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Research Article

Impacts of large herbivores on mycorrhizal fungal communities across the Arctic

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Mycorrhizal fungi play an integral role in nutrient and carbon cycling in soils, which may be especially important in the Arctic, one of the world's most soil carbon-rich regions. Large mammalian herbivores can influence these fungi through their impacts on vegetation and soil conditions, however the strength and prevalence of these interactions in the Arctic is still uncertain. We collected soils from 15 large mammal exclusion experiments across the Arctic. We sequenced both ITS regions and partial SSU regions using two sets of amplicons to determine the composition of soil mycorrhizal fungal communities. This allowed us to assess how these communities are impacted by exclusion of large mammalian herbivores, plant communities, and climate and soil

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properties. Large mammalian herbivore exclusion had a significant impact on the arbuscular mycorrhizal (AM) community dissimilarity between sites. The AM community was also influenced by growing season temperature and pH, which may indicate that conditions are becoming more favourable for these species in some Arctic communities. Large herbivore exclusion did not have a coherent impact on ectomycorrhizal and ericoid mycorrhizal fungal community dissimilarity, which were primarily correlated with $\delta^{15}N$ signature in the soil, rather than herbivory, climate, or plant functional types. The consistent detection of arbuscular mycorrhizal fungi identified highlights the need for more thorough evaluations of these communities and their role in Arctic carbon and nutrient dynamics, as these fungi are currently understudied in the Arctic.

Keywords: amplicon sequencing, arbuscular mycorrhiza, arctic, ectomycorrhiza, ericoid mycorrhiza, herbivory

Introduction

Large mammalian herbivores play a central role in regulating environmental conditions by actively shaping plant and soil properties (Harrison and Bardgett 2008, Vowles and Björk 2019, Koltz et al. 2022, Ylänne and Stark 2025). These interventions influence soil fungi, including those associated with specific plant species (Ruotsalainen and Eskelinen 2011, Ylänne et al. 2021). Soil fungi contribute critically to the cycling of soil carbon (C) and nutrients in ecosystems (Read and Perez-Moreno 2003, Högberg and Read 2006, Orwin et al. 2011, Averill et al. 2014), especially in nutrient-poor ecosystems (Clemmensen et al. 2021, Parker et al. 2021) such as most Arctic ecosystems (Shaver and Chapin 1991, Schulze et al. 1994, Jonasson et al. 2001, Clemmensen et al. 2006). Arctic soils store a substantial portion of the global terrestrial belowground C pool (Schuur et al. 2015). Large mammalian herbivores influence soil fungal communities through both direct and indirect pathways. They disturb soils physically by trampling, and through urine and feces deposition, which alters soil structure, raises soil temperature, and increases nutrient availability (Wang et al. 2018, 2023, Yan et al. 2018, Ylänne et al. 2018, Kytöviita and Olofsson 2021). These impacts can affect fungal composition and may impact future C and nutrient cycling in the Arctic (Olofsson et al. 2009, Vowles et al. 2017, Sundqvist et al. 2019, Vowles and Björk 2019, Lindén et al. 2021, Ylänne et al. 2021, Ylänne and Stark 2025). Concurrently, large mammalian herbivores shape plant communities through selective foraging by altering dominance patterns among plant functional groups, which may in turn influence the proportion of their respective mycorrhizal fungi (Vowles et al. 2018, Vowles and Björk 2019, Ahonen et al. 2021, Ylänne et al. 2021, Castaño et al. 2023), such as ectomycorrhiza (EcM), ericoid mycorrhiza (ErM), and arbuscular mycorrhiza (AM). Despite these known mechanisms, current understanding of large mammalian herbivore–mycorrhizal interactions across the Arctic remains limited, and no systematic evaluation has yet addressed their strengths and consistency.

Mycorrhizal fungal community composition reflects the dominant plant community, as well as soil and climate properties at a given site (Timling et al. 2012, Martínez-García et al. 2015, Soudzilovskaia et al. 2015), all of which large mammalian herbivores can influence. The relative abundance of host plant species often correlates with the prevalence of their associated mycorrhizal fungal types, particularly at local-scales where plant and fungal diversity tend to co-vary (Fei et al. 2022). Locally, variation in herbivory intensity plays a pivotal role in shaping plant community composition and the structure of associated mycorrhizal fungal communities. When large mammalian herbivores exert little or no pressure, competitive deciduous shrubs expand, along with their associated EcM fungi (Myers-smith et al. 2011). Moderate herbivory tends to favor Ericaceous shrubs and their associated ErM fungi, as large mammalian herbivores selectively consume the more palatable EcM deciduous shrubs (Vowles et al. 2017). Under high herbivory pressure, grasses and forbs, which commonly associate with AM fungi, dominate (Olofsson and Post 2018). Additionally, the primarily non-mycorrhizal sedges, especially common in wetter meadow communities, may also become more abundant under heavy grazing conditions.

Soil properties influence mycorrhizal fungal communities, predominantly through reciprocal relationships with C and nutrient dynamics. In turn, mycorrhizal fungal actively modify the soil as they absorb nutrients, store carbon, and contribute to decomposition processes (Hodge et al. 2010, Orwin et al. 2011, Fernandez et al. 2016). Mycorrhizal types influence soil organic matter in two main ways, the degree to which they can decompose organic material to access nutrient stores (Hobbie et al. 2009, Wild et al. 2014), and the recalcitrance of their own necromass (Ekblad et al. 2016, Zhou et al. 2024). 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), however, the influence of AM fungi specifically on soil C turnover has not been evaluated in tundra environments. In addition, large-scale climatic conditions can affect regional distribution of mycorrhizal fungal species, but do not necessarily relate to finer scale processes (Mikryukov et al. 2023). As fungi have different optimal growth conditions, soil temperature and precipitation can affect the balance of different mycorrhizal types in the soil (Ruotsalainen and Kytöviita 2004, Kytöviita 2005). Therefore, changes in temperature and moisture can act as a strong selection factor on the mycorrhizal fungal community as they shift the species most optimally suited to an area. As Arctic soils warm, productivity and subsequently microbial activity generally increases, with the strength of this change connected to soil moisture (Geml et al. 2015). The interplay between soil conditions, climatic factors, and large mammalian herbivores in shaping mycorrhizal fungal communities across the Arctic remains poorly understood, particularly how these interactions influence the distribution of mycorrhizal fungi at both regional and finer scales.

Arctic regions have experienced approximately 2–4 times greater warming since 1979 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, b, Bjorkman et al. 2015, 2020), resulting in increased aboveground productivity and a general greening trend in the Arctic (Myers-Smith et al. 2020). Due to these wide-spread, drastic changes in Arctic ecosystems, understanding direct and indirect environmental and trophic effects on mycorrhizal fungal communities is integral to better understand future changes in the Arctic including C storage, nutrient exchange, and vegetation shifts. The current distribution of mycorrhizal fungal communities across the Arctic can provide valuable insights into the function of these environments and how they might be impacted by future changes moderated by large mammalian herbivores. For example, although AM fungi form associations with almost 80% of terrestrial plant species globally (Smith and Read 2008), their distribution in Arctic communities is generally limited due to low tolerance to cold (Wang et al. 2002, Ruotsalainen and Kytöviita 2004, Kytöviita 2005, Kilpeläinen et al. 2016). However, AM fungal species may respond quickly to climate warming if their host-species become more prevalent, and soils become more amenable to growth as climate conditions improve (Olsson et al. 2004, Hollister and Flaherty 2010, Gao et al. 2016, Newsham et al. 2017, Bennett and Classen 2020). Evaluating mycorrhizal fungal communities in the Arctic is critically important for understanding future ecosystem services in these areas as they are undergoing drastic changes.

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 investigate the effect of these herbivores on mycorrhizal fungal composition and the proportion of mycorrhizal types, alongside edaphic and climate properties and vegetation dynamics. We hypothesize 1) that differences in plant communities, and soil and climate properties will correlate with mycorrhizal fungal community dissimilarity between sites as these properties can act both directly and indirectly on the mycorrhizal fungi in terms of optimal environmental conditions. We also hypothesize 2) that large mammalian herbivores will have a significant impact on mycorrhizal fungal community composition via a myriad of indirect effects through plant consumption, nutrient input, and trampling.

Material and methods

Site descriptions

The study was conducted at 15 sites across the Arctic tundra: five sites in Sweden, four in Finland, two in USA, two in Canada, one in Iceland, and one in Russia (Fig. 1, Table 1). Most sites had three large mammal exclosure fences paired with three ambient plots of equal size, except for SAP1/2 (which had one large fence and ambient plot for each site), 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 YUK1/2 (which had three replicate 1 m^2 fences and three ambient subplots for each site; Supporting information). 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 dominant large mammalian herbivore at most sites is reindeer/caribou, *Rangifer tarandus*, while at AUD it is sheep, *Ovis ares*. Moose, *Alces alces,* are also likely present in most or all sites to some degree. Large mammalian herbivore effect is referring to the total effects of large mammalian herbivores including foraging, trampling, and urine and feces deposition, processes that all interact to influence vegetation and soil properties.

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 as it is generally the depth of highest activity/concentration of bacteria and fungi and accounts for the organic horizon and part of the mineral fraction for most sites. Five cores were retrieved per subplot. Since the fenced area varies between sites, three separate sampling schemes were followed depending on site configuration (Table 1, Supporting information). Soil samples were immediately collected 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, to remove small rocks and any large pieces of organic material and roots and freeze-dried for a minimum of 24 hours with any samples still moist dried an additional 24 hours. Samples were then dry stored until further analyses. All soil samples within a fence or ambient plot were combined and mixed thoroughly into a single composite soil sample for DNA extraction. In total, there were 116 soil samples across all sites.

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 PCRs were performed using two pairs of primers targeting different regions of the fungal genome. ITS1, ITS2, and partial LSU regions were amplified using the ITS1ngs–LR5 primer pair (ITS1m: 5′-TCCGTAGGTGAACCTGC-3′ Tedersoo et al. (2015); LR5: 5′-TCCTGAGGGAAACTTCG-3′ Vilgalys and Hester 1990) to broadly capture fungal groups (Eshghi

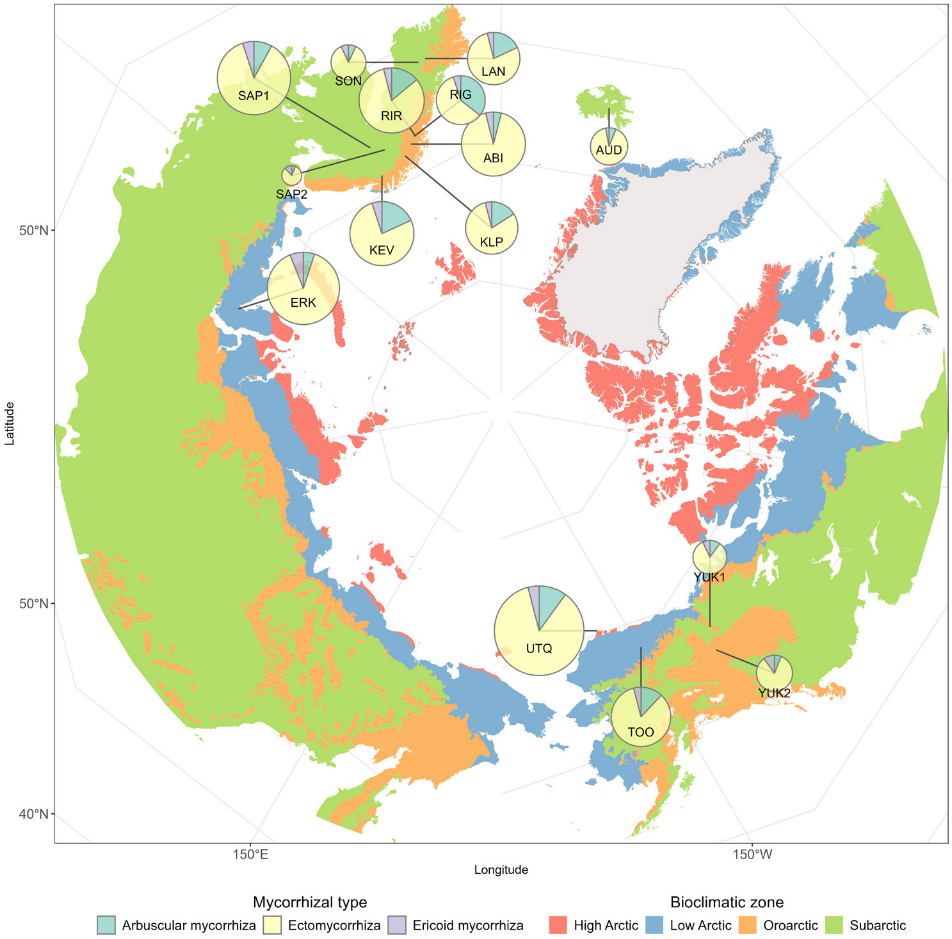

Figure 1. Map of site locations with pie charts showing proportion of mycorrhizal fungal types with the size of the pie charts scaled to the relative abundance of reads attributed to each mycorrhizal fungal type within sites. The bioclimatic zones for Subarctic, Oroarctic, Low Arctic, and High Arctic are included (Berner et al. 2024). AUD is an alpine site within the Icelandic subarctic and should therefore be considered as Oroarctic.

Sahraei et al. 2022). These ITS-LSU region primers may have difficulty targeting some groups of saprotrophic and pathogenic fungi, as well as AM fungi (Tedersoo et al. 2022), although these groups (aside from AM fungi below) were not of interest for this study. Partial SSU region was amplified using the SSU515Fngs–AML2 primer pair (SSU515Fngs: 5′-GCCAGCAACCGCGGTAA-3′ Tedersoo et al. (2015); AML2: 5′-CCCAAACACTTTGGTTTCC-3′ Lee et al. 2008) to target AM fungi specifically. A reaction volume of 50 μl was used for PCR with 5 μl each of template DNA (approximately 1.0–1.5 μg of DNA per sample), forward and reverse barcoded primers with sample specific tags (Supporting information, Tedersoo et al. 2015, Eshghi Sahraei et al. 2022) and 0.5 μl of Phusion High-Fidelity DNA polymerase. A negative control with no template DNA was included with each PCR run. Thermocycling conditions for the ITS1ngs–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 min 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 min after the final cycle. A total of 232 PCR products were cleaned using Agencourt AMpure XP magbeads 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. Library preparation and sequencing was performed by Uppsala Genome Centre, in Uppsala, Sweden using two SMRT cells on the Sequel platform (Pacific Biosciences, Menlo Park, CA, USA).

Bioinformatics

Circular consensus sequence (CCS) reads (218 250 total, Supporting information) were demultiplexed and primers removed for the ITS1ngs-LR5 samples using 'cutadapt' ver.4.4 (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

Table 1 . Description of each site contributing to the data. SAP and YUK both consisted of two subsites that were initially sampled as replicates. No. of 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 approximates moisture conditions at each site.

Country	Site name	ID	Coordinates	No. Fence and ambient plots	Fence area (m^2)	No. Soil cores	No. 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	68°12′21.6″ N,69°11′ 2.4″E	15+15	0.25	5/plot	30	2014	6	Yes	−6.1	561		Dwarf shrubs and sedges	*Rangifer tarandus*	Baubin et al. 2016

(*continued*)

Table 1. Continued.

Country	Site name	ID	Coordinates	No. Fence and ambient plots	Fence area (m²)	No. Soil cores	No. 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
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

had to be removed. Reads from all samples were pooled for the two primers sets and analysed with the 'DADA2' pipeline (ver. 1.26.0). The pooled reads were treated as one dataset in all downstream analysis. Amplicons were filtered using the *filterAndTrim* function with default parameters including maxEE = 2, rm.Phix = TRUE, which sets the expected error rate of sequencing and removes any reads that match the Phix genome and are considered the default values for these parameters when they are included, and minLen = 50, which removes any sequence shorter than 50 bp which is longer than the default 20 but still very conservative for long read samples. Samples were denoised with the *DADA2* function using default parameters, and chimeras removed using the *removeBimera* function. Denoised ASVs for the ITS1ngs–LR5 primer reads were taxonomically assigned with PlutoF SH matching ver. 2.0.0 (Abarenkov et al. 2010) which assigns taxonomy through the UNITE database (ver. 9.0; Nilsson et al. 2019) at thresholds from 97–99% sequence similarity to species hypotheses (SH). The 97% threshold for sequence similarity between sample and reference was selected for downstream statistics. After taxonomic assignment, 1,094 SH's that were taxonomically assigned to family or below were sorted into functional guilds using FUNGuild (Nguyen et al. 2016) and 247 SH's corresponding to mycorrhizal fungi were selected for further analysis. All SH assigned to mycorrhizal type through FUNguild that stated potential membership in multiple guilds with a probability rating of 'possible' were manually checked to ensure they were EcM fungi, which removed an additional 53 SH from our dataset. A final check was performed to ensure only SH that were present in at least one plot, which reduced the final number of SH to 166. 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. Multiple SH may be identified to the same taxonomic species name due to uncertainty in classification or different genotypes within a species, but they are all identified by unique SH code in the UNITE database (ver. 9.0). It is important to note that the guild assignments, much like the SH's themselves, are tentative classifications and an SH can be assigned into multiple potential guilds. For example, many Helotiaceae species are saprotrophs though some can potentially form EcM (Tedersoo et al. 2009, Tedersoo and Smith 2013), and so all identified as potentially EcM by FUNguild were retained in our analyses to ensure full capture of the EcM community rather than potentially excluding some EcM species. ErM fungal species are especially difficult as they are often facultative and can exist as fungal endophytes in non-host plants (Perotto et al. 2018). Indeed, all SH's assigned as ErM were also co-assigned to EcM but were treated as only ErM in the analyses. SH's identified as EcM were manually assigned to exploration type following Agerer (2001). Taxonomy was assigned for the SSU515Fngs–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 ITS1ngs–LR5 assignments and any ASVs overlapping in assignment at species level were removed from the AM fungal sequence dataset. All of the 22 identified genera from the SSU515ngs–AML2 dataset represent AM genera. Relative abundance, separately for the ITS1ngs–LR5 SH's and SSU515ngs–AML2 ASVs, was calculated as proportion of reads out of the total mycorrhizal fungal reads for each plot as it is least affected by the low sequencing depth of our samples compared to absolute abundance or species presence/absence. Dissimilarity in community composition between plots or sites was primarily used to evaluate differences in mycorrhizal fungal communities, over diversity or richness metrics, to avoid biases from low sequencing depth as much as possible. For evaluation of changes in species richness between sites a total community presence/absence dataset was produced by combining the ITS1ngs–LR5 SH's with the SSU515ngs–AML2 ASVs/virtual taxa across all samples (Supporting information; Fig. 1).

Soil and climate properties

All soil samples were also analysed for pH, soil organic matter (SOM) content, total C, total N, δ^{13}C and δ^{15}N. Isotopic analyses of the soil were included as they relate to complex C and N processes relevant for fungal communities, both in how the soil influences fungal groups and how the fungi in turn alter soil isotopes (Kohl et al. 2015). pH was measured after adding 50 ml water and 0.5 ml 2M KCl to 10 g soil (except for SAP and YUK samples which used 150 ml water and 1.5 ml KCl to 5 g soil, and 50 ml water and 0.5 ml KCl to 5 g soil; respectively, as they contained a higher amount of organic material) and allowing to settle overnight before measuring with a pH meter. The addition of 2M KCl removes any potential effect of soil electrolyte concentration on the measurements (Kome et al. 2018). SOM was measured using the Loss-on-Ignition method where the soil was ignited at 550°C for 8 hours with mass loss approximating the mass of organic material in the sample. Total C, δ^{13}C, total N and δ^{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 based on satellite-derived measurements, for the period 1979–2016 for each site (ver. 1.1; Karger et al. 2017). The CHELSA-W5E5 ver. 1.1 has a horizontal resolution of 1 km, which is a downscaled product of its previous version, W5E5 ver. 1.0, using the CHELSA V2.0 algorithm (Karger et al. 2017, 2022). These data were used to determine mean annual temperature (MAT), mean growing season temperature, mean annual precipitation (MAP) and mean growing season precipitation across the sites.

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 20 subplots were used (Sundqvist et al. 2019), KEV used 12 subplots (Lindén et al. 2021), 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 evenly spaced points and counting the number of times individual plant species intercepted the pins. All data were normalized to 100 pins per subplot, upscaling the plots inventoried with fewer than 100 pins, and averaged per plot (Väisänen et al. 2014). These data were further used to calculate the abundance of plant functional types (grasses, sedges, forbs, evergreen and deciduous dwarf shrubs, and tall deciduous shrubs).

Statistics

All data analyses were carried out with R (ver. 4.2.2, www.r-project.org). 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 fungal communities were split into two datasets: EcM/ErM species identified from the ITS1ngs– LR5 primer pair sequences, and AM species identified from the SSU515Fngs–AML2 primer pair sequences.

Non-metric multi-dimensional scaling (NMDS) ordinations were used to evaluate the dissimilarity of mycorrhizal fungal communities between each site for each treatment condition (i.e. exclosure and ambient plots), using Bray-Curtis distances. Three sets of Permutational Analysis of Variance (PERMANOVA) were performed for each dataset to evaluate the effects of large mammalian herbivores on soil properties 1), climate properties 2), and plant functional types (PFTs; 3) on the dissimilarity of mycorrhizal fungal communities between plots. Variable selection for the PERMANOVA was performed using correlation matrices and variance inflation factor (VIF) testing to reduce multicollinearity in the resulting independent variables. The final model for the soil PERMANOVA 1) included site, treatment, pH, SOM, C:N, δ^{13}C, δ^{15}N, and log-transformed sequencing depth. The final model for the climate PERMANOVA 2) included treatment, mean annual temperature, mean growing season temperature and mean growing season precipitation. To disentangle the effects of climate properties and geographic distance a Principal Coordinates of Neighbour Matrices (PCNM) was used on the coordinates for each site, with the resulting scores added as a variable in a PERMANOVA and distance-based redundancy analysis (db-RDA) with post-hoc analysis of variance (ANOVA), conditioning by sequencing depth and PCNM scores. The final model for the PFT PERMANOVA 3) included site, treatment, log-transformed sequencing depth, and percent cover of deciduous tall shrubs, deciduous dwarf shrubs, evergreen dwarf shrubs, grasses, sedges, and forbs.

To account for the overwhelming effect of Site on the mycorrhizal fungal community dissimilarity a second set of PERMANOVA were performed to evaluate the same parameters but with site as a block to restrict the permutations. Additionally, a db-RDA with post-hoc ANOVA following the same permutation scheme was also run to evaluate treatment effect only, which allowed us to condition by both site and sequencing depth, ostensibly removing their influence from the treatment results.

The relative contribution of each set of soil, climate and PFT variables to explaining the overall variance in mycorrhizal fungal community dissimilarity was explored using variance partitioning. Since the climate variables are only relevant at the site level, two sets of variance partitioning were performed for each dataset, one evaluating soil, climate and PFTs at the site level (Supporting information), and a second evaluating just soil and PFTs at the plot level (Supporting information). Additionally, Mantel tests were performed to explore if sites more dissimilar in vegetation community were likewise more dissimilar in fungal community, which if true would indicate a connection between these two communities, either directly or through responding to similar drivers. Differences in soil properties between treatments, fenced and unfenced plots, were calculated using student's t-test for each site individually (Supporting information).

All statistics use an alpha of 0.05, and p-values between 0.1 and 0.05 are referred to as marginally significant which is appropriate due to the low replication inherent in this study and to increase statistical power and reduce the risk of type II errors.

Results

Mycorrhizal fungal types

Three major types of mycorrhizae were captured by the sequence data: EcM, ErM, and AM (Fig. 1, Supporting information), corresponding to 16% of the total fungal reads in the dataset. Across all samples, there were 166 unique SH and 22 unique virtual taxa identified. Only two ErM fungi species were identified: *Hyaloscypha hepaticicola* (species complex including syn. *Pezoloma ericae* and *Leohumicola incrustata* from our sequences) and *Oidiodendron maius*, both in the order Helotiales in the phylum Ascomycota. EcM fungi were a mix of Basidiomycota and Ascomycota, across 3 classes, 9 orders, and 22 families, whereas AM fungi were found across 3 classes, 4 orders, and 8 families within Glomeromycota. Ambient and exclosure plots were generally quite different in the relative proportion of EcM/ErM fungal orders and AM fungal families across the sites (Fig. 2). However, Helotiales were the most abundant EcM/ErM order across all sites, and

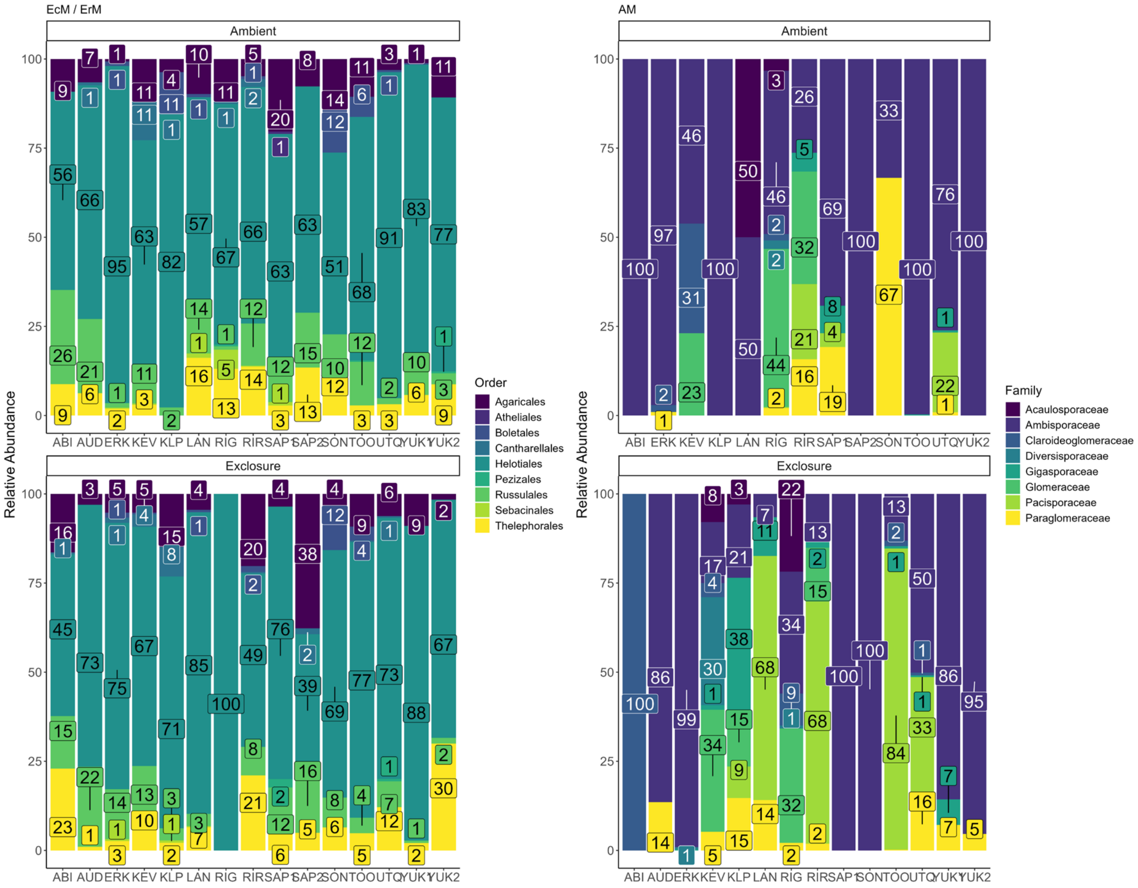

Figure 2. Relative abundance of EcM/ErM fungal orders, and AM fungal families between ambient and exclosure plots at each site. The percent contribution of each Order/Family is labelled on its corresponding bar.

Ambisporaceae was typically the most abundant AM family. The composition of EcM exploration types at each plot was not affected by exclusion of large mammalian herbivores (Supporting information).

Mycorrhizal fungal community composition

Soil properties explained the highest proportion of variance in dissimilarity of EcM/ErM communities compared to climate or PFTs (Supporting information). The total variance explained by all variables at the site-level on EcM/ErM community dissimilarity was approximately 34%. For the AM fungal communities, climate explained a small portion of the variance at site-level, but neither PFTs or soil explained any variance. The total variance explained by all variables at the site-level on AM community dissimilarity was approximately 23%. At the plot level both PFTs and soil parameters explained a small percentage of the variance in AM community dissimilarity. Overall, the measured parameters explained a relatively small portion of the variance in mycorrhizal fungal community dissimilarity for EcM/ErM or AM.

At the plot-level, the large mammalian herbivore exclusion treatment had a significant effect on the AM fungal community composition (Table 2d). Site was significant for both the EcM/ErM and AM mycorrhizal fungal communities, making up between 23–72% of the explained variance depending on the set of explanatory variables tested (Supporting information). When controlling for site, pH and $\delta^{15}N$ signature were significant for explaining dissimilarity in the EcM/ErM fungal community composition, while $\delta^{13}C$ signature was marginally significant (Table 2a). pH was significant for the AM fungal community dissimilarity, while SOM and mean growing season temperature were marginally significant (Table 2a, b).

The NMDS plot for the EcM/ErM community dissimilarity between each site and treatment condition indicated a slight clustering of the Fennoscandian sites that was correlated with higher relative abundance of *Suillus variegatus* (Fig. 3a). NMDS axis 1 was differentiated by changes in the relative abundance of key EcM SH, with one group correlated to positive values, including *Inocybe* sp., *Helotiaceae* sp., and *Tomentella* sp., and another correlated to negative values, including *Oidiodendron chlamydosporicum, Oidiodendron tenuissium,* and *Russula vinosa*. For the AM community, the NMDS confirmed the impact of the exclosures on the AM community dissimilarity, with *Claroideoglomus* sp. showing a correlation adjacent to the treatment vector (Fig. 3b).

Vegetation influence

The relative cover of PFTs was significant for explaining dissimilarity in the EcM/ErM fungal community at the plot-level, but not for the AM community (Supporting information, Fig. 4). Site, percent cover of deciduous dwarf shrubs, percent cover of evergreen dwarf shrubs, percent cover of grasses, percent cover of sedges, and percent cover of forbs all significantly influenced the EcM/ErM fungal community dissimilarity, with percent cover of deciduous tall shrubs showing a marginal significant effect (Supporting information). The shrubs increased towards KEV, LAN, and RIR plots, and away from SAP and RIG (Fig. 4). Sedges primarily increased towards AUD, SAP, and RIG plots, while grasses and forbs increased towards RIR exclosure and SON plots. However, when accounting for the influence of site, PFT's were no longer significant for EcM/ErM mycorrhizal fungal community dissimilarity (Table 2c).

Discussion

We found that large mammalian herbivores exerted the strongest impact on AM fungal communities at the Pan-Arctic scale. This response suggests that AM fungi are particularly sensitive to changes in disturbance regimes, likely because they are already near their ecological tolerance limits (Wang et al. 2002, Ruotsalainen and Kytöviita 2004, Kytöviita 2005, Kilpeläinen et al. 2016). Shifts in environmental conditions, such as host plant prevalence and soil conditions, could have an amplified impact on the AM community. Additionally, the few AM species observed further increases this sensitivity, as reduced diversity can limit functional redundancy and resilience. Consequently, changes affecting individual species may disproportionately alter the structure and function of the entire AM fungal community. While AM fungi are extensively studied in most biomes, they remain understudied in the Arctic (Ruotsalainen and Eskelinen 2011, Větrovský et al. 2023). However, herbivory has been demonstrated to reduce AM colonization of plant roots in acidic, non-fertile sites, coinciding with a higher proportion of evergreen shrubs, rather than grasses and forbs (Ruotsalainen and Eskelinen 2011). Under heavy grazing, graminoids, which associate with AM fungi, usually dominate (Barthelemy et al. 2017). A synthesis of vegetation changes linked with Arctic warming (Bjorkman et al. 2018) showed that nine of the ten most rapidly increasing plant species were species that associate with AM fungi. Despite these patterns, our data did not reveal any significant association between AM fungal community dissimilarity and PFTs. Instead, we found that pH, SOM, and growing season temperature had the strongest influence on AM fungal communities, although we could only assess the temperature relationship at the site level due to the coarseness of the climate data. The relationship to growing season temperature could indicate that climate conditions are becoming more favorable for AM fungal growth, especially as the Arctic continues to warm rapidly (Rantanen et al. 2022). pH has been previously identified as an important driver of fungal community composition (Ruotsalainen and Eskelinen 2011, Hewitt et al. 2013). The influence of both pH and SOM on AM dissimilarity is potentially due to increased productivity in soils with higher pH and SOM. Further, site was a strong predictor of AM community dissimilarity at the plot scale. Sequencing depth was identified as limitation influencing our fungal community dissimilarity estimates, highlighting that deeper sequencing could reveal additional diversity and provide a more complete picture of community composition across plots. However, by including or controlling for

Table 2. PERMANOVA model output for effects of a) soil properties, b) climate properties, and c) PFT's along with large mammalian herbivore effect (treatment) on Hellinger-transformed EcM/ErM and AM mycorrhizal fungal community composition, while accounting for (a–c) or removing (d) the effect of Site. d) Shows the outcome of a PERMANOVA to evaluate just treatment and sequencing depth to explore the effect sequencing depth has on our data, as well as a distance-based redundancy analysis that allows to remove the effect of Site and sequencing depth completely from the analysis of treatment on the mycorrhizal fungal communities. C:N ratio is carbon:nitrogen ratio, and log(SeqDepth) refers to log-transformed sequencing depth to account for the varied sequencing depth between samples. Bold values indicate marginally significant difference at an alpha of 0.1, bold and italic indicate significance below 0.05.

	EcM/ErM			AM		
	R^2	F	p	R^2	F	p
a)						
Treatment	0.009	1.008	0.270	**0.018**	**1.576**	**0.095**
pH	***0.023***	***2.459***	***0.050***	***0.033***	***2.829***	***0.012***
SOM	0.014	1.524	0.543	**0.019**	**1.636**	**0.075**
C:N	0.020	2.171	0.620	0.025	2.171	0.391
δ^{13}C	**0.018**	**1.868**	**0.095**	0.017	1.414	0.397
δ^{15}N	***0.024***	***2.526***	***0.034***	0.012	1.003	0.517
b)						
Treatment	0.013	0.416	0.947	0.033	0.949	0.102
Mean annual temp.	0.054	1.722	0.947	0.052	1.496	0.400
Mean growing season temp.	0.085	2.723	0.947	**0.110**	**3.163**	**0.060**
Mean growing season precip.	0.072	2.308	0.947	0.043	1.247	0.154
c)						
Treatment	0.019	0.445	0.924	0.036	0.711	0.240
Deciduous tall shrub	0.038	0.903	0.927	0.057	1.131	0.908
Deciduous dwarf shrub	0.072	1.700	0.620	0.046	0.910	0.420
Evergreen dwarf shrub	0.056	1.331	0.865	0.024	0.464	0.652
Grass	0.062	1.459	0.952	0.082	1.617	0.496
Sedge	0.067	1.592	0.593	0.023	0.460	0.607
Forb	0.094	2.219	0.657	0.122	2.407	0.170
d)						
PERMANOVA						
Treatment	0.009	0.986	0.249	**0.018**	**1.526**	**0.095**
log(SeqDepth)	***0.041***	***4.264***	***< 0.001***	***0.029***	***2.387***	***0.004***
db-RDA						
Treatment		0.627	0.920		***2.879***	***0.028***

sequencing depth in our analyses, we effectively account for the variance it explains. This approach strengthens our confidence in the accuracy of the remaining identified drivers and supports the robustness of our ecological interpretations. Our findings suggest that both herbivory and climate change are simultaneously shaping Arctic AM fungal communities, highlighting a complex interplay of factors operating across multiple scales.

EcM/ErM fungal community dissimilarity was primarily influenced by plot-level soil properties. Large mammalian herbivores did not have a coherent impact on EcM/ErM communities across the Arctic, but rather site-level differences were the most consistent drivers of community dissimilarity. Among the soil properties, pH and δ^{15}N showed the strongest relationship with EcM/ErM community dissimilarity. Soil δ^{15}N signature can serve as an indicator of dominant mycorrhizal fungal types, with low δ^{15}N values are typically associated with ErM and EcM fungi (Michelsen et al. 1996, 1998, Read and Perez-Moreno 2003, Barthelemy et al. 2017). Following this pattern, all identified exploration types of EcM species were associated with low δ^{15}N values in our data. This isotopic gradient reflects differences in N acquisition strategies, as ErM and EcM fungi efficiently mine N from organic matter and transfer ^{15}N-depleted N compounds to their host plants (Hobbie and Hobbie 2008, Hobbie et al. 2009, Schweiger 2016). Similar to the δ^{15}N gradient, mining of organic matter for nutrients can coincide with a release of carbon from these substrates which will affect the δ^{13}C of the soil (Lindahl et al. 2021, Parker et al. 2021, Clemmensen et al. 2024). Basidiomycete EcM fungi have been shown to be enriched in ^{13}C compared to soil and even differ in δ^{13}C signature from basidiomycete saprotrophs (Hobbie et al. 1999, Henn and Chapela 2001). The amount of C entering the soil through different EcM fungi, their host plants, and breakdown of soil organic matter could explain a portion of the variance in δ^{13}C between sites which is reflected in our data. PFT's impacted EcM/ErM mycorrhizal fungal dissimilarity, but only when site was included as a covariate, when the site-effect was accounted for statistically these relationships were no longer significant. The differences in vegetation between sites was stronger than the effect of PFT cover itself, indicating that vegetation was not directly important for mycorrhizal fungal dissimilarity. The low number of ErM species observed, low sequencing depth, and difficulty assigning species to this mycorrhizal group may explain the limited influence of evergreen dwarf shrubs on mycorrhizal community dissimilarity. While PFTs showed some influence, their overall contribution was weak

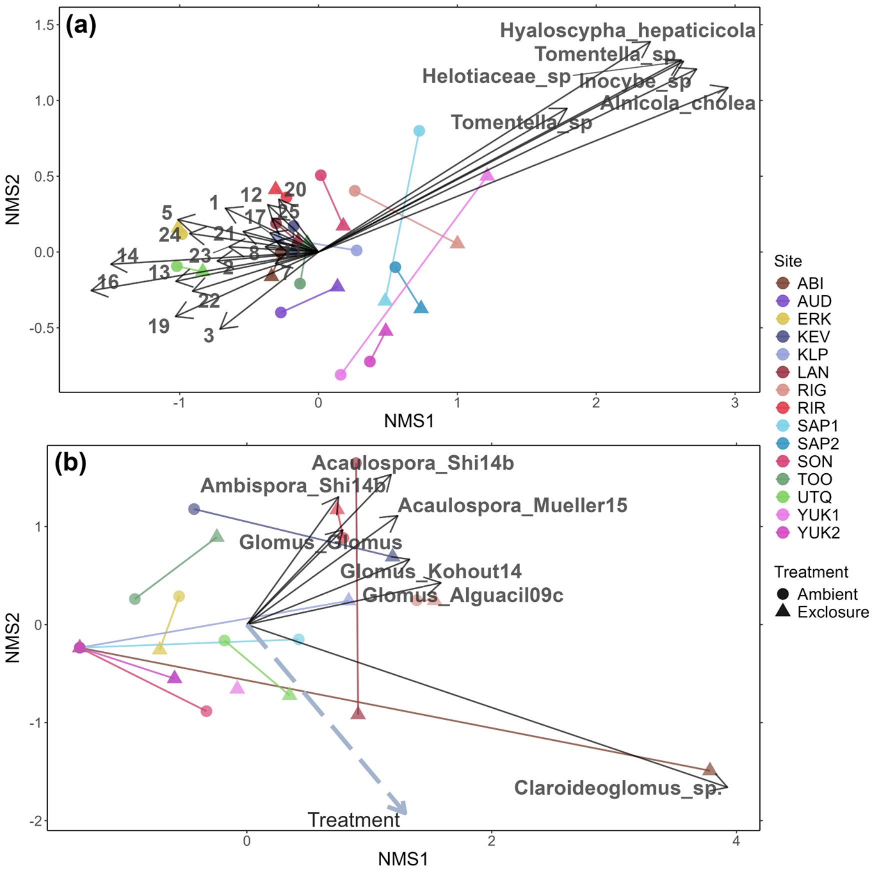

Figure 3. Non-metric multidimensional scaling (NMDS) plot of Bray–Curtis dissimilarity matrix based on Hellinger-transformed relative abundance of mycorrhizal fungal species for: (a) EcM/ErM fungal community composition and (b) the AM fungal community composition (note that no AM species were found in SON and AUD). Each point corresponds to a plot's mycorrhizal fungal community ordinated relative to other plots according to their dissimilarity in community composition. Coloured lines connect the paired treatment conditions for each site. Triangles are exclosure plots while circles are ambient plots. Grey vectors correspond to significance from PERMANOVA results, where dashed vectors are marginally significant for explaining variance in mycorrhizal fungal communities. Treatment points towards the exclosure condition. Black vectors highlight fungal species hypotheses (SH) that show a significant correlation along the direction they point. SH are numbered where space is limited. 1 indicates *Glarea lozoyensis*, 2 indicates *Oidiodendron* sp., 3 indicates *Oidiodendron maius*, 5 indicates Helotiaceae sp., 7 indicates Helotiaceae sp., 8 indicates *Hyaloscypha hepaticicola*, 11 indicates *Lactarius subdulcis*, 12 indicates *Tomentella* sp., 13 indicates *Tomentella* sp., 14 indicates *Tomentella* sp., 16 indicates *Fayodia gracilipes*, 17 indicates *Hydnangium kanuka*, 19 indicates *Russula versicolor*, 20 indicates *Suillus variegatus*, 21 indicates *Russula vinosa*, 22 indicates *Russula vinososordida*, 23 indicates *Oidiodendron tenuissimum*, 24 indicates *Oidiodendron chlamydosporicum*, and 25 indicates *Cortinarius subscotoides*.

compared to soil and climate factors. This underscores the greater importance of abiotic conditions in shaping current and future changes in mycorrhizal community composition. Nevertheless, greater than 65% of the variance remains unexplained, suggesting that additional, unmeasured drivers may influence regional-scale patterns in EcM/ErM fungal composition across the Arctic.

EcM represented the majority of mycorrhizal fungal species, spanning 22 families, with Thelephoraceae as the most species-rich family, accounting for 18% of SHs. The most abundant ErM species in our data, *H. hepaticicola*, also dominated in a herbivory study in subarctic Fennoscandia (Ylänne et al. 2021), where grazing pressure and plant composition influenced its abundance. AM fungi accounted for 13% of the SH/VTs in our study. Their host plants – primarily grasses and forbs – have been shown to respond sensitively to warming in some Arctic communities (Bjorkman et al. 2020). However, AM fungi themselves exhibit variable responses to herbivory, even when their host plants increase in abundance (Kytöviita and Olofsson 2021). Comparing the relative abundance of EcM/ErM fungal orders between exclosure and ambient conditions across sites reveals substantial shifts at several locations, such as KLP, LAN, RIG, and YUK2. In contrast, other sites show minor changes at the order level, which aligns with the overall non-significant effect of large mammalian herbivore exclusion on EcM/ErM community dissimilarity. AM fungal families had much higher changes in relative abundance between exclosure and ambient plots, however, some of this may be explained by the low number of AM reads identified to genera. Changes in the prevalence

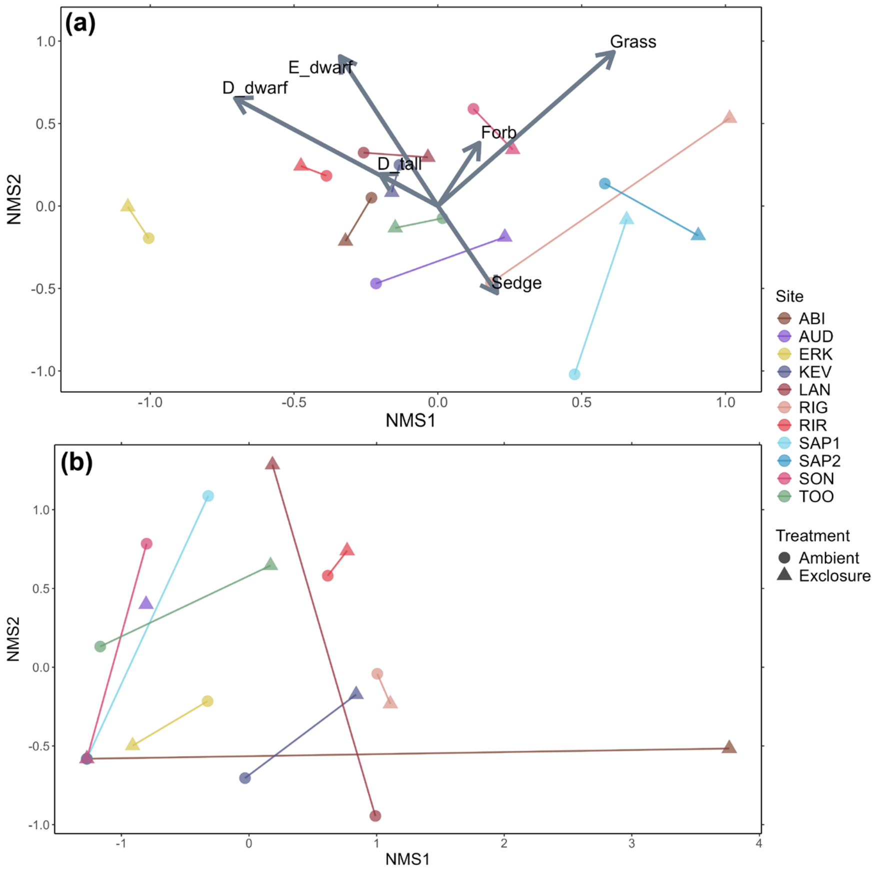

Figure 4. NMDS ordination plot comparing mycorrhizal fungi communities between sites based on percent cover of Plant Functional Types (PFT) at each site with available data. Each point corresponds to the mycorrhizal fungi community composition for (a) EcM/ErM and (b) AM communities using Hellinger-transformed relative abundance data for each site and treatment condition ordinated relative to the other sites by their Bray-Curtis dissimilarity in community composition. Triangles are exclosure plots while circles are ambient plots. Vectors belong to significant percent cover of PFT predictors. D_tall = Deciduous tall shrub, D_dwarf = deciduous dwarf shrub, E_dwarf = evergreen dwarf shrub.

of AM fungal families can impact the rate and extent of root colonization (Hart and Reader 2002), and the capacity for nutrient supply and pathogen protection to host plants (Powell et al. 2009). Large mammal herbivores may therefore impact key plant–fungal interactions at the community level.

In conclusion, our study reveals that herbivory plays a role in shaping Arctic AM fungal communities, however, effects on EcM/ErM communities are inconsistent across the Arctic. The interplay between bottom-up processes (climate and edaphic properties) and top-down processes (large mammalian herbivores and biotic interactions) has a complex, scale-dependent influence on the composition of mycorrhizal fungal communities. However, across the Arctic, soil properties emerged as stronger determinants of mycorrhizal community composition than PFTs, with climate properties integral at a regional scale particularly for AM fungi. The widespread presence of AM species across sites, combined with their sensitivity to environmental change, underscores the need to adapt fungal survey protocols in tundra ecosystems. Without including AM fungi, community-level evaluations risk being incomplete. Mycorrhizal fungi play a crucial role in Arctic soil carbon and nutrient dynamics, and their impact may become increasingly important as the Arctic warms and vegetation shifts. Understanding these dynamics is essential for predicting the future of Arctic ecosystems. Further research into a biogeographical synthesis of Arctic fungi could help clarify these missing pieces, especially to evaluate joint species modelling within the fungal communities to explore how fungal species interact – whether through competitive exclusion or facilitation – across Arctic regions. Although we did not find direct evidence linking mycorrhizal fungal communities to carbon storage, the strong associations with soil $\delta^{13}C$ and $\delta^{15}N$ (for EcM/ErM) and SOM (for AM) suggest that mycorrhizal composition is closely tied to soil carbon and nitrogen dynamics across the Arctic. While single-site studies have shown links between mycorrhizal fungi and carbon cycling, our Pan-Arctic results suggest these relationships are not yet resolved at broader spatial scales.

Significance statement

This study advances our understanding spatial variation in Arctic mycorrhizal fungi and the multi-trophic level interactions among herbivores, plants, and soil microbes. The study leverages a unique dataset of long-read DNA amplicons from a pan-Arctic network of large herbivore exclosures, it represents the most extensive assessment of herbivory impacts on soil fungi in the Arctic to date. Our findings offer novel insights into Arctic soil ecology, highlighting connections between fungal communities, plant composition, soil properties, and climate. While recent studies have explored herbivory-driven changes in plant-fungal interactions at a local scale (Le Noir de Carlan et al. 2024, Parisy et al. 2024, Tyvijärvi et al. 2024), our work significantly extend these observations to the entire Arctic.

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Author contributions

Cole G. Brachmann: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Martin Ryberg**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Resources (equal); Writing – review and editing (equal). **Brendan R. Furneaux**: Data curation (equal); Investigation (equal); Writing – review and editing (equal). **Anna Rosling**: Data curation (equal); Investigation (equal); Writing – review and editing (equal). **Tinghai Ou**: Data curation (equal); Investigation (equal); Writing – review and editing (equal). **Alf Ekblad**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Resources (equal); Writing – review and editing (equal). **Isabel C Barrio**: Investigation (equal); Writing – review and editing (equal). **M. Syndonia Bret-Harte**: Investigation (equal); Writing – review and editing (equal). **Hannu Fritze**: Investigation (equal); Writing – review and editing (equal). **Laura Gough**: Investigation (equal); Writing – review and editing (equal). **Robert D. Hollister**: Investigation (equal); Writing – review and editing (equal). **Ingibjörg S. Jónsdóttir**: Investigation (equal); Writing – review and editing (equal). **Oula Kalttopää**: Investigation (equal); Writing – review and editing (equal). **Elin Lindén**: Investigation (equal); Writing – review and editing (equal). **Päivi Mäkiranta**: Investigation (equal); Writing – review and editing (equal). **Johan Olofsson**: Investigation (equal); Writing – review and editing (equal). **Rauni Partanen**: Investigation (equal); Writing – review and editing (equal). **Kirsten A. Reid**: Investigation (equal); Writing – review and editing (equal). **Aleksandr Sokolov**: Investigation (equal); Writing – review and editing (equal). **Svetlana Abdulmanova**: Investigation (equal); Writing – review and editing (equal). **Maija S. Sujala**: Investigation (equal); Writing – review and editing (equal). **Maja K. Sundqvist**: Investigation (equal); Writing – review and editing (equal). **Otso Suominen**: Investigation (equal); Writing – review and editing (equal).. **Craig E. Tweedie**: Investigation (equal); Writing – review and editing (equal). **Amanda Young**: Investigation (equal); Writing – review and editing (equal). **Robert G. Björk**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Resources (equal); Writing – review and editing (equal);

Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/ecog.08045.

Data availability statement

Data are available from the Swedish National Data Service: https://doi.org/10.5878/zf1c-vz95 (Brachmann et al. 2025). Raw sequence reads are available from the Sequence Read Archive under accession number: PRJNA1362997; https://www.ncbi.nlm.nih.gov/sra/PRJNA1362997.

Supporting information

The Supporting information associated with this article is available with the online version.

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