effects on soil conditions.

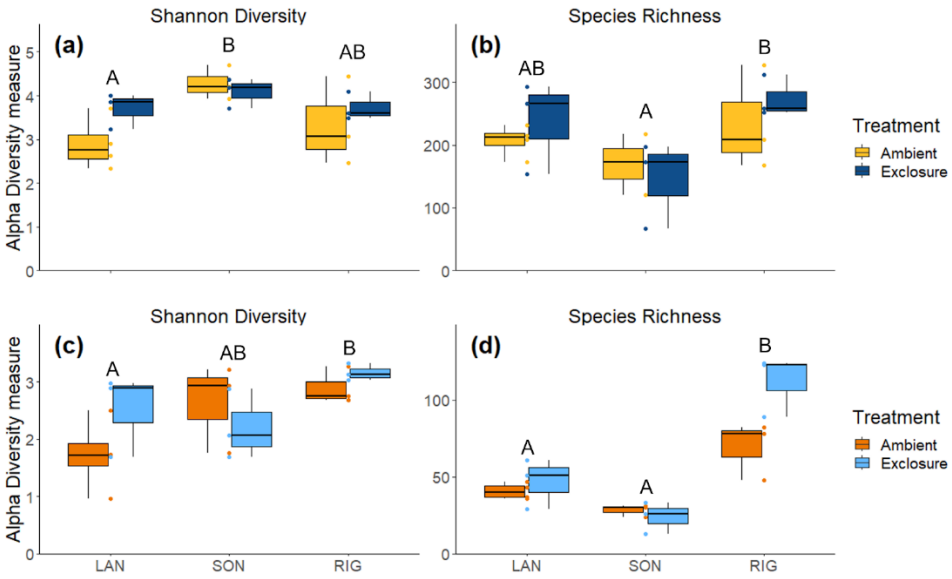

Fig. 10. *Total fungal and mycorrhizal specific fungi species richness and Shannon diversity between sites and treatment conditions.* ***a)*** *Shannon diversity, which incorporates both richness and evenness, for the total fungal communities,* ***b)*** *species richness in the total fungal communities.* ***c)*** *Shannon diversity for the mycorrhizal fungal communities and* ***d)*** *species richness in the mycorrhizal fungal communities. Letters within each panel denote significance between sites, there were no significant effects of herbivory on species richness or diversity.*

The mycelial carbon, both biomass and total mass, is a bit lower than that reported previously in forests (Ekblad *et al.*, 2016; Hagenbo *et al.*, 2017), but higher than previous values reported for tundra (Vowles *et al.*, 2018). There was a large amount of fungal necromass in the mesh bags, but this did not follow a consistent pattern over time. Mycelia production varies seasonally (Šťursová *et al.*, 2020), and this variation is also tied to different components of the fungal community, where different fungal assemblages contribute to production of mycelia at different magnitudes (Hagenbo *et al.*, 2018, 2021; Šťursová *et al.*, 2020; Cheeke *et al.*, 2021). Interannual variation in mycelia production could be influenced by the amount of fungal species turnover (Cook *et al.*, 2023), and variation in climate and soil conditions between years (Ernakovich *et al.*, 2014).

4 CONCLUSION

Herbivory alters BVOC emission composition by altering the proportion of shrub species in a community. It also affects the magnitude of ER in a productive meadow community; however, this effect was not related to differences in vegetation composition. The differences in CO_2 emission from a site is related to the cycling of carbon belowground in terms of decomposition and stabilization of organic matter. Herbivory influenced stabilization under *Betula* but did not affect decomposition rates. Rather, decomposition was primarily related to plant community and soil conditions at the heath communities. Intraspecific shrub traits had a marginal impact on decomposition rates, but soil properties were more important for both decomposition and stabilization. Our results suggest that the microbial community associated with dominant vegetation types may have a large control over decomposition and stabilization. In particular, mycorrhizal fungi likely have a strong effect on these parameters and the mycorrhizal community may be impacted by herbivory. Herbivory negatively influenced the number of AM fungal species across the whole Arctic, while EcM were important only on local scales. Vegetation and soil conditions were important for mycorrhizal fungi community composition across the Arctic, with gradients in total carbon, pH, and cover of sedges were particularly important for community dissimilarity. Within Sweden, herbivory primarily affected EcM fungal groups and reduced mycorrhizal fungi species richness in a productive meadow community. Differences in plant community types in terms of dominant plant functional types and soil conditions drove the variation in soil fungal communities. Mycelia biomass was similar between both community types but was not impacted by herbivory. Overall, herbivores tend to have localized, indirect, but significant effects on mycorrhizal fungi communities, which may drive differences in decomposition and stabilization which in turn impact the magnitude of carbon released from the soil. Of particular interest to all of these processes seems to be high productive, grass-dominated meadow communities which seem to be sensitive to herbivory driven changes in plant and fungal composition with potential carry-over effects on ER.

The influence of large mammals on graminoid and shrub dynamics likely drives the effects on ER, decomposition, and mycorrhizal community, as these species have a substantial effect on ecosystem productivity and the species richness of mycorrhizal fungi. Predicted changes in plant communities, especially shrub encroachment, will feedback onto climate change through

their effect on carbon fluxes and these effects may be situationally mediated by herbivory. The variation in vegetation communities across the Arctic likely influences how readily mycorrhizal fungi types will react to altered biotic or environmental conditions. The simultaneous interaction between bottom-up processes by climate and edaphic properties and top-down processes by herbivores and biotic interactions on vegetation communities determines the species likely to comprise the mycorrhizal community in an area.

5 FUTURE PERSPECTIVES

This thesis highlights several processes connecting microbial communities and carbon emissions from tundra ecosystems. Considerable focus should be put on linking these processes explicitly to determine the magnitude of interactions between mycorrhizal fungi communities, decomposition/ stabilization, and ER, and their net effect on carbon storage and release from tundra soils.

Paper I indicates effects of herbivores on trace gas fluxes, however, higher temporal resolution may be useful to uncover seasonality in these processes and identify when they are most sensitive to herbivory impacts. Also, linking the differences in these parameters to the microbial communities in the soil may provide a clearer picture of the mechanisms by which herbivore-plant-soil interactions affect carbon emissions.

Paper II highlights differences in decomposition and stabilization under different shrub types and links these processes to potential differences in mycorrhizal fungi. Explicit consideration of the active fungal community under these shrubs and its subsequent effect on decomposition is necessary to elucidate the effect of fungal communities on carbon cycling in the soil.

Papers III and **IV** demonstrate differences in soil fungal communities across the Arctic, which may also be related to the variation in tundra community types. Identifying differences in response to climate impacts by different tundra communities can provide a better understanding of the overall change in the Arctic. Detailed examination of mycelia production and turnover across the Arctic will elucidate differences in carbon cycling connected to mycorrhizal fungi community assemblages.

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