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RESEARCH ARTICLE

Fungal microbiome biodiversity in *Larix sibirica* Ledeb. needles under biotic and technogenic stress in the Arctic

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Abstract

Biodiversity plays a crucial role in maintaining the stability of both ecosystems (biocenoses) and individual trees, as it enhances resistance to biotic and abiotic stressors. This study focuses on the phyllosphere fungal communities of *Larix sibirica* Ledeb. and their role in host resilience under combined stresses from the root pathogen *Porodaedalea niemelaei* M. Fisch. and technogenic pollution. Samples were collected from four groups of trees: infected with the root pathogenic fungus *P. niemelaei*, exposed only to technogenic pollution, subjected to both *P. niemelaei* infection and technogenic pollution, and control trees, which were neither infected nor affected by pollution. DNA was amplified, sequenced, and analyzed using Illumina sequencing technology, yielding 598,891 raw ITS sequences. Varying degrees of larch needle necrosis were observed across the groups, likely influenced by different microbial genera under specific environmental conditions. In samples infected with *P. niemelaei*, *Fusarium* and

Alternaria dominated, whereas in the group exposed to both *P. niemelaei* and technogenic pollution, *Valsa* and *Cytospora* were the most represented. Notably, the latter group also exhibited a reduced number of unique taxa compared to others, though further studies are needed to confirm statistical significance. The dominant pathogenic genera detected – *Fusarium*, *Alternaria*, *Valsa*, and *Cytospora* – likely interact with other fungi such as *Exobasidium*, *Ophiognomonia*, *Sarocladium*, *Phomopsis*, and *Taphrina*, exacerbating damage and altering the microbiome, particularly under pollution-induced stress.

Keywords
Microbiome, *Larix sibirica*, *Porodaedalea niemelaei*

Introduction

Of the various factors influencing the equilibrium of forest ecosystems in the Arctic, the most crucial is the predominant presence of larch (*Larix* spp.). These species demonstrate remarkable biological resilience and a strong capacity to extend their range, even in the most extreme climatic conditions. Larch species is typically recognized for its tolerance to pests, diseases, and abiotic stressors, particularly in Nordic environments where it has a relatively recent introduction and limited co-evolution with native pests and pathogens. The species' resilience is largely attributed to its broad heartwood, thick latewood rings, and the high concentration of secondary metabolites in its stem and deciduous foliage (Jalkanen 2016; Fakhrutdinova et al. 2017). However, the numerous industrial enterprises of the Norilsk Industrial Region (NIR) have triggered an environmental crisis in the Siberian Arctic forest. The NIR encompasses a wide range of products, resulting in a diverse array of harmful emissions from its enterprises. The total mass of waste exceeds 1 billion tons, covering more than 6,000 hectares. NIR enterprises account for 78% of harmful emissions in the Krasnoyarsk Territory (Bogorodskaya et al. 2012; Yurkevich et al. 2021). The most harmful pollutants include sulfur and several heavy metals: copper, nickel, cobalt, and lead. Sulfur dioxide contributes the most to environmental pollution in the NIR, accounting for 96–98% of all emissions in recent years. The intensive industrial exploitation of forest-tundra zones in European Russia, utilizing outdated and environmentally harmful technologies, has inevitably led to widespread degradation of natural ecosystems, destruction of forest habitats, loss of their ecological stabilization functions, and an increased incidence of pathogenic organisms (Ziganshin et al. 2017; Bobushkina et al. 2018; Kirdyanov et al. 2020; Kirpotin et al. 2021; Kharuk et al. 2023a; Kharuk et al. 2023b). The basidiomycete fungus *Porodaedalea niemelaei* M. Fisch. is widely distributed across Siberia in permafrost regions. The uniqueness of this phytopathogen lies in its ability to maintain high aggressiveness even under extreme low-temperature conditions. The proliferation of *P. niemelaei* leads to widespread clusters of declining trees and windthrown larches, characterized by corrosive heart rot. Root rot is pervasive throughout the area, affecting not only mature larches but also saplings (Litovka et al. 2017; Pavlov et al. 2018). In addition, over the past decade, larch forests on the Taimyr Peninsula have experienced widespread needle necrosis. The necrosis begins at the tip of the needles in mid-summer and rapidly spreads throughout the entire needle. The most intense damage is observed in the lower part of the crown, which suggests that direct needle burn due to industrial pollution from the Norilsk industrial area can be ruled out, indicating a potential infectious nature of the disease. This hypothesis is further supported by the presence of similar patterns in larch forests outside the zone of anthropogenic pollution (control).

Therefore, the objective of this study was to identify the microorganism (or group of fungi and bacteria) responsible for this new needle disease in *Larix sibirica*. The first step is to understand the microbiome changes that have led to the rapid needle necrosis under the conditions of climate change and chronic background atmospheric pollution. Despite the important role of Siberian larch, there are still few studies focused on its microbiome. Kauhanen et al. (2006) suggested that, since larch is a unique deciduous conifer whose needles grow for only one season, the species diversity of endophytic fungi would differ from that of evergreen conifers, where the rate of infection tends to increase with needle age. They were the first to publish a report on endophytic fungi in the Siberian larch (Kauhanen et al. 2006). However, additional studies are required to gain a comprehensive understanding of the interactions between the microbiome and host trees.

Materials and methods

Sampling

For the study of the Siberian larch microbiome, 17 needle samples were collected from trees growing in the Norilsk industrial region (NIR). The needles were collected on August 1–2, 2018, from trees aged 30–50 years according to a factorial design:

- techno: Trees under high air pollution levels and absence of the phytopathogenic fungus *P. niemelaei* in the trunk wood (location: 69.32°N, 88.30°E).
- inf&tech: Trees affected by *P. niemelaei* under high air pollution levels (location: 69.32°N, 88.30°E).
- infected: Trees under background air pollution levels but affected by *Porodaedalea niemelaei* M. Fisch (location: 69.34°N 86.87°E).
- control: Trees under background air pollution levels and absence of wood-destroying phytopathogenic fungi in the trunk wood (Boganidskoye Lake area, 50 km from Norilsk; coordinates: 69.34°N 86.87°E).

In total, 17 trees (L1–L112; W1–W5) were sampled, distributed across four groups: infected (4 trees), techno (5 trees), inf&tech (4 trees), and control (4 trees). From each tree, needles were collected from multiple locations within the crown (upper, middle, and lower branches) to account for potential spatial variability in microbial communities. The samples from each tree were pooled to create a composite sample per tree, which was then used for DNA extraction and subsequent analysis. Samples were collected using sterile tools, placed in sterile containers, and stored at −20°C until DNA extraction.

The presence of *P. niemelaei* infection was determined by extracting cores from preselected trees showing signs of heartwood rot and isolating pure fungal cultures. The sampling sites were characterized by a subarctic climate, with short, cool summers and long, extremely cold winters. Figure 1 illustrates the state of trees within the study sites.

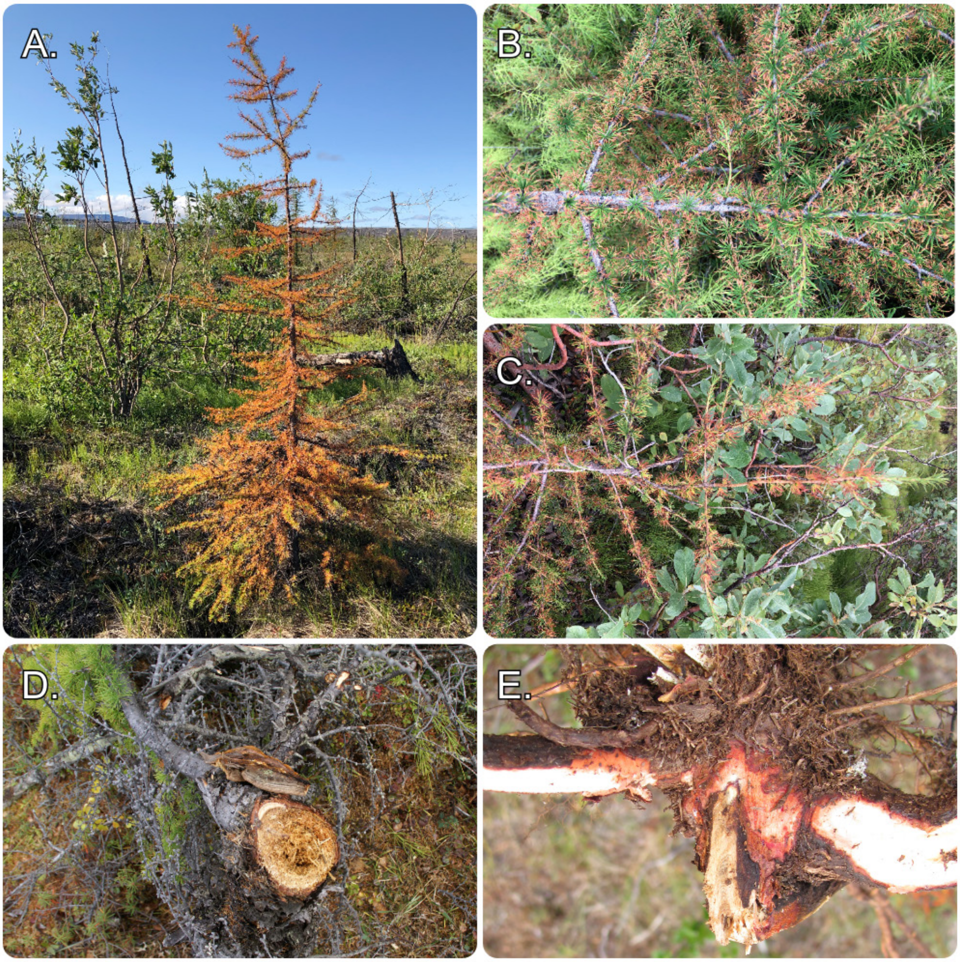


Figure 1. Siberian larch in the study areas: general view of an affected tree (**A**); shoots with needles showing mild (**B**) and severe (**C**) degrees of damage; heartwood decay and the fruiting body of the fungus *Porodaedalea niemelaei* (**D**); damage to the central root of the larch caused by the pathogenic effects of *P. niemelaei* (**E**).

In 2018, the growing period in Norilsk was marked by average monthly temperatures ranging from 5°C to 14°C. During the winter months, temperatures averaged between −27°C and −23°C, highlighting the region's severe subarctic climate. The total annual rainfall for the year was approximately 585 mm, with most precipitation concentrated in the summer. These weather patterns are characteristic of Norilsk, where the climate is defined by brief, cool summers and prolonged, intensely cold winters. The climatic data were obtained from the historical weather records available at http://www.pogodaiklimat.ru/history/23078.htm.

Extraction of DNA and Sequencing

DNA was extracted from the samples using the MACHEREY-NAGEL NucleoSpin Soil kit (MACHEREY-NAGEL, Germany) following the manufacturer's instructions. The quality of the extracted DNA was assessed by electrophoresis in a 1% agarose gel, while its concentration was measured using Qubit (Life Technologies) and Nanodrop (Thermo Fisher Scientific). The ITS2 region of fungal ribosomal operons was amplified using the ITS1F/ITS2 primers (GCATCGATGAAGAACGCAGC/TCCTCCGCTTATTGATATGC), which included Illumina adapter sequences, linkers, and a barcodes. The 15 μL PCR reaction mixture contained 10 ng of DNA template, 5 μM of each primer (forward and reverse), 2 nM of each deoxynucleoside triphosphate (Life Technologies), and 0.5–1 unit of Q5® High-Fidelity DNA Polymerase (NEB, USA). The reaction mixture was denatured at 94°C for 1 minute, followed by 35 cycles of amplification: denaturation at 94°C for 30 seconds, annealing at 50°C for 30 seconds, and extension at 72°C for 30 seconds. The final elongation was performed at 72°C for 3 minutes. PCR products were purified using the AMPure XP system (Beckman Coulter, USA) in accordance with Illumina's recommendations. Library preparation was conducted according to the MiSeq Reagent Kit Preparation Guide (Illumina). Sequencing was performed on the Illumina MiSeq platform (Illumina, USA) using the MiSeq® Reagent Kit v3 (600 cycle), which supports paired-end reads (2×300 base pairs), strictly following the manufacturer's protocol.

Bioinformatics analysis

Sequencing data were processed in RStudio using the DADA2 (Callahan et al. 2016) package version 1.28.0. Primer removal was performed with CUTADAPT version 1.15 (Martin 2011), following the removal of ambiguous bases (Ns) from the reads to prevent errors in downstream analyses. Quality profiles were inspected, and quality filtering was applied with the parameters truncLen=c(220,190), maxN=0, maxEE=8, truncQ=8, rm.phix=TRUE, minLen=50, which were selected based on preliminary quality profile inspections to balance read length and error rates. Chimeric sequences were identified and removed using the DADA2 algorithm to eliminate artifacts generated during PCR amplification. Taxonomy was assigned using the assignTaxonomy method with the ITS UNITE database for fungal sequences (Kõljalg et al. 2020; Abarenkov et al. 2024) version 25.07.2023, using default parameters and enabling the tryRC = TRUE option to ensure comprehensive identification by considering both forward and reverse complement sequences. Diversity metrics, including alpha diversity (e.g., Shannon index, observed species) and beta diversity (e.g., Bray-Curtis dissimilarity), were calculated using the VEGAN (Oksanen et al. 2024) and PHYLOSEQ (McMurdie and Holmes 2013) packages. Visualizations were performed with the FANTAXTIC (Teunisse 2022) and METACODER (Foster et al. 2017) to explore taxonomic composition and hierarchical relationships, while ggplot2 was used for creating publication-quality plots.

For investigating the functions of the fungal community, FUNGuild (Nguyen et al. 2016) and FungalTraits (Põlme et al. 2020; Tanunchai et al. 2022) were used for the identification of functional groups (guilds) in all groups of samples. The resulting datasets were categorized into three trophic modes based on fungal feeding strategies: symbiotrophs (mutualistic relationships with plants), saprotrophs (decomposers of organic matter), and pathotrophs (pathogens).

Results

Fungal Taxonomic Richness and Dominant Species

In total, 598,891 raw ITS sequences were obtained from the DNA of needle samples. There were 287,441 complete ITS sequences that were recovered from 17 samples and represented 155 ASVs after the low-quality, singletons, and non-fungal sequences were eliminated. As shown in the nested bar plot (Figure 1), Ascomycetes were highly dominant in all groups, comprising between 85.2% and 99% of the total, with the genera *Alternaria*, *Cladosporium*, and *Eustilbum* being the most prevalent. Basidiomycetes accounted for 1.5% to 13.8% across all groups and were represented by the genera *Phaeotremella*, *Phyllotopsis*, and *Porotheleum*. In some groups, Rozellomycota (inf&tech and infected) and Chytridiomycota (inf&tech) were detected, but their abundance was less than 0.1% (Figure 2). The most prevalent ASVs identified across all groups were assigned as *Alternaria eichhorniae* Nag Raj & Ponnappa, *Cladosporium herbarum* (Pers.) Link, and *Eustilbum aureum* (Pers.) Seifert & S.E. Carp. (Suppl. material 1: Table S1).

infected:

In the group infected with *P. niemelaei*, the dominant classes of the phylum Ascomycota are Sordariomycetes and Dothideomycetes. Among Sordariomycetes, the genus *Fusarium* is predominant, represented by *Fusarium nirenbergiae* L. Lombard & Crous and *Fusarium chlamydosporum* Wollenw. & Reinking. These species are phytopathogens and are absent in other sample groups. Dothideomycetes are also represented by pathogenic species of the genus *Alternaria* (*Alternaria metachromatica* E.G. Simmons and *A. eichhorniae*) as well as saprotrophs of the genus *Cladosporium*. Based on relative abundance, the dominant ASVs were identified as *Alternaria eichhorniae* (19.8%), *Fusarium* sp. (15.2%), *Fusarium chlamydosporum* (7.5%), *Cladosporium cladosporioides* (Fresen.) G.A. de Vries (6.0%), and *Cladosporium herbarum* (5.7%) (Figure 3A, Suppl. material 1: Table S1).

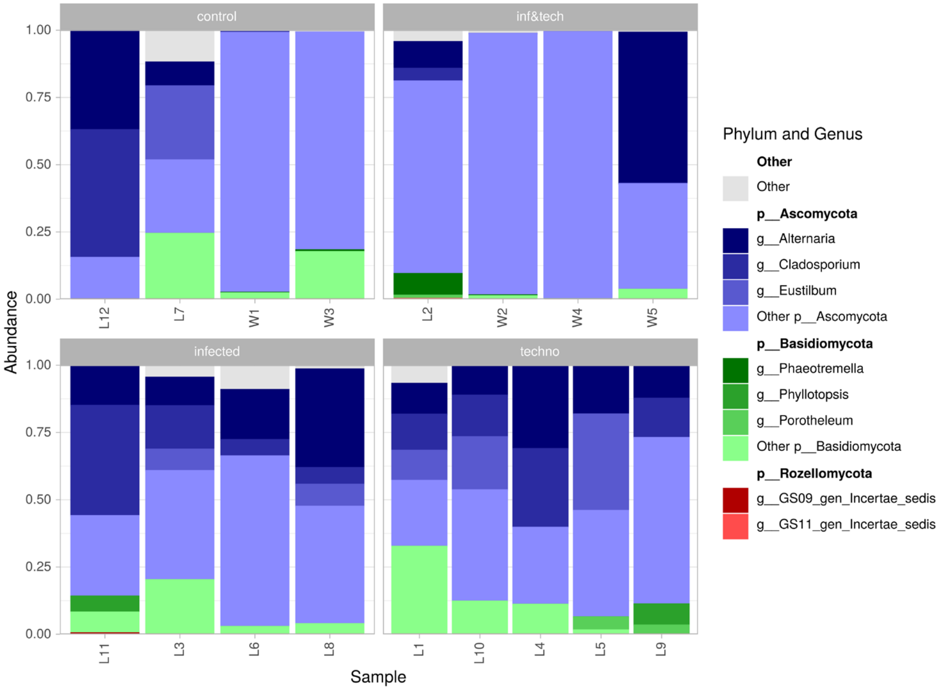


Figure 2. A bar plot of the most abundant fungal phyla and the most represented genera within these phyla, found in the Siberian larch needle samples.

inf&tech:

In the community of the group subjected to both *P. niemelaei* infection and technogenic pollution, the dominant classes remain the same as in the infected group – Sordariomycetes and Dothideomycetes. However, unlike the infected group, Sordariomycetes are predominantly represented by phytopathogens from the family Valsaceae (Cytospora and Valsa). Dothideomycetes are characterized by pathogenic species of the genus *Alternaria*. The most abundant sequences were assigned to *Cytospora* sp. (51.7%), *Valsa sordida* Nitschke (22.1%), *A. metachromatica* (6.9%), an unidentified member of Ascomycota (2.8%), and *Cadophora* sp. (2.6%) (Figure 3B, Suppl. material 1: Table S1).

techno:

In the group subjected exclusively to technogenic influence, the predominant classes within the phylum Ascomycota were Dothideomycetes and Leotiomycetes, with the most abundant genera identified as *Alternaria*, *Cladosporium*, and *Eustilbum*. Among Basidiomycota, the dominant classes were Agaricomycetes and Tremellomycetes. In terms of relative abundance, the leading taxa in this group were *Alternaria eichhorniae* (13.7%), *Eustilbum aureum* (10.9%), *Cladosporium herbarum* (10.6%), an unidentified representative of Ascomycota (5.8%), and Sordariomycetes (5.7%) (Figure 3C, Suppl. material 1: Table S1).

control:

In the control group, the most represented classes of Ascomycota were Dothideomycetes, Eurotiomycetes, and Sordariomycetes. Among Dothideomycetes, the dominant genera were *Perusta* and *Parafenestella*. The primary representative of the class Eurotiomycetes was the genus *Phaeomoniella*, while the most significant genus within Sordariomycetes was *Cytospora*. Basidiomycota were represented by the classes Agaricomycetes and Tremellomycetes, with the genus Peniophora being the most abundant among them. In terms of relative abundance, the most prevalent taxa were the non-pathogenic species *Perusta inaequalis* Egidi & Stielow (15.2%), an unidentified representative of Ascomycota (14.7%), *Peniophora polygonia* (Pers.) Bourdot & Galzin (9.3%), *Phaeomoniella* sp. (9.1%), and *Cytospora* sp. (8.7%). Pathogenic species such as *Parafenestella alpina* Jaklitsch & Voglmayr and *A. eichhorniae* were also detected, though their relative abundance was low (Figure 3D, Suppl. material 1: Table S1).

Microbial diversity

In all groups, alpha diversity metrics such as 'Observed', 'Chao1', 'Shannon', 'Simpson', 'InvSimpson' and 'Fisher' were measured (Suppl. material 3: Table S3). The Kruskal-Wallis test was implemented to compare these metrics across the groups. No significant differences were found for 'Observed', 'Chao1', 'Shannon,' and 'Fisher (Figure 4A). For the 'Simpson' and 'InvSimpson' metrics, the Kruskal-Wallis test rejected the null hypothesis with a p-value of 0.04626; however, the post-hoc Dunn test did not confirm significant differences between any of the groups (Table 1). Multidimensional scaling (or principal coordinate analysis; PCoA) on microbial abundance data didn't show prominent clustering among groups (Figure 4B).

Functional Prediction Analysis

The analysis of predicted fungal functional communities revealed that the communities in all groups were predominantly represented by saprotrophs and pathogens. The proportion of saprotrophs exceeded that of pathogens in the control and technogenic impact groups, whereas in the group infected with *P. niemelaei* and the group exposed to both *P. niemelaei* infection and technogenic impact, the proportion of pathogens markedly exceeded that of saprotrophs and all other functional groups (Figure 5, Suppl. material 2: Table S2). In the inf&tech group, plant pathogens account for 91.2%, with less than 8% of saprotrophs, whereas in the infected group, plant pathogens make up 61%, saprotrophs 16.9%, and multifunctional organisms 9%. The proportions of saprotrophs and pathogens in the techno and control groups are nearly identical, with both groups comprising 45-47% saprotrophs and 25-27% plant pathogens.

The main pathogenic genera identified include *Alternaria*, *Fusarium*, *Cytospora*, *Valsa* and others, as illustrated in Figure 7. In the infected group, *Alternaria* and *Fusarium* are the dominant pathogens, while less abundant genera include *Bryochiton* and *Stagonospora*. In the inf&tech group, the predominant pathogens are *Cytospora* and *Valsa*. Additionally, *Alternaria* and *Fusarium* are present, along with other genera such as *Exobasidium*, *Ophiognomonia*, *Sarocladium*, *Betamyces*, *Taphrina* and *Venturia*. In the techno group, the identified pathogens include *Alternaria*, *Bryochiton*, *Pyrenochaeta*, and *Phomopsis*. In the control group, a diverse range of pathogenic genera is present in low abundance, with *Phaeomoniella* and *Cytospora* being the most abundant (Figure 6, Suppl. material 2: Table S2).

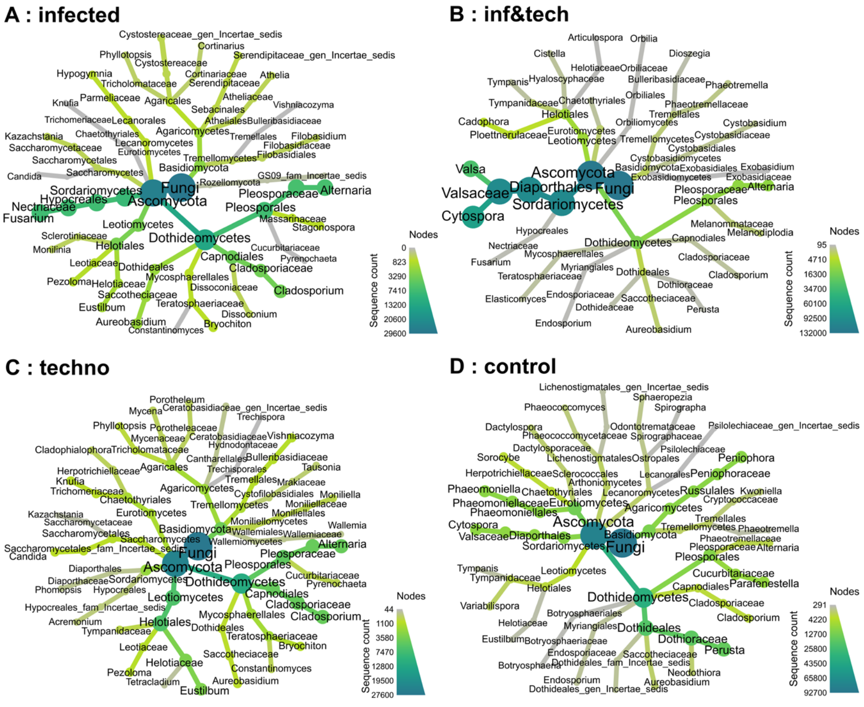


Figure 3. The heat tree format illustrates absolute abundances across taxonomic ranks, from phylum to genus, highlighting the top 20 taxa for each group. Node color represents the fungal load within a group, while node size facilitates comparisons between groups.

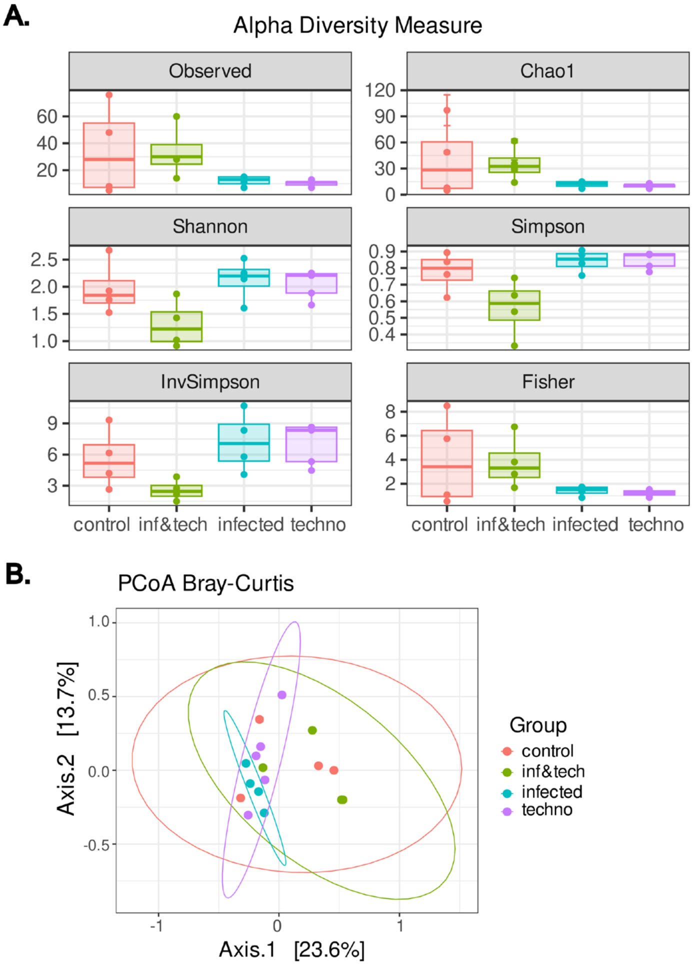


Figure 4. Alpha diversity metrics (**A**) and PCoA based on the Bray-Curtis distance matrix (**B**) for fungal communities associated with the Siberian larch phyllosphere. The two principal coordinates in the PCoA explain approximately 37% of the variation.

Table 1. Pairwise Comparison of Groups by Simpson Metric Using Post-hoc Dunn Test

Comparison	Z	P.unadj	P.adj
control-inf&tech	1.7503501	0.08005792	0.16011584
control-infected	-0.560112	0.575403023	0.69048363
inf&tech-infected	-2.3104621	**0.020862582**	0.06258775
control-techno	-0.7527727	0.451586543	0.67737981
inf&tech-techno	-2.5978037	**0.009382212**	0.05629327
infected-techno	-0.1623627	0.871020219	0.87102022

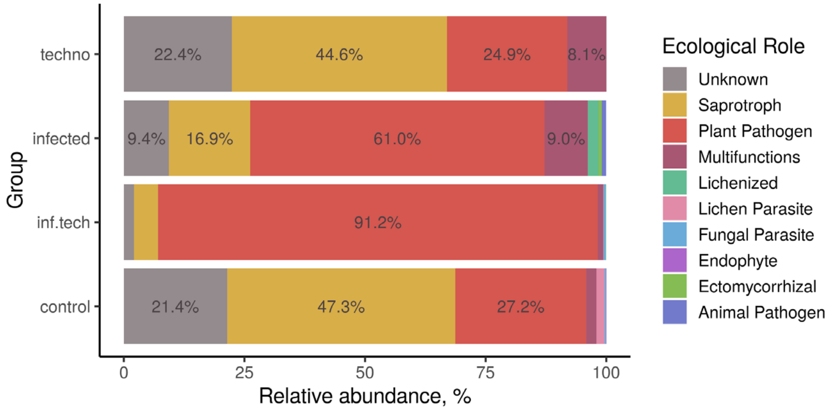
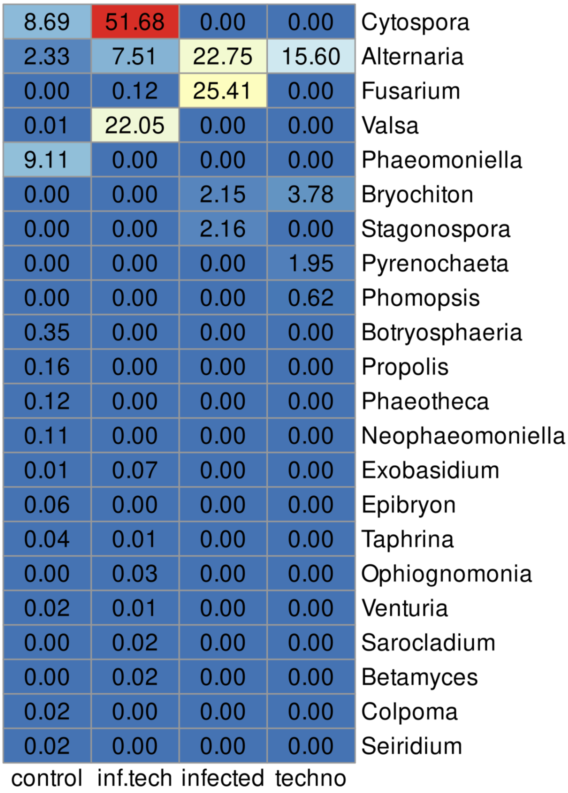


Figure 5. Relative abundance of fungal functional groups (pathotrophs, saprotrophs, and symbiotrophs) inferred using FUNGuild and FungalTraits across different sample groups from Siberian larch phyllosphere.



control	inf.tech	infected	techno	
8.69	51.68	0.00	0.00	Cytospora
2.33	7.51	22.75	15.60	Alternaria
0.00	0.12	25.41	0.00	Fusarium
0.01	22.05	0.00	0.00	Valsa
9.11	0.00	0.00	0.00	Phaeomoniella
0.00	0.00	2.15	3.78	Bryochiton
0.00	0.00	2.16	0.00	Stagonospora
0.00	0.00	0.00	1.95	Pyrenochaeta
0.00	0.00	0.00	0.62	Phomopsis
0.35	0.00	0.00	0.00	Botryosphaeria
0.16	0.00	0.00	0.00	Propolis
0.12	0.00	0.00	0.00	Phaeotheca
0.11	0.00	0.00	0.00	Neophaeomoniella
0.01	0.07	0.00	0.00	Exobasidium
0.06	0.00	0.00	0.00	Epibryon
0.04	0.01	0.00	0.00	Taphrina
0.00	0.03	0.00	0.00	Ophiognomonia
0.02	0.01	0.00	0.00	Venturia
0.00	0.02	0.00	0.00	Sarocladium
0.00	0.02	0.00	0.00	Betamyces
0.02	0.00	0.00	0.00	Colpoma
0.02	0.00	0.00	0.00	Seiridium

Figure 6. Heat map of plant pathogenic genera found in sample groups from Siberian larch phyllosphere. The numbers represent percentages of sequences among all sequences.

Discussion

The needles of *L. sibirica* support a diverse fungal community, primarily composed of Ascomycetes, a group commonly found in conifer needle tissues (Oono et al. 2015; Würth et al. 2019; Ata et al. 2022; Agan et al. 2021). Although no significant differences were observed between groups in diversity indices, a higher number of identified taxa was recorded in the control and inf&tech groups, whereas the infected group and the group exposed to technogenic impact were characterized by a lower number of taxa. A decrease in the number of taxa in groups exposed to infection or technogenic impact individually may indicate their specific effects on biodiversity. In the inf&tech group, both factors may potentially neutralize each other or create a unique ecological niche that allows for the preservation of a greater number of species. Both infected groups displayed an elevated relative abundance of pathogenic fungi compared to uninfected groups. However, regarding the number of detected pathogenic taxa, the control group was not inferior to, and even slightly exceeded, the infected groups, potentially indicating a shift in community composition favoring pathogenic species under pathogenic pressure. Notably, in the infected group, dominant pathogens were primarily species of genera *Fusarium* and *Alternaria*, whereas in the inf&tech group, *Valsa* and *Cytospora* were predominant, suggesting that additional environmental factors may modulate the prevalence and activity of specific pathogens.

Many important forestry and agricultural species are infected by the cosmopolitan fungi *Alternaria* and *Fusarium*. Due to their widespread distribution, there is global interest in gaining a better understanding of various pathogenic species and strains. *Fusarium* is one of the most studied fungal genera and one of the most economically significant in the world (Rampersad 2020; Dobbs et al. 2024). Among the diseases of coniferous species caused by the genus *Fusarium*, the most significant is pine pitch canker, caused by *Fusarium circinatum* Nirenberg & O'Donnell. It is an example of a new invasive disease in Europe and one of the most damaging pine diseases in the world (Elvira-Recuenco et al. 2020; Amaral et al. 2022).

The genus *Alternaria*, belonging to the phylum Ascomycota, is also widespread and includes pathogenic, saprophytic, and endophytic species. Necrotrophic phytopathogens of the genus *Alternaria* are globally prevalent and have a substantial impact on agricultural and forest ecosystems (Ozkilinc et al. 2018; Ali et al. 2023). Zhang M. J. et al. (2023) reported the discovery of a new needle blight disease in conifers caused by *Alternaria alternata* (Fr.) Keissl. Through detailed morphological analysis and molecular identification, supported by phylogenetic analysis of multiple gene sequences, they confirmed *A. alternata* as the pathogen responsible for this disease on Bunge's pine (Pinus bungeana Zucc. ex Endl.) in China. This marks the first documentation of *A. alternata* infecting *P. bungeana* (Zhang et al. 2023). Among our model trees, sample W5 stands out with 80% needle damage and no new growth, which is characteristic of the genus *Larix*. A possible reason lies in the abundance of the highly pathogenic fungus *A. metachromatica* within the studied microbiome. The pathogenicity of *A. metachromatica* has been confirmed through studies on a range of cultures (Bashir et al. 2014; Al-Lami et al. 2018; Al-Lami et al. 2019; Florea and Puia 2020).

Both *Cytospora* and *Valsa* are harmful ascomycetes that belong to the Valsaceae family (Diaporthales, Sordariomycetes). Valsa canker is one of the most prevalent canker diseases. Due to their opportunistic nature, species of *Cytospora* thrive in trees that have been weakened by late frost, drought, or bark damage from other pathogens. *Cytospora*, with its broad host range, is one of the most significant pathogenic fungi affecting both coniferous and hardwood trees globally. The stem cankers and dieback it causes lead to host plant death or weakened growth, resulting in major ecological and economic losses. In mature conifers, cankers caused by *Cytospora* are usually found on the lowest branches and seldom spread to the trunk (Adams et al. 2005; Adams et al. 2006; Yin et al. 2015; Pan et al. 2018; Kepley and Jacobi 2000; Pan et al. 2021; Lin et al. 2023; Lin et al. 2024).

Frascella A. et al. (2024) reported a high abundance of species from the genera *Valsa*, *Cytospora* (including the anamorphs of *Valsa*), and *Rhizosphaera* on the needles of *Abies nebrodensis* (Lojac.) Mattei. These fungi were predominant on both reddened and green needles. The authors propose that these species likely function as endophytes, reactivating growth when needles are subjected to stress factors such as wind, hail, or mechanical damage, and do not pose a direct biotic threat to *A. nebrodensis*. The observed needle disorders are primarily attributed to the harsh environmental conditions characteristic of this relic species' habitat. The presence of fungi on both symptomatic and asymptomatic needles suggests that *A. nebrodensis* has adapted to its modified environment and demonstrates resilience to these conditions (Frascella et al. 2024).

Among other noteworthy pathogenic fungal genera identified in our study, Exobasidium stood out. Species of the genus *Exobasidium* are known to cause leaf spots on blueberry, cranberry, and other *Vaccinium* species (Brewer et al. 2014). Additionally, tea plants are prone to blister blight disease caused by *Exobasidium* (Han et al. 2024; Zhou et al. 2024).

The genus *Ophiognomonia* encompasses leaf-associated fungi that exhibit diverse ecological roles, functioning as endophytes, pathogens, or saprobes on host plants belonging to the families Rosaceae, Betulaceae, Malvaceae, Fagaceae, Lauraceae, Juglandaceae, Salicaceae, Platanaceae, and Sapindaceae. Comprehensive studies and collections have demonstrated that this species-rich genus has a cosmopolitan distribution, with a primary occurrence in temperate regions and a smaller representation in subtropical zones (Walker et al. 2012).

The majority of species within the genus *Sarocladium* are saprophytic fungi inhabiting soil or plant pathogens. *Sarocladium strictum* (W. Gams) Summerb., initially recognized as an endophyte, has later been identified as a pathogen in maize crops, causing symptoms such as chlorosis, leaf and stem necrosis, plant barrenness, and wilting. This species has also been reported to induce diseases in strawberry plants. Sheath rot in rice is linked to S. oryzae (Sawada) W. Gams & D. Hawksw., *S.*

sparsum J.H. Ou, G.C. Lin & C.Y. Chen, and *S. attenuatum* W. Gams & D. Hawksw.; in Bangladesh, *S. oryzae* has also been found to be the causative agent of bamboo blight. Correspondingly, a secondary metabolite known to inhibit rice leaf blast, cerulenin, is also produced by this species. Furthermore, *S. kiliense* (Grütz) Summerb. has been identified for the first time in India as a stalk rot pathogen in maize (Hou et al. 2019; Peeters et al. 2020; Harish et al. 2024).

Microfungi of considerable phytopathological significance, with a wide variety of host associations and a worldwide distribution, are found in the genus *Phomopsis*. Climate, host plant susceptibility, and the range of regions studied in biodiversity studies all affect the taxa's prevalence. Despite its low average annual temperatures, the Scandinavian Peninsula (Finland and Sweden) has been home to a number of species. In North America, pathogenic species infecting conifers (*Phomopsis occulta* Traverso), junipers (*Phomopsis juniperivora* G.G. Hahn), blueberries (*Phomopsis vaccinii* Shear; current name *Diaporthe vaccinii* Shear), grapevines (*Phomopsis viticola* (Sacc.) Sacc.; current name *Diaporthe ampelina* (Berk. & M.A. Curtis) R.R. Gomes, Glienke & Crous), and elms (*Phomopsis oblonga* (Desm.) Traverso; current name Diaporthe eres Nitschke) are found (Udayanga et al. 2011; Mihaescu et al. 2021). Notably, *Phomopsis* species can cause Tip Blight (Blalock and Baysal-Gurel 2015; Behnke-Borowczyk et al. 2020).

Taphrina species cause the tumor-like plant structure, infection symptoms include leaf spots, leaf curl, deformed fruits, and witches' brooms (Tsai et al. 2014). In Siberian forests and urban areas, M. Tomoshevich et al. documented thirteen years of observations on foliar fungal pathogens that target woody broadleaved species from Europe and Eurasia. They discovered that fruit deformation was linked to *Taphrina pruni* Tul. (Tomoshevich et al. 2013). *Taphrina carpini* (Rostr.) Johanson is a species which have been reported from studies on Norway spruce needle communities and can be a member of normal phyllosphere fungal communities (Elfstrand et al. 2020).

Other species of the genus *Porodaedalea* are of significant interest to researchers. For instance, Wojciech Szewczyk et al. conducted a study aimed at investigating fungi inhabiting knotwood of *Pinus sylvestris* L. infected by *Porodaedalea pini* (Brot.) Murrill. Their findings revealed that the fungal community primarily consisted of endophytes, saprotrophs, and lichens. The most frequently identified genera included *Coniochaeta*, *Lecanora*, *Infundichalara*, *Rhinocladiella* and *Sarea*. They discovered that in pines impacted by *P. pini*, *Coniochaeta hoffmannii* (J.F.H. Beyma) Z.U. Khan, Gené & Guarro and *Coniochaeta fodinicola* Vázq.-Camp. were the most prevalent. The pathogen effectively competes with certain fungal species, according to the authors, and does not impede the growth of survivors (Szewczyk et al. 2017).

Conclusions

A total of 598,891 raw ITS sequences were obtained from larch needle samples. Sequences were clustered into 155 ASVs for fungal taxa. The fungal community was mainly represented by Ascomycetes and Basidiomycetes. The dominant pathogenic fungi included *Fusarium*, *Alternaria*, *Valsa*, and *Cytospora*. These pathogens may interact with other species from the genera *Exobasidium*, *Ophiognomonia*, *Sarocladium*, *Phomopsis* and *Taphrina*, contributing to damage and microbiome alterations, especially when combined with the weakening effects of technogenic pollution on larch. Future research will focus on the isolation of pure fungal cultures and subsequent inoculation of plants under controlled conditions to elucidate their specific role in needle damage.

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Supplementary material 1

Table S1. Fungal taxa identified in phyllosphere of Siberian larch and their relative abundance in sample groups

Authors: Ksenia A. Miroshnikova, Yulia A. Litovka, Anton A. Timofeev, Igor N. Pavlov

Data type: table

Link: https://journal.asu.ru/biol/article/view/18453/15847

Supplementary material 2

Table S2. Relative abundance of fungal functional groups inferred using FUNGuild and FungalTraits in Siberian larch needles

Authors: Ksenia A. Miroshnikova, Yulia A. Litovka, Anton A. Timofeev, Igor N. Pavlov

Data type: table

Link: https://journal.asu.ru/biol/article/view/18453/15848

Supplementary material 3

Table S3. Alpha diversity metrics of fungal communities derived from Siberian larch phyllosphere

Authors: Ksenia A. Miroshnikova, Yulia A. Litovka, Anton A. Timofeev, Igor N. Pavlov

Data type: table

Link: https://journal.asu.ru/biol/article/view/18453/15849