Herbivory effects on soil fungi communities across the Arctic

Cole G. Brachmann*[1,2], Martin Ryberg[3], Brendan R. Furneaux[4], Anna Rosling[5], Tingrui Xu[1], Alf Ekblad[6], Isabel C. Barrio[7], M. Syndonia Bret-Harte[8,9], Hannu Fritze[10], Laura Gough[11], Robert D. Hollister[12], Ingibjörg S. Jónsdóttir[13], Oula Kalttopää[14], Elin Lindén[15], Päivi Mikkola[16], Johan Olofsson[15], Rauni Partanen[14], Kirsten A. Reid[16], Aleksandr Sokolov[17], Svetlana Abdulmanova[17], Maija S. Sujala[14], Maja K. Sundqvist[18], Otso Suominen[19], Craig E. Tweedie[20], Amanda Young[9], and Robert G. Björk[1,2]

[1]Department of Earth Sciences, University of Gothenburg, SE-405 30 Gothenburg, Sweden.

[2]Gothenburg Global Biodiversity Centre, University of Gothenburg, SE-405 30 Gothenburg, Sweden.

[3]Department of Organismal Biology, Uppsala University, SE-752 36 Uppsala, Sweden.

[4]Department of Biological and Environmental Science, University of Jyväskylä, FI-40014 Jyväskylä, Finland.

[5]Department of Ecology and Genetics, Uppsala University, SE-752 36, Uppsala, Sweden.

[6]School of Science and Technology, Örebro University, Örebro, Sweden.

[7]Faculty of Environmental and Forest Sciences, Agricultural University of Iceland, Árleynir 22, 112 Reykjavík, Iceland.

[8]Department of Biology and Wildlife, University of Alaska Fairbanks, 99775 Fairbanks, Alaska, USA.

[9]Toolik Field Station, Institute of Arctic Biology, University of Alaska Fairbanks, 99775 Fairbanks, Alaska, USA.

[10]Natural Resources Institute Finland, Latokartanonkaari 9, 00790 Helsinki, Finland.

[11]Department of Biology, Towson University, Towson, MD 21252 USA.

[12]Department of Biology, Grand Valley State University, Allendale, MI 49504 USA.

[13]Institute of Life and Environmental Sciences, University of Iceland, 102 Reykjavík, Iceland

[14]Kilpisjärvi Biological Station, University of Helsinki, FI-99490, Kilpisjärvi, Finland.

[15]Department of Ecology and Environmental Science, Umeå University, SE90187 Umeå, Sweden.

[16]Department of Geography, Memorial University of Newfoundland and Labrador, St. John's, NL, A1B 3X9.

[17]Arctic research station of Institute of plant and animal ecology, Ural branch, Russian academy of sciences, 629400, Zelenaya Gorka Str., 21, Labytnangi, Russia.

[18]Department of Forest Ecology and Management, Swedish University of Agricultural Sciences (SLU), Umeå, 901 83 Sweden.

[19] Biodiversity Unit, Kevo Subarctic Research Institute, FI-20014 University of Turku, Finland.

[20]Department of Biological Sciences and the Environmental Science and Engineering Program, The University of Texas at El Paso, El Paso, Texas 79968, USA.

*Corresponding author: Cole G. Brachmann, cole.brachmann@gu.se

ORCIDs

Cole G. Brachmann; 0000-0001-8345-3141

Martin Ryberg; 0000-0002-6795-4349

Brendan R. Furneaux; 0000-0003-3522-7363

Anna Rosling; 000-0002-7003-5941

Tinghai Ou; 0000-0002-6847-4099

Alf Ekblad; 0000-0003-4384-5014

Isabel C Barrio; 0000-0002-8120-5248

M. Sydonia Bret-Harte; 0000-0001-5151-3947

Hannu Fritze; 0000-0003-4347-4444

Laura Gough; 0000-0002-9312-7910

Robert D. Hollister; 0000-0002-4764-7691

Ingibjörg S. Jónsdóttir; 0000-0003-3804-7077

Elin Lindén; 0000-0002-4060-011

Päivi Mäkiranta; 0000-0002-9

Johan Olofsson; 0000-0002-6

Rauni Partanen; 0009-

Kirsten A. Reid; 000

Aleksandr Sokolov; 0000-0002-1521-3856

Svetlana Abd

Maija S. S

Maja Sund

Otso S

Craig E. Tweedie; 0000-0002-3409-8881

Amanda Young; 0000-0002-3580-8603

Robert G. Björk; 0000-0001-7346-666X

Abstract

Plants form symbiotic relationships with mycorrhizal fungi, which are vital for soil carbon and nutrient cycling. In the Arctic, one of the most soil carbon rich biomes of the world, herbivores can strongly influence vegetation, but their impacts on mycorrhizal fungi communities and subsequently on soil carbon and nutrient cycling are uncertain. We collected soils from 15 sets of herbivore exclusion fences across the Arctic. We sequenced across both ITS2 regions and partial SSU region with two sets of amplicons to determine the composition of soil mycorrhizal fungi communities and how these are impacted by herbivory, climate, and edaphic properties. Herbivore exclusion had an overall weak effect on the arbuscular mycorrhizal (AM) fungi community across the tundra, but the effect was variable across sites. pH differences among sites were correlated with changes in AM composition. Ectomycorrhizal fungi had the highest number of species, followed by AM. Consistent Arctic wide differences observed in mycorrhizal fungi communities were generally tied to edaphic and climatic properties, whereas herbivores seem to influence mycorrhizal species predominantly at individual sites. Soil carbon storage is affected by the composition of mycorrhizal fungi and shifts in the proportion of mycorrhizal types will have subsequent impacts on carbon in Arctic soils.

Key words: Amplicon sequencing; Arbuscular mycorrhiza; Arctic; Ectomycorrhiza; Ericoid mycorrhiza; Herbivory

1. Introduction

Large mammalian herbivores can modify plant communities through selective foraging which may allow herbivores to impact future carbon (C) and nutrient cycling in the Arctic (Olofsson et al., 2009; Vowles et al., 2017a; Sundqvist et al., 2019; Lindén et al., 2021). For instance, herbivores may give evergreen shrubs a competitive advantage as herbivores preferentially consume deciduous shrubs, forbs, and graminoids (Christie et al., 2015; Vowles and Björk, 2019). By altering dominance patterns among plant functional groups, herbivores can indirectly affect mycorrhizal fungi communities (Vowles et al., 2018; Vowles and Björk, 2019; Ahonen et al., 2021; Ylänne et al., 2021; Castaño et al., 2023). Trampling and waste deposition by herbivores may also benefit mycorrhizal fungi by increasing soil temperature and nutrient availability (Wang et al., 2018, 2023; Yan et al., 2018; Ylänne et al., 2018; Kytöviita and Olofsson, 2021). The magnitude of herbivore impact has been shown to be sensitive to local climate, where for instance herbivores have the largest effect on shrub radial growth at intermediate Arctic air temperature ranges (Vuorinen et al., 2022). Herbivory mediated changes in the dominance of different plant functional groups will affect their associated types of mycorrhizal fungi, where deciduous shrubs primarily associate with ectomycorrhizal fungi (EcM), ericaceous shrubs which are predominantly evergreen associate with ericoid mycorrhizal fungi (ErM), and grasses and forbs primarily associate with arbuscular mycorrhizal fungi (AM)

(Smith and Read, 2008; Vowles and Björk, 2019). The proportion of different plant functional types and their associated mycorrhizal fungi can alter soil properties which feedback onto the dominant vegetation and mycorrhizal fungi (Clemmensen et al., 2015, 2021; Castaño et al., 2023). These multi-trophic interactions between herbivores and soil fungi may be important for Arctic ecosystems as climate change continues (Vowles and Björk, 2019; Ylänne et al., 2021), however, they have not been evaluated across the Arctic.

Soil fungi are likely to respond to herbivory-driven shifts in vegetation and soil properties, as they generally have close connections to the plant species comprising the community (Parker et al., 2022). These soil fungi, including both saprotrophic and mycorrhizal fungi, play a key role in the cycling of soil C and nutrients globally (Read and Perez-Moreno, 2003; Högberg and Read, 2006; Orwin et al., 2011; Averill et al., 2014), including in nutrient-poor ecosystems (Clemmensen et al., 2021; Parker et al., 2021) such as most Arctic communities (Shaver and Chapin, 1991; Schulze et al., 1994; Jonasson et al., 2001; Clemmensen et al., 2006). Mycorrhizal fungi function as a C sink in soils, as they receive photosynthates from their host plant, and as a result are less C limited than saprotrophic fungi and can thereby outcompete free living microbes for organic nitrogen (N) (Högberg and Read, 2006; Orwin et al., 2011; Averill et al., 2014). Different mycorrhizal groups, such as ectomycorrhiza, ericoid mycorrhiza and arbuscular mycorrhiza have been linked to different degrees of recalcitrance of soil organic material where shifts in mycorrhizal dominance along a gradient from AM-EcM-ErM corresponds to slower C turnover and subsequently higher C storage in the soil (Phillips et al., 2013; Clemmensen et al., 2015, 2021; Parker et al., 2021; Fanin et al., 2022). Thus, clarifying the distribution of different mycorrhizal groups is important for understanding the Arctic's future C storage potential (Dahlberg and Bültmann, 2013).

Climatic conditions can affect regional processes of mycorrhizal fungi distribution, but do not necessarily describe finer scale patterns (Mikryukov et al., 2023). However, soil conditions, which are more variable than climate at the site level, may have stronger effects on mycorrhizal fungi communities, in some cases acting as stronger drivers than vegetation (Dumbrell et al., 2010; Grau et al., 2017; Bennett and Classen, 2020). The amount of nutrients in the soil and the form they take, i.e. organic or inorganic, impact the abundance and production of mycorrhizal fungi (Avolio et al., 2009; Nicolás et al., 2019). EcM fungi are lower in abundance when inorganic N is high (Kjøller et al., 2012) potentially due to the benefit of the mycorrhizal relationship to the plant host decreases under such conditions and the plants subsequently reduce the investment into mycorrhizal symbionts. The proportion of fungi can also be impacted by the differences in soil C as saprotrophs are less competitively excluded when labile C is abundant (Bödeker et al., 2016; Marañón-Jiménez et al., 2021). Likewise, soil temperature and precipitation can affect the balance of mycorrhizal types in the soil as fungi have different optimal growth conditions (Ruotsalainen and Kytöviita, 2004; Kytöviita, 2005). As soils warm,

productivity and subsequently microbial activity may increase in the tundra, with the strength of this change connected to soil moisture (Geml et al., 2015).

Arctic regions have experienced approximately 2-4 times greater warming since 19[illegible] than the rest of the globe (Rantanen et al., 2022). This warming trend has led to vegetation shifts (Myers-Smith et al., 2011; Elmendorf et al., 2012a, 2012b; Bjorkman et al., 2015, 2020), which have resulted in aboveground productivity increases and a general greening trend in Arctic communities (Myers-Smith et al., 2020). Increasing productivity has the potential to decrease the long-term C storage in tundra soils (Hartley et al., 2012), which currently account for nearly 50% of global terrestrial belowground C pool (Schuur et al., 2015, Crowther et al., 2016; Van Gestel et al., 2018; Bjorkman et al., 2020). In addition, shifting plant abundance and composition potentially impact decomposition rates, C turnover and nutrient cycling as microbial communities shift concomitantly (Ekblad et al., 2013). The ongoing climate-driven shifts in tundra vegetation (Elmendorf et al., 2012b; Bjorkman et al., 2018), are expected to trigger changes in soil fungal communities as well. For instance, shrub species are expanding and becoming more prevalent (Myers-Smith et al., 2011), which should correspond to increases in EcM and ErM depending on shrub type (Vowles et al., 2018; Vowles and Björk, 2019; Clemmensen et al., 2021; Parker et al., 2022); whereas tundra communities with a greater proportion of grass and forb species, which may become more prevalent under high intensity grazing, should correspond with an increase in AM fungi (Walker et al., 2006; Berner et al., 2020; Betway-May et al., 2022). Thus, the dominance of functionally distinct shrub or graminoid vegetation in the landscape may be a major determinant of the fungal community in tundra ecosystems (Vowles and Björk, 2019).

Tundra ecosystems are comprised of multiple community types, such as heath and meadow communities, which have different dominant mycorrhizal types according to their dominant vegetation (Martínez-García et al., 2015; Sizonenko et al., 2020; Clemmensen et al., 2021; Defrenne et al., 2023). Thus, factors that influence the proportion of plant functional types, such as herbivory, will affect the proportion of different mycorrhiza types in the soil as well (Dahlberg and Bültmann, 2013; Martínez-García et al., 2015; Grau et al., 2017). These community types are partially determined by the strength of herbivory at each location, where no or low herbivory may allow for easier expansion of deciduous shrubs (Myers-Smith et al., 2011; Parker et al., 2021), moderate herbivory could give ericaceous shrubs an advantage by consuming highly competitive deciduous shrubs (Vowles et al., 2017a), and high herbivory promotes grass and forb species (Olofsson and Post, 2018). Although AM fungi form associations with almost 80% of terrestrial plant species globally (Smith and Read, 2008), AM fungi are generally limited in distribution in Arctic communities due to their low tolerance to cold (Wang et al., 2002; Ruotsalainen and Kytöviita, 2004; Kytöviita, 2005; Kilpeläinen et al., 2016). However, AM fungi species may respond quickly to climate warming if their host-species

become more prevalent and climate conditions for AM fungi improve (Olsson et al., 2004; Hollister and Flaherty, 2010; Gao et al., 2016; Newsham et al., 2017; Bennett and Classen, 2020).

Our study aims to investigate the effect of large mammalian herbivores on mycorrhizal fungal communities across multiple Arctic sites. We use a network of large mammalian herbivore exclosures to evaluate the effect of herbivores on mycorrhizal fungi composition and the proportion of mycorrhizal types, alongside edaphic and climate properties and vegetation dynamics. We hypothesise that i) large mammalian herbivores will impact mycorrhizal fungi community composition through soil property and vegetation community changes as a response to the combined effects of selective foraging, waste deposition, and trampling. However, we predict that the observation of this effect will likely be site-specific due to the differences between Arctic community types and the magnitude of herbivory pressure. We also hypothesise that ii) mycorrhizal fungi communities will shift across the Arctic due to differences in climate and vegetation. We predict ErM will be most species rich under dominant ericaceous shrub cover, EcM under dominant deciduous shrub cover, and AM under dominant grass and forb vegetation. Furthermore, iii) we hypothesise a greater richness of ErM species when herbivores are present, but only in sites where herbivore exclusion significantly alters mycorrhizal fungi community composition, as evergreen ericaceous shrubs may increase when deciduous shrubs are suppressed by herbivores. Finally, iv) we also predict that soil properties, such as pH and soil C and N, will influence the proportion of each mycorrhizal type, where non-acidic, low C:N ratio soil conditions benefit AM species the most.

2. Materials and Methods

2.1. Site descriptions

The study was conducted at 15 sites across the tundra; five sites in Sweden, four in Finland, two in USA, two in Canada, one in Iceland, and one in Russia (Fig. 1; Tab. 1). The site designations listed in Tab. 1 will be used throughout the paper to refer to those sites. 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 for each of the two sites; Fig. S1). Sites that had large fences and ambient plots (i.e. > 1 m^2) were sampled from five subplots (approx. 1 m^2) within each plot, while sites with small fences (i.e. ≤ 1 m^2) were sampled once within each plot. The term herbivory used throughout this manuscript is specifically referring to the effects of large mammalian herbivores including foraging, trampling and waste deposition, events that all interact to influence vegetation and soil properties.

Herbivory effect is used to denote the effects of excluding these herbivores from the fenced plots.

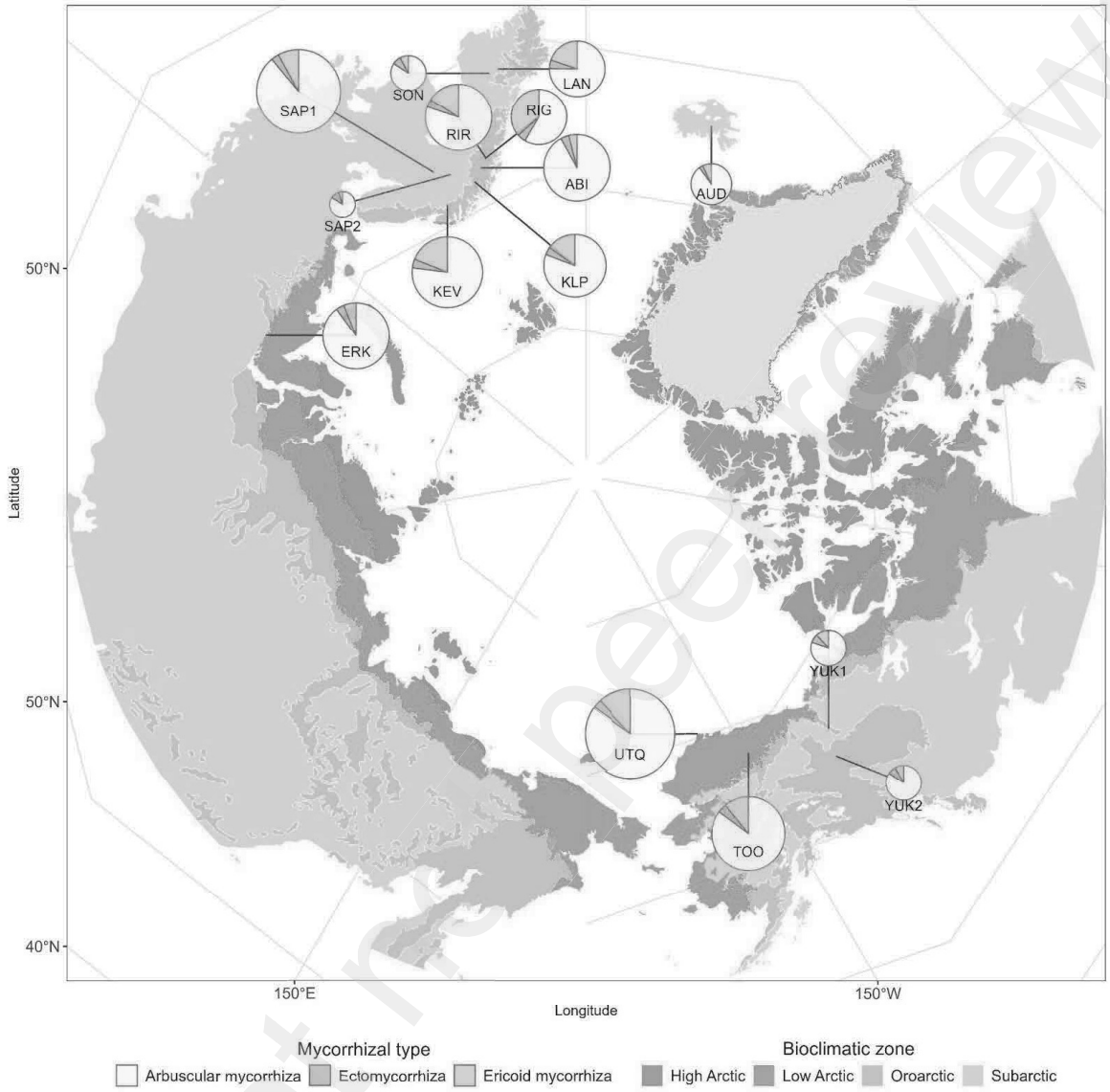

Fig. 1. *Map of site locations with pie charts showing proportion of mycorrhiza types with the size of the pie charts scaled to the number of unique mycorrhizal fungi species within sites. The bioclimatic zones for Subarctic, Oroarctic, Low Arctic, and High Arctic are included (Berner et al., 2024).*

Table 1. *Description of each site contributing to the data. SAP and YUK both consisted of two subsites that were initially sampled as replicates. # fences and paired ambient plots refer to the number of fences at the site and therefore also the number of paired ambient plots, i.e. ABI has three fences and three ambient plots. Two of the KLP fences covered an area of 1994 m^2, while the third fence covered an area of 562 m^2. SAP fences were also different sizes, so they are treated as separate sites. Soil moisture class is an approximation of moisture conditions at each site.*

# 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
6	1998	22	Yes	-1.6	637	Dry	*Empetrum nigrum, Betula nana*	*Rangifer tarandus*	Lindén et al. 2021
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
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
6	1995	25	Yes	-3.5	847	Dry	*Empetrum nigrum, Betula nana*	*Rangifer tarandus*	Vowles et al. 2017b, Sundqvist et al. 2019
6	1995	25	Yes	-1.5	773	Dry	*Empetrum nigrum, Deschampsia flexuosa*	*Rangifer tarandus*	Sundqvist et al. 2019
6	1970	50	Yes	-2.0	481		*Empetrum nigrum, Deschampsia flexuosa, Vaccinium myrtillus*, and *V. vitis-idaea*	*Rangifer tarandus*	Lehtonen and Heikkinen 1995
6	2020	0	No	-2.3	553	Dry	*Betula nana, Empetrum nigrum, Vaccinium myrtillus* and *V. vitis-idaea*	*Rangifer tarandus*	*N/A*
2	2001	19	No	0.4	567	Wet	*Eriophorum vaginatum, Carex sp. Andromeda polifolia, Vaccinium oxycoccos, Betula nana*	*Rangifer tarandus*	Meinander et al. 2020
2	2017	3	No	-0.9	592	Wet	*Carex rostrata, Menyanthes trifoliata, Comarum palustre, Betula nana*	*Rangifer tarandus*	Meinander et al. 2020
6	1996	24	Yes	-8.8	245	Moist	*Eriophorum vaginatum, Betula nana, Rubus chamaemorous*	*Rangifer tarandus*	Lindén et al. 2021
24	1959	61	No	-11.1	211	Dry-Wet	Deciduous shrubs and graminoids	*Rangifer tarandus*	Johnson et al. 2011
6	2016	4	Yes	2.8	708	Dry	*Betula nana*	*Ovis aries*	Mulloy et al. 2021
30	2014	6	Yes	-6.1	561		Dwarf shrubs and sedges	*Rangifer tarandus*	Baubin et al. 2016
2	2019	1	Yes	-16.8	207		*Betula nana, Eriophorum vaginatum, and Empetrum nigrum*	*Rangifer tarandus*	N/A
2	2019	1	Yes	-6.36	326		*Betula nana, Eriophorum vaginatum, and Empetrum nigrum*	*Rangifer tarandus*	*N/A*

Country	Site name	ID	Coordinates	# Fence and ambient plots	Fence area (m^2)	# Soil cores
Sweden	Abisko	ABI	68° 19' 23" N, 18° 51' 57" E	3+3	64	25 / plot
Sweden	Långfjället	LAN	62° 06' 53" N, 12° 16' 30" E	3+3	625	25 / plot
Sweden	Ritsem meadow	RIG	67° 49' 35" N, 17°43'02" E	3+3	625	25 / plot
Sweden	Ritsem shrub heath	RIR	67° 46' 33" N, 17° 32' 22" E	3+3	625	25 / plot
Sweden	Sonfjället	SON	62° 16' 55" N, 13° 28' 21" E	3+3	625	25 / plot
Finland	Kevo	KEV	69° 42' 28" N, 27° 04' 55" E	3+3	400	25 / plot
Finland	Kilpisjärvi	KLP	69° 02' 35" N, 20° 48' 22" E	3+3	1994/562	25 / plot
Finland	Sodankylä	SAP1	67° 22' 02" N, 26° 39' 02" E	1+1	5000	25 / plot
Finland	Pallas	SAP2	67° 59' 49" N, 24° 12' 42" E	1+1	2000	25 / plot
USA	Toolik lake	TOO	68° 37' 27" N, 149° 36' 36" W	3+3	100	25 / plot
USA	Utqiaġvik	UTQ	71° 18' 49" N, 156° 36' 11" W	12+12	1	5 / plot
Iceland	Auðkúluheiði	AUD	65° 12' 0" N, 19° 42' 0" W	3+3	144	25 / plot
Russia	Erkuta	ERK	68° 12' 21.6" N, 69° 11' 2.4" E	15+15	0.25	5 / plot
Canada	Yukon sites - North	YUK1	66° 36' 12" N, 136° 17' 13.2" W	3+3	1	5 / plot
Canada	Yukon sites - south	YUK2	64° 55' 49" N, 138° 16' 23" W	3+3	1	5 / plot

2.2. Soil sampling

Soil samples were collected at each site during the 2020 growing season using a 2 cm diameter soil corer to a depth of 10 cm, with five cores retrieved per subplot. Since the fenced area varies between sites, three separate sampling schemes were followed depending on site configuration (Table 1, Fig. S1). Soil samples were immediately put in a bag with silica gel, and frozen at -20 °C as soon as possible before being shipped to the University of Gothenburg, Sweden, where they were stored at -20 °C until processed. Each soil sample was sieved at 2 mm and freeze-dried for 24 hours to be dry stored until further analyses. All soil samples within a fence or ambient plot were homogenized into a single composite soil sample for DNA extraction. In total, there were 116 soil samples across all sites.

2.3. Extraction and sequencing

The Qiagen DNeasy PowerSoil Pro extraction kit was used to isolate environmental DNA from the processed soil samples following the manufacturer's protocol. DNA was extracted

from approximately 250 mg of soil from each sample. 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. ITS1, IT2, and partial LSU regions were amplified using a ITS1m–LR5 primer pair (ITS1m: 5'-TCCGTAGGTGAACCTGC-3'; LR5: 5'-TCCTGAGGGAAACTTCG-3') to capture general fungal groups (Eshghi Sahraei et al., 2022). Partial SSU region was amplified using an SSU515Fngs–AML2 primer pair (SSU515Fngs: 5'-GCCAGCAACCGCGGTAA-3'; AML2: 5'-CCCAAACACTTTGGTTTCC-3') to target AM fungi 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. 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. Samples were then sequenced by Uppsala Genome Centre (UGC, Science for Life Laboratory, Dept. of Immunology, Genetics and Pathology, Uppsala University, BMC, Box 815, SE-752 37 UPPSALA) in Uppsala, Sweden using two SMRT cells on the Sequel platform (Pacific Biosciences, Menlo Park, CA, USA).

2.4. Bioinformatics

Circular consensus sequence (CCS) reads (218,250 total, Table S1) 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 Centre, so only primers had to be removed. Reads from all samples were pooled for the two primers sets and analysed 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 readswere 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 (SH) (although duplication was still high; approximately 70%). After taxonomic assignment, 1837 unique SH's that were taxonomically assigned to family or below were sorted into functional guilds using FUNGuild (Nguyen et al., 2016) and 539 SHs corresponding to mycorrhizal fungi were selected for further analysis. SH identified as orchid mycorrhiza were removed from further analysis. All mycorrhizal types referred to throughout the paper refer to fungi not plants, unless otherwise specified and species is used to refer to the generated SHs. It is important to note that the guild assignments, much like the SHs themselves, are tentative and an SH can be assigned into multiple potential guilds depending on the level of taxonomic assignment. ErM fungal species are especially difficult as they are often facultative and do not necessarily form mycorrhiza unless conditions are right. Indeed, all SHs assigned as ErM were also co-assigned to EcM but were retained as ErM only in the analyses. SHs identified as EcM were manually assigned to exploration type following Agerer (2001). Taxonomy was assigned for the SSU515ngs–AML2 ASVs using the assignTaxonomy function from DADA2 with default settings, 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 from further analysis. 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 of the 26 identified species from the SSU515ngs–AML2 dataset represent AM species. A final total community dataset was produced by combining the ITS1m–LR5 SH's assigned to taxonomy and identified as mycorrhizal fungi, with the SSU515ngs–AML2 SH's taxonomically assigned as Glomeromycota across all samples (Table S1). All three datasets used species presence/absence data and not relative abundance differences between sites due to low sequencing depth, unless otherwise stated for a specific test (Fig. S13).

2.5. Soil and climate properties

All soil samples were also analysed for pH, soil organic matter (SOM) content, total C, total N, $\delta^{13}C$ and $\delta^{15}N$. First, pH was measured after adding 50 ml water to 10 g soil (except for SAP and YUK samples which used 150 ml to 5 g and 50 ml to 5 g, respectively as they contained a higher amount of organic material) and allowing to settle overnight before measuring with a pH meter (Mettler Toledo S91 pH meter). A second pH measurement was performed after adding 0.5 ml (1.5 ml for SAP and YUK) 2M KCl to reach a final concentration of 0.02 M KCl, which removes any potential effect of soil electrolyte concentration on the measurements (Kome et al., 2018). SOM 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 C, $\delta^{13}C$, total N and $\delta^{15}N$ were analysed on an elemental analyser (GSL, Sercon Ltd., Crewe, UK) coupled to an isotope ratio mass spectrometer (20-22, Sercon Ltd., Crewe, UK).

Daily mean near-surface air temperature and precipitation data were retrieved from CHELSA-W5E5 downscaled climate data for the period 1979-2016 for each site (version 1.1: Karger et al., 2017). The CHELSA-W5E5 v1.1 has a horizontal resolution of 1km, which is a downscaled product of its previous version, W5E5 v1.0, using the CHELSA V2.0 algorithm (Karger et al., 2017, 2022). These data were used to determine mean annual temperature (MAT), maximum annual temperature, minimum annual temperature, mean growing season temperature, maximum growing season temperature, minimum growing season temperature, mean annual precipitation (MAP) and mean growing season precipitation across the sites.

2.6. Vegetation data

Plant species abundance was evaluated previously for eleven of the sites using point intercept method (Goodall, 1952) on subplots within all exclosures and their paired controls across our study system. For LAN, RIG, RIR, and SON a total of 24 subplots were used (Sundqvist et al., 2019), KEV used 12 subplots, ABI and TOO used 8 subplots (Lindén et al., 2021), and AUD used 24 subplots (Kushbokov et al., 2023). In each subplot, species abundance was determined by lowering pins at 25–100 pins at even spacing and counting the number of times that the vegetation intercepted the pins. All data were normalized to 100 pins per subplot and averaged per plot (Väisänen et al., 2014). These data were further used to calculate the abundance of plant functional groups (grasses, sedges, forbs, evergreen and deciduous dwarf shrubs, and tall deciduous shrubs).

2.7. Statistics

All data analyses were carried out with R (version 4.2.2, (R Core Team, 2022). The phyloseq package (McMurdie and Holmes, 2013) was used for handling bioinformatic data, and relevant functions from the vegan and ecodist packages (Goslee and Urban, 2007; Oksanen et al., 2022) were used for community dissimilarity ordinations. The mycorrhizal fungi 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); hereafter referred to as EcM/ErM, AM, and total community, in the results. Mycorrhizal fungi species presence/absence (P/A) data was used for ordinations as we had low sequence sampling depth for relative abundance differences between our sites.

To investigate the impact of herbivory and soil conditions on mycorrhizal fungi community composition between plots we use Canonical Correspondence Analysis (CCA) as a constrained ordination according to mycorrhizal species composition dissimilarity based on presence/absence matrices, using Bray-Curtis distances, against soil properties and treatment. Variable selection was performed by correlation matrix and variance inflation factor tests to reduce multicollinearity in the resulting independent variables. The final model for the CCA

ordinations was the community dissimilarity matrix against Site, Treatment, pH, total C, C:N ratio, δ13C, and δ15N. A follow-up Analysis of Variance (ANOVA) was also performed to evaluate the effect of the independent variables on the mycorrhizal fungi community. A Permutational Analysis of Variance (PERMANOVA) was also performed to evaluate the dissimilarity of mycorrhizal fungi communities between plots, after using the ordiR2step function from vegan for forward model selection as the models were overfit with the full parameters (Tab. S3). For the EcM/ErM and total mycorrhizal fungi communities Site and total N were selected, and for the AM community, Site, Treatment, C:N, and Precipitation were selected. Treatment was added to all models as it is the parameter of interest.

The differences between sites in mycorrhizal community composition were evaluated against mean air temperature and precipitation using a separate CCA. An ANOVA was performed to evaluate the effect of these climate properties on the dissimilarity in mycorrhizal fungi composition between sites.

Another CCA was used to evaluate community dissimilarity influenced by vascular plant functional types (deciduous tall shrubs, deciduous dwarf shrubs, evergreen dwarf shrubs, grasses, sedges/rushes, and forbs) for the eleven sites with vegetation data available, as plant community is expected to be a major driver of mycorrhizal community composition. Differences in soil properties between treatments, fenced and unfenced plots, were calculated using student's t-test for each site individually.

All statistics use an alpha of 0.05 and p-values between 0.1 and 0.05 are referred to as marginally significant which may be appropriate due to the low replication in this study.

3. Results

3.1. Fungal guilds

Three major types of mycorrhizae were captured by the sequence data: EcM, ErM, and AM (Fig. 1, Fig. 2). Together these corresponded to 38% of the total fungal reads in the dataset. Across all samples 450 unique mycorrhizal fungi species within 3 phyla, 6 classes and 13 orders were captured (Fig. 2). Among these species, EcM accounted for 82%, while ErM comprised 2% and AM contained the remaining 14%. The ErM identified to species were assigned to the phylum Ascomycota, specifically, the order Helotiales. EcM were a mix of Basidiomycota and Ascomycota, across three classes and nine orders. The herbivore exclosure treatment generally did not affect the mean number of species of either total mycorrhizal fungi, or of EcM/ErM, or AM fungi respectively (Fig. 3). However, the mean number of total mycorrhizal fungi species, and EcM/ErM species, was higher in KLP, EcM/ErM were fewer in LAN, and AM were higher in UTQ in exclosures compared to ambient plots (Fig. S2). Further, the composition of

ectomycorrhizal fungi exploration types at each plot was not affected by exclusion of herbivores (Fig. S3 and S4).

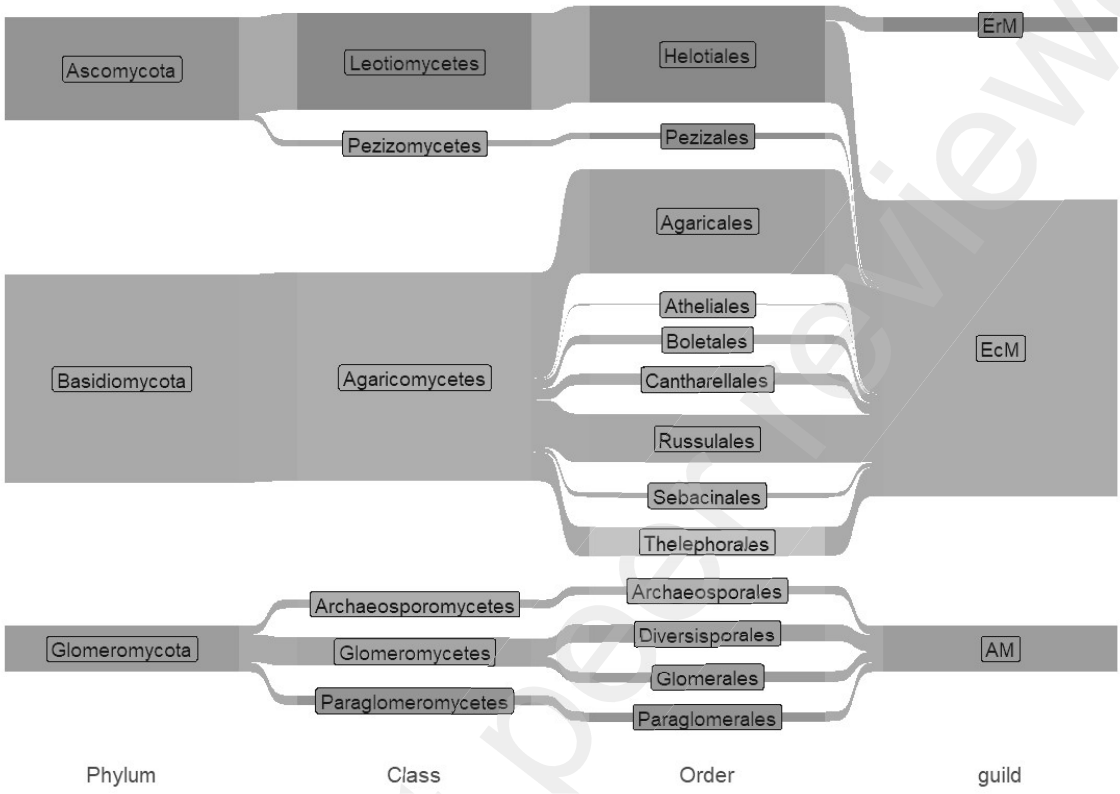

Fig. 2. *Overall proportion of unique mycorrhizal species separated into phylum, class, order and guild across all sites. The height of each rectangle represents the number of species belonging to that group, and connections between columns indicate the proportion which belongs to both groups. EcM refers to ectomycorrhiza, ErM to ericoid mycorrhiza, and AM to arbuscular mycorrhiza.*

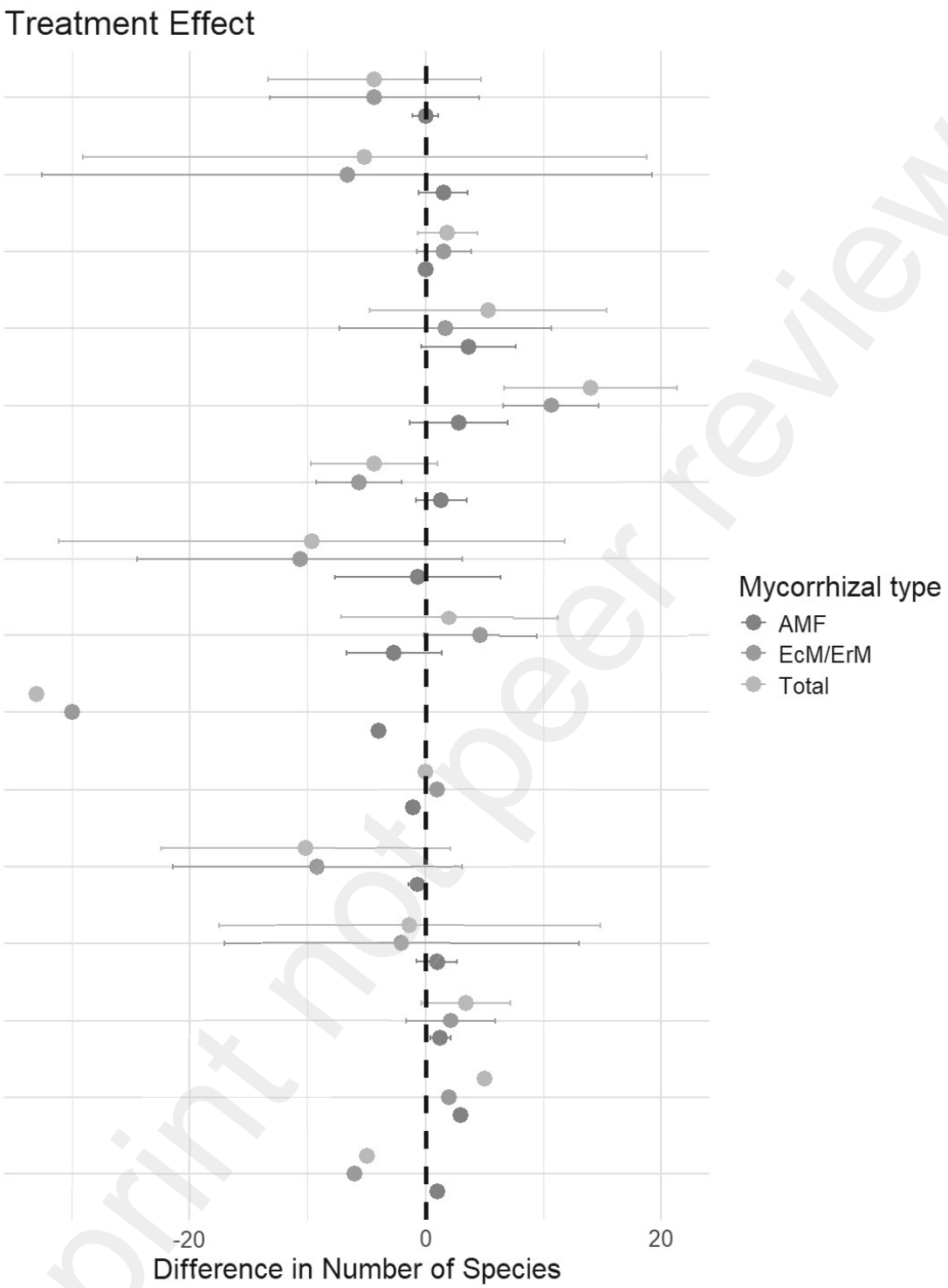

Fig. 3*. Difference of exclosure from ambient conditions in mean number of species of each mycorrhizal type at each site. Error bars represent 85% confidence intervals around the mean (corresponding to a α = 0.05 test; see Payton et al., 2000, 2003). The sites SAP1, SAP2, YUK1, and YUK2 have no error bars as there was one composite sample for the ambient and exclosure condition at each of these sites and so they couldn't be compared.*

3.2. Mycorrhizal fungi community composition

A consistent pattern of differentiation in mycorrhizal fungi communities occurred for all three subsets of mycorrhizal data in the ordination analyses, where the Russian, North American and Icelandic sites (UTQ, ERK, YUK, TOO and AUD) were broadly separated from the Fennoscandian sites (Fig. 4; Fig. S5). Site was significant for all three subsets of mycorrhizal fungi communities (Fig. 4A: $F_{14,83} = 2.196$, $p < 0.001$; B: $F_{14,61} = 2.718$, $p < 0.001$; C: $F_{14,83} = 2.264$, $p < 0.001$).

The separation of the EcM/ErM community in the cluster with Russian, Icelandic, and North American sites UTQ, ERK, YUK, TOO and AUD, and the Fennoscandian cluster is primarily driven by the genera *Cortinarius*, *Entoloma*, and *Lactarius* being more abundant in Fennoscandia, and *Russula* more abundant in the non-Fennoscandian sites (Fig. S5A).

In the AM community dataset CCA, pH was significantly correlated with community composition where the vector pointed primarily towards RIG, as well as some individual plots in KEV, ERK, and ABI (Fig. 4B: $F_{1,61} = 1.917$, $p = 0.046$). The AM genera *Acaulospora*, *Diversispora*, *Glomus*, and *Claroideoglomus* increase with pH along this gradient (Fig. S5B). In addition, total C was marginally significant and increased towards ERK primarily with a tendency of all cold sites moving in the same direction (Fig. 4B: $F_{1,61} = 1.711$, $p = 0.063$). Treatment (removal of herbivores) was also marginally significant and nearly followed the same direction as total C (Fig. 4B: $F_{1,61} = 1.474$, $p = 0.076$) with the AM genus *Ambiospora* showing species specific responses either increasing or decreasing along the total C and treatment gradient (Fig. S5B). In cold sites, the AM genera *Pacispora*, *Paraglomus* and *Scutellospora* contributed more species compared to warmer sites (Fig. S5B).

Total C was marginally significantly related to the total mycorrhizal community composition and increased along a gradient towards the coldest sites ERK, TOO, UTQ and YUK (Fig. 4C: $F_{1,83} = 1.257$, $p = 0.068$). The separation of the cold sites seems to be driven by increased abundance of *Salicaceae* spp. and *Fayodia gracilipes,* as well as a decreased abundance of *Lactarius* spp. and *Polyozellus umbrinus* (Fig. S5C). A few other EcM genera (e.g. *Mycosymbioces*, *Russula*, *Tomentella*) had some mixed species-specific responses along this gradient (Fig. S5C). Another distinct pattern in the total mycorrhizal community is the separation of RIG in the ordination space, driven by the AM genera *Acaulospora*, *Diversispora*, *Glomus*, and *Claroideoglomus*, but also by EcM fungi in the genera *Entoloma* (Fig. S5C).

Overall, the soil CCA models accounted for a small proportion of variance within the mycorrhizal data (ranging from 6.7-18.4% in the first two axes). Significant effects on mycorrhizal fungi composition were found for pH and total C, however there were no significant effects of SOM, total N, $\delta^{13}C$ or $\delta^{15}N$ for any mycorrhizal fungi community. Individual site CCAs identified a significant treatment effect in RIG ($F_{1,2} = 1.350$, $p = 0.042$), and marginally

significant treatment effects in LAN and TOO (LAN: $F_{1,4} = 1.250$, $p = 0.074$; TOO: $F_{1,4} = 1.215$, $p = 0.067$; Fig. S6). The number of AM fungal species tended to increase in exclosures when treatment effects were observed (Fig. S6).

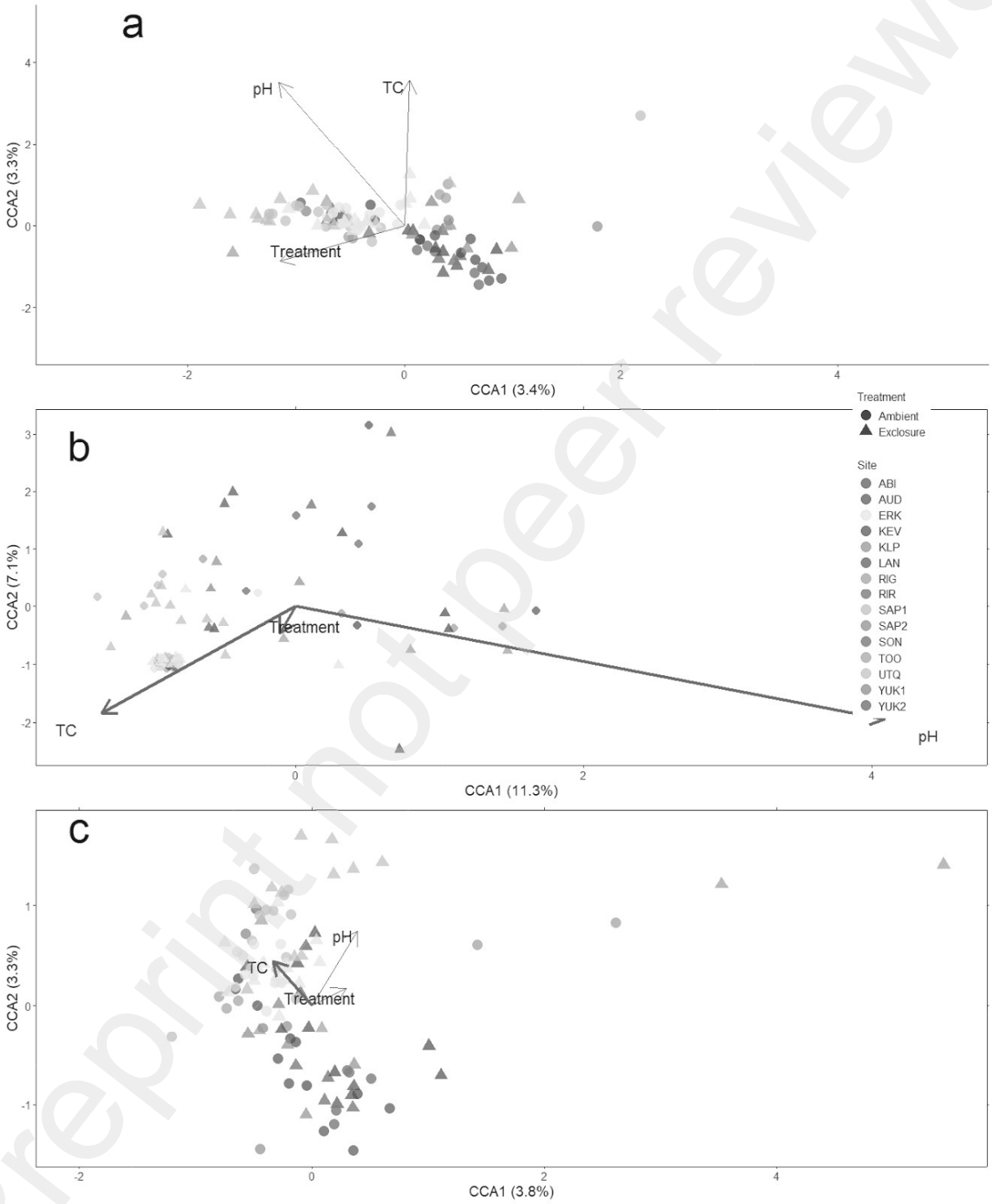

Fig. 4. *Canonical Correspondence Analysis (CCA) plot of Bray-Curtis dissimilarity matrix based on the presence of mycorrhizal species for: a) the EcM/ErM community composition, b) the AM community composition (note that no AM species was found in SON and AUD), and c) the total community composition. Each point corresponds to a plot's mycorrhizal community ordinated relative to other plots by their dissimilarity in community composition. Triangles are exclosure plots while circles are ambient plots. 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.*

When evaluating climate variables across the sites, mean air temperature was a significant explanatory variable for EcM/ErM and total mycorrhizal fungi communities, and marginally significant for AM fungi communities (Fig. S7A: $F_{1,12}$ = 1.472, p = 0.005; B: $F_{1,12}$ = 2.043, p = 0.059; C: $F_{1,12}$ = 1.390, p = 0.020), while precipitation was marginally significant across all mycorrhizal communities (Fig. S7A: $F_{1,12}$ = 1.254, p = 0.058; B: $F_{1,12}$ = 1.644, p = 0.100; C: $F_{1,12}$ = 1.248, p = 0.062). Both mean air temperature and precipitation tended to increase towards the Fennoscandian and Icelandic sites, and away from the North American and Russian sites. Overall, the climate CCA models accounted for 21.2-33.4% of the variance within the site-level mycorrhiza data in the first two axes.

The PERMANOVA supported the CCA by indicating site as significant for all three mycorrhizal community datasets (Tab. 2). Additionally, total N was found to be significant for the EcM/ErM and total communities, with treatment marginally significant in the total community. The model for total community accounted for approximately 34% of the variation within the data, predominantly due to site differences.

Table 2. *PERMANOVA model output for three subsets of the mycorrhizal community. Model structure was determined based on forward model selection criteria. TN refers to total N, and C:N ratio is Carbon:Nitrogen ratio. Bold values indicate significant difference between treatment conditions within the indicated site below alpha 0.1, bold and italic indicate significance below 0.05.*

Community	Model structure	Site			Treatment			TN			C:N			Precipitation		
		R^2	*F*	*p*	R^2	*F*	*p*	R^2	*F*	*p*	R^2	*F*	*p*	R^2	*F*	*p*
EcM/ErM	Site + Treatment + TN	0.291	3.151	***0.001***	0.008	1.081	0.379	0.014	1.828	***0.026***						
AM	Site + Treatment + C:N + Precipitation	0.436	4.524	***0.001***	0.010	1.213	0.308				0.010	1.279	0.264	0.013	1.676	0.146
Total	Site + Treatment + TN	0.316	3.551	***0.001***	0.012	1.558	**0.062**	0.013	1.724	***0.033***						

3.3. Vegetation influence

The CCA using relative cover of plant functional types (PFT) as predictors was significant for explaining dissimilarity in mycorrhiza data ($F_{17,55}$ = 1.876, p < 0.001; Fig. 5). Site ($F_{10,55}$ = 2.416, p < 0.001) and percent cover of sedges ($F_{1,55}$ = 1.790, p < 0.027) were significant factors for explaining difference in mycorrhizal fungi composition. The effect of sedges on mycorrhizal fungi dissimilarity was likely driven primarily by RIG as the vector points almost exclusively towards those plots.

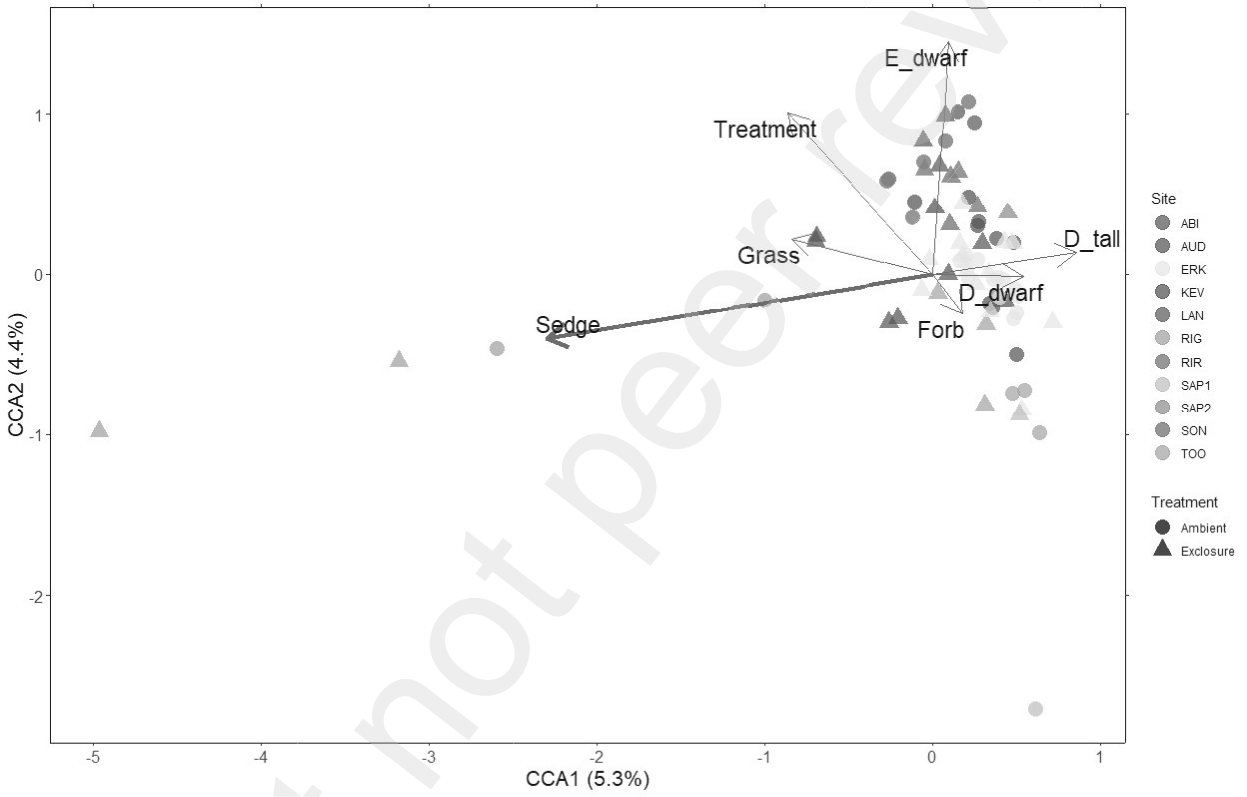

Fig. 5. *CCA analysis comparing mycorrhizal communities between sites based on percent cover of Plant Functional Types (PFT) at each site with available data. Each point corresponds to a plot's mycorrhizal community ordinated relative to other plots by their dissimilarity in community composition. Triangles 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.*

4. Discussion

4.1 Mycorrhizal communities across the Arctic

EcM comprised the majority of mycorrhiza species in our data as they made up 82% of the species identified. The EcM species in our study were distributed across 34 families with the most species-rich family accounting for 10% of the unique species. A previous study of Arctic EcM found that the majority of sequences belonged to four families indicating a 'big' degree of dominance of a few taxa (Timling et al., 2012). Similar proportions of taxonomic numbers to our data were previously found in tundra sites (Blaalid et al., 2014; Geml et al., 2014; Botnen et al., 2020), which also showed more EcM species than ErM, although not to the degree shown in this study. Two ErM species were identified in our data; however, they were ubiquitous across all sites. Previous studies have found more ErM species, predominantly in Helotiaceae and Hyaloscyphaceae (Van Geel et al., 2020; Fanin et al., 2022). However, this difference may be partially attributed to the different biogeographic areas evaluated in the studies, as neither were focused on tundra ecosystems, as well as differences in detection of rare species in the samples as our sequencing depth was low. The most prevalent ErM species in our data, *Pezoloma ericae*, was likewise the most abundant ErM species in a grazing study in northern Fennoscandia (Ylänne et al., 2021). They found that grazing conditions and plant composition influenced the abundance of *P. ericae*. The remaining 14% of species were AM which, while well-known elsewhere, are vastly understudied in tundra communities (Ruotsalainen and Eskelinen, 2011; Větrovský et al., 2023). The large number of AM species hypotheses identified in this study indicates a necessity to adapt protocols to include these species when evaluating soil fungi in the tundra, otherwise community evaluations may be incomplete. This is especially important in communities with a high abundance of grass and forb species (Ravolainen et al., 2020; Gignac et al., 2022; Spitzer et al., 2022), as these species have shown a tendency to increase with warming in some locations(Bjorkman et al., 2020). However, AM fungi have shown variable responses to herbivory, even with increases in their plant partners (Kytöviita and Olofsson, 2021). Better understanding of the drivers of AM community change may aid understanding of the variation in grass and forb community responses in the tundra.

4.2 Large herbivore impacts on mycorrhizal fungi composition

Large mammalian herbivores had a weak effect on only AM fungal species across our sites, where *Archaeospora* spp. seems to be the most sensitive genera to herbivory across Arctic sites. This is in opposition to our hypothesis iii, where we expected herbivory to increase the number of ErM fungi by increasing ericaceous shrubs. Rather, the effect of herbivory on mycorrhizal fungi community composition depends on the dominant vegetation when herbivores are present, the specific site conditions (such as edaphic and climatic properties), and the strength of the herbivory pressure. It is possible that changes in the cover of sedges

and differences in pH across the sites contributed to the consistent weak effect on AM fungi. The response of AM fungi to herbivory is not consistent across previous studies (Ruotsalainen and Eskelinen, 2011; Kytöviita and Olofsson, 2021); however, herbivory has been demonstrated to decrease AM colonization of plant roots in acidic, non-fertile sites with the opposite response in non-acidic sites with high soil fertility (Ruotsalainen and Eskelinen, 2011). The difference in the response of AM fungi to herbivory could therefore be tied to local soil conditions, as AM fungi were also impacted by pH in our study. Although, it was also argued that the difference in AM colonization is primarily due to vegetation differences where nutrient-rich non-acidic communities have a higher proportion of graminoids and forbs and nutrient-poor acidic communities have more ericaceous shrubs (Ruotsalainen and Eskelinen, 2011). Higher proportion of graminoid vegetation that associates with AM fungi can be observed under heavy grazing conditions (Barthelemy et al., 2017). Our data suggested that the cover of primarily non-mycorrhizal sedges (Muthukumar et al., 2004; Tedersoo, 2017) had the largest correlation with mycorrhizal fungi community composition dissimilarity. This may be due to some sedges being capable of forming AM associations (Muthukumar et al., 2004) while *Kobresia* sp. can form EcM associations (Tedersoo, 2017), which may contribute to the observed dissimilarity in mycorrhizal fungi communities related to differences in sedge cover. The sites where significant herbivory impacts were observed did not have similar vegetation communities, but all showed a greater number of AM species present in the ambient condition. The strength of herbivory pressure applied at a location can shift the current vegetation towards a more graminoid dominated community (Olofsson et al., 2001, 2004; van der Wal, 2006; Vowles et al., 2017b), where communities with high grazing pressure increase in AM and saprotrophic fungal abundance (Ahonen et al., 2021). 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 (Yang et al., 2018; Ylänne et al., 2018; Fischer et al., 2022). Changes in conditions suitable for AM fungi, such as warmer temperatures and grass dominated plant communities, may increase their prevalence in the tundra.

In support of the prediction derived from hypothesis i, the herbivory effect was not consistent across the Arctic for EcM/ErM or total mycorrhizal fungi communities. Herbivory had previously been identified as an important driver for Arctic EcM and ErM fungi community composition (Grimling et al., 2012; Santalahti et al., 2018; Vowles and Björk, 2019; Botnen et al., 2020; Van Geel et al., 2020; Ahonen et al., 2021), however, these conclusions were for single sites and not across the Arctic. In our data, herbivory had a local scale impact at four sites. Herbivory likely impacts mycorrhizal fungi communities within a site by changing local vegetation and soil conditions; for example, herbivore driven changes in evergreen shrub abundance and differences in C:N ratio had large effects on the total soil fungi community at

the Norwegian-Finland border (Ylänne et al., 2021). Abiotic conditions have also been shown to have a large effect on mycorrhizal fungi composition differences (Dumbrell et al., 2010; Grau et al., 2017; Bennett and Classen, 2020), and can be more important for fungal community composition than vegetation composition (Grau et al., 2017). Although many studies indicated close connection between plant functional types and mycorrhizal types (Vowles et al., 2018; Vowles and Björk, 2019; Ahonen et al., 2021; Ylänne et al., 2021), EcM do not have strong host species specificity in the tundra (Ryberg et al., 2011; Abrego et al., 2020). The ability of individual plants to form multiple types of mycorrhizae, which varies by species and environmental gradient (Abrego et al., 2020), makes the complex relationships between PFTs and mycorrhizal types difficult to elucidate.

4.3 Soil properties influence mycorrhizal fungi community composition

In support of hypothesis iv, soil properties were found to coincide with mycorrhizal fungi composition where total C varies along with the total mycorrhizal fungi community, and pH and total C shifts with AM fungi community. Soil C can be differentially affected by different types of mycorrhizal fungi (Wurzburger and Brookshire, 2017) related to differences in their resource acquisition strategies and their response to increases in inorganic N (Kjøller et al., 2012; Wurzburger and Brookshire, 2017; Averill et al., 2019). Mycorrhizal fungi community composition was correlated with the total soil C vector which pointed primarily towards the North American and Russian sites. Increases in soil C have been linked to higher cover of EcM forming tundra plants and relative abundance of EcM fungi corresponding to heath communities (Clemmensen et al., 2021). Conversely, AM plants reduced soil C relative to soil-only controls while EcM plants did not (Wurzburger and Brookshire, 2017). pH has been identified as an important driver of fungal community composition; however, it was argued as a correlative property and not the main driver of fungal community change (Ruotsalainen and Eskelinen, 2011; Hewitt et al., 2013). Previous studies have also found impacts of warming on fungal communities (Geml et al., 2015, 2021; Shi et al., 2021), but these effects differed between tundra habitats primarily related to soil moisture. Warming impacts on fungal community composition were stronger in moist communities than dry (Geml et al., 2021) and may decrease the mycorrhizal component of the fungal community (Geml et al., 2015); however, there was no response to warming in an AM community (Shi et al., 2021). Our data show an impact of air temperature on all mycorrhizal fungi communities, but that may be due to the large gradient in air temperature among sites. In addition, our data showed a significant precipitation gradient among the sites that was consistently correlated to mycorrhizal fungi community composition, but not for AM fungi specifically. The large gradient in precipitation and air temperature that our study sites span account for at least 20% of the variance among the sites in mycorrhizal fungi composition. Overall, large scale changes in water and C availability and acid-stress are likely regional drivers for mycorrhiza composition.

Overall, herbivory is likely acting locally on mycorrhizal fungi communities while large-scale patterns coincide with climatic gradients in the Arctic. The variation in vegetation communities across the tundra likely influences how readily mycorrhizal fungi types will react to altered biotic or abiotic 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 fungi community in an area. Additionally, it is important to evaluate both EcM/ErM and AM fungi species in tundra ecosystems as AM species were found to be more sensitive to changes in herbivory and constitute a substantial portion of the mycorrhizal fungi community. Thus, changes in the balance between AM-EcM-ErM in the tundra will most likely have associated consequences on total soil C, and may influence the capacity of the tundra soils to store C.

Acknowledgements

The authors would like to acknowledge support of the National Genomics Infrastructure (NGI) / Uppsala Genome Centre and UPPMAX for providing assistance in massive parallel sequencing and computational infrastructure. Work performed at NGI / Uppsala Genome Center has been funded by RFI / VR and Science for Life Laboratory, Sweden. We would also like to acknowledge all field assistants who assisted in collecting the data from all sites including Violetta Filippova and Kirill Shklyar for ERK, Peppi Heikkilä, Mirella Karppinen, and Samira Terzenbach for KEV, and Petri Salovaara for SAT. Finally, we would like to thank Logan Berner for sharing shapefiles for making the Arctic map.

Competing interests

The authors declare no competing interests.

Author contributions

RBG, MR, AE: conceptualization, methodology, resources, funding acquisition, writing – review and editing. CGB: conceptualization, methodology, investigation, formal analysis, writing – original draft. AR, BRF, TO: investigation, data curation. All coauthors contributed to investigation and writing – review and editing.

Funding Sources

The authors would like to acknowledge the following funding agencies that allowed for the collection of the data; Swedish Research Council (Vetenskapsrådet) grant no 2018-04202 to RGB, Carl Tryggers foundation (grant no CTS 21:1470) to RGB, the Academy of Finland grant no 315415 to HF, Russian Ministry of Science and Higher Education program No. 122021000089-9 for AS and SA, US National Science Foundation DEB-1637459 to LG, US National Science

Foundation OPP-2221133 to SBH & ABY, US National Science Foundation OPP-1836861 to CET, University of Iceland Research Fund to ISJ, Soil Conservation Service of Iceland, Orkurannsóknasjoður Landsvirkjunar (NÝR-09-2017, NÝR-14-2018, NÝR-12-2019) to ICB and ISJ the W. Garfield Weston Award in Northern Research, The W. Garfield Weston Foundation Fellowship Program, a program of the Wildlife Conservation Society Canada funded by The W. Garfield Weston Foundation, Northern Scientific Training Program, Aurora Research Institute Research Fellowship, to KAR. This research was conducted with permission from the Vuntut Gwitchin Government and Yukon Government (18-28S&E; 19-10S&E; 20-05S&E) where applicable. The research has received funding from INTERACT III under the European Union H2020 Grant Agreement No.871120.

Data availability

Data and code will be submitted to a repository upon acceptance of the manuscript.

References

Abarenkov, K., Tedersoo, L., Nilsson, R.H., Vellak, K., Saar, I., Veldre, V., Parmasto, E., Prous, M., Aan, A., Ots, M., Kurina, O., Ostonen, I., Jõgeva, J., Halapuu, S., Põldmaa, K., Toots, M., Truu, J., Larsson, K.H., Kõljalg, U., 2010. Plutof-a web based workbench for ecological and taxonomic research, with an online implementation for fungal its sequences. Evolutionary Bioinformatics 2010, 189–196. doi:10.4137/EBO.S6271

Abrego, N., Huotari, T., Tack, A.J.M., Lindahl, B.D., Tikhonov, G., Somervuo, P., Martin Schmidt, N., Ovaskainen, O., Roslin, T., 2020. Higher host plant specialization of root-associated endophytes than mycorrhizal fungi along an arctic elevational gradient. Ecology and Evolution 10, 8989–9002. doi:10.1002/ece3.6604

Agerer, R., 2001. Exploration types of ectomycorrhizae: A proposal to classify ectomycorrhizal mycelial systems according to their patterns of differentiation and putative ecological importance. Mycorrhiza 11, 107–114. doi:10.1007/s005720100108

Ahonen, S.H.K., Hänne, H., Väisänen, M., Ruotsalainen, A.L., Männistö, M.K., Markkola, A., Stark, S., 2021. Reindeer grazing history determines the responses of subarctic soil fungal communities to warming and fertilization, New Phytologist. doi:10.1111/nph.17623

Averill, C., Bhatnagar, J.M., Dietze, M.C., Pearse, W.D., Kivlin, S.N., 2019. Global imprint of mycorrhizal fungi on whole-plant nutrient economics. Proceedings of the National Academy of Sciences of the United States of America 116, 23163–23168. doi:10.1073/pnas.1906655116

653 Averill, C., Turner, B.L., Finzi, A.C., 2014. Mycorrhiza-mediated competition between
654 plants and decomposers drives soil carbon storage. Nature 505, 543–545.
655 doi:10.1038/nature12901

656 Avolio, M.L., Tuininga, A.R., Lewis, J.D., Marchese, M., 2009. Ectomycorrhizal
657 responses to organic and inorganic nitrogen sources when associating with two
658 host species. Mycological Research 113, 897–907.
659 doi:10.1016/j.mycres.2009.05.001

660 Barthelemy, H., Stark, S., Kytöviita, M.M., Olofsson, J., 2017. Grazing decreases N
661 partitioning among coexisting plant species. Functional Ecology 31, 2051–2060.
662 doi:10.1111/1365-2435.12917

663 Bennett, A.E., Classen, A.T., 2020. Climate change influences mycorrhizal fungal–plant
664 interactions, but conclusions are limited by geographical study bias. Ecology 101,
665 1–11. doi:10.1002/ecy.2978

666 Berner, L.T., Massey, R., Jantz, P., Forbes, B.C., Macias-Fauria, M., Myers-Smith, I.,
667 Kumpula, T., Gauthier, G., Andreu-Hayles, L., Gaglioti, B. V., Burns, P., Zetterberg,
668 P., D'Arrigo, R., Goetz, S.J., 2020. Summer warming explains widespread but not
669 uniform greening in the Arctic tundra biome. Nature Communications 11, 1–12.
670 doi:10.1038/s41467-020-18479-5

671 Betway-May, K.R., Hollister, R.D., May, J.L., Harris, J.A., Gould, W.A., Oberbauer, S.F.,
672 2022. Can plant functional traits explain shifts in community composition in a
673 changing Arctic? Arctic Science 8, 899–915. doi:10.1139/as-2020-0036

674 Bjorkman, A.D., Elmendorf, S.C., Beamish, A.L., Vellend, M., Henry, G.H.R., 2015.
675 Contrasting effects of warming and increased snowfall on Arctic tundra plant
676 phenology over the past two decades. Global Change Biology 21, 4651–4661.
677 doi:10.1111/gcb.13051

678 Bjorkman, A.D., García Criado, M., Myers-Smith, I.H., Ravolainen, V., Jónsdóttir, I.S.,
679 Westergaard, K.B., Lawler, J.P., Aronsson, M., Bennett, B., Gardfjell, H.,
680 Heiðmarsson, S., Stewart, L., Normand, S., 2020. Status and trends in Arctic
681 vegetation: Evidence from experimental warming and long-term monitoring. Ambio
682 49, 678–692. doi:10.1007/s13280-019-01161-6

683 Bjorkman, A.D., Myers-Smith, I.H., Elmendorf, S.C., Normand, S., Thomas, H.J.D.,
684 Alatalo, J.M., Alexander, H., Anadon-Rosell, A., Angers-Blondin, S., Bai, Y.,
685 Baruah, G., te Beest, M., Berner, L., Björk, R.G., Blok, D., Bruelheide, H., Buchwal,
686 A., Buras, A., Carbognani, M., Christie, K., Collier, L.S., Cooper, E.J., Cornelissen,
687 J.H.C., Dickinson, K.J.M., Dullinger, S., Elberling, B., Eskelinen, A., Forbes, B.C.,
688 Frei, E.R., Iturrate-Garcia, M., Good, M.K., Grau, O., Green, P., Greve, M., Grogan,

P., Haider, S., Hájek, T., Hallinger, M., Happonen, K., Harper, K.A., Heijmans, M.M.P.D., Henry, G.H.R., Hermanutz, L., Hewitt, R.E., Hollister, R.D., Hudson, J., Hülber, K., Iversen, C.M., Jaroszynska, F., Jiménez-Alfaro, B., Johnstone, J., Jorgensen, R.H., Kaarlejärvi, E., Klady, R., Klimešová, J., Korsten, A., Kulera, S., Kulonen, A., Lamarque, L.J., Lantz, T., Lavalle, A., Lembrechts, J.J., Lévesque, E., Little, C.J., Luoto, M., Macek, P., Mack, M.C., Mathakutha, R., Michelsen, A., Milbau, A., Molau, U., Morgan, J.W., Mörsdorf, M.A., Nabe-Nielsen, J., Nielsen, S.S., Ninot, J.M., Oberbauer, S.F., Olofsson, J., Onipchenko, V.G., Petraglia, A., Pickering, C., Prevéy, J.S., Rixen, C., Rumpf, S.B., Schaepman-Strub, G., Semenchuk, P., Shetti, R., Soudzilovskaia, N.A., Spasojevic, M.J., Speed, J.D.M., Street, L.E., Suding, K., Tape, K.D., Tomaselli, M., Trant, A., Treier, U.A., Tremblay, J.P., Tremblay, M., Venn, S., Virkkala, A.M., Vowles, T., Weijers, S., Wilmking, M., Wipf, S., Zamin, T., 2018. Tundra Trait Team: A database of plant traits spanning the tundra biome. Global Ecology and Biogeography 27, 1402–1411. doi:10.1111/geb.12821

Blaalid, R., Davey, M.L., Carlsen, T., Halvorsen, R., Høiland, K., Eidesen, P.B., 2014. Arctic root-associated fungal community composition reflects environmental filtering. Molecular Ecology 23, 649–659. doi:10.1111/mec.12622

Bödeker, I.T.M., Lindahl, B.D., Olson, Å., Clemmensen, K.E., 2016. Mycorrhizal and saprotrophic fungal guilds compete for the same organic substrates but affect decomposition differently. Functional Ecology 30, 1967–1978. doi:10.1111/1365-2435.12677

Botnen, S.S., Thoen, E., Eidesen, P.B., Krabberød, A.K., Kauserud, H., 2020. Community composition of arctic root-associated fungi mirrors host plant phylogeny. FEMS Microbiology Ecology 96, 1–12. doi:10.1093/femsec/fiaa185

Castaño, C., Hallin, S., Egelkraut, D., Lindahl, B.D., Olofsson, J., Clemmensen, K.E., 2023. Contrasting plant–soil–microbial feedbacks stabilize vegetation types and uncouple topsoil C and N stocks across a subarctic–alpine landscape. New Phytologist 238, 2621–2633. doi:10.1111/nph.18679

Christie, K.S., Bryant, J.P., Gough, L., Ravolainen, V.T., Ruess, R.W., Tape, K.D., 2015. The Role of Vertebrate Herbivores in Regulating Shrub Expansion in the Arctic: A Synthesis. BioScience 65, 1123–1133. doi:10.1093/biosci/biv137

Clemmensen, K.E., Durling, M.B., Michelsen, A., Hallin, S., Finlay, R.D., Lindahl, B.D., 2021. A tipping point in carbon storage when forest expands into tundra is related to mycorrhizal recycling of nitrogen. Ecology Letters 24, 1193–1204. doi:10.1111/ele.13735

Clemmensen, K.E., Finlay, R.D., Dahlberg, A., Stenlid, J., Wardle, D.A., Lindahl, B.D., 2015. Carbon sequestration is related to mycorrhizal fungal community shifts during long-term succession in boreal forests. New Phytologist 205, 1525–1536. doi:10.1111/nph.13208

Clemmensen, K.E., Michelsen, A., Jonasson, S., Shaver, G.R., 2006. Increased ectomycorrhizal fungal abundance after long-term fertilization and warming of two arctic tundra ecosystems. New Phytologist 171, 391–404. doi:10.1111/j.1469-8137.2006.01778.x

Crowther, T.W., Todd-Brown, K.E.O., Rowe, C.W., Wieder, W.R., Carey, J.C., MacHmuller, M.B., Snoek, B.L., Fang, S., Zhou, G., Allison, S.D., Blair, J.M., Bridgham, S.D., Burton, A.J., Carrillo, Y., Reich, P.B., Clark, J.S., Classen, A.T., Dijkstra, F.A., Elberling, B., Emmett, B.A., Estiarte, M., Frey, S.D., Guo, J., Harte, J., Jiang, L., Johnson, B.R., Kroël-Dulay, G., Larsen, K.S., Laudon, H., Lavallee, J.M., Luo, Y., Lupascu, M., Ma, L.N., Marhan, S., Michelsen, A., Mohan, J., Niu, S., Pendall, E., Peñuelas, J., Pfeifer-Meister, L., Poll, C., Reinsch, S., Reynolds, L.L., Schmidt, I.K., Sistla, S., Sokol, N.W., Templer, P.H., Treseder, K.K., Welker, J.M., Bradford, M.A., 2016. Quantifying global soil carbon losses in response to warming. Nature 540, 104–108. doi:10.1038/nature20150

Dahlberg, A., Bültmann, H., 2013. Fungi. In: Meltofte, H. (Ed.), Arctic Biodiversity Assessment. Status and Trends in Arctic Biodiversity. Akureyri: Conservation of Arctic Flora and Fauna, Arctic Council, pp. 303–319.

Defrenne, C.E., Moore, J.A.M., Tucker, C.L., Lamit, L.J., Kane, E.S., Kolka, R.K., Chimner, R.A., Keller, J.K., Lilleskov, E.A., 2023. Peat loss collocates with a threshold in plant–mycorrhizal associations in drained peatlands encroached by trees. New Phytologist 240, 412–425. doi:10.1111/nph.18954

Dumbrell, A.J., Nelson, M., Helgason, T., Dytham, C., Fitter, A.H., 2010. Relative roles of niche and neutral processes in structuring a soil microbial community. ISME Journal 4, 337–345. doi:10.1038/ismej.2009.122

Ekblad, A., Wallander, H., Godbold, D.L., Cruz, C., Johnson, D., Baldrian, P., Björk, R.G., Epron, D., Kieliszewska-Rokicka, B., Kjøller, R., Kraigher, H., Matzner, E., Neumann, J., Plassard, C., 2013. The production and turnover of extramatrical mycelium of ectomycorrhizal fungi in forest soils: Role in carbon cycling. Plant and Soil 366, 1–27. doi:10.1007/s11104-013-1630-3

Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Björk, R.G., Bjorkman, A.D., Callaghan, T. V., Collier, L.S., Cooper, E.J., Cornelissen, J.H.C., Day, T.A., Fosaa, A.M., Gould, W.A., Grétarsdóttir, J., Harte, J., Hermanutz, L., Hik, D.S., Hofgaard, A., Jarrad, F., Jónsdóttir, I.S., Keuper, F., Klanderud, K., Klein, J.A., Koh, S., Kudo, G.,

762 Lang, S.I., Loewen, V., May, J.L., Mercado, J., Michelsen, A., Molau, U., Myers-
763 Smith, I.H., Oberbauer, S.F., Pieper, S., Post, E., Rixen, C., Robinson, C.H.,
764 Schmidt, N.M., Shaver, G.R., Stenström, A., Tolvanen, A., Totland, Ø., Troxler, T.,
765 Wahren, C.H., Webber, P.J., Welker, J.M., Wookey, P.A., 2012a. Global
766 assessment of experimental climate warming on tundra vegetation: Heterogeneity
767 over space and time. Ecology Letters 15, 164–175. doi:10.1111/j.1461-
768 0248.2011.01716.x

769 Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Björk, R.G., Boulanger-Lapointe, N.,
770 Cooper, E.J., Cornelissen, J.H.C., Day, T.A., Dorrepaal, E., Elumeeva, T.G., Gill,
771 M., Gould, W.A., Harte, J., Hik, D.S., Hofgaard, A., Johnson, D.R., Johnstone, J.F.,
772 Jónsdóttir, I.S., Jorgenson, J.C., Klanderud, K., Klein, J.A., Koh, S., Kudo, G., Lara,
773 M., Lévesque, E., Magnússon, B., May, J.L., Mercado-Diaz, J.A., Michelsen, A.,
774 Molau, U., Myers-Smith, I.H., Oberbauer, S.F., Onipchenko, V.G., Rixen, C., Martin
775 Schmidt, N., Shaver, G.R., Spasojevic, M.J., Þórhallsdóttir, P.E., Tolvanen, A.,
776 Troxler, T., Tweedie, C.E., Villareal, S., Wahren, C.H., Walker, X., Webber, P.J.,
777 Welker, J.M., Wipf, S., 2012b. Plot-scale evidence of tundra vegetation change and
778 links to recent summer warming. Nature Climate Change 2, 453–457.
779 doi:10.1038/nclimate1465

780 Eshghi Sahraei, S., Furneaux, B., Kluting, K., Yakeh, M., Rydin, H., Hytteborn, H.,
781 Rosling, A., 2022. Effects of operational taxonomic unit inference methods on soil
782 microeukaryote community analysis using long-read metabarcoding. Ecology and
783 Evolution 12, 1–14. doi:10.1002/ece3.8676

784 Fanin, N., Clemmensen, K.E., Lindahl, B.D., Farrell, M., Nilsson, M.C., Gundale, M.J.,
785 Kardol, P., Wardle, D.A., 2022. Ericoid shrubs shape fungal communities and
786 suppress organic matter decomposition in boreal forests. New Phytologist 236,
787 684–697. doi:10.1111/nph.18353

788 Fischer, W., Thomas, C.K., Zimov, N., Göckede, M., 2022. Grazing enhances carbon
789 cycling but reduces methane emission during peak growing season in the Siberian
790 Pleistocene Park tundra site. Biogeosciences 19, 1611–1633. doi:10.5194/bg-19-
791 1611-2022

792 Gao, C., Kim, Y.C., Zheng, Y., Yang, W., Chen, L., Ji, N.N., Wan, S.Q., Guo, L.D.,
793 2016. Increased precipitation, rather than warming, exerts a strong influence on
794 arbuscular mycorrhizal fungal community in a semiarid steppe ecosystem. Botany
795 94, 459–469. doi:10.1139/cjb-2015-0210

796 Gaml, J., Morgado, L.N., Semenova, T.A., Welker, J.M., Walker, M.D., Smets, E., 2015.
797 Long-term warming alters richness and composition of taxonomic and functional

groups of arctic fungi. FEMS Microbiology Ecology 91, 1–13. doi:10.1093/femsec/fiv095

Geml, J., Morgado, L.N., Semenova-Nelsen, T.A., 2021. Tundra Type Drives Distinct Trajectories of Functional and Taxonomic Composition of Arctic Fungal Communities in Response to Climate Change – Results From Long-Term Experimental Summer Warming and Increased Snow Depth. Frontiers in Microbiology 12. doi:10.3389/fmicb.2021.628746

Gignac, C., Rochefort, L., Gauthier, G., Lévesque, E., Maire, V., Desch amps, L., Pouliot, R., Marchand-Roy, M., 2022. N/P Addition Is More Likely than N Addition Alone to Promote a Transition from Moss-Dominated to Graminoid-Dominated Tundra in the High-Arctic. Atmosphere 13. doi:10.3390/atmos13050676

Goodall, D.W., 1952. Some Considerations in the Use of Point Quadrats for. Australian Journal of Biological Sciences 5, 1–41.

Goslee, S.C., Urban, D.L., 2007. The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software 22, 1–19. doi:doi:10.18637/jss.v022.i07

Grau, O., Geml, J., Pérez-Haase, A., Ninot, J.M., Semenova-Nelsen, T.A., Peñuelas, J., 2017. Abrupt changes in the composition and function of fungal communities along an environmental gradient in the high Arctic. Molecular Ecology 26, 4798–4810. doi:10.1111/mec.14227

Hartley, I.P., Garnett, M.H., Sommerkorn, M., Hopkins, D.W., Fletcher, B.J., Sloan, V.L., Phoenix, G.K., Wookey, P.A., 2012. A potential loss of carbon associated with greater plant growth in the European Arctic. Nature Climate Change 2, 875–879. doi:10.1038/nclimate1575

Hewitt, R.E., Bent, E., Hollingsworth, T.N., Chapin, F.S., Taylor, D.L., 2013. Resilience of arctic mycorrhizal fungal communities after wildfire facilitated by resprouting shrubs. Ecosphere 20, 296–310. doi:10.2980/20-3-3620

Högberg, P., Read, D.J., 2006. Towards a more plant physiological perspective on soil ecology. Trends in Ecology and Evolution 21, 548–554. doi:10.1016/j.tree.2006.06.004

Hollister, R.D., Flaherty, K.J., 2010. Above- and below-ground plant biomass response to experimental warming in northern Alaska. Applied Vegetation Science 13, 378–387. doi:10.1111/j.1654-109X.2010.01079.x

Jonasson, S., Chapin, F.S., Shaver, G.R., 2001. Biogeochemistry in the Arctic, in: Schulze, E.-D., Harrison, S.P., Heimann, M., Holland, E.A., Lloyd, J.J., Prentice,

I.C., Schimel, D. (Eds.), Global Biogeochemical Cycles in the Climate System. Academic Press, New York, NY, USA., pp. 139–150. doi:10.1016/b978-012631260-7/50012-1

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2017. Climatologies at high resolution for the earth's land surface areas. Scientific Data 4, 1–20. doi:10.1038/sdata.2017.122

Karger, D.N., Lange, S., Hari, C., Reyer, C.P.O., Zimmermann, N.E., 2022. CHELSA-W5E5 v1.0: W5E5 v1.0 downscaled with CHELSA v2.0. doi:10.48364/ISIMIP.836809.1

Kilpeläinen, J., Vestberg, M., Repo, T., Lehto, T., 2016. Arbuscular and ectomycorrhizal root colonisation and plant nutrition in soils exposed to freezing temperatures. Soil Biology and Biochemistry 99, 85–93. doi:10.1016/j.soilbio.2016.04.025

Kjøller, R., Nilsson, L.O., Hansen, K., Schmidt, I.K., Vesterdal, L., Gundersen, P., 2012. Dramatic changes in ectomycorrhizal community composition, root tip abundance and mycelial production along a stand-scale nitrogen deposition gradient. New Phytologist 194, 278–286. doi:10.1111/j.1469-8137.2011.04041.x

Kome, G.K., Enang, R.K., Yerima, B.P.K., Lontsi, M.G.R., 2018. Models relating soil pH measurements in H2O, KCl and CaCl2 for volcanic ash soils of Cameroon. Geoderma Regional 14, e00185. doi:10.1016/j.geodrs.2018.e00185

Kushbokov, A.U., Barrio, I.C., Jónsdottir, I.S., 2023. Estimating the effects of grazing exclusion on the seed bank in Icelandic rangelands. Icelandic Agricultural Sciences 36, 35–40.

Kytöviita, M.M., 2005. Asymmetric symbiont adaptation to Arctic conditions could explain why high Arctic plants are non-mycorrhizal. FEMS Microbiology Ecology 53, 27–32. doi:10.1016/j.femsec.2004.09.014

Kytöviita, M.M., Olofsson, J., 2021. Idiosyncratic responses to simulated herbivory by root fungal symbionts in a subarctic meadow. Arctic, Antarctic, and Alpine Research 53, 80–92. doi:10.1080/15230430.2021.1878738

Lindén, E., Gough, L., Olofsson, J., 2021. Large and small herbivores have strong effects on tundra vegetation in Scandinavia and Alaska. Ecology and Evolution 11, 12741–12752. doi:10.1002/ece3.7977

Naranon-Jiménez, S., Radujković, D., Verbruggen, E., Grau, O., Cuntz, M., Peñuelas, J., Richter, A., Schrumpf, M., Rebmann, C., 2021. Shifts in the Abundances of

Saprotrophic and Ectomycorrhizal Fungi With Altered Leaf Litter Inputs. Frontiers in Plant Science 12, 1–17. doi:10.3389/fpls.2021.682142

Martin, M., 2011. Cutadapt removes adapter sequences from high-throughput sequencing reads. EMBnet Journal 17, 10–12.

Martínez-García, L.B., Richardson, S.J., Tylianakis, J.M., Peltzer, D.A., Dickie, I.A., 2015. Host identity is a dominant driver of mycorrhizal fungal community composition during ecosystem development. New Phytologist 205, 1565–1576. doi:10.1111/nph.13226

McMurdie, P.J., Holmes, S., 2013. Phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data. PLoS ONE 8. doi:10.1371/journal.pone.0061217

Mikryukov, V., Dulya, O., Zizka, A., Bahram, M., Hagh-Doust, N., Anslan, S., Prylutskyi, O., Delgado-Baquerizo, M., Maestre, F.T., Nilsson, H., Pärn, J., Öpik, M., Moora, M., Zobel, M., Espenberg, M., Mander, Ü., Khalid, A.N., Corrales, A., Agan, A., Vasco-Palacios, A.M., Saitta, A., Rinaldi, A., Verbeken, A., Sulistyo, B., Tamgnoue, B., Furneaux, B., Ritter, C.D., Nyamukondiwa, C., Sharp, C., Marín, C., Gohar, D., Klavina, D., Sharmah, D., Dai, D.Q., Nouhra, E., Biersma, E.M., Rähn, E., Cameron, E., De Crop, E., Otsing, E., Davydov, E., Albornoz, F., Brearley, F., Buegger, F., Zahn, G., Bonito, G., Hiiesalu, I., Barrio, I., Heilmann-Clausen, J., Ankuda, J., Doležal, J., Kupagme, J., Macià-Vicente, J., Fovo, J.D., Geml, J., Alatalo, J., Alvarez-Manjarrez, J., Põldmaa, K., Runnel, K., Adamson, K., Bråthen, K.A., Pritsch, K., Issifou, K.T., Antanaitis, K., Hyde, K., Newsham, K.K., Panksep, K., Lateef, A.A., Hansson, L., Lamit, L., Saba, M., Tuomi, M., Gryzenhout, M., Bauters, M., Piepenbring, M., Vijayawardene, N.N., Yorou, N., Kurina, O., Mortimer, P., Meidl, P., Kohout, P., Puusepp, R., Drenkhan, R., Garibay-Orijel, R., Godoy, R., Alkahtani, S., Rahimlou, S., Dudov, S., Põlme, S., Ghosh, S., Mundra, S., Ahmed, T., Netherway, T., Henkel, T., Roslin, T., Nteziryayo, V., Fedosov, V., Onipchenko, V., Yasanthika, W.A.E., Lim, Y., Van Nuland, M., Soudzilovskaia, N., Antonelli, A., Kõljalg, U., Abarenkov, K., Tedersoo, L., 2023. Connecting the multiple dimensions of global soil fungal diversity. Science Advances 9, 1–15. doi:10.1126/sciadv.adj8016

Muthukumar, T., Udaiyan, K., Shanmughavel, P., 2004. Mycorrhiza in sedges - An overview. Mycorrhiza 14, 65–77. doi:10.1007/s00572-004-0296-3

Myers-Smith, I.H., Forbes, B.C., Wilmking, M., Hallinger, M., Lantz, T., Blok, D., Tape, K.D., Maclas-Fauria, M., Sass-Klaassen, U., Lévesque, E., Boudreau, S., Ropars, P., Hermanutz, L., Trant, A., Collier, L.S., Weijers, S., Rozema, J., Rayback, S.A., Schmidt, N.M., Schaepman-Strub, G., Wipf, S., Rixen, C., Ménard, C.B., Venn, S.,

Goetz, S., Andreu-Hayles, L., Elmendorf, S., Ravolainen, V., Welker, J., Grogan, P., Epstein, H.E., Hik, D.S., 2011. Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. Environmental Research Letters 6. doi:10.1088/1748-9326/6/4/045509

Myers-Smith, I.H., Kerby, J.T., Phoenix, G.K., Bjerke, J.W., Epstein, H.E., Assmann, J.J., John, C., Andreu-Hayles, L., Angers-Blondin, S., Beck, P.S.A., Berner, L.T., Bhatt, U.S., Bjorkman, A.D., Blok, D., Bryn, A., Christiansen, C.T., Cornelissen, J.H.C., Cunliffe, A.M., Elmendorf, S.C., Forbes, B.C., Goetz, S.J., Hollister, R.D., de Jong, R., Loranty, M.M., Macias-Fauria, M., Maseyk, K., Normand, S., Olofsson, J., Parker, T.C., Parmentier, F.J.W., Post, E., Schaepman-Strub, G., Stordal, F., Sullivan, P.F., Thomas, H.J.D., Tømmervik, H., Treharne, R., Tweedie, C.E., Walker, D.A., Wilmking, M., Wipf, S., 2020. Complexity revealed in the greening of the Arctic. Nature Climate Change 10, 106–117. doi:10.1038/s41558-019-0688-1

Newsham, K.. K., Eidesen, P.B., Davey, M.L., Axelsen, J., Courtecuisse, E., Flintrop, C., Johansson, A.G., Kiepert, M., Larsen, S.E., Lutherau, K.E., Maurset, M., McQuilkin, J., Misiak, M., Pop, A., Thompson, S., Read, D.J., 2017. Arbuscular mycorrhizas are present on Spitsbergen. Mycorrhiza 27, 725–731.

Nguyen, N.H., Song, Z., Bates, S.T., Branco, S., Tedersoo, L., Menke, J., Schilling, J.S., Kennedy, P.G., 2016. FUNGuild: An open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecology 20, 241–248. doi:10.1016/j.funeco.2015.06.006

Nicolás, C., Martin-Bertelsen, T., Floudas, D., Bentzer, J., Smits, M., Johansson, T., Troein, C., Persson, P., Tunlid, A., 2019. The soil organic matter decomposition mechanisms in ectomycorrhizal fungi are tuned for liberating soil organic nitrogen. ISME Journal 13, 977–988. doi:10.1038/s41396-018-0331-6

Nilsson, R.H., Larsson, K.H., Taylor, A.F.S., Bengtsson-Palme, J., Jeppesen, T.S., Schigel, D., Kennedy, P., Picard, K., Glöckner, F.O., Tedersoo, L., Saar, I., Kõljalg, U., Abarenkov, K., 2019. The UNITE database for molecular identification of fungi: Handling dark taxa and parallel taxonomic classifications. Nucleic Acids Research 47, D259–D264. doi:10.1093/nar/gky1022

Oksanen, J.F., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J., 2022. Vegan: Community Ecology Package.

940 Olofsson, J., Kitti, H., Rautiainen, P., Stark, S., Oksanen, L., 2001. Effects of summer
941 grazing by reindeer on composition of vegetation, productivity and nitrogen cycling
942 Ecography 24, 13–24. doi:10.1034/j.1600-0587.2001.240103.x

943 Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P.E., Oksanen, T., Suominen, O.,
944 2009. Herbivores inhibit climate-driven shrub expansion on the tundra. Global
945 Change Biology 15, 2681–2693. doi:10.1111/j.1365-2486.2009.01935.x

946 Olofsson, J., Post, E., 2018. Effects of large herbivores on tundra vegetation in a
947 changing climate, and implications for rewilding. Philosophical Transactions of the
948 Royal Society B: Biological Sciences 373. doi:10.1098/rstb.2017.0437

949 Olofsson, J., Stark, S., Oksanen, L., 2004. Reindeer influence on ecosystem processes
950 in the tundra. Oikos 105, 386–396. doi:10.1111/j.0030-1299.2004.13048.x

951 Olsson, P.A., Eriksen, B., Dahlberg, A., 2004. Colonization by arbuscular mycorrhizal
952 and fine endophytic fungi in herbaceous vegetation in the Canadian High Arctic.
953 Canadian Journal of Botany 82, 1547–1556. doi:10.1139/B04-111

954 Öpik, M., Vanatoa, A., Vanatoa, E., Moora, M., Davison, J., Kalwij, J.M., Reier, Ü.,
955 Zobel, M., 2010. The online database MaarjAM reveals global and ecosystemic
956 distribution patterns in arbuscular mycorrhizal fungi (Glomeromycota). New
957 Phytologist 188, 223–241. doi:10.1111/j.1469-8137.2010.03334.x

958 Orwin, K.H., Kirschbaum, M.U.F., St John, M.G., Dickie, I.A., 2011. Organic nutrient
959 uptake by mycorrhizal fungi enhances ecosystem carbon storage: A model-based
960 assessment. Ecology Letters 14, 493–502. doi:10.1111/j.1461-0248.2011.01611.x

961 Parker, T.C., Chomel, M., Clemmensen, K.E., Friggens, N.L., Hartley, I.P., Johnson, D.,
962 Kater, I., Krab, E.J., Lindahl, B.D., Street, L.E., Subke, J.A., Wookey, P.A., 2022.
963 Resistance of subarctic soil fungal and invertebrate communities to disruption of
964 below-ground carbon supply. Journal of Ecology 110, 2883–2897.
965 doi:10.1111/1365-2745.13994

966 Parker, T.C., Thaston, A.M., Raundrup, K., Subke, J.A., Wookey, P.A., Hartley, I.P.,
967 2021. Shrub expansion in the Arctic may induce large-scale carbon losses due to
968 changes in plant-soil interactions. Plant and Soil 463, 643–651.
969 doi:10.1007/s11104-021-04919-8

970 Phillips, R.P., Brzostek, E., Midgley, M.G., 2013. The mycorrhizal-associated nutrient
971 economy: A new framework for predicting carbon-nutrient couplings in temperate
972 forests. New Phytologist 199, 41–51. doi:10.1111/nph.12221

973 Rantanen, M., Karpechko, A.Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja,
974 K., Vihma, T., Laaksonen, A., 2022. The Arctic has warmed nearly four times faster

than the globe since 1979. Communications Earth and Environment 3, 1–10. doi:10.1038/s43247-022-00498-3

Ravolainen, V., Soininen, E.M., Jónsdóttir, I.S., Eischeid, I., Forchhammer, M., van der Wal, R., Pedersen, Å., 2020. High Arctic ecosystem states: Conceptual models of vegetation change to guide long-term monitoring and research. Ambio 49, 667–677. doi:10.1007/s13280-019-01310-x

Read, D.J., Perez-Moreno, J., 2003. Mycorrhizas and nutrient cycling in ecosystems - A journey towards relevance? New Phytologist 157, 475–492. doi:10.1046/j.1469-8137.2003.00704.x

Ruotsalainen, A.L., Eskelinen, A., 2011. Root fungal symbionts interact with mammalian herbivory, soil nutrient availability and specific habitat conditions. Oecologia 166, 807–817. doi:10.1007/s00442-011-1928-x

Ruotsalainen, A.L., Kytöviita, M.M., 2004. Mycorrhiza does not alter low temperature impact on Gnaphalium norvegicum. Oecologia 140, 226–233. doi:10.1007/s00442-004-1586-3

Ryberg, M., Andreasen, M., Björk, R.G., 2011. Weak habitat specificity in ectomycorrhizal communities associated with Salix herbacea and Salix polaris in alpine tundra. Mycorrhiza 21, 289–298. doi:10.1007/s00572-010-0335-1

Santalahti, M., Sun, H., Sietiö, O.M., Köster, K., Berninger, F., Laurila, T., Pumpanen, J., Heinonsalo, J., 2018. Reindeer grazing alter soil fungal community structure and litter decomposition related enzyme activities in boreal coniferous forests in Finnish Lapland. Applied Soil Ecology 132, 74–82. doi:10.1016/j.apsoil.2018.08.013

Schulze, E.D., Chapin, F.S., Gebauer, G., 1994. Nitrogen nutrition and isotope differences among life forms at the northern treeline of Alaska. Oecologia 100, 406–412. doi:10.1007/BF00317862

Schuur, E.A.G., McGuire, A.D., Schädel, C., Grosse, G., Harden, J.W., Hayes, D.J., Hugelius, G., Koven, C.D., Kuhry, P., Lawrence, D.M., Natali, S.M., Olefeldt, D., Romanovsky, V.E., Schaefer, K., Turetsky, M.R., Treat, C.C., Vonk, J.E., 2015. Climate change and the permafrost carbon feedback. Nature 520, 171–179. doi:10.1038/nature14338

Shaver, G.R., Chapin, F.S., 1991. Production : Biomass Relationships and Element Cycling in Contrasting Arctic Vegetation Types. Ecological Monographs 61, 1–31.

Shi, G., Yao, B., Liu, Y., Pan, J., Jiang, S., Wang, Y., Wang, Z., Feng, H., Zhou, H., 2021. The effects of long-term warming on arbuscular mycorrhizal fungal

communities depend on habitat type on the Qinghai-Tibet Plateau. Applied Soil Ecology 167, 104030. doi:10.1016/j.apsoil.2021.104030

Sizonenko, T.A., Dubrovskiy, Y.A., Novakovskiy, A.B., 2020. Changes in mycorrhizal status and type in plant communities along altitudinal and ecological gradients—a case study from the Northern Urals (Russia). Mycorrhiza 30, 445–454. doi:10.1007/s00572-020-00961-z

Smith, S.E., Read, D.J., 2008. Mycorrhizal symbiosis, Third edit. ed. Elsevier Ltd. doi:https://doi.org/10.1016/B978-0-12-370526-6.X5001-6

Spitzer, C.M., Wardle, D.A., Lindahl, B.D., Sundqvist, M.K., Gundale, M.J., Fanin, N., Kardol, P., 2022. Root traits and soil micro-organisms as drivers of plant–soil feedbacks within the sub-arctic tundra meadow. Journal of Ecology 110, 466–478. doi:10.1111/1365-2745.13814

Sundqvist, M.K., Moen, J., Björk, R.G., Vowles, T., Kytöviita, M.M., Parsons, M.A., Olofsson, J., 2019. Experimental evidence of the long-term effects of reindeer on Arctic vegetation greenness and species richness at a larger landscape scale. Journal of Ecology 107, 2724–2736. doi:10.1111/1365-2745.13201

Team, R.C., 2022. R: A Language for Statistical Computing.

Tedersoo, L., 2017. Biogeography of Mycorrhizal Symbiosis. Springer International Publishing, Cham, Switzerland. doi:10.1007/978-3-319-56363-3

Timling, I., Dahlberg, A., Walker, D.A., Gardes, M., Charcosset, J.Y., Welker, J.M., Taylor, D.L., 2012. Distribution and drivers of ectomycorrhizal fungal communities across the North American Arctic. Ecosphere 3, art111. doi:10.1890/es12-00217.1

Väisänen, M., Ylänne, H., Kaarlejärvi, E., Sjögersten, S., Olofsson, J., Crout, N., Stark, S., 2014. Consequences of warming on tundra carbon balance determined by reindeer grazing history. Nature Climate Change 4, 384–388. doi:10.1038/nclimate2147

van der Wal, R., 2006. Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. Oikos 114:1, 177–186.

Van Geel, M., Jacquemyn, H., Peeters, G., van Acker, K., Honnay, O., Ceulemans, T., 2020. Diversity and community structure of ericoid mycorrhizal fungi in European bogs and heathlands across a gradient of nitrogen deposition. New Phytologist 228, 1640–1651. doi:10.1111/nph.16789

Van Gestel, N., Shi, Z., Van Groenigen, K.J., Osenberg, C.W., Andresen, L.C., Dukes, J.S., Hovenden, M.J., Luo, Y., Michelsen, A., Pendall, E., Reich, P.B., Schuur,

E.A.G., Hungate, B.A., 2018. Predicting soil carbon loss with warming. Nature 554, E4–E5. doi:10.1038/nature25745

Větrovský, T., Kolaříková, Z., Lepinay, C., Awokunle Hollá, S., Davison, J., Gromyko, A., Jelínková, B., Kolařík, M., Krüger, M., Lejsková, R., Michalčíková, L., Michalová, T., Moora, M., Moravcová, A., Moulíková, Š., Odriozola, I., Öpik, M., Pappová, M., Piché-Choquette, S., Popelářová, A., Skřivánek, J., Vlk, L., Zobel, M., Baldrian, P., Kohout, P., 2023. GlobalAMFungi: a global database of arbuscular mycorrhizal fungal occurrences from high-throughput-sequencing metabarcoding studies. Fungal Diversity In review, 2151–2163. doi:10.1111/nph.19283

Vowles, T., Björk, R.G., 2019. Implications of evergreen shrub expansion in the Arctic. Journal of Ecology 107, 650–655. doi:10.1111/1365-2745.13031

Vowles, T., Gunnarsson, B., Molau, U., Hickler, T., Klemedtsson, L., Björk, R.G., 2017a. Expansion of deciduous tall shrubs but not evergreen dwarf shrubs inhibited by reindeer in Scandes mountain range. Journal of Ecology 105, 1547–1561. doi:10.1111/1365-2745.12753

Vowles, T., Lindwall, F., Ekblad, A., Bahram, M., Hurmeaux, B.R., Ryberg, M., Björk, R.G., 2018. Complex effects of mammalian grazing on extramatrical mycelial biomass in the Scandes forest-tundra ecotone. Ecology and Evolution 8, 1019–1030. doi:10.1002/ece3.3657

Vowles, T., Lovehav, C., Molau, U., Björk, R.G., 2017b. Contrasting impacts of reindeer grazing in two tundra grasslands. Environmental Research Letters 12. doi:10.1088/1748-9326/aa6a2a

Vuorinen, K.E.M., Austrheim, G., Tremblay, J.P., Myers-Smith, I.H., Hortman, H.I., Frank, P., Barrio, I.C., Dalerum, F., Björkman, M.P., Björk, R.G., Ehrich, D., Sokolov, A., Sokolova, N., Ropars, P., Boudreau, S., Normand, S., Prendin, A.L., Schmidt, N.M., Lecheco-Solana, A., Post, E., John, C., Kerby, J., Sullivan, P.F., Moullec, M. Le, Hansen, B.B., Van Der Wal, R., Pedersen, Å.O., Sandal, L., Gough, L., Young, A., Li, B., Magnússon, R.I., Sass-Klaassen, U., Buchwal, A., Welker, J., Grogan, P., Andruko, R., Morrissette-Boileau, C., Volkovitskiy, A., Terekhina, A., Speed, J.D.M., 2022. Growth rings show limited evidence for ungulates' potential to suppress shrubs across the Arctic. Environmental Research Letters 17. doi:10.1088/1748-9326/ac5207

Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H.R., Ahlquist, L.E., Alatalo, J.M., Bret-Harte, M.S., Calef, M.P., Callaghan, T. V., Carroll, A.B., Epstein, H.E., Jónsdóttir, I.S., Klein, J.A., Magnússon, B., Molau, U., Oberbauer, S.F., Rewa, S.P., Robinson, C.H., Shaver, G.R., Suding, K.N., Thompson, C.C., Tolvanen, A., Totland, Ø., Turner, P.L., Tweedie, C.E., Webber, P.J., Wookey, P.A., 2006. Plant

community responses to experimental warming across the tundra biome. Proceedings of the National Academy of Sciences of the United States of America 103, 1342–1346. doi:10.1073/pnas.0503198103

Wang, B., Funakoshi, D.M., Dalpé, Y., Hamel, C., 2002. Phosphorus-32 absorption and translocation to host plants by arbuscular mycorrhizal fungi at low root-zone temperature. Mycorrhiza 12, 93–96. doi:10.1007/s00572-001-0150-9

Wang, Yanan, Li, F.Y., Liu, Y., Cheng, J., Wang, Yadong, Liu, J., Wang, X., Li, Y., 2023. Herbivore Dung Promotes Plant Litter Decomposition Rate in a Semi-arid Grassland Ecosystem. Ecosystems 26, 661–674. doi:10.1007/s10021-022-00784-3

Wang, Z., Yuan, X., Wang, D., Zhang, Y., Zhong, Z., Guo, Q., Peng, C., 2018. Large herbivores influence plant litter decomposition by altering soil properties and plant quality in a meadow steppe. Scientific Reports 8, 1–11. doi:10.1038/s41598-018-26835-1

Wurzburger, N., Brookshire, E.N.J., 2017. Experimental evidence that mycorrhizal nitrogen strategies affect soil carbon. Ecology 98, 1491–1497. doi:10.1002/ecy.1827

Yan, Y., Yan, R., Chen, Jiquan, Xin, X., Eldridge, D.J., Shao, C., Wang, X., Lv, S., Jin, D., Chen, Jinqaing, Guo, Z., Chen, B., Xu, L., 2018. Grazing modulates soil temperature and moisture in a Eurasian steppe. Agricultural and Forest Meteorology 262, 157–165. doi:10.1016/j.agrformet.2018.07.011

Ylänne, H., Madsen, R.L., Castaño, C., Metcalfe, D.B., Clemmensen, K.E., 2021. Reindeer control over subarctic treeline alters soil fungal communities with potential consequences for soil carbon storage. Global Change Biology 27, 4254–4268. doi:10.1111/gcb.15720

Ylänne, H., Olofsson, J., Oksanen, L., Stark, S., 2018. Consequences of grazer-induced vegetation transitions on ecosystem carbon storage in the tundra. Functional Ecology 32, 1091–1102. doi:10.1111/1365-2435.13029