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Opportunistic partner choice among arctic plants and root-associated fungi is driven by environmental conditions

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Abstract

Interactions between plants and soil microbes play a key role in structuring plant communities. In a rapidly changing Arctic environment, we urgently need to uncover how these interactions are responding to environmental changes. Here, we disentangle two contributions to variation in plant–fungus interactions along geographic and environmental gradients of the Arctic: abiotic impacts on the pool of fungal species present in the soil, and abiotic *and* biotic impacts on variation in the pool of fungi associated with plant roots. Given the low species richness and harsh conditions in the Arctic, we expected opportunistic associations to emerge, along with strong impacts of the environment on interaction structure. Across multiple spatial scales, we sampled roots of 12 widely distributed plant taxa. To characterize the pool of species available for colonization, we quantified the pool of fungi present in the soil, and to characterize realized interactions, we quantified root-associated fungal communities. Data from DNA metabarcoding of each fungal community were

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modeled by Hierarchical Modeling of Species Communities (HMSC). To determine whether the realized networks deviated from random expectations, we compared the observed networks to those expected under null models. Overall, we found strong support for opportunistic associations, along with some level of selectivity. Fungal communities within the soil and rhizosphere shared 85% of their fungal genera, but the composition of these communities significantly differed among ecosystem compartments. The two compartments showed similar responses to the environment, with low levels of partner fidelity among both plant and fungal taxa. Plant–fungus networks showed a distinctly nonrandom structure, which was driven by gradients in pH and temperature. Across the Arctic, the structure of fungal communities in the plant rhizosphere is thus mainly driven by abiotic rather than by biotic conditions (i.e., host identity or microbes–microbes associations). Environmental conditions will dictate what interaction partners occur where, but interactions among locally occurring plants and fungi are dominated by opportunistic partner choice. Overall, our findings suggest that the dynamics and structure of plant–root-associated interactions will be altered by abiotic changes in the Arctic realm, and that the flexibility of associations may contribute to the resilience of the system.

KEYWORDS

Arctic, eDNA metabarcoding, Hierarchical Modeling of Species Communities (HMSC), network analyses, plant–fungus interactions, root-associated fungi, soil fungi

INTRODUCTION

The importance of soil microbiota in driving the dynamics of plant communities and ecosystem functioning has long been recognized (Bahram & Netherway, 2021; Bardgett & Wardle, 2010). There is an increasing recognition that the community dynamics of plants cannot be separated from the dynamics of soil microbiota (Bahram & Netherway, 2021; Tedersoo et al., 2020). Understanding the links between above- and belowground communities, and between the micro- and macrobiome, is now more urgent than ever. With globally changing abiotic conditions (Calvin et al., 2023; IPCC, 2014), species are rapidly changing their ranges in pursuit of shifting abiotic conditions (IPBES, 2019). What is much less known is how these changes at the species level reflect in biotic interactions, and in full networks of such interactions (Tylianakis et al., 2008; Tylianakis & Morris, 2017; Woodward et al., 2010). Overall, interactions among and between communities of different kingdoms are likely to change with environmental stress (Classen et al., 2015; Vandenkoornhuysen et al., 2015).

Belowground microbiomes can affect the composition of plant communities in many ways. For one, root-associated microbial communities can have a

strong influence on plant nutrient acquisition (Bowles et al., 2018; Tedersoo et al., 2020; Van Der Heijden et al., 2008). They can also affect the survival of individual plants by improving defense against pathogens (Bever et al., 2010; Friesen et al., 2011; Li et al., 2020). These effects are so strong that recent studies have shown that the distributional ranges of plants can be modulated by the presence of suitable mycorrhizal fungi (Bahram & Netherway, 2021; Bowles et al., 2018; McCormick et al., 2018). Ultimately, ecological dynamics may change plant community composition and diversity, leading to concordant and predictable changes in soil microbial communities and vice versa (Bardgett, 2011; Reynolds et al., 2003; Wardle et al., 2004).

Changes in plant–fungal associations are likely accentuated in the Arctic realm, since this region has recently been warming at a rate three to four times faster than the global average (Box et al., 2019; Post et al., 2019; Rantanen et al., 2022). Arctic plants will also allocate a large proportion of biomass belowground, which is likely to increase the resource availability for arctic soil microbial communities (Bowles et al., 2018; Eisenhauer et al., 2017; Iversen et al., 2015). However, the precise mechanisms behind—and the microbes involved in—the dynamics of arctic plant–microbe interactions in

response to environmental conditions are still poorly understood (Mohan et al., 2014; Trivedi et al., 2022). While Arctic ecosystems are sensitive to disturbance, there is little information on how soil microbial communities respond to environmental changes (Bardgett & Caruso, 2020; Frindte et al., 2019). As a general feature potentially buffering the system against both biotic and abiotic variation, several studies have reported opportunistic associations among plants and fungi in arctic and alpine areas (Abrego et al., 2020; Bjorbækmo et al., 2010; Botnen et al., 2014). For mutualistic interactions, such opportunistic foraging can be an efficient strategy to find alternative hosts and/or increase bargaining power in harsh environments (Chagnon et al., 2020; Lekberg et al., 2010).

In this paper, we address both the direct and indirect effects of abiotic conditions on plant–microbe interactions. Specifically, we disentangle two contributions to variation in plant–fungus interactions along geographic and environmental gradients of the Arctic: abiotic impacts on the pool of fungal species present in the soil and abiotic *and* biotic impacts on variation in the pool of fungi associated with plant roots (and thereby present in the plant rhizosphere). Working across multiple spatial scales, we sampled roots of 12 widely distributed plant

taxa across local environmental gradients and across a large latitudinal gradient. We then characterized the pool of species present in the soil and the set of realized interactions, that is, the fungal communities emerging on the roots themselves. Drawing on this explicit characterization of each ecosystem compartment (i.e., bulk soil vs. rhizosphere) and of their relation to environmental conditions, we aimed to (1) compare environmental responses among fungi in the soil versus in the rhizosphere; (2) disentangle the extent to which plant-associated fungal communities are shaped by biotic influences (most prominently: the identity of the host plant) and the climatic environment, respectively, (Figure 1A); (3) relate overall variation in network features to variation in the abiotic environment across the Arctic (Figure 1B).

To target these objectives, we took a threefold approach: We first disentangled the effect of the environment from effects of the plants themselves (Figure 1). For that, we compared paired communities to each other: the fungi found associated with the rhizosphere and the fungi found in nearby soil. Second, we used a joint species distribution model to quantify the relative importance of the abiotic and biotic environment (i.e., host identity, vegetation coverage, or microbe–microbe associations) in shaping the composition of fungi communities

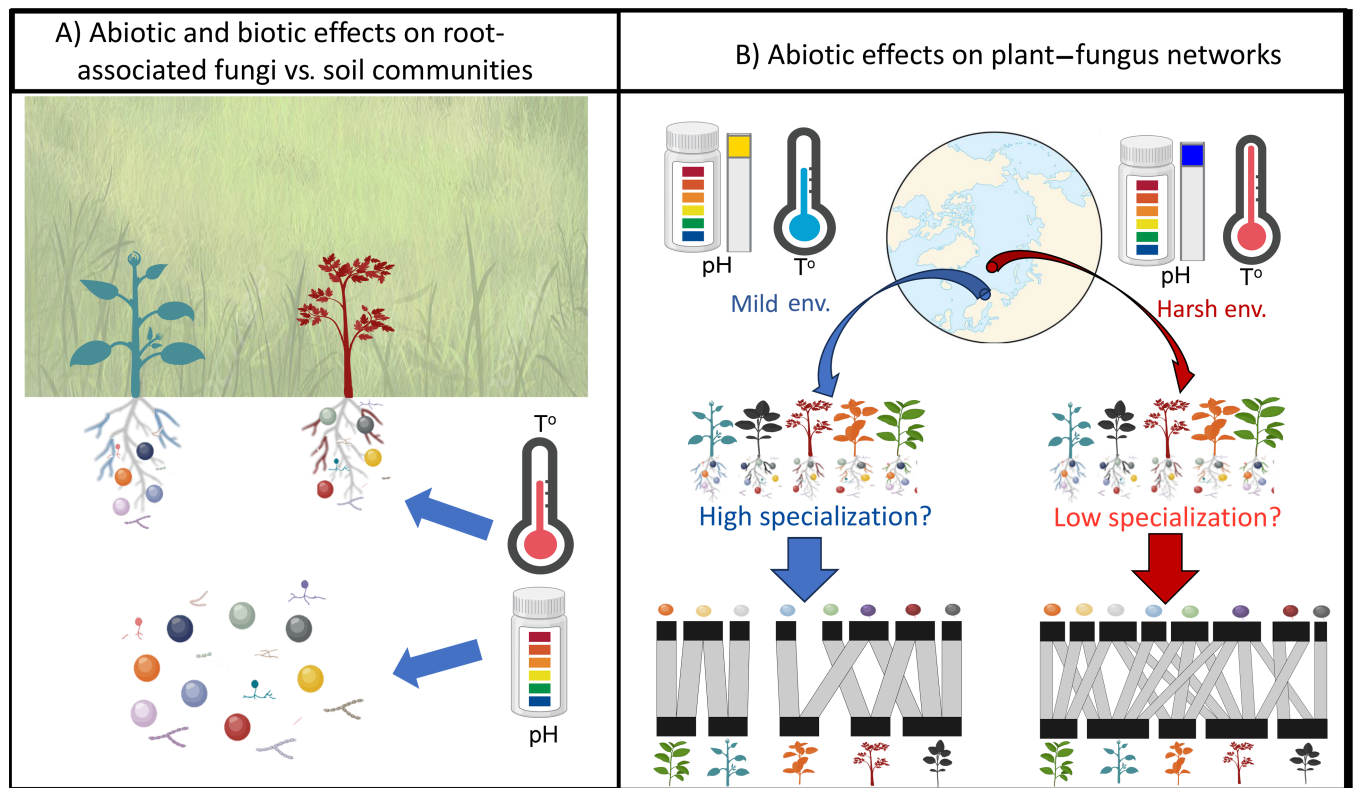


FIGURE 1 Conceptual setting and approach of this study. To quantify biotic versus abiotic imprints on fungal communities across the Arctic, we examined (A) bioclimatic responses among fungi in the soil vs in the rhizosphere and (B) changes in association specificity along geographic and environmental gradients in the Arctic. The figure was partially created in BioRender. Parisy, B. (2025b) <https://BioRender.com/w131598>.

(Figure 1A). Finally, we explored how the associations between plants and fungi change with environmental conditions (Figure 1B) by using network analyses applied to plants and their root-associated fungi along environmental gradients.

At the level of different ecosystem compartments (the soil vs. the rhizosphere), we a priori expected a strong concordance in community composition, inferred by a substantial overlap between compartments (Bahram et al., 2018; Soudzilovskaia et al., 2015; Tedersoo et al., 2022). In line with this a priori assumption, we expected congruent changes in the composition of these two communities in response to environmental gradients across the Arctic. As an alternative hypothesis, we posited the plant to provide a pronounced “physical buffer” (Sikes, 2010). If so, then we expected to observe differences in how the root-associated fungal communities versus fungi present in the soil respond to environmental gradients. More specifically, we expected that soil fungal communities would be mainly driven by abiotic conditions, while root-associated fungal communities would rather be driven by the identity of the interaction partner.

Given the low species richness and harsh conditions typical of the Arctic realm, we expected opportunistic associations and strong impacts of environmental gradients on interaction structure across the region. Within the region, we expected higher generalism and thus an increase in the Eltonian niche width of both plants and fungi toward more stressful conditions—and thus toward higher latitudes and elevations.

MATERIALS AND METHODS

Sample collection

To evaluate the impact of community assembly processes across multiple spatial scales, we coordinated sampling at two spatial scales: a pan-Arctic scale and a regional scale. During the summers of 2020 and 2021, we collected a total of 2900 root and soil samples by sampling seven **sites** across a gradient of 14.5° latitudes. These sites ranged over various ecotones from the Subarctic through the Low Arctic to the High Arctic (Figure 2).

To characterize variation along local environmental gradients within each of our seven sites, we defined at least three local **transects** (Figure 2). These transects were located at least 250 m apart from each other across a joint elevation gradient. To capture differences in microclimatic environmental conditions, we selected the strongest elevational gradients available in the vicinity of each site (i.e., the gradients spanning the

largest difference in meters above sea level). Within three sites (Kilpisjärvi, Varanger, and Zackenberg), we sampled more intensively following a stratified random sampling design across multiple elevational gradients (Figure 2).

Along each transect, we established four **plots** with a radius of ca. 25 m each. These plots were selected at least 100 m from each other along the slope. A plot was selected only if at least three of the five target species occurred within the plot (no matter which species; see list below). At each site, we sampled at least eight plots, and all geographical coordinates and altitudes were recorded using a GPS (Garmin, GPSmap 62s, Switzerland).

As focal plant species, we selected species common and widespread enough to be sampled across the Arctic region. Thus, within each site, the set of target species to be sampled was defined as the five most locally abundant species out of the following list: *Betula nana*; *Bistorta vivipara*; *Cassiope tetragona*; *Dryas* spp.; *Empetrum nigrum*; *Salix arctica*; *Salix polaris*; *Saxifraga oppositifolia*; *Silene acaulis*; *Vaccinium myrtillus*; *Vaccinium uliginosum*; and *Vaccinium vitis-idaea* (for the list of species collected within each site, see Figure 2A). Of these taxa, *Dryas* spp. represents a species complex. In North America, the dominant species is *Dryas integrifolia*, and in Europe, it is *Dryas octopetala*. Nonetheless, the two species interbreed, with individuals in Northeast Greenland (Zackenberg) mainly being hybrids *D. octopetala* × *integrifolia* (Elkington, 1965; Philipp & Siegismund, 2003).

Importantly, these plant taxa were a priori selected to represent different mycorrhizal types: *B. nana*, *B. vivipara*, *Dryas* spp., *S. polaris*, and *S. arctica* have previously been assumed to be associated with ectomycorrhiza (ECM; Abrego et al., 2020; Cripps & Eddington, 2005; Gardes & Dahlberg, 1996); *C. tetragona*, *V. myrtillus*, *V. uliginosum*, *Vaccinium vitis-idaea*, and *E. nigrum* to be mainly associated with ericoid mycorrhiza (ErM), though sometimes with ECM too (Daghino et al., 2022; Koizumi & Nara, 2017; Treu et al., 1995; Wang & Qiu, 2006); *S. acaulis* and *S. oppositifolia* are often nonmycorrhizal (NM; Kytöviita, 2005), but can also be associated with arbuscular mycorrhiza (AM; Abrego et al., 2020; Rasmussen et al., 2022).

To characterize fungal communities in the rhizosphere (i.e., fungi directly interacting with the target plant species), we collected three root fragments (length >3 mm) from different parts of the root architecture from two to three individuals of each target plant species found within the plot. To this aim, we gently dug and/or scraped 2–3 cm around the focal plant individual until we found the roots (clearly identified as connected to the stem). We then excavated the roots without breaking their fine parts and collected the soil adhered to the root.

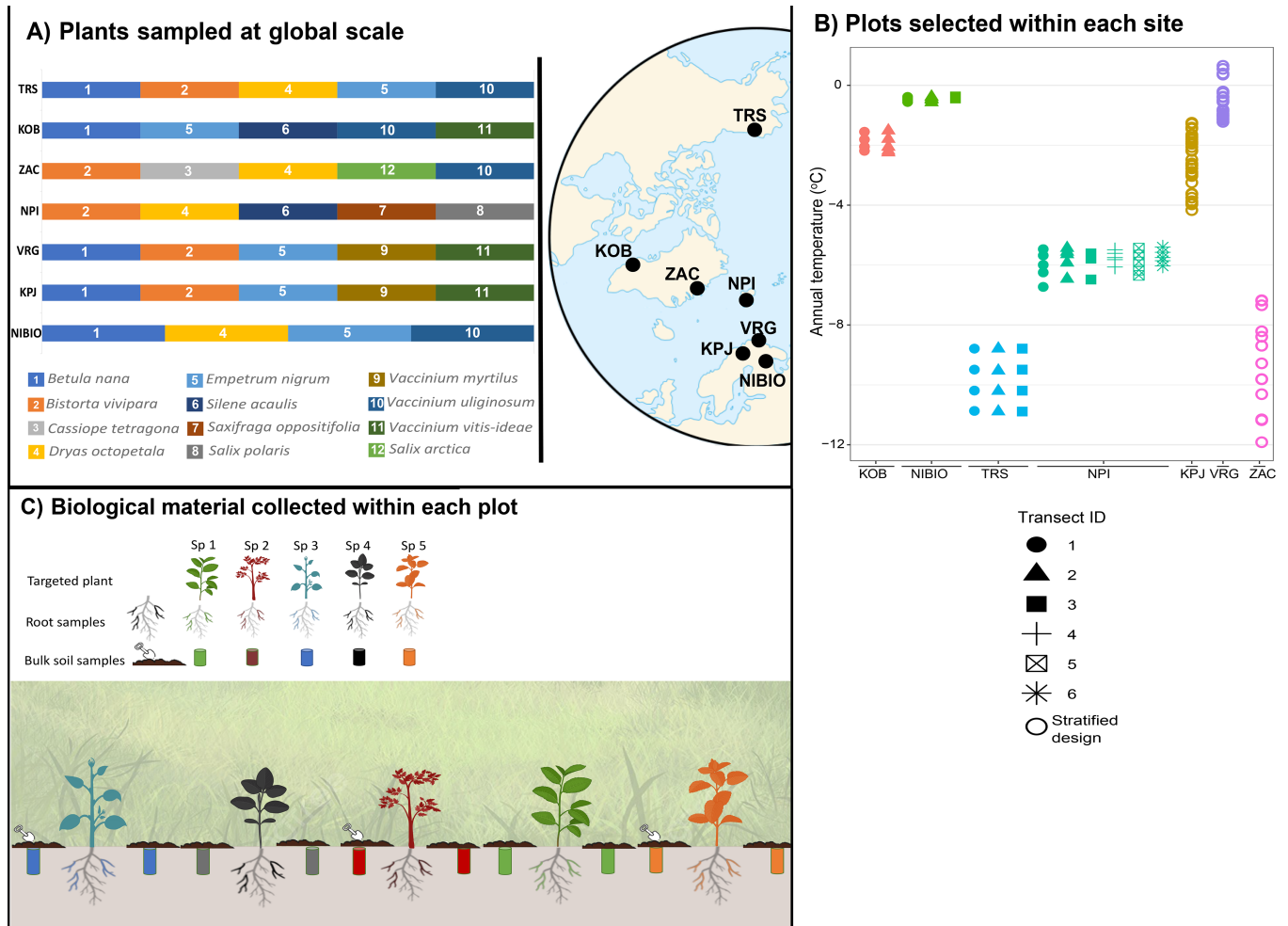


FIGURE 2 Sampling design and data collection. Panel (A) shows our seven sampling sites across the Arctic. At each **site**, we sampled at least 8 **plots** (each with a radius of 25 m) across local elevation gradients. In the plot, each slice of the site-specific bar chart represents a focal plant species sampled per site, with the color and number revealing its identity (see below). Panel (B) shows the estimated temperature of the plots selected within each site. The sites are first sorted according to the number of transects locally sampled (from left to right) and then by the number of plots for each site. Panel (C) shows the biological sampling design within each plot. We collected roots of three individuals of each targeted plant as well as two soil cores in the vicinity of each plant. Each plant color represents one of the five plant species targeted per site. Site-specific acronyms: KPJ = Kilpisjärvi, Finland; VRG = Varanger Peninsula, Norway; NIBIO = Gandvik valley, Norway; KOB = Kobbefjord, Greenland; TRS = Toolik Research Station, USA; NPI = Norsk Polarinstitut, Ny Alesund, Svalbard; ZAC = Zackenberg, Greenland. The top-left bar chart has a color legend for the plant species: N°1 = *Betula nana*; N°2 = *Bistorta vivipara*; N°3 = *Cassiope tetragona*; N°4 = *Dryas* spp. (which includes *Dryas octopetala*, *Dryas integrifolia*, and *Dryas octopetala* × *integrifolia* hybrids); N°5 = *Empetrum nigrum*; N°6 = *Silene acaulis*; N°7 = *Saxifraga oppositifolia*; N°8 = *Salix polaris*; N°9 = *Vaccinium myrtillus*; N°10 = *Vaccinium uliginosum*; N°11 = *Vaccinium vitis-idaea*; N°12 = *Salix arctica*. Panel C was partially created in BioRender. Parisy, B. (2025b) <https://BioRender.com/w13i598>.

The resulting sample was then considered a compound ecological compartment: the rhizosphere. To characterize the fungal community of the soil, we collected two bulk soil samples on opposite sides of each targeted plant individual (ca. 10 cm). For each soil core (ca. 5 cm diameter), we collected the upper 5–10 cm of the soil layers, with the two soil cores pooled into one for analysis. Coarse roots (>0.2 mm in diameter) and stones were removed. The soil was then stored within a paper bag and put into a ZIP-lock bag filled with silica gel, which was then stored at –20°C.

In total, we collected 1450 roots and 1450 soil samples across 129 plots spread across the Arctic (Figure 2).

Environmental data

To characterize the local climate, we extracted the annual mean temperature (BIO1) of each site from the WorldClim database (version 1.4; Fick & Hijmans, 2017). We then associated the average elevation of each plot

within a site with a mean annual temperature. Assuming a decline of 0.7°C for every 100 m above sea level (asl), we used the mean elevation as the baseline and then subtracted or added 0.7°C for every 100 m below or above the average, respectively. This 0.7°C factor was defined following the standard lapse rate (Mane et al., 2022) and is consistent with highly resolved data collected by Peña-Aguilera et al. (2023).

Vegetation cover surrounding each focal plant individual in a 1 m^2 area was estimated visually. The average vegetation coverage of each plot was then calculated from all the individual estimates. For three plots at the Zackenberg site (ZAC10, 11, and 12), we lacked information on plot-level vegetation. For these plots, we used the mean of all other plots within the site as a conservative measure of vegetation coverage.

From a subsample of the soil samples that remained after DNA metabarcoding (see below), we measured soil chemistry as represented by pH, carbon, and nitrogen content measured at the plot level. From all the soil samples collected within each plot, we pooled soil samples collected around each target plant species sampled locally. The pooled soil was then oven-dried at 70°C and homogenized using a sieve with a mesh size of 2 mm. 0.15 mg of soil was weighed under an air-vacuumed balance, placed in tin foil, and analyzed for carbon and nitrogen content using a Leco series 828 series analyzer (Leco, United States). Nitrogen and carbon content was measured for each pooled soil sample using the LCRM method and calibrated with soil samples of known concentration. Another part of the pooled soil sample was used to measure pH following the ISO 10390:2021 standards (International Organization for Standardization; <https://standards.iteh.ai/>). For this, we prepared a 1:5 (volume fraction) suspension of soil with water, shook the suspension for 60 min using a mechanical shaker, and left it to rest at least 1 h before measurement. The pH probe was calibrated with three buffers of pH 4.00, 6.88, and 9.22, respectively.

DNA metabarcoding

The bulk soil and rhizosphere samples were used for the laboratory analysis, implemented by Bioname Ltd. (www.bioname.fi) as a turn-key service from sample handling through bioinformatics to final data as a taxa \times sample matrix.

Five milliliters of the bulk soil samples was transferred to a sterile 50-mL Falcon tube and 1.25 mL of 2.5-mm ceramic beads was added to the tube. The tube containing the sample was homogenized in a Bullet Blender DX50 for 5 min. An amount of 50–100 mg of the

homogenized sample was then used for DNA extraction. The rhizosphere samples were first cut into small pieces using DNA-clean scissors and then homogenized together with the rhizosphere soil with ceramic 2-mm beads in a sterile 50-mL Falcon tube for 10 min in a Bullet Blender 50DX (Next Advance, Inc., Troy, NY, USA). DNA was extracted following the protocol of Vesterinen et al. (2016), with some modifications as follows: A fixed volume (30 mL) of preheated 60°C lysis buffer (Aljanabi & Martinez, 1997; Vesterinen et al., 2016) and 30 μL of proteinase K were added to the sample, and the mix was incubated for exactly 2:45 h at $+60^{\circ}\text{C}$ in a shaking incubator. After incubation, 200 μL of the lysate was transferred to the next step, and excess lysate was stored in a clean 50-mL tube at -20°C . To purify the DNA, 200 μL of the lysate was mixed with 400 μL in-house SPRI bead solution (Vesterinen et al., 2016) and purified using an Opentrons OT-2 automated liquid-handling robot (New York, USA). During the robotic steps, the DNA was bound to the SPRI beads, drawn to the magnet, and the supernatant was discarded. Then, the DNA pellet was washed twice using 40 μL freshly prepared 80% ethanol. After removing all ethanol, the pellet was dried, and DNA was eluted to 200 μL of pure RNase, DNase-free water. A DNA extraction control was added to each extraction batch, containing all the reagents, except the sample material. DNA purity and integrity were assessed by polymerase chain reaction (PCR) success rate.

The fungal ITS2 gene region was amplified by using primer pair tagF-ITS7 (5'-GTGARTCATCGAATCTTTG-3'; Ihrmark et al., 2012) and tagR-ITS4 (5'-TCCTCCGCTT ATTGATATGC-3'; White et al., 1990). This primer pair is designed to amplify fungi over plants (Høyer & Hodkinson, 2021). All the primers included a linker-tag, enabling the subsequent attachment of next-generation sequencing adapters. To increase the diversity of the amplicon library, each primer was used as two different versions, including so-called heterogeneity spacers between the linker-tag and the actual locus-specific oligo. All PCRs were carried out as two technical replicates, and each replicate contained two heterogeneity versions of each primer. The reaction setup followed Kankaanpää et al. (2020) and included 5 μL of $2\times$ MyTaq HS Red Mix (Bioline, UK), 2.4 μL of H_2O , 150 nM of each primer (two forward and two reverse primer versions), and 2 μL of DNA extract per sample in 10 μL total volume. A blank PCR control was added to each PCR batch to ensure reagent purity and detect any cross-contamination. PCR was performed under the following cycling conditions: 3 min at 95°C , then 35 cycles of 20 s at 95°C , 30 s at 55°C , and 20 s at 72°C , ending with 7 min at 72°C .

Library preparation followed Vesterinen et al. (2016) with minor modifications as follows: A dual indexing

strategy was used, where each reaction (including technical replicates) was prepared with a unique combination of forward and reverse indices. All index sets were perfectly balanced so that each nucleotide position included either T/G or A/C, as this ensures base calling for each channel in the sequencing. For a reaction volume of 10 μL , we mixed 5 μL of MyTaq HS RedMix, 500 nM of each tagged and indexed primer (i7 and i5) and 3 μL of the locus-specific PCR product from the first PCR. For library preparation PCR, the following protocol was used: initial denaturation for 3 min at 98°C, then 12 cycles of 20 s at 95°C, 15 s at 60°C and 30 s at 72°C, followed by 3 min at 72°C. All the indexed samples were then pooled and purified using magnetic beads (Vesterinen et al., 2018). Sequencing was done on an Illumina NovaSeq6000 SP Flowcell 2x250 (Illumina Inc., San Diego, California, USA) run, including PhiX control library by the Turku Centre for Biotechnology, Turku, Finland.

The bioinformatics pipeline closely followed Kaunisto et al. (2020). Paired-end reads were merged and trimmed for quality using 64-bit VSEARCH version 2.14.2 (Rognes et al., 2016). The primers were removed from the merged reads using software CUTADAPT version 2.7 (Martin, 2011), with a 20% rate for primer mismatches and 100 bp minimum length. The reads were then collapsed into unique sequences with command “fastx_uniques” using VSEARCH. Unique reads were denoised (i.e., chimeras were removed), and reads were clustered into ZOTUs (“ZOTU” = “zero-radius operational taxonomic unit”) with command “unoise3” using 32-bit USEARCH version 11 (Edgar, 2010). All samples with fewer than 50 reads in total were removed, and all ZOTUs from a sample with less than 20 reads for that ZOTU or with less than 0.05% of the total read number (all reads assigned to ZOTUs) of that sample were removed. Finally, ZOTUs were assigned to taxa by using the UNITE database (Abarenkov et al., 2020) with SINTAX (Edgar, 2010) in VSEARCH (Rognes et al., 2016). All ZOTUs with under 97% similarity to any reference database sequence were discarded. Finally, ZOTUs were assigned to a functional group by using the FUNGUILD python script (<https://github.com/UMNFuN/FUNGuild>), which matches taxonomic assignment against the FUNGuild database (Nguyen et al., 2016). Importantly, the FUNGuild database and script assign function to genus-level taxonomy. In doing so, function is assigned with different levels of confidence. For the analyses, we kept the original assignments for genera assigned to guilds at levels “highly probable (=absolutely certain)” and “probable (=fairly certain).” For uncertain cases where genera were assigned at level “Possibly (=suspected but not proven, conflicting reports given, etc.),” we created a separate category “Mixed Function (Uncertain)” for the subsequent analyses.

Statistical analyses

Fungal communities of the soil versus rhizosphere

To first characterize the level of specificity between fungi and plants, we calculated a simple measure of interaction probability (Equation 1). To distinguish potential differences in specificity between functional guilds, this analysis was focused on the fungal genera that could be attributed to a specific functional group. In brief, we calculated the conditional probability that an interaction occurs between a plant species i and a fungus j (i.e., that fungus j occurs on the rhizosphere of plant species i) within the plot y (L_{ijy}), given that fungus j is recorded within the soil around i at the same location y (X_{ijy}). For each plot, this conditional probability was calculated by dividing the frequency with which each plant–fungus pair was found by the frequency of occurrence of the fungus within the soil:

$$P(L_{ijy} \cup X_{ijy}) = L_{ijy} / X_{ijy}. \quad (1)$$

Rare fungi will easily be defined as specialists, since, for example, a fungus appearing only once on a plant will per necessity be observed on this plant species alone. Thus, we discarded fungal taxa occurring in less than 10% of the plots (i.e., in less than 14 plots). However, many fungi were only detected within the rhizosphere while never being found within the soil ($n = 53$, 10.6%) or were more often observed within the rhizosphere than in the soil, resulting in $P(L_{ijy} | X_{ijy}) > 1$ ($n = 57$, 23.2%). As further experiments would be required to determine whether this is caused by obligate symbionts or molecular detectability issues, these fungi were discarded from the current analysis.

Biotic versus abiotic effect on root-associated fungi communities

In interpreting patterns of co-occurrence, it is important to note that $P(L_{ijy} | X_{ijy}) = 1$ could arise either because fungus j is specialized on plant i or because fungus j shares the exact same environmental preferences as plant i . To disentangle these effects (Figure 1A), we used Hierarchical Modeling of Species Communities (HMSC, Ovaskainen et al., 2017; Ovaskainen & Abrego, 2020). This model partitions the variation in species occurrences and co-occurrences to variation explained by the abiotic covariates versus variation remaining after accounting for these abiotic effects, in the form of residual associations (Ovaskainen et al., 2010, 2017). In this multivariate

framework, a matrix of taxon-by-sample observations (the Y community-matrix, with entries Y_{yj} for taxon j at plot y) is modeled as a function of a matrix of the plot-level environmental covariates (the X matrix, with entries X_{yk} for covariate k at plot y).

As a basis for analyses, we created a data matrix of fungus taxa \times plant taxa \times plot \times compartment (soil or rhizosphere), resolved to the level of plant individuals. In other words, each row of this matrix will correspond to a target plant, with individual microbial taxa as columns. Following the terminology of Ovaskainen and Abrego (2020), this matrix is henceforth referred to as the Y community matrix. We note that any fungal genus j could potentially occur two times in the Y community matrix, if recorded as present in both the soil and the rhizosphere. The two records were then treated as separate taxa and the ecosystem compartment as a trait (summarized in the T matrix, with entries “soil” for fungi recorded in the soil and “root” for fungi detected within the rhizosphere). Matrix Y was reduced to data on the presence/absence of taxa and fitted to a probit HMSC model (Ovaskainen & Abrego, 2020). Since very rare or very common species will contribute little information on the factors affecting species’ presence or absence, we included only genera that occurred in at least 40 samples (3%), in at least one of the datasets (soil or roots).

The occurrences of taxa were modeled as a function of edaphic conditions and bioclimatic variables relevant for fungal communities within the soil and within the rhizosphere (Burns et al., 2015; Ni et al., 2018; Rasmussen et al., 2020; Zhang et al., 2016). As each sample corresponds to the fungal community found around a specific plant, or on its roots, we include plant identity as a categorical fixed effect to test for differences in fungal incidence across plants. For each plot, we included temperature (a continuous covariate), soil pH (a continuous covariate), soil nitrogen content (in percentage, a continuous covariate), and the average of total coverage of plants surrounding the targeted plant within each plot, named below as vegetation cover (in percentage, a continuous covariate; cf. *Environmental data* section). To control for the effects of variation in sequencing depth, we included $\log(\text{total number of reads})$ as a compartment-specific covariate (with one value for the soil sample and one for the rhizosphere sample). All covariates were scaled to a mean of 0 and a variance of 1.

The HMSC models were fitted with the R-package *Hmsc* (Ovaskainen & Abrego, 2020; Tikhonov et al., 2020). The models were fitted with eight chains in total, each with 1,500,000 iterations, which we discarded 500,000 as transient and which we thinned the remaining 1,000,000 by 4000 for a total of 2000 samples from the posterior. Markov chain Monte Carlo (MCMC) convergence was

assessed by examining the potential scale reduction factors of the model parameters. The discriminatory power of the probit model was measured by calculating two different metrics, that is, species-specific “areas under the curve” (AUC; Pearce & Ferrier, 2000) and Tjur’s coefficient of discrimination (Tjur’s R^2 ; Tjur, 2012).

In the fitted models, the responses of taxa to fixed effects (as representing not only abiotic conditions but also the plant host effect) will inform us about the responses of fungal taxa to their bioclimatic environment, whereas the residual variance–covariance matrix will inform us about either biotic associations among microbes or about joint responses to environmental covariates unmeasured in the study (Ovaskainen & Abrego, 2020).

Network analyses

To quantify the relative impact of environmental conditions on partner selection in plant–fungus networks across the Arctic (Figure 1B), we quantified interaction structure in terms of overall network association specificity at the plot and site scales. For this purpose, we used the $H2'$ index of Blüthgen et al. (2006). This metric quantifies to what extent interactions are restricted to given partners rather than randomly spread across all partners available (Blüthgen et al., 2006). Moreover, since our networks explicitly differ in size due to our sampling design (see *Sample collection*), $H2'$ serves as a more robust and scale-independent index than qualitative indices like “connectance” or the number of links—which are both strongly influenced by network size.

As a basis for network analyses, we created an adjacency matrix of fungus taxa \times plant taxa \times plot. In other words, we aggregated the fungal composition of individual plants of the same species within each plot. Ultimately, each row of this matrix will correspond to a target plant species, sampled within a specific plot, and each column to a fungal taxon observed in the rhizosphere. For the site-level networks, we aggregated plot-scale networks (i.e., rows) within sites. As our focal response, we used the presence or absence of fungi.

To quantify whether local (i.e., site-scale) networks show any clear ecological structuring pattern, we used a null model approach. To this aim, we generated randomly assembled networks based on random reallocation of links in the plant–rhizosphere association matrix of each local network using the “swap.web” algorithm of package *bipartite* (v.2.18; Dormann et al., 2018; Dormann, 2022). This algorithm allows the removal of any systematic patterns while controlling for both the marginal totals (i.e., maintaining species-specific probabilities of

interaction) and the connectance (i.e., maintaining the overall number of links in the network). Thus, we compared the observed network-level specialization $H2'$ (I_{observed}) with the average value of the $H2'$ value across 1000 iterations of the null model (\bar{I}_{null} ; Equation 2). We then expressed the difference between the null expectation and the observed value in units of SDs of the null distribution (σ_{null}):

$$Z_I = \frac{I_{\text{observed}} - \bar{I}_{\text{null}}}{\sigma_{I_{\text{null}}}} \quad (2)$$

If the Z score is higher than 2 or lower than -2 , then we consider that the local network showed significantly more structure than expected by chance alone. Consequently, it would reflect a detectable imprint of ecological processes structuring plant–fungus interactions.

Null models can also be used to evaluate the role of functional traits in structuring ecological networks. To test whether the functional matching of interactions is stricter than expected under random associations, we applied the same approach as above to the subset of fungi in each local network to which functions could be assigned by matching with the FUNGuild database (Nguyen et al., 2016; see *DNA-metabarcoding*). As an example, we extracted all the rhizosphere-associated fungi assigned to “mycorrhiza” and produced a local network containing only the interactions observed between these mycorrhizae and the different plants within a site (henceforth “the meta-web of functional mycorrhizae”). Again, we quantified the deviation (i.e., z -score) between the value of the network index (i.e., $H2'$) observed for plant–mycorrhiza and the mean expectation from randomized networks in units of SDs across 1000 iterations of the null model.

Does plant–fungus association specificity change across environmental gradients?

To explore whether the level of association specificity at the plot-level networks changed across environmental gradients (for a definition of plots vs. sites, see *Sample collection*), we followed a hypothesis-based meta-web approach (Pellissier et al., 2018). Thus, we compared association specificity at the plot level to null models generated at the site level (and thus containing all the interactions observed within the *site*).

For each type of network based on the type of interactions (i.e., the full network or the sub-networks consisting of mycorrhizal, saprotrophic, or pathogenic fungi alone) of each site, we generated a site-level null model by randomizing the full set of links in the plant–rhizosphere association matrix using the “swap-web” algorithm from package *bipartite* (version 2.18;

Dormann et al., 2018, Dormann, 2022). Focusing on $H2'$, we then modeled the z -scores of the deviations between the observed $H2'$ values of each local web to the site-level null web as a function of bioclimatic variables (estimated temperature, nitrogen [N] and carbon [C] content in the soil, pH, and vegetation coverage). As mentioned above, we split the overall network into networks representing specific types of interactions (i.e., the full network or the sub-networks consisting of mycorrhizal, saprotrophic, or pathogenic fungi alone). To test whether these functional networks follow similar patterns across environmental gradients, we fitted a linear model assuming a Gaussian distribution for each network type, for each site, following:

$$\text{lm}(z - \text{score} \sim \text{Temperature} \\ + \text{pH} + \text{N} + \text{C} + \text{vegetation.coverage}).$$

For each of the resulting 28 models (i.e., 4 network types \times 7 sites), the covariates were scaled and centered around 0. To validate model fit, we used functions implemented in package “DHARMA” (version 0.4.6; Hartig, 2022). Model checks included visual inspection of residuals using quantile–quantile plots (to detect overall deviations from the expected distribution), with additional tests to assess the adherence of residuals to the distribution assumed, as well as for dispersion and for outliers (KS test; Hartig, 2022). To identify systematic deviations from model assumptions, we also checked residuals plotted against predicted values.

RESULTS

Fungal communities differ between the soil and the rhizosphere

The DNA sequencing produced a total of 384 million reads reliably assigned to fungi. Out of this set, 156 million sequence reads were retained for soil samples and 228 million for rhizosphere samples. For soil samples, 7053 ZOTUs were reliably assigned to 444 genera of fungi; for rhizosphere samples, 7973 ZOTUs were reliably assigned to 459 genera (Appendix S1: Table S1). Rarefaction curves of fungi showed that the sequencing effort was sufficient among sites and ecosystem compartments (i.e., the sampling depth sufficed to recover more or less the full microbial communities within both the rhizosphere and the soil; Appendix S1: Figure S2). Out of the 459 fungal genera detected in rhizosphere samples, 278 were assigned to a functional group (60.6%). Among these fungal genera, 28 were assigned to ECM, one (genus *Oidiodendron*) to ErM, one (genus *Rhizophagus*)

to AM, and one (genus *Sebacina*) to a mycorrhizal type whose precise nature was uncertain. Additionally, 112 genera were assigned to saprotrophs and 33 to plant pathogens.

At a pan-Arctic scale, we found a similar diversity of fungal genera in the rhizosphere and in the soil (459 genera in rhizosphere vs. 444 in soil), with ratios ranging from 1.1:1 to 3.1:1 for fungal genera (Appendix S1: Figure S3). As a result, for each compartment, a minority (13%–41%) of the fungal genera detected was unique to the rhizosphere or to the soil (7%–33%) and a relatively large proportion of taxa (44%–76%) was shared between the two communities. Nonetheless, this pattern across the Arctic hid substantial variation between the two compartments at individual sites: at this level, the two compartments were more distinct from each other, with much species turnover between bulk soil and the rhizosphere and little evidence of nestedness of the rhizosphere community within the soil community (Appendix S1: Figure S4).

The above patterns were supported by the multivariate ordination non-metric multidimensional scaling (NMDS) which highlighted not only partial overlap but also substantial differences between fungal community

composition in the soil versus the rhizosphere. In the NMDS plots, we see little or no separation between plant species, but strong separation between presumed mycorrhizal type (Figure 3). Fungal composition within the rhizosphere or within bulk soil did not differ in its distance to its respective centroid (Figure 3; Tukey's honestly significant difference (HSD) of beta dispersion, $p > 0.05$).

Fungal recruitment varies across plants

In terms of the frequency of occurrence in the rhizosphere when present in the soil, mycorrhizal fungi showed the highest incidence (Figure 4). These taxa, such as the genera *Tomentella* or *Russula*, were also characterized by the widest distribution across plant species, with several fungal genera showing high incidence across all plant taxa—regardless of the presumed mycorrhizal type of these plants. Endophytes and saprotrophic fungi formed an intermediary group, whereas pathogenic fungi were less frequently encountered in the rhizosphere and were typically associated with only a few plant species.

Of the plants, *B. vivipara* and *B. nana* were the species with the highest proportion of strongly associated fungi

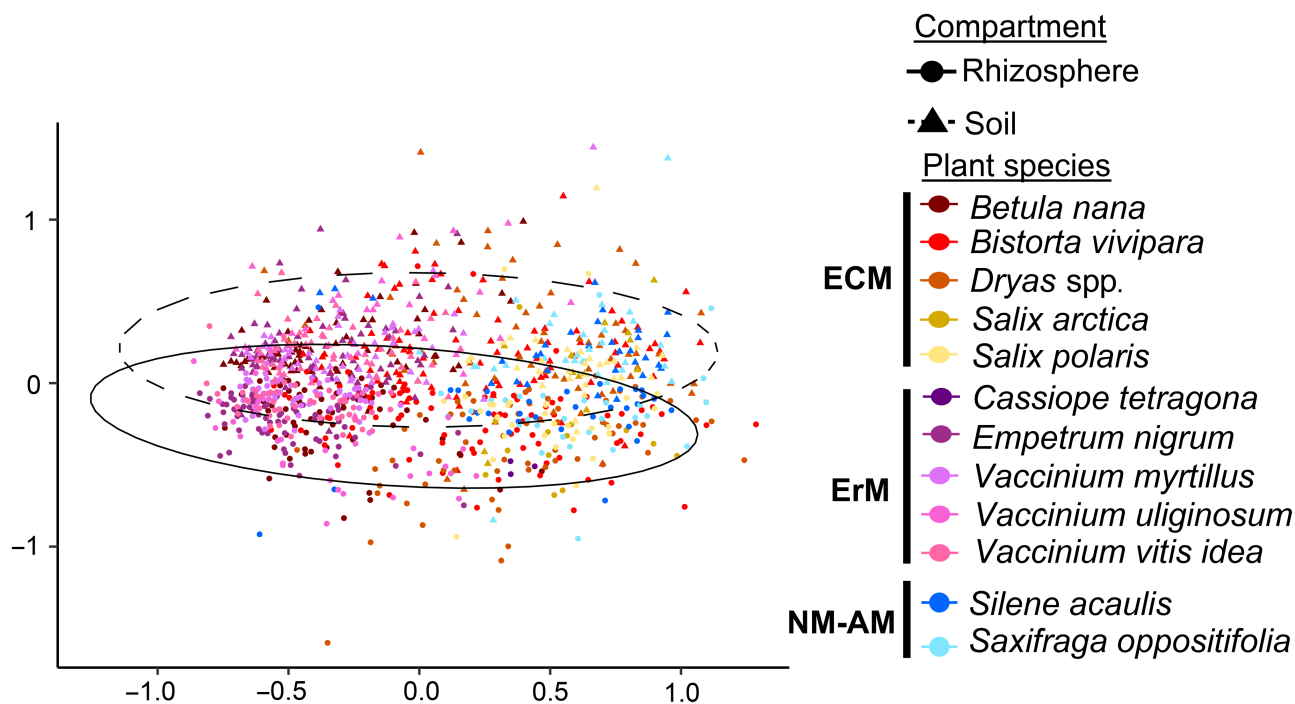


FIGURE 3 Multivariate ordination (Non-metric MultiDimensional Scaling, NMDS) of fungal community composition found within the roots (filled line) of different plant species versus bulk soil (dashed line). Ellipses summarize the within-community variability (75%) of each compartment. Each color represents a plant species categorized into the type of mycorrhiza it is presumed associated with; ECM = Ectomycorrhiza, ErM = Ericoid mycorrhiza, and NM-AM = Often nonmycorrhizal but sometimes arbuscular mycorrhiza. The NMDS was performed on species presence–absence data using the Jaccard distance. The stress value of the NMDS is 0.20; number of permutations = 1000, 2 dimensions, $R^2 = 0.82$.

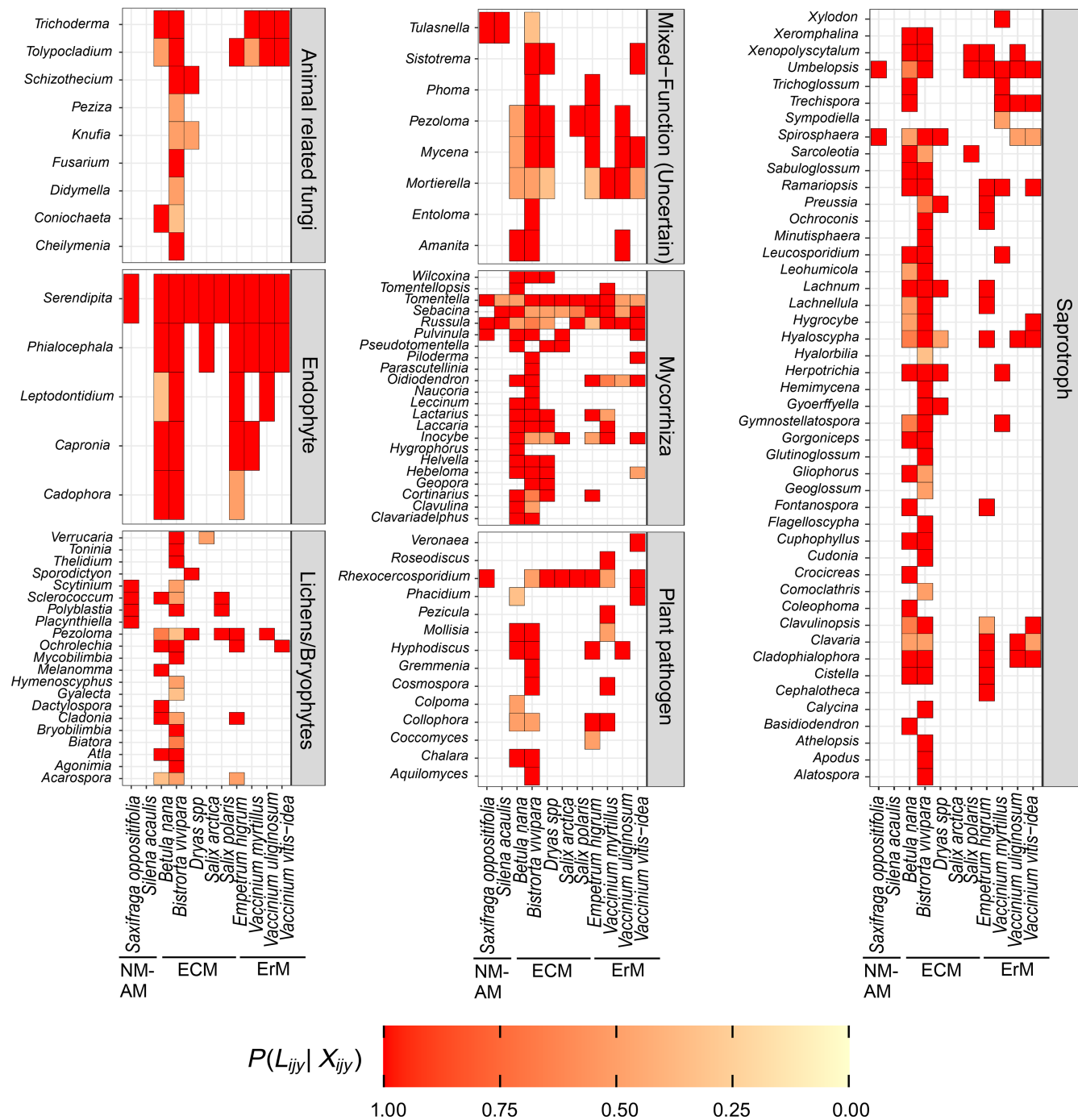


FIGURE 4 Frequency of association between fungal occurrence in the soil and in the rhizosphere around the same plants. As a simple measure of interaction probability, we show a heat map of the probability that an interaction between a plant species i and a fungus j occurs at location y (L_{ij}) when the fungus j is recorded within the soil around the same plant i at the same location x (X_{ij}). Each row represents a fungus assigned to a functional group and each column a plant species, with the color proportional to $P(L_{ij}|X_{ij})$. Plant species on the x -axis are sorted according to their assumed mycorrhizal types, where ECM = Ectomycorrhiza and ErM = Ericoid mycorrhiza; NM-AM = Often Nonmycorrhizal but sometimes arbuscular mycorrhiza.

within their rhizosphere (Figure 4). Moreover, *B. vivipara* showed frequent associations with almost every fungal genus (as assigned to a functional group) whenever the fungus was recorded within the soil (Figure 4). In

contrast, *S. acaulis* showed the lowest proportion of fungi strongly associated with its rhizosphere. For this species, only four fungal genera were frequently found in its rhizosphere when recorded in the soil (Figure 4).

Fungi in the soil and in the rhizosphere respond similarly to their environment

The HMSC model used to quantify the relative importance of the abiotic and biotic environment in shaping the composition of fungi communities (Figure 1A) was successfully fitted to the data. MCMC convergence was satisfactory and the potential scale reduction factors were close to the theoretical optimum of one. The model achieved satisfactory discriminatory performance with a mean $T_{\text{jur}} R^2$ of 0.22 and a mean AUC value of 0.90 (Appendix S1: Table S2). However, the explanatory power ($T_{\text{jur}} R^2$) was similar among taxa present within the rhizosphere compared to the fungi present in the soil (rhizosphere: mean $T_{\text{jur}} R^2 = 0.22$, AUC = 0.89; soil: mean $T_{\text{jur}} R^2 = 0.24$, AUC = 0.90). Predictive performance assessed by cross-validation was lower than explanatory performance (mean $cvT_{\text{jur}} R^2 = 0.16$, mean $cvAUC = 0.80$). On average, these cross-validation indices were similar between compartments (rhizosphere: mean $cvT_{\text{jur}} R^2 = 0.13$, $cvAUC = 0.80$; soil: mean $cvT_{\text{jur}} R^2 = 0.14$, $cvAUC = 0.80$ s).

Overall, the bioclimatic environment explained the presence/absence of fungal taxa equally across compartments (Appendix S1: Table S2). The random effects, especially at the sample level, explained the highest proportion of raw variance for both compartments (rhizosphere = 5.8%; soil = 6.0%), followed by abiotic conditions (rhizosphere = 5.0%; soil = 5.0%) and the host effect (rhizosphere = 2.9%; soil = 2.2%). Similarly, across compartments, pH accounted for the highest proportion of variation explained by abiotic conditions, followed by temperature. As expected, the host effect explained slightly more variance for the fungi within the rhizosphere than for fungi in the soil. Overall, the variance explained by individual covariates was largely consistent among different functional groups of fungi, with the strongest host effect for mycorrhizal fungi occurring within the rhizosphere.

In terms of responses to abiotic conditions, the taxon-specific occurrences responded similarly to the given environmental features across the two compartments (soil vs. rhizosphere; Figure 5) and we found no posterior support for a significant directional effect of the type of sample (i.e., soil vs. rhizosphere) on taxon-specific responses to environmental variables (Appendix S1: Figure S5A). This was evidenced by consistency in the sign and significance of effects across the two communities (Figure 5; see Appendix S1: Figure S6, compare the color of juxtaposed tiles between compartments within taxa).

Overall, only 31.3% of all fungal taxa detected within the rhizosphere and 19.9% of all fungi within the soil

responded significantly (i.e., with at least 0.95 posterior probability) to the identity of the host plant. By comparison, 32.1% of the fungi detected in the rhizosphere and 32.5% of the taxa detected in the soil responded significantly to abiotic covariates (i.e., temperature, nitrogen content, pH, vegetation coverage, and the C:N ratio; Figure 5). Among these abiotic covariates, the C:N ratio elicited the strongest response, with 40.8% and 54.1% of fungal taxa in the soil and rhizosphere, respectively, showing significant and mainly negative responses (Figure 5). The second most frequent response was observed for temperature, to which 46.1% of fungal taxa in the soil and 37.9% of fungi in the rhizosphere showed a significant and predominantly positive response (Figure 5). Fungi within the rhizosphere and the soil again showed similar responses to pH, with mixed positive and negative responses among individual taxa (Figure 5). Overall, both the variance-partitioning results (Appendix S1: Table S2) and strong heterogeneity in the estimated beta parameters revealed taxon-specific responses to the environmental covariates (Figure 5; Appendix S1: Figure S6). In a similar manner, community-level predictions showed consistency in predicted species richness along environmental gradients (Appendix S1: Figure S7). Across host plant species, the predicted richness of fungi in the rhizosphere was higher than richness predicted in the soil (Appendix S1: Figure S7A). Across environmental gradients, the predicted richness of fungal taxa responded similarly between compartments (Appendix S1: Figure S7B–F). In terms of residual covariance, we found little evidence for biotic interactions (Appendix S1: Figure S5B). Thus, fungal occurrence in the soil and in the rhizosphere seems governed by abiotic imprints.

Plant–rhizosphere networks are relatively nonspecialized across the Arctic and mainly driven by local environmental conditions

Fungal interaction partners were widely shared between plants (Figures 1B and 6A). Across plants, roughly one-third of the fungi found within the rhizosphere were unique to a specific plant even when plants co-occurred within the same plot (Figure 6B). The overall proportion of fungi shared among co-occurring plants was relatively evenly distributed among plant pairs (Figure 6B). However, the proportion of shared fungi showed a clustering between the presumed mycorrhizal type of the plant species, that is, arbuscular and ericoid mycorrhizal plants shared only a few fungi, while ectomycorrhizal plants shared as many fungi with plants presumed to be associated with AM as with plants presumed to be

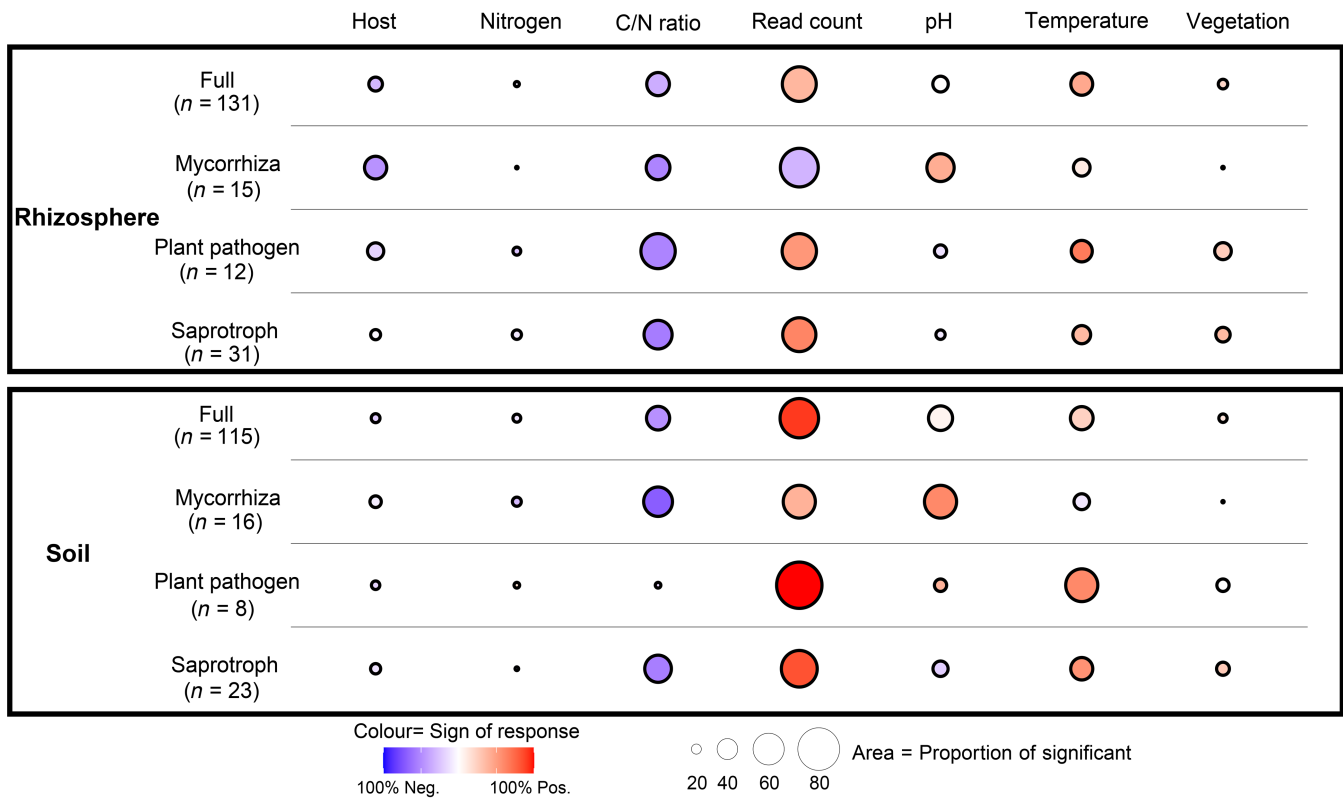


FIGURE 5 Summary of taxon-specific responses to environmental covariates for Hierarchical Modeling of Species Communities (HMSC) model of the presence-absence of fungal genera among compartments. Circle size corresponds to the proportion of taxa for which a statistically supported response was detected (i.e., a response with at least 0.95 posterior probability), whereas circle color shows the balance between negative (neg.) and positive (pos.) responses (see color scale at the bottom of the graph; white indicates that an equal number of taxa responded positively and negatively to the predictor in question). Statistical inference was based on the posterior distribution of the beta parameters, equivalent to regression coefficients. Ranges of values for individual covariates: Temperature: -11.9 to $+0.62^{\circ}\text{C}$; pH: 4.12–7.54; nitrogen content [i.e., nitrogen]: 0.062%–2.3%; carbon/nitrogen ratio [i.e., C/N ratio]: 8.8%–32.9%; vegetation coverage [i.e., Vegetation]: 5%–99.4%; sequencing depth, which is log transformed of total number of reads per sample [i.e., Readcount]: 2.6–13.3).

associated with ErM (Figure 6B). The highest proportion of fungi shared in the rhizosphere was found between *C. tetragona* and *E. nigrum* (21.2%; Figure 6B). *E. nigrum* shared a particularly high number of partners with *V. vitis-idaea*, *B. nana*, and *V. myrtilus* (Figure 6A). *S. arctica* and *V. uliginosum* showed the highest rates of unique nonshared fungi, with 48.4% and 45.7% of all fungi uniquely found within their rhizosphere (Figure 6B). In terms of functional groups of fungi, the majority of fungi unique to a plant were assigned to saprotrophs, whereas most fungi shared between plants were assigned to symbiotic or antagonistic functions (i.e., mycorrhiza, endophytes, and pathogenic fungi; Appendix S1: Figure S8). Mycorrhizal fungi represented around a third of fungi commonly shared between plant species, whereas pathogens accounted for around 15% of shared fungi.

To further quantify whether the local host preferences for each site varied across the Arctic, we explored the site-level network specialization index (as quantified by

$H2'$). The $H2'$ index varied considerably between ecological groups (i.e., between the mycorrhiza and plant pathogens) and between sites. The deviation between observed values and values expected under the null model slightly increased with latitude, but few networks appeared significantly more structured than expected by random (Figure 7A). The mean structure of sub-networks including only mycorrhiza or plant pathogens did not differ from random expectations (Figure 7A). Although association specificity was not significantly different from what we can expect by chance, the patterns shifted over space: with increasing latitude, deviations from the null model became increasingly negative for the mycorrhizal and saprotrophic network, while they became increasingly positive for the plant-pathogen networks. In other words, mycorrhizal and saprotrophic networks tend to become more generalized with increasing latitude, while the pathogenic network and the full networks tend to become more specialized than expected by chance.

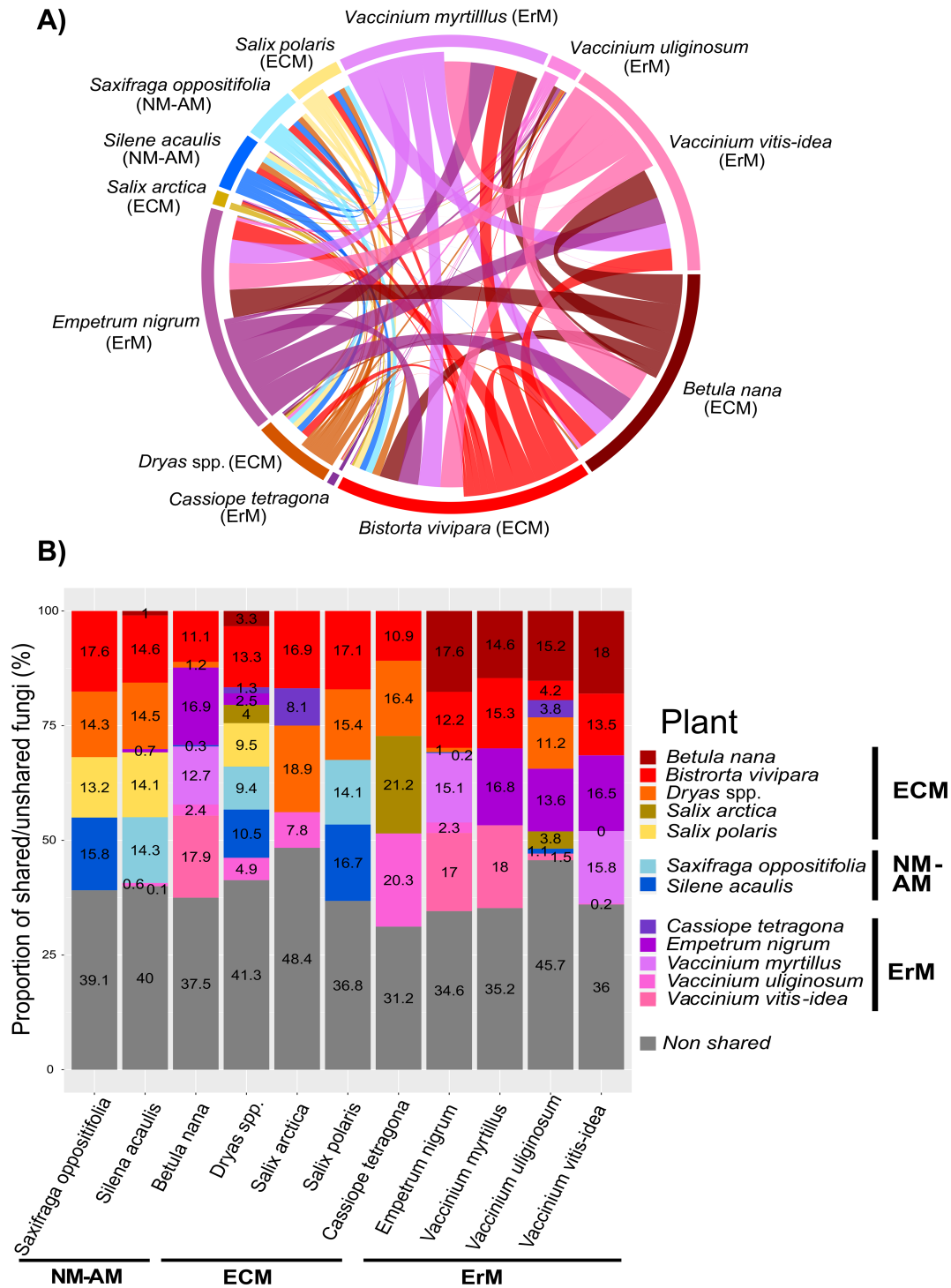


FIGURE 6 Overlap in rhizosphere-associated fungi between co-occurring plants. For each plot across all our sites, we quantified the number of rhizosphere-associated fungi recorded for each combination of plant species. Panels (A) and (B) show the numbers and proportions of rhizosphere-associated fungi shared between two plant species when present in the same plot. Panel (A) is a chord diagram showing overlap between specific plant pairs, whereas (B) decomposes the number of all rhizosphere-associated fungi detected on a plant species (individual columns) into the specific proportion unique to this plant (in gray) versus shared with other plant species (colored sections). Plants species in panel (B) are sorted according to their assumed mycorrhizal types where NM-AM = Often Nonmycorrhizal but sometimes arbuscular mycorrhiza; ECM = Ectomycorrhiza and ErM = Ericoid mycorrhiza.

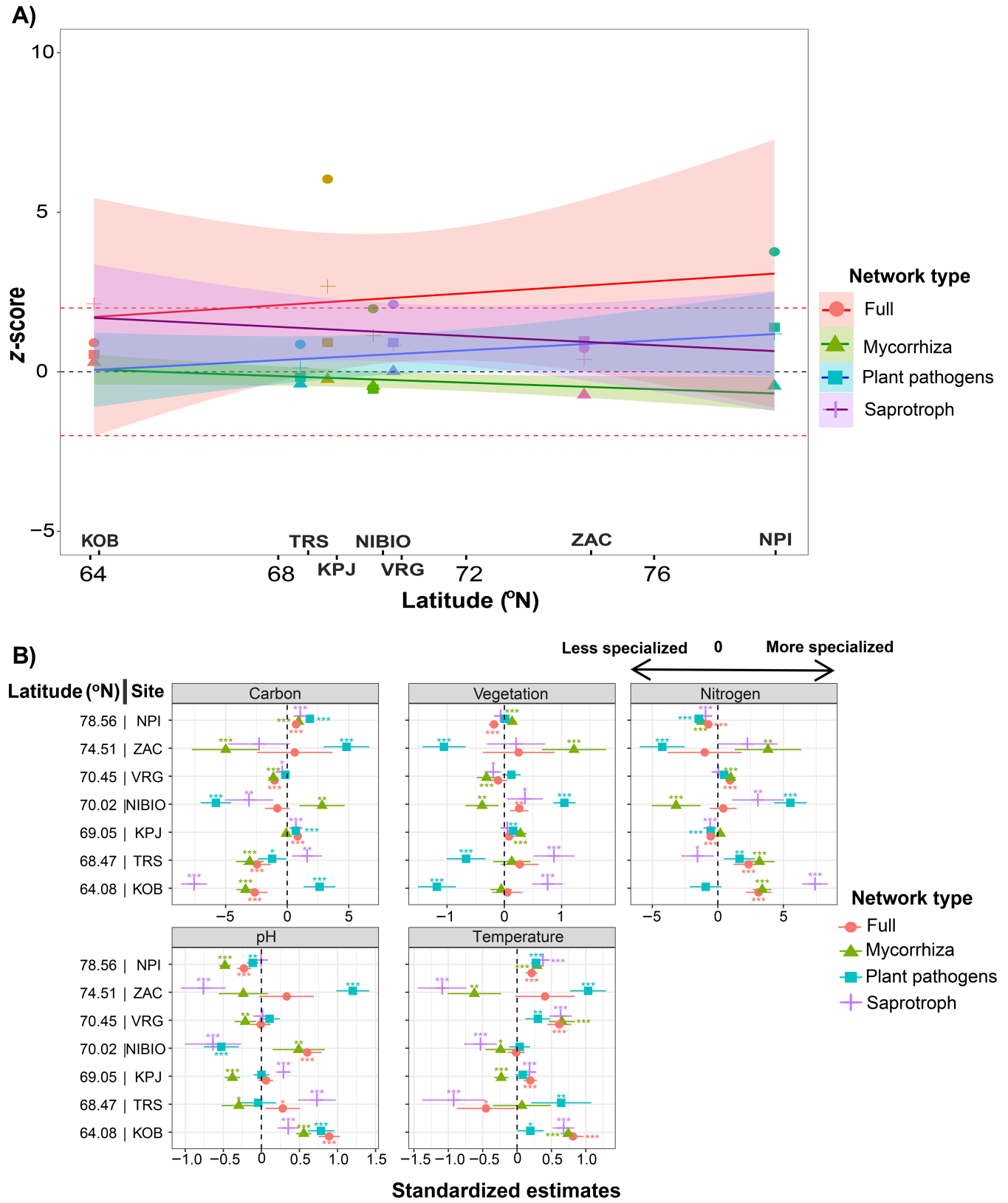


FIGURE 7 Legend on next page.

Thus, we further investigated the level of association specificity across local environmental gradients (Figure 7B). The linear models (Figure 7B) identified temperature and soil pH as significant predictors of local association specificity, with notable site specificity in local responses (Figure 7B). Moreover, the responses of the different network compartments (i.e., the full network vs. plant–mycorrhizal and plant–pathogenic interactions) differed strongly from each other in terms of their responses to environmental conditions (Figure 7B).

DISCUSSION

Studies of full communities and ecological interaction networks are key to understanding the biotic consequences of global change (Pellissier et al., 2018; Tylianakis & Morris, 2017; Woodward et al., 2010). Here, we dissected the effects of biotic and abiotic drivers on networks consisting of plants and rhizosphere-associated fungi across the Arctic. While the fungal composition of the soil and the rhizosphere proved significantly different from each other, the occurrence of a fungus in the plant rhizosphere was strongly dependent on its presence in the soil. Within both the rhizosphere and the soil, fungal occurrence was mainly driven by abiotic environmental conditions, with little effect of host plant or biotic interactions. In terms of the interaction networks of fungi and plants, we found a generally low but variable level of host specificity of fungi. Variation in association specificity across the Arctic was mainly driven by conditions at the local rather than the regional scale. At the local scale, temperature, pH, and vegetation coverage appeared to be the main environmental factors impacting network specialization. With increasing pH and temperature, the networks tended to be more generalized in nature. Below, we will discuss each of these findings in turn.

Soil- and root-associated fungal communities respond similarly to their environment

As our first key objective, we assessed how the probability of plant–fungus interaction is modulated by the occurrences of the fungi within the soil and by the bioclimatic environment (Figure 1A), respectively. Based on global patterns (Bahram et al., 2018; Soudzilovskaia et al., 2015; Tedersoo et al., 2022), we expected congruent changes in the composition of soil and rhizosphere-associated fungal communities. As an alternative hypothesis, we proposed differential change in the two ecological compartments (i.e., rhizosphere and soil), as based on the “physical buffering” capacity of plants (Sikes, 2010). Had this expectation been supported, then we would have expected soil fungi to respond more strongly than rhizosphere-associated fungi to abiotic conditions, with more pronounced biotic imprints on the latter group.

Of these alternatives, the first expectation was clearly supported by our results, whereas the second was refuted. Overall, the fungal composition of the rhizosphere was significantly different from that of the soil, and the rhizosphere of plants sustained a higher diversity of fungi than the soil. We found 54 fungal genera unique to roots (11% of the full set of fungi) and 34 fungal genera unique to soil (8% of the full set of fungi). However, the results of our joint species distribution (HMSC) model revealed that fungal occurrence in both communities was mainly driven by pH and temperature (Appendix S1: Table S2). When treated as a trait, the compartments (soil vs. rhizosphere) did not modify species responses. Neither did we detect any signs of strong residual associations among rhizosphere-associated fungi after accounting for the abiotic effects (Appendix S1: Figure S10A), suggesting a general lack of pronounced biotic interactions among fungi. Predictions of emergent community features (here: overall species richness) were largely

FIGURE 7 Deviations from randomness in the specialization of networks as a function of latitude (Panel A) and across local environmental gradients (Panel B). Panel (A) shows the z -score, that is, the deviation (in units of SDs) between the observed $H2'$ specialization index and the expected value, as derived from 1000 realizations of a null model. If the z -score is higher than 2 or lower than -2 , then the observed specialization is significantly different from the value expected under the null model. Panel (B) shows dot-and-whisker plots of the responses of network specialization to different features of the environment across sites. Shown are standardized estimates of site-specific linear models of specialization (measured by z -scores between plot specialization and the randomized specialization of the network at site level) as functions of variation in carbon, nitrogen, pH, temperature, and vegetation coverage within each site. Each color and shape represents a standardized estimate of a specific type of network, with estimates ordered by latitude along the y -axis. In both panels (A) and (B) “Full network” represents the full plant–fungus matrix, whereas “Mycorrhiza” represents the site-specific sub-network including only fungi assigned to the functional group of mycorrhizae. “Plant-pathogens” represent the site-specific sub-network including only fungi assigned to the functional group of plant-pathogens. Site acronyms: KPJ = Kilpisjärvi, Finland; VRG = Varanger Peninsula, Norway, NIBIO = Gandvik valley, Norway; KOB = Kobbefjord, Greenland; TRS = Toolik Research Station, USA; NPI = Norsk Polarinstitut, Ny Alesund, Svalbard; ZAC = Zackenberg, Greenland.

consistent among compartments along the environmental gradients.

In the current results, there are little if any suggestions of biotic interactions among fungal taxa as being strong drivers of community assembly. Only two mycorrhizal fungi from the genus *Geospora* and *Lactarius* showed a positive residual association between compartments (i.e., rhizosphere vs. soil), suggesting that the occurrence of these genera in the soil is positively associated with their presence within the roots in a way not accounted for by their environment (Appendix S1: Figure S5B). This partly contrasts with previous studies suggesting more pronounced associations between fungal guilds (Hannula & Trager, 2020). In sites characterized by low fertility (which is generally the case in Arctic ecosystems), abundances of mutualists (mycorrhizal fungi) and saprotrophs have been found to be negatively related to each other, suggesting antagonistic competition for nutrients (Hannula & Trager, 2020). In our case, the residual co-occurrences (estimated after considering the effect of environment) of fungi in the rhizosphere showed a sparse pattern (Appendix S1: Figure S10B). Only 1% of all possible associations between saprotrophic and mycorrhizal genera were detectably positive and 1% negative.

Overall, these findings attest to a lack of strong biotic imprints on either compartment and rather suggest that abiotic drivers (i.e., environmental filtering) dominate the fungal community assembly across both the arctic soil and the rhizosphere. Our current results are thus well in line with previous reports suggesting that fungal richness in the rhizosphere is more closely linked to abiotic than biotic variables (Alzarhani et al., 2019; Blaaid et al., 2014).

Root communities are weakly impacted by plant identity

As our second key objective, we aimed to evaluate fungal partner selection among plant species (Figure 1B). Here, we found little imprint of host identity, but rather a strong signal of opportunistic associations with taxa present in the soil. Thus, arctic fungi appear to show largely opportunistic patterns of associations with individual plants. In support of this inference, the presence of individual fungal taxa in the soil had a strong influence on their presence in the plant rhizosphere, and individual plant species shared massive amounts of fungi with each other. Low levels of host specificity extended to all functional groups (i.e., to fungal taxa identified as saprotrophs, mycorrhiza, plant pathogens, and endophytes; Appendix S1: Figure S9).

The current findings may appear surprising, given that we had a priori selected plants representing different

types of fungal associations (ECM, AM, ErM, etc.). Nonetheless, individual fungi showed relatively low fidelity to these groups. Overall, out of all 459 root-associated fungal genera detected across the Arctic, only 15% were unique to a plant species, and 85% were found within the rhizosphere of at least two different plant species. Among plant mycorrhizal types, we found no clustering of shared fungi between plant species that are known to be associated with similar mycorrhizal types (Figure 3; Figure 6). In fact, the distribution and proportion of shared fungi between plant species were relatively even (Figure 6B,C). However, we observed two distinct clusters in root-associated fungi between plant species presumed to be associated with arbuscular and ErM (Figure 3; Figure 6A,B).

From a methodological viewpoint, it is important to emphasize that the fungal ITS2-primers provide a skewed picture of arbuscular mycorrhizal fungi (Lekberg et al., 2018; Tedersoo et al., 2015). Among fungi, the primers in our study were chosen for their wide target range and selectivity against plants; thus, providing a general overview of the soil communities with a restricted by-yield of plant sequences (Ihrmark et al., 2012). However, these primers generally fail to amplify important mutualistic symbionts such as AM (Lekberg et al., 2018; opik et al., 2013, 2014). In our current study, ectomycorrhizal fungi were frequently detected on plants originally defined as lacking mycorrhiza or being associated with AM (Kytoviita, 2005). Moreover, we were surprised to systematically record *Oidiodendron* in the rhizosphere of *B. vivipara* (cf. Figure 4)—as *B. vivipara* is assumed to be mainly colonized by ectomycorrhizal fungi or sometimes by AM (Eriksen et al., 2002), whereas *Oidiodendron* belongs to the group of ErM. This finding underscores the complexity of plant–fungus interactions and suggests that the associations between plants and mycorrhizal fungi may be more nuanced and variable than previously thought.

Overall, the opportunistic sharing of fungi among plants detected is in line with several studies from arctic and alpine areas, which have shown that the dominant plants associated with ECM or ErM share the same pool of fungal symbionts (Botnen et al., 2014, 2020; Timling et al., 2012; Toju & Sato, 2018). To frequently associate with different plants occurring in the same plot may reflect efficient host foraging behavior by fungi benefiting widely from plant associations (Lekberg et al., 2010). Indeed, such opportunistic foraging may be an efficient strategy to find alternative hosts in harsh environments (Chagnon et al., 2020; Lekberg et al., 2010).

From a plant perspective, *B. nana* and *B. vivipara* showed frequent associations with almost every fungal genus assigned to a functional group. This may reflect a high degree of generalism on the plants' part, or even opportunistic behavior. Highly generalist plants have

been considered key regulators of ecosystem dynamics (e.g., promoters of community “stability” or “robustness”; Chagnon, 2016; Chagnon et al., 2020). As an example, *B. nana* may potentially facilitate the revegetation by shrubs and possibly the expansion of trees into the Arctic by maintaining ectomycorrhizal communities during tundra fire (Hewitt et al., 2013; Timling et al., 2014). Surprisingly, though, we found *S. acaulis*—a plant species mainly recorded in arctic and in the relatively “harsher” environments in our study—to be the plant species associated with the lowest proportion of the fungal taxa of the surrounding soil, suggesting high selectivity of partners or low rewards for the fungi associating with this plant. This finding runs opposite to our initial expectations, since in an arctic environment, fungi benefitting from plant associations should do better in teaming up with any available partner than to associate with no partner at all (i.e., there should be a high cost to partner rejection; Chagnon et al., 2020; Steidinger & Bever, 2014). However, we note that our method for establishing association (i.e., the scoring of co-occurrence based on DNA-metabarcoding) will reveal neither the nature of the association nor its fitness consequences for the fungus or the plant. Thus, whether or not this prediction remains strictly applicable to the current data remains a question of conjecture.

Be this as it may, our study paints a clear picture of arctic plants and fungi as being generalists in terms of association specificity. Whether specific taxa will co-occur and interact is mainly driven by environmental conditions.

Plant–fungus networks are mainly structured by local environmental gradients

Until recently, networks involving plants and microorganisms belowground have received little attention—and to this date, plant–fungus networks in the Arctic remain poorly known (Bahram et al., 2014; Wong et al., 2023). As our third key objective, we aimed to describe and explore the processes that shape plant–fungus networks in the Arctic (Figure 1B). At a regional scale (i.e., at the site level; Figure 2), the overall “preference” of fungi for plant interaction partners was no higher than expected by chance. Neither at the level of the full root-associated community nor at the level of functional groups did we find consistent evidence for host specificity. This lack of association specificity is in line with previous studies reporting low specificity among root-associated fungi and plants in the Arctic (Botnen et al., 2014; Monard et al., 2016). The lack of network specialization and of partner preferences suggests that environmental

conditions might override the effects of the host plant in fungal community assembly (Maciá-Vicente & Popa, 2022; Timling et al., 2014; Wong et al., 2023).

As described by Pellissier et al. (2018), indices calculated at the level of site-wide meta-webs do not adequately capture how networks respond at a local scale. Site-specific networks can still be structured by their location along environmental gradients (Pellissier et al., 2018). In this context, we found that the deviation of the local networks (i.e., the plot-level associations) from the randomized site-level meta-web was strongly structured by environmental gradients (Figure 7B). In response to temperature, networks shifted toward higher levels of association specificity. This finding contradicts the “stress gradient hypothesis” where, under increasingly harsh environmental conditions, resources are primarily allocated to survival and reproduction rather than to competition—avoiding the risks associated with host specialization (Botnen et al., 2014; Tylianakis & Morris, 2017).

Interestingly, partial networks consisting of mycorrhizal, pathogenic, and saprotrophic associations alone showed lower network-level association specificity than full networks encompassing plants and all fungi. This finding resonates with the results of Toju et al. (2018) from temperate Japanese forests. There they reported higher specialization at the level of the full interaction network than at the level of the partial networks of mycorrhizal and saprotrophic associations. Nonetheless, our analyses of different compartments of the networks were clearly challenged by the difficulties in assigning fungal taxa to functions. As mentioned above, 40% of fungal genera could not be assigned to any functional group. Thus, the pooling of these different unidentified interaction types may generate different conclusions regarding the structure of the full plant–fungus networks. Clearly, much more work is needed to improve reference databases and define the ecological role of arctic fungi before we can fully comprehend ecological networks in these ecosystems.

CONCLUSIONS

Our analyses reveal complex relationships between the environment and fungal community structure and diversity. Local communities in the plant rhizosphere are formed from the species pool available in the local soil, with strong imprints of the environment on the species present. Nonetheless, among locally co-occurring plant and fungal species, we found major variation in plant–fungus associations and low levels of partner specificity. This level of plasticity suggests high adaptability of plant–fungus networks in the face of environmental changes. As our current study is clearly observational in

nature, we urge experimental studies exploring the rewiring achieved under controlled conditions.

AUTHOR CONTRIBUTIONS

Bastien Parisy, Niels M. Schmidt, and Tomas Roslin designed the study. Bastien Parisy, Mikko Tiusanen, Paul Eric Aspholm, and Tomas Roslin collected the biological samples. Bastien Parisy measured a part of the edaphic variables used in this study. Eero J. Vesterinen generated metabarcoding libraries from root and soil samples and produced fungal community data, with assistance by Bioname. Bastien Parisy, Alyssa R. Cirtwill, Edith Villa-Galaviz, and Tomas Roslin designed the statistical analyses. Bastien Parisy and Jukka Sirén analyzed the data, with input from Tomas Roslin, Alyssa R. Cirtwill, Helena Wirta, Niels M. Schmidt, and Edith Villa-Galaviz. Bastien Parisy, Tomas Roslin, and Helena Wirta wrote the first draft of the manuscript. All authors then helped to revise the manuscript or provided comments on the final manuscript.

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CONFLICT OF INTEREST STATEMENT


The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT


Data and code (Parisy, 2025a) are available in Figshare at <https://doi.org/10.6084/m9.figshare.25516735.v1>. The raw sequences for the soil and root samples are available in the National Center for Biotechnology Information's Sequence Read Archive under BioProjects PRJNA1256308 (<https://www.ncbi.nlm.nih.gov/bioproject/PRJNA1256308>) and PRJNA1178551 (<https://www.ncbi.nlm.nih.gov/bioproject/PRJNA1178551>), respectively.

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SUPPORTING INFORMATION

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