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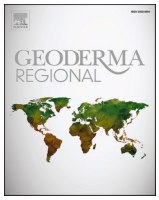

Microbial communities of urban and industrial polluted soils in the Russian Arctic

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ABSTRACT

The Russian Arctic presents a unique environment for studying the effects of anthropogenic pressure on soil microbial communities under severe climatic conditions. This study investigated the impact of chemical pollution on soil microbial properties by comparing urban and industrially polluted soils in Murmansk region with natural Podzols. Urban soils exhibited significant alterations, including shifts in pH and increased carbon and nutrient contents compared to natural soils. Industrially polluted soils near the copper-nickel smelter were characterized by elevated heavy metal concentration, while those near the aluminum smelter showed high fluorine and aluminum content. In both cases, carbon content and pH remained similar to natural soils. Industrial emissions significantly changed the soil microbiome, with effects varying depending on the pollution source and chemical composition of the emissions. Soils near the copper-nickel smelter showed a decline in bacterial gene copies and actinomycete mycelium length, with a predominance of Chloroflexii and Ascomycota. Conversely, soils near the aluminum smelter exhibited less pronounced changes, with Proteobacteria and Basidiomycota being prevalent. Despite these differences, both industrially impacted sites displayed reduced microbial diversity, regardless of the composition of the emissions. In contrast, urban soils demonstrated increased microbial diversity, likely attributed to the emergence of new, favorable ecological niches. Microbial communities in both cities were similar, dominated by Proteobacteria and Ascomycota, and displayed an increase in bacterial gene copies compared to natural soils. These findings highlight the contrasting influences of urban and industrial development on soil microbial communities. While industrial activities suppress microbial life, urbanization fosters the creation of new niches, promoting microbial diversity. This underscores the potential of urban soils to support diverse microbial communities, which is crucial for sustainable development and ecological strategies in Arctic cities.

1. Introduction

Soil health in Arctic regions has emerged as an important research area in the context of ongoing climate change (Ford et al., 2021; Gao et al., 2023; Madani et al., 2023). Arctic soils are particularly vulnerable to climate change, especially when subjected to anthropogenic disturbances (Vincent, 2020; Korneykova et al., 2023b). The economic development of Arctic regions, a priority for Russia and other northern countries, has led to industrial expansion and urbanization (Körber et al., 2017; Laruelle, 2019; Abakumov et al., 2023). The Murmansk region, located in the Russian Arctic, is a hub for mining industries, nonferrous metallurgy, and nuclear power plants. Industrial emissions in this region have resulted in the degradation of vegetation and the depletion of soil functionality in areas surrounding factories and smelters (Slukovskaya et al., 2019, 2020; Dvornikov et al., 2022). Urbanization in the region has led to the development of gray and green infrastructures, which can have diverse effects on soils. Soil sealing, pollution from inorganic (heavy metals) and organic (petroleum

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products, pesticides, and dyes) substances (Yang and Zhang, 2015; Beroigui et al., 2020; Ananyeva et al., 2021), alkalization by concrete dust and construction waste (Ivashchenko et al., 2019), and oversaturation with phosphorus (Cheng et al., 2014) are among the most widespread negative impacts of urbanization on soils in the region. Conversely, the urban heat island effect, which has led to a significant increase in ambient temperature in polar cities, has a positive effect on soils by increasing the thickness of the functional soil-forming layer (Laruelle, 2019; Abakumov et al., 2023) and creating more favorable conditions for urban greening initiatives (Shi et al., 2012; Konstantinov et al., 2018). These urban green spaces often feature constructed soils composed of soil mixtures and amendments, which can have higher carbon and nutrient contents than natural soils (Lorenz and Lal, 2009; Shchepeleva et al., 2017; Korneykova et al., 2022). Despite previous studies on the chemical properties of urban and industrial soils in the Arctic, the consequences of these changes for the soil microbiome remain largely unexplored.

Industrial and mining activities in the Arctic are known to cause significant heavy metal pollution in soils, negatively affecting soil microbial communities compared to pristine ecosystems (Xie et al., 2016; Ji et al., 2021; Korneykova et al., 2022; Yan-Hui et al., 2022; Abakumov et al., 2023). While low concentrations of heavy metals can stimulate microbial growth, high concentrations can severely inhibit soil microbial communities (Ji et al., 2021; Korneykova et al., 2021b, 2022). Despite extensive research on the impact of pollutants on the biological activity of Arctic urban soils (Kumar et al., 2011; Enya et al., 2020; Ji et al., 2021; Fokina et al., 2022), there is limited information on the specific composition and abundance of microbial communities in these contaminated environments. Previous studies on urban soil microbial communities have primarily relied on plating methods (Bridge and Spooner, 2012; Ball and Virginia, 2014) or estimated total microbial biomass (Oechel et al., 1997; Ananyeva et al., 2006), with a focus on sanitary and hygienic indicators (Peretrukhina, 2011; Beroigui et al., 2020). However, a comprehensive understanding of microbial diversity and activity in anthropogenically disturbed soils is crucial to fully elucidate how urbanization and industrial activities alter microbial community structure and function.

To address this research gap, we employed molecular genetic techniques to investigate the structure and taxonomic diversity of microbial communities in industrial and urban soils in the Murmansk region. This study had two primary objectives: 1) Quantify and characterize microbial communities: the number, biomass structure, and taxonomic diversity of soil microbial communities in industrial and urban soils; 2) Assess the impact of anthropogenic and environmental factors: compare the effects of anthropogenic disturbance (urban or industrial) and bioclimatic conditions (forest-tundra or north taiga) on the composition and diversity of soil microbial communities. We hypothesized that industrial pollution would suppress soil microbial activity and reduce microbial diversity, regardless of the bioclimatic conditions. Conversely, we predicted that urban green infrastructure and the urban heat island effect would create unique ecological niches, fostering distinct soil microbial communities in Arctic environments.

2. Methods and materials

2.1. Research area

This study was conducted in the Murmansk region, which comprises the onshore area of the Arctic zone of the Russian Federation. This region is characterized by three distinct bioclimatic zones: tundra, forest-tundra, and northern taiga. The northernmost tundra zone remains largely pristine, while the forest-tundra and northern taiga zones host significant industrial and urban development. To understand how human activities impact soil microbes in these varied environments, we focused on the largest city and the most impactful industrial enterprise within each of the forest-tundra and northern taiga zones. Specifically, we selected the following locations for our study: 1) Forest-tundra: Murmansk is the region's largest city, and the Pechenganikel copper-nickel plant is a major industrial polluter. 2) Northern taiga: Apatity is a smaller town, and the Kandalaksha aluminum smelter is another significant industrial source (Fig. 1).

The Kandalaksha aluminum smelter (AL) holds a unique distinction as the only aluminum smelter in the world located above the Arctic Circle, near Kandalaksha city (67°09′N, 32°24′E). Its inland location, roughly 300 km from the Barents Sea, results in a more continental climate, transitional between temperate and subarctic. Although the smelter produces valuable aluminum products (primary aluminum, aluminum alloys, foil, and alumina), its operations also release a range of pollutants, including hydrogen fluoride, hydrofluoric acid salts, aluminum oxide, benzo(*a*)pyrene, tarry substances, naphthalene, carbon monoxide, and sulfur dioxide. In contrast, the Pechenganikel copper-nickel smelter (CU-NI) is located in the northwestern Kola Peninsula, near the Nickel settlement. This area is characterized by temperate climate, though heavily influenced by the warm North Atlantic Gulf Stream, resulting in significant variability. Since 1998, this facility has focused on mining and enriching sulfide copper-nickel ores, processing approximately 7.5 million tons annually to produce matte. Further refining yields nickel, copper, cobalt, and sulfuric acid, which are the primary pollutants of concern in areas affected by the smelter's emissions.

Murmansk (68°58′ N, 33°05′E) is located on the Kola Bay's eastern coast. Benefiting from the warm Gulf Stream current, it has an Atlantic-Arctic temperate climate. As the world's largest city above the Arctic Circle, Murmansk boasts a population exceeding 290,000 and a diverse economy encompassing fish processing, maritime transport, ship repair, food production, and Arctic geological exploration. In contrast, Apatity (67°34′N, 33°24′E), the region's second-largest city, lies on the Belaya River's left bank, nestled between Lake Imandra and the Khibiny Mountains. Characterized by low hills averaging 150–200 m above sea level, Apatity experiences a continental climate that is cold and humid (Kottek et al., 2006). With a population of 55,200, its economy centers on apatite-nepheline ore extraction and processing, and the production of phosphorus fertilizers.

2.2. Site description and soil sampling

To capture the diverse impacts of human activities on soil microbes, we tailored our sampling strategies to the specific characteristics of industrial and urban areas. In industrial areas, where pollution sources are typically well-defined, we employed a transect-based approach. This involved collecting soil samples along gradients extending from the pollution source, allowing us to systematically assess the spatial impact of industrial activities on soil properties. Urban areas, in contrast, present a more complex challenge due to the varied and spatially heterogeneous nature of human influences. To account for this complexity, we used a random stratified sampling strategy. We divided the urban area into strata based on functional zones (e.g., residential, recreational) and then randomly sampled within each stratum. This approach ensured that we captured the variability in soil properties across different urban land uses and activities.

Our sampling design was developed considering the previous research emphasizing the importance of distance from emission sources and functional zones in predicting soil chemical properties (Evdokimova et al., 2013; Evdokimova et al., 2014; Korneykova et al., 2021b, 2022; Korneykova and Nikitin, 2023). It was thus optimized to ensure representative and informative data.

To assess the impact of industrial emissions on soil microbial communities, we collected soil samples along transects extending outwards from each smelter. Sampling distances were based on previous zoning of the territory, which considered the level of soil pollution and the state of vegetation (Evdokimova et al., 2013; Evdokimova et al., 2014). Specifically, samples were collected at the following distances: Kandalaksha

Fig. 1. Research area and sampling scheme.

aluminum smelter (1.5 km, 8 km, 15 km, and 50 km (background)); Pechenganikel copper-nickel smelter (3 km, 8 km, 30 km, and 50 km (background)). At each distance (pollution zone), a representative 100 m^2 plot was established, and within each plot, soil samples were collected from 5 randomly selected locations (spatial replicates). This resulted in a total of 20 sampled locations per industrial area (Table 1). This design allowed us to evaluate the influence of industrial activities on soil properties across a gradient of pollution impact.

In urban areas, soil samples were taken at residential zones and recreational areas (public green spaces), selected randomly inside the city boundaries. Considering different size of the cities (~40 km^2 and ~ 30 km^2 of urbanized areas in Murmansk and Apatity respectively) and dominating functional zones (Korneykova et al., 2021b, 2022; Dvornikov et al., 2021), the sample size was also different. In Murmansk, in total 40 urban sites were sampled (20 in residential and 20 in recreational zones). In addition, 10 background sites were selected in the undisturbed forest-tundra landscapes located within 5 km from the city boundaries and considered as natural references. In Apatity, in total 28 sites were sampled (21 in residential and 7 in recreational zones) and compared to 6 background sites. In total, 84 locations were sampled from urban areas and corresponding natural background areas (Table 2).

At each study site (pollution zones for industrial areas, functional zones for urban areas, and natural background areas), a single soil pit was excavated for description, morphological analysis, and classification according to the World Reference Base for Soil Resources (WRB). At each location, composite topsoil samples (0–10 cm depth) were collected during the summer. Each composite sample consisted of soil collected from five points within a 2 × 2 m subplot, including the center and corners, using an auger. These samples were used for various analyses. Bulk density was determined using ring samples and analyzed in the laboratory using the dry weight approach (Shein et al., 2007). For the chemical analysis, the samples were taken from topsoil horizons, transported to the lab, air-dried (22 °C), and sieved (mesh 2 mm). For the microbiological analysis, the samples were collected from a depth of 0–10 cm according to the standard sampling procedure with measures to prevent contamination (ISO 18400-206, 2018) and stored at −18 °C for luminescent microscopy and at −70 °C for molecular analyses. The taxonomic diversity of microbial communities was determined in the most representative soils from industrial and urban sites, including heavily polluted sites in industrial areas, located 3 km from the CU-NI and 1.5 km from the AL facilities and residential areas in cities, designated as RZ and RZ-I. Soil samples from background sites were analyzed as references to provide a baseline for comparison.

2.3. Soil chemical analysis

The following soil properties were measured. The pH_w was measured in a 1:5 soil:water suspension using an electrometric method with a

Table 1
Description of the industrial sites (aluminum and copper-nickel smelters emission areas).

Distance from the smelter, km	Level of pollution*	Vegetation	Soil (WRB)
Kandalaksha aluminum smelter			
1.5	Maximum	Crowberry pine forest; ground cover: crowberry	Folic Leptic Albic Podzol (Arenic)
8	Intense	Cowberry–sphagnum pine forest; ground cover: crowberry > blueberry> cowberry>wild rosemary	Folic Leptic Albic Podzol (Arenic)
15	Moderate	Cowberry–sphagnum pine forest; ground cover: crowberry > blueberry> cowberry>wild rosemary; mosses	Folic Leptic Albic Podzol (Arenic)
50	Background	Bilberry–sphagnum pine forest; ground cover: crowberry > blueberry> cowberry; lichens; mosses	Folic Leptic Albic Podzol (Arenic)
Pechenganickel copper nickel smelter			
3	Strong	Lingonberry pine stand with birch trees	Folic Leptic Albic Podzol (Arenic)
16	Moderate	Pine stand with dwarf shrubs and birch trees; ground cover, lingonberry > crowberry > Labrador tea	Folic Leptic Albic Podzol (Arenic)
30	Weak	Lingonberry pine stand with birch trees; ground cover, lingonberry > Labrador tea and lichens	Dystric Leptic Hemic Folic Histosol
50	Background	Lichen–dwarf shrub pine stand; ground cover, bog bilberry > European blueberry > crowberry and lichens	Folic Leptic Albic Podzol (Arenic)

* According to Evdokimova et al. (2013, 2014).

Table 2
Description of the urban sites (Murmansk and Apatity).

Functional zone		Vegetation	Soil (WRB)
Murmansk			
FT	Background	Birch woodlands; ground cover: crowberry lingonberry, horsetail, Labrador tea, mosses	Folic Leptic Albic Podzol (Arenic)
SR	Residential zone, private house	Mixed lawn with the dominance of dandelion officinalis, nettle dioecious	Folic Leptic Albic Podzol (Arenic)
RZ	Residential zone, inner courtyard	Asberry stand with birch trees; ground cover: Kupyr forest > nettle dioecious	Urbic Technosol
SD	Abandoned green area	Willow bushes; ground cover: Kupyr forest > Gramineae	Urbic Technosol
UR	Public green space	Willow bushes; mixed lawn	Urbic Technosol
Apatity			
FT	Background	Pine-spruce forest with birch trees; ground cover: blueberry > cowberry > crowberry	Folic Leptic Albic Podzol (Arenic)
RZ-I	Residential zone, inner courtyard	Birch and rowan trees; mixed grass lawn	Someriumbric Leptic Albic Podzol (Arenic)
SR	Public green space	Birch stand; mixed grass lawn, Gramineae > clover	Someriumbric Leptic Entic Podzol (Arenic, Technic)
RZ-O	Residential zone, external courtyard	Birch trees; mixed grass lawn with hogweed, cuff	Someriumbric Leptic Entic Podzol (Arenic, Technic); Urbic Technosol
RZ-AR	Residential zone, urban farming	Mixed lawn with the dominance of Kupyr forest	Anthroumbric Entic Podzol

Starter pH meter. Total carbon and nitrogen contents were determined by dry combustion using a Vario TOC Elementar CN analyzer. Available phosphorus was determined using a spectrophotometric method with a HACH DR-3900 spectrophotometer. Available potassium content was measured using a flame photometer. The concentrations of heavy metals (Ni, Cu, Pb, Zn, Cd, and Co) extracted by 5.0 M HNO_3 were determined by inductively coupled plasma atomic emission spectrometry (ICP-AES) using a Perkin Elmer AVIO 200 instrument. Soil samples were digested using a microwave-assisted acid digestion method (3 mL HNO_3 + 2 mL HF + 1 mL HCl + 5 mL H_2O per 0.25 g of soil) following the standard M-MVI-80-2008 method. All acids were of reagent grade (Baum-Lux, Moscow, Russia). Quality control and quality assurance (QA/QC) were ensured using a multi-element calibration standard and a verification standard (GSO 2499–83, SDPS-2). Total fluorine content was determined using an ion-selective electrode method with a Radelkis Budapest pH/ION ANALYZER ion meter.

2.4. Soil microbiological properties

2.4.1. Microbial biomass

The number of cells and prokaryotes biomass were determined by luminescence microscopy method («Zeiss Axioskop 2 plus» microscope (Germany), × 100, oil immersion) using acridine orange fluorescence. Desorption of cells from soil particles was carried out by ultrasound «UDNZ-1» device (2 min, 22 kHz, 0.44 A) (Polyanskaya and Zvyagintsev, 2005). Six preparations were made from each soil sample and cells were counted in 30 observation fields.

The number of fungal propagules and mycelium length were also measured using luminescence microscopy («Biomed 5PR LUM» microscope (Russia), × 40) with calcofluor white fluorescence. Cell desorption from soil particles was carried out with the «MSV-3500» vortex (Latvia) at a speed of 3500 rpm for 10 min) (Polyanskaya and Zvyagintsev, 2005). From each sample, 3 preparations were made, and cells were counted in 90 observation fields. Detailed methodology was presented in the article by Korneykova et al. (2022).

2.4.2. Quantification of ribosomal genes

The abundance of bacterial, archaeal, and fungal ribosomal genes was quantified using quantitative real-time polymerase chain reaction (qPCR). Primers for the 16S rRNA gene were used to account for archaea and bacteria, and primers for the ITS region were used to account for fungi.qPCR reactions were performed using a Bio-Rad CFX96 Touch real-time PCR system with Bio-Rad SuperMix Eva Green. The *Escherichia coli* (Sigma) ribosomal operon was used as the control for bacteria, the FG-07 *Halobacterium salinarum* strain for archaea (Jurgens and Saano, 1999), and the *Saccharomyces cerevisiae* Meyen 1B—D1606 yeast strain for fungi. For each sample, the reaction was performed in 3 repetitions. Gene concentrations were calculated using CFX Manager software. The concentration of genes in the DNA preparations was converted into the number of genes per gram of soil, considering the dilutions and weight of the sample.

2.4.3. Taxonomic diversity of microbial community

To characterize the taxonomic diversity of soil microbial communities, we used a high-throughput sequencing approach. This involved DNA extraction, PCR amplification of marker genes, library preparation, and next-generation sequencing.

2.4.3.1. DNA extraction. Total DNA was extracted from 10 g composite soil samples using the Fast DNA Spin Kit (MPBio, Solon, Ohio, USA)

according to the manufacturer's instructions. DNA concentration was quantified using a Qubit 2.0 Fluorometer (Invitrogen/Life Technologies, Carlsbad, CA, USA). The extracted DNA served as a template for subsequent PCR reactions.

2.4.3.2. PCR amplification, library preparation, and sequencing. Bacterial 16S rRNA and fungal ITS genes were amplified via PCR, followed by library preparation and Illumina MiSeq sequencing conducted by Sequentia Biotech SL (Barcelona, Spain). The V3-V4 hypervariable regions of the bacterial 16S rRNA gene were amplified using the universal primer pair 341F-805R (Herlemann et al., 2011). These primers included sample-specific barcodes and Illumina sequencing adaptors (Illumina Inc., San Diego, CA, USA).

The fungal ITS region was amplified using the ITS1 and ITS4 primers (White et al., 1990). After PCR amplification, the amplicons were quantified, purified, and used to construct separate libraries for bacteria and fungi according to the 16S Metagenomic Sequencing Library Preparation protocol. Paired-end sequencing (2 × 300 nt) was performed on an Illumina MiSeq sequencer (MiSeq Reagent kit v2, Illumina Inc., San Diego, CA, USA) using the manufacturer's recommended protocols.

2.5. Bioinformatic analysis

Raw sequencing reads were quality-trimmed, and adapter sequences were removed using Trimmomatic v0.32 (Bolger et al., 2014). Sequence quality was assessed using the FastQC toolkit (Babraham Bioinformatics, Cambridge, UK). Taxonomic profiling and quantification were performed using the GAIA software package (version 2.02, Sequentia Biotech, Spain). This analysis utilized databases of 16S and ITS1 + ITS2 sequences obtained from the NCBI "nr" database. Sequences from each sample were clustered into operational taxonomic units (OTUs) based on 97 % sequence similarity.

2.6. Statistical analysis

Descriptive statistics were calculated to estimate the mean, standard error of the mean, and 95 % confidence intervals for each measured variable. Normality of the collected data was checked by Shapiro-Wilk test, and the homogeneity of variances was assessed by Levene's test (Tables 1S—2S). To compare quantitative parameters of the microbial community (gene copy numbers and microbial biomass) between different areas (industrial, urban, and background), we used one-way analysis of variance (ANOVA) followed by Tukey's Honestly Significant Difference (HSD) test for pairwise multiple comparisons. These analyses were performed separately for each microbial indicator (gene copy number or biomass) and for each smelter/city. For data that did not conform to a normal distribution, the non-parametric Kruskal-Wallis test was used to assess the significance of differences. Effect sizes were calculated using Cohen's *d* with 95 % confidence intervals (Tables 3S—4S). Multivariate analysis of variance (MANOVA) was used to evaluate the influence of qualitative parameters (zone type, ecosystem type, anthropogenic impact type, and vegetation cover type) on the variability of quantitative microbial community parameters. Because the data on gene copy numbers and microbial biomass were not normally distributed, a logarithmic transformation was applied prior to MANOVA. To identify the primary factors influencing the quantitative parameters of the microbial community, we performed principal component analysis (PCA). PCA was conducted using the "FactoMineR" (Lê et al., 2008) and "factoextra" (Kassambara and Mundt, 2020) packages in R. Sampling adequacy for PCA was verified using the Kaiser-Meyer-Olkin (KMO) test with the "psych" package (Revelle, 2024). An individual factor map was constructed to illustrate the relationships between physicochemical and microbiological soil properties, the type of anthropogenic disturbance, and the identified principal components. We visualized the diversity of fungal operational taxonomic units (OTUs) at the class level using a heatmap generated with the "pheatmap" package (Kolde, 2019) in R, based on Bray-Curtis distances. A Venn diagram, created using the "ggVennDiagram" package (Gao and Duşa, 2024), illustrates the number of unique and shared bacterial and fungal OTUs across different sample groups. Fungal functional diversity was predicted using the FUNGuild database (Nguyen et al., 2016). The relative abundance of fungal OTUs assigned to different functional guilds was visualized using a bubble plot created with the "ggplot2" and "reshape2" packages (Wickham, 2007, 2016). We performed cluster analysis to group samples based on similarities in fungal functional guilds, using Euclidean distance and Ward's method in the "vegan" package (Oksanen et al., 2022). All statistical analyses and data visualizations were conducted in R 4.3.3 using R Studio (R Core Team, 2024).

3. Results

3.1. Morphological and chemical properties

3.1.1. Industrially polluted soils

The soils surrounding the non-ferrous metallurgy enterprises were chemically contaminated natural Albic/Entic Podzols and Histosols, with no visible signs of anthropogenic disturbance within the studied soil profiles. These soils exhibited an acidic reaction, with pH_w decreasing gradually with increasing distance from the smelters. The surface organic horizons (peat and litter) were characterized by high organic carbon (39–63 %) and total nitrogen (0.2–2.2 %) contents. However, there were no significant differences in the mean values of pH_w, C, and N between the two industrial sites. In contrast, the mean values and spatial patterns of heavy metals were distinct between the sites. Along the gradient from CU-NI, the concentrations of Ni and Cu decreased by several orders of magnitude: from 2143 to 22 mg kg^{-1} for Ni and from 1587 to 26 mg kg^{-1} for Cu at 5 and 50 km from the smelter, respectively. Soils impacted by AL had significantly lower concentrations of Ni, Cu, Cd, and Fe compared to those impacted by CU-NI, and did not exhibit clear gradient changes with distance (Fig. 2). This difference is attributed to the unique technological processes and the distinct composition of pollutants in the smelter aerosols, which were dominated by fluorine (F) at the AL site. Total F content decreased gradually with distance from the AL smelter, from 990 mg kg^{-1} at 1.5 km to 46 mg kg^{-1} at the background site.

3.1.2. Urban soils

Urban soils in Murmansk and Apatity were classified as natural Albic and Entic Podzols with varying degrees of disturbance, as well as artificially created urban Technosols. These soils exhibited high variability due to factors such as functional zoning, soil construction practices, and the management of urban green infrastructure, including the introduction of new soil material onto excavated and leveled subsoil. These factors strongly influenced the formation of surface organic horizons. In some cases, gray humus horizons with well-decomposed organic matter were observed under urban herbaceous vegetation (Apatity: SR, RZ-I, RZ-O). Such horizons are not typical for the natural Al-Fe-humic Podzols of the region. In other cases, anthropogenic peaty horizons were formed due to the introduction of peat mixtures (Murmansk: RZ, UR; Apatity: RZ-O). The carbon content in these peaty topsoil horizons reached 15 % and was primarily composed of partially decomposed peat, compost, and soil mixtures. These horizons were typically observed at sites where green infrastructure was recently created or renovated. In contrast, gray humus horizons had an average carbon content of 3–5 % and were mainly observed in older, unmanaged green spaces. In these areas, slow humification of plant biomass (roots and leaves) is the primary source of organic matter, although remnants of previously introduced organic substrates can also be found. The lowest carbon content (1–2 %) was observed in the most disturbed sites within residential and public areas, where organic horizons were poorly

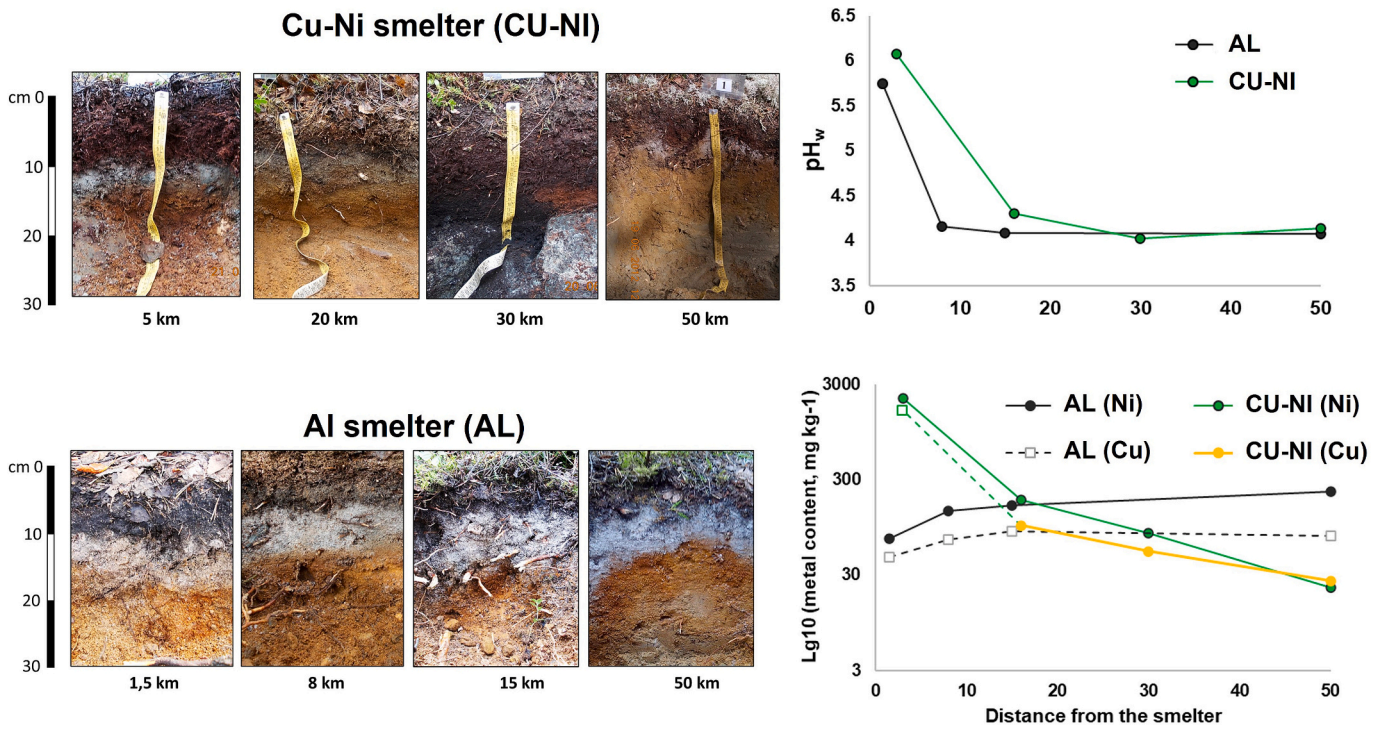

Fig. 2. Soil profiles at the industrial sites (measuring bar has 10 cm unit) and spatial patterns in pH_w and logarithm of Cu and Ni contents along the gradient from the smelters.

developed or absent. Soil pH_w in urban areas was significantly higher than in background areas (Fig. 3). Urban Technosols exhibited a neutral to slightly alkaline reaction (pH_w 7.0–7.8), which is typical for urban soils in various bioclimatic zones, including the Kola Arctic (Korneykova et al., 2021b, 2022). Heavy metal concentrations in urban soils exceeded background values but were significantly lower than those found in industrial areas (Table 5S).

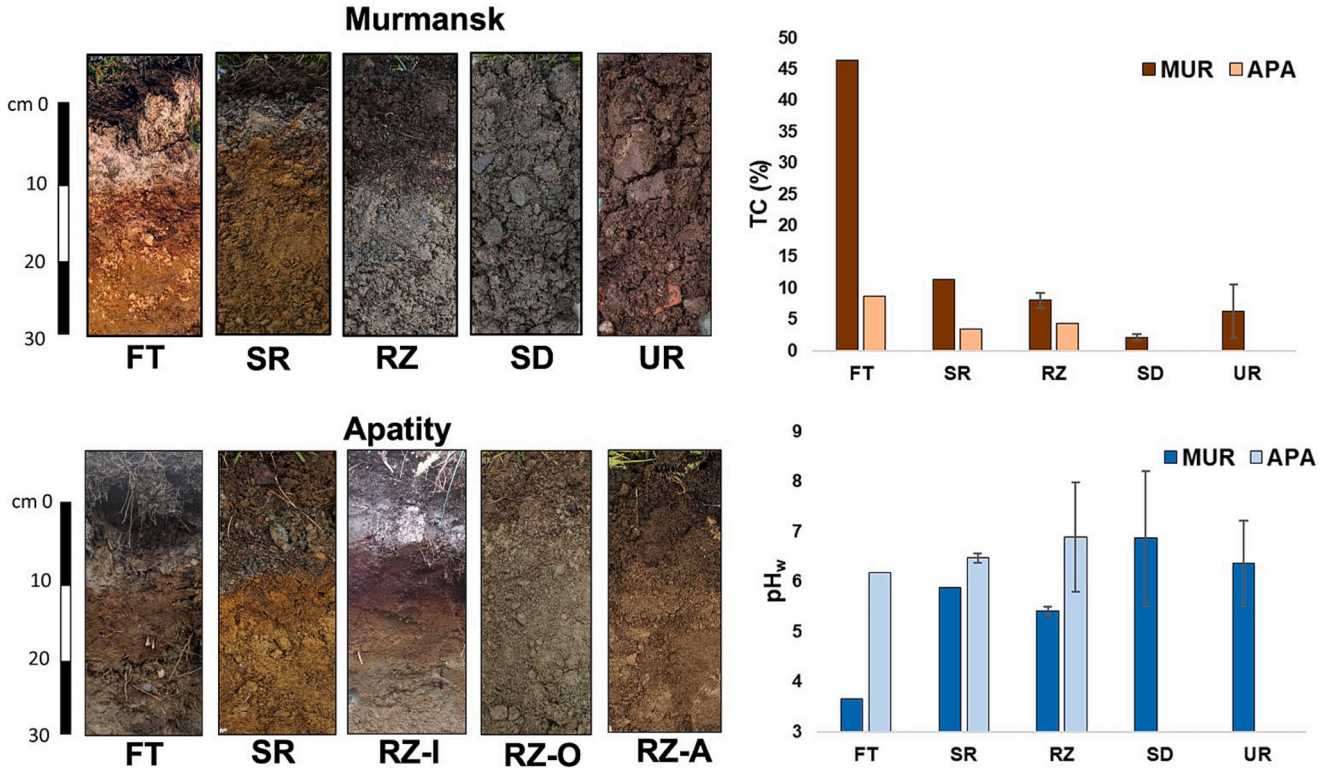

Fig. 3. Soil profiles at the urban sites (measuring bar has 10 cm unit) and average (mean ± sd) total C content and pH_w in soils of different functional zones (see Table 2 for abbreviations, data for the RZ-I site is used to represent RZ zone of Apatity on the graphs).

3.2. Number of microorganism gene copies

3.2.1. Industrially polluted soils

Industrial emissions significantly altered the structure of soil microbial communities compared to background soils. In soils near CU-NI, at distances less than 16 km, the microbial community was dominated by bacteria and archaea, each comprising approximately 40 % of the community, with fungi representing only 7 %. At more remote sites (≥16 km from CU-NI), bacteria accounted for 80 % of the microbial community, similar to the background soil. In the vicinity of AL, the most pronounced changes in community structure were observed at 1.5 km from the emission source. Here, fungal gene copies comprised 30 % of the microbial community, archaea accounted for 20 %, and bacteria made up 50 % (Fig. 4 A, B). This site also exhibited the highest number of archaeal (2.2×10^{10}) and fungal (3×10^{10}) gene copies, with values comparable to background levels (1×10^{10} and 1.3×10^{10}, respectively). However, bacterial gene copy numbers were lowest at this location, with 4×10^{10} copies compared 7×10^{10} in the background soil (Table 3). At distances of 16 km or greater from CU-NI, a significant increase of bacterial gene abundance was observed ($p < 0.01$, Cohen's $d = -4$ to -32). Even greater differences were found for archaea ($p < 0.001$, $d = -8$ to -31) and fungi ($p < 0.05$, $d = -3$ to -11), which were 3–10 times more abundant than background levels at these distances.

3.2.2. Urban soil

Bacteria dominated the microbial communities in both urban and background soils. In urban soils, bacteria represented 70–85 % of the total microbial community (Fig. 4 C, D), with an average number of 4×10^{10} gene copies per gram of soil, reaching 10^{11} gene copies in some instances. Fungal gene copies accounted for less than 10 % of the microbial community, with an average number of 2×10^{9} and a maximum of 9×10^{9} gene copies per gram of soil in Apatity (Table 4). Interestingly, the proportion of fungi was higher in background soils compared to urban soils. In the background soil near Murmansk, archaea constituted 40 % of the microbial community, a pattern not observed in the background soil near Apatity. The microbial community structure in the Apatity background soil was more similar to that of urban soils. Overall, the number of bacterial, archaeal, and fungal gene copies was lower in Murmansk soils compared to Apatity soils, while the opposite pattern was observed in the corresponding background soils.

In the residential areas of Apatity, we observed a significant increase in the number of bacterial and fungal genes compared to the background soil ($p = 0.002$–0.0002, Cohen's $d = -3.6$ to -3.8). However, the

Table 3
Microorganisms ribosomal genes number of the industrial sites (aluminum and copper-nickel smelters emission areas).

Distance, km	Archaea, $*10^{10}$	Bacteria, $*10^{10}$	Fungi, $*10^{9}$
Kandalaksha aluminum smelter			
50	0.98 ± 0.04^{a}	6.59 ± 0.88^{a}	1.36 ± 0.21^{a}
15	0.42 ± 0.24^{a}	10.27 ± 2.60^{a}	0.49 ± 0.24^{a}
8	1.03 ± 0.18^{a}	7.39 ± 0.39^{a}	1.45 ± 0.04^{a}
1.5	2.19 ± 0.72^{a}	4.25 ± 1.72^{a}	3.09 ± 0.72^{a}
Copper nickel smelter			
50	0.32 ± 0.03^{a}	3.05 ± 0.2^{a}	0.50 ± 0.03^{a}
30	1.90 ± 0.1^{a}	7.20 ± 0.5^{b}	0.55 ± 0.05^{a}
16	10.8 ± 0.3^{b}	9.50 ± 0.02^{c}	1.48 ± 0.4^{b}
3	11.2 ± 1.2^{b}	12.00 ± 1.5^{d}	1.60 ± 0.3^{b}

Note: Data are presented as mean ± standard error. Different lowercase letters indicate significant differences in gene copy numbers between sampling distances for each gene and smelter, as determined by ANOVA or the Kruskal-Wallis test, where appropriate.

Table 4
Microorganisms ribosomal genes number of the urban sites (Murmansk and Apatity).

Site	Archaea,$*10^{10}$	Bacteria, $*10^{10}$	Fungi $*10^{9}$
Murmansk			
FT	3.1 ± 0.9^{a}	3.9 ± 0.8^{a}	5.90 ± 0.2^{a}
SR	1.83 ± 0.4^{ab}	6.96 ± 1.2^{b}	2.46 ± 1.0^{ab}
RZ	0.41 ± 0.08^{b}	2.92 ± 0.3^{a}	1.31 ± 0.3^{ab}
SD	0.22 ± 0.01^{b}	1.28 ± 0.07^{a}	0.42 ± 0.07^{b}
UR	0.86 ± 0.1^{b}	1.9 ± 0.01^{a}	0.94 ± 0.1^{b}
Apatity			
FT	0.35 ± 0.01^{a}	2.48 ± 0.2^{a}	2.86 ± 0.09^{a}
RZ-I	1.45 ± 0.8^{a}	10.00 ± 2.1^{b}	8.90 ± 1.3^{a}
SR	0.40 ± 0.02^{a}	1.73 ± 0.9^{a}	0.50 ± 0.08^{a}
RZ-O	0.67 ± 0.03^{a}	4.00 ± 1.1^{a}	0.84 ± 0.02^{a}
RZ-AR	1.20 ± 0.07^{a}	4.29 ± 0.8^{a}	2.00 ± 0.07^{a}

Note: Data are presented as mean ± standard error. Different lowercase letters indicate significant differences in gene copy numbers between functional zones within each city, as determined by ANOVA or the Kruskal-Wallis test, where appropriate.

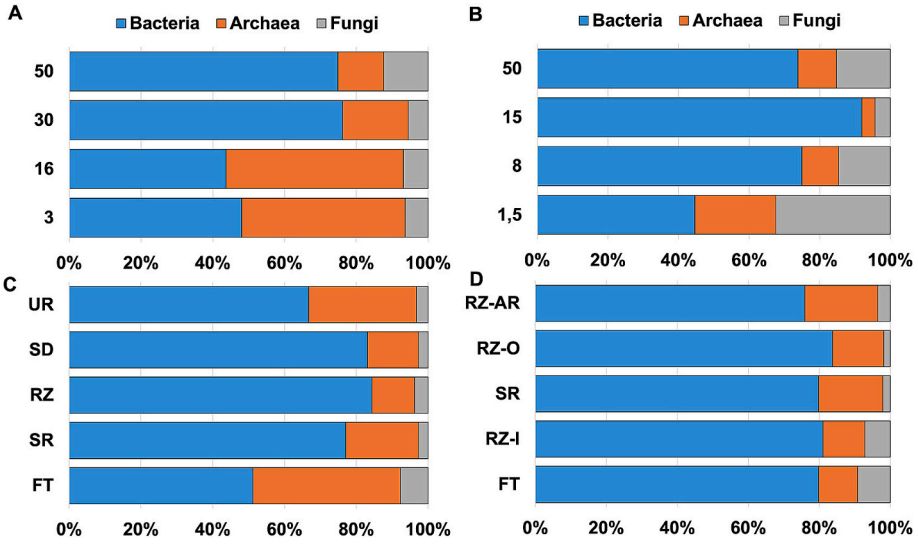

Fig. 4. The proportion of bacteria, archaea and fungi in industrially polluted soils – CU-NI (A), AL (B), in urban soils - Murmansk (C), Apatity (D).

number of archaeal genes did not differ significantly between residential areas and the background. A contrasting trend was observed in Murmansk. Here, urban soils exhibited a lower abundance of archaeal, bacterial, and fungal genes compared to the background soil ($p < 0.01$, $d = 2$–19). The exception to this pattern was the residential zone, where bacterial gene abundance was significantly higher than in the background soil ($p = 0.047$, $d = -1.6$). For both Murmansk and Apatity, the number of microorganism genes in recreational zone soils was closer to the values in background soils compared to residential zone soils.

3.3. Microbial biomass

3.3.1. Industrially polluted soils

Industrial emissions had varying effects on soil microbial biomass. Actinomycetes appeared to be the most sensitive to industrial pollution. In the impact zone of AL (1.5 km), the length of actinomycete mycelium increased to 31.2 m/g of soil, whereas in the background area (50 km) this parameter was 2 times lower (16.0 m/g). However, a statistically significant increase in mycelium length was only observed at 15 km from the AL smelter ($p = 0.003$, Cohen's $d = -4$). In contrast, at 3 km from CU-NI, a significant decrease in actinomycete mycelium length was observed (1.7 m/g) compared to the background value of 20.5 m/g ($p > 0.05$, $d = 2$). In the area impacted by CU-NI, fungal biomass was 4 times higher than at the background site ($p = 0.03$, $d = -6$). Emissions from the AL smelter did not have a pronounced effect on bacterial biomass, whereas emissions from the CU-NI smelter had a significant suppressive effect ($p = 0.02$–0.03, $d = 2.1$–2.3) (Table 5).

Industrial emissions also influenced the structure of fungal biomass. Near the emission sources, the proportion of spores increased relative to mycelium. In areas distant from AL, the proportion of mycelium ranged from 60 to 75 %, while at 8 km from the smelter, it decreased to 48 %, indicating a higher proportion of spores (Fig. 1S, A). Near CU-NI, the proportion of mycelium was 52 %, increasing to 70–85 % in more distant areas. The number of fungal spores varied from thousands to hundreds of thousands per gram of soil. Small spores (≤ 3 μm) dominated in almost all areas, comprising over 97 % of the total spore count. Large spores were absent near the CU-NI smelter but appeared at distances greater than 16 km. In contrast, near the AL smelter, the proportion of large spores increased, particularly at a distance of 8 km (Table 5).

We observed a significant shift in the structure of the prokaryotic community near AL. The proportion of actinomycete mycelium increased to 30 % in this area, compared to 5 % in more distant areas. Conversely, near CU-NI, actinomycetes dominated over unicellular prokaryotes, comprising 90–95 % of the prokaryotic community, whereas at the background site, they represented only 40 % (Fig. 1S, B).

3.3.2. Urban soils

The proportion of resting spores and mycelium in fungal biomass provides insights into the composition and functional role of the soil mycobiota. In the background soils, fungi were predominantly present as mycelium (70–80 % of total fungal biomass), while in urban soils, the proportion of spores increased (Fig. 2S). In Apatity, spores constituted up to 75 % of the fungal biomass, and in Murmansk, up to 65 %. The number of fungal spores ranged from thousands to hundreds of thousands per gram of soil (Table 6). Fungal spores were categorized as small (2–3 μm) or large (3–5 μm). Small spores were more abundant (10^4–10^5 cells/g soil), while large spores did not exceed 10^3 cells/g soil. Although large spores represented only 10–15 % of the total number of fungal propagules across all sites, their total mass exceeded that of the small spores. In Apatity, large spores were mainly found in the background soil, whereas in Murmansk, they were also present in urban soils. The proportion of thin mycelium (< 3 μm in diameter) was twice as high in urban soils (43 %) compared to background soils (26 %). The abundance of single-celled fungal propagules (spores and yeasts) in the studied soils ranged from 10^4 to 10^5 cells/g soil.

Unicellular forms dominated the prokaryotic biomass. However, in some urban soil samples, the proportion of actinomycete mycelium reached 30 %, while in background soils, it reached 40 %. Overall, the proportion of mycelial prokaryotes was lower in urban soils compared to background soils. The length of actinomycete mycelium in urban soils varied considerably. In Murmansk, it ranged from 9 to 30 m/g, significantly lower than the background average of 79 m/g ($p < 0.001$, Cohen's $d = 5$–11). In Apatity, the length of actinomycete mycelium was even lower, ranging from 1.7 to 19.4 m/g, compared to a background average of 34.5 m/g ($p < 0.05$, $d = 2$–5). Small nanoforms constituted the majority (up to 55 %) of prokaryotic cells in both urban and background soils (Table 6).

3.4. Taxonomic structure of soil microbial communities in Urban and industrially impacted soils

A total of 33 bacterial phyla were identified across all soil samples (Fig. 5). The dominant phyla were Proteobacteria (8.7–53.4 %), Acidobacteriota (11.6–26.7 %), and Actinobacteriota (5.56–21.4 %). A notable exception was observed in the contaminated soils near CU-NI, where Chloroflexi exhibited a high relative abundance of 48 %.

The relative abundance of Proteobacteria varied across cities and bioclimatic zones, without a consistent pattern. In Apatity, the relative abundance of Proteobacteria was similar in industrially polluted and background soils (53 % in both), but decreased to 33 % in urban soils. In Murmansk, however, Proteobacteria exhibited a declining trend across urban, background, and industrially polluted soils, with relative abundances of 38 %, 23 %, and 8 %, respectively. In contrast to the variable patterns observed for Proteobacteria, Actinobacteriota showed a clear

Table 5
Biomass structure of procaryotes and fungi of the industrial sites (aluminum and copper-nickel smelters emission areas).

Distance, km	Biomass, mg/g		Actinomycete mycelium length, m/g	Fungal mycelium biomass, mg/g, $\times 10^{-2}$	Number of spores (diameter, μ), units/g		
	Bacteria, $\times 10^{-3}$	Fungi, $\times 10^{-2}$			≤2, $\times 10^5$	2–3, $\times 10^4$	3–5, $\times 10^3$
Kandalaksha aluminum smelter							
50	3.1 ± 0.7^{a}	28.2 ± 6.2^{a}	15.9 ± 3.6^{ab}	16.9 ± 2.5^{ab}	1.38 ± 0.30	4.6 ± 1.0	2.1 ± 0.5
15	3.6 ± 0.8^{a}	31.4 ± 7.1^{a}	2.2 ± 0.5^{b}	23.6 ± 4.6^{b}	1.01 ± 0.23	2.4 ± 0.6	3.12 ± 0.05
8	2.3 ± 0.5^{a}	25.3 ± 6.3^{a}	13.9 ± 3.1^{ab}	12.3 ± 3.3^{ab}	1.04 ± 0.23	4.7 ± 1.0	8.3 ± 2.8
1.5	2.6 ± 0.6^{a}	39.5 ± 8.1^{a}	31.2 ± 6.9^{a}	26.2 ± 5.2^{a}	1.31 ± 0.27	5.3 ± 1.2	3.5 ± 1.2
Copper nickel smelter							
50	2.9 ± 0.9^{b}	12.2 ± 3.4^{a}	20.5 ± 8.8^{a}	8.4 ± 2.4^{a}	0.66 ± 0.05	5.7 ± 2.2	6.93 ± 1.25
30	1.8 ± 0.3^{ab}	57.4 ± 3.5^{b}	16.4 ± 7.5^{a}	43.5 ± 5.5^{a}	0.93 ± 0.06	3.8 ± 0.7	3.12 ± 0.43
16	0.5 ± 0.0^{a}	45.4 ± 9.5^{b}	22.6 ± 1.7^{a}	38.4 ± 3.8^{a}	1.34 ± 0.09	2.7 ± 0.2	0.87 ± 0.20
3	0.2 ± 0.0^{a}	39.7 ± 1.7^{b}	1.7 ± 0.3^{a}	20.9 ± 4.2^{a}	0.81 ± 0.01	2.4 ± 0.3	–

Note: Data are presented as mean ± standard error. Different lowercase letters indicate significant differences in the proportion of actinomycetes, unicellular prokaryotes, fungal spores, and mycelium between sampling distances for each smelter, as determined by ANOVA or the Kruskal-Wallis test, where appropriate.

Table 6
Biomass structure of prokaryotes and fungi of the urban sites (Murmansk and Apatity).

Site	Biomass, mg/g		Actinomycete mycelium length, m/g	Fungal mycelium biomass, mg/g,$\times10^{-2}$	Number of spores (diameter, μ), units/g		
	Bacteria, $\times10^{-3}$	Fungi, $\times10^{-2}$			≤2, $\times10^{5}$	2–3, $\times10^{4}$	3–5, $\times10^{3}$
Murmansk							
FT	8.53 ± 1.3^{a}	83.7 ± 9.8^{a}	79.00 ± 5.0^{a}	56.9 ± 4.5 ^{a}	1.27 ± 0.05	10.23 ± 1.3	7.57 ± 0.9
SR	2.3 ± 0.1^{ab}	63.9 ± 6.7^{ab}	16.63 ± 1.3^{bc}	53.9 ± 3.2 ^{b}	1.46 ± 0.03	9.76 ± 1.2	7.21 ± 0.9
RZ	1.5 ± 0.3^{b}	29.4 ± 5.3^{c}	9.28 ± 0.6^{c}	21.2 ± 1.8 ^{b}	0.69 ± 0.01	4.36 ± 1.1	10.4 ± 2.1
SD	2.1 ± 0.1^{ab}	20.8 ± 2.2^{c}	9.27 ± 0.3^{c}	14.1 ± 1.5 ^{b}	0.69 ± 0.02	2.75 ± 0.6	12.59 ± 3.2
UR	9.37 ± 0.1^{a}	41.1 ± 9.9^{ab}	30.67 ± 5.5^{ab}	16.4 ± 3.3 ^{ab}	1.40 ± 0.9	8.39 ± 1.2	5.76 ± 0.3
Apatity							
FT	3.7 ± 0.3^{a}	95.5 ± 9.9^{a}	34.52 ± 4.9^{a}	70.7 ± 5.0^{a}	1.36 ± 0.2	8.28 ± 1.3	9.81 ± 2.3
RZ-I	0.3 ± 0.04^{b}	12.1 ± 3.3^{b}	1.69 ± 0.8^{c}	3.3 ± 0.2^{b}	0.49 ± 0.05	0.97 ± 0.9	1.04 ± 0.3
SR	2.2 ± 0.9^{ab}	30.3 ± 4.2^{b}	19.40 ± 1.3^{b}	17.6 ± 2.3^{b}	1.13 ± 0.02	6.59 ± 0.02	4.16 ± 1.2
RZ-O	1.3 ± 0.7^{ab}	19.7 ± 2.5^{b}	15.81 ± 3.3^{bc}	12.6 ± 1.4^{b}	0.92 ± 0.02	3.78 ± 0.04	3.12 ± 0.8
RZ-AR	2.6 ± 0.5^{ab}	86.8 ± 8.5^{ab}	17.96 ± 3.9^{b}	6.41 ± 1.1^{b}	1.53 ± 0.01	9.97 ± 0.9	5.87 ± 0.02

Note: Data are presented as mean ± standard error. Different lowercase letters indicate significant differences in the proportion of actinomycetes, unicellular prokaryotes, fungal spores, and mycelium between functional zones within each city, as determined by ANOVA or the Kruskal-Wallis test, where appropriate.

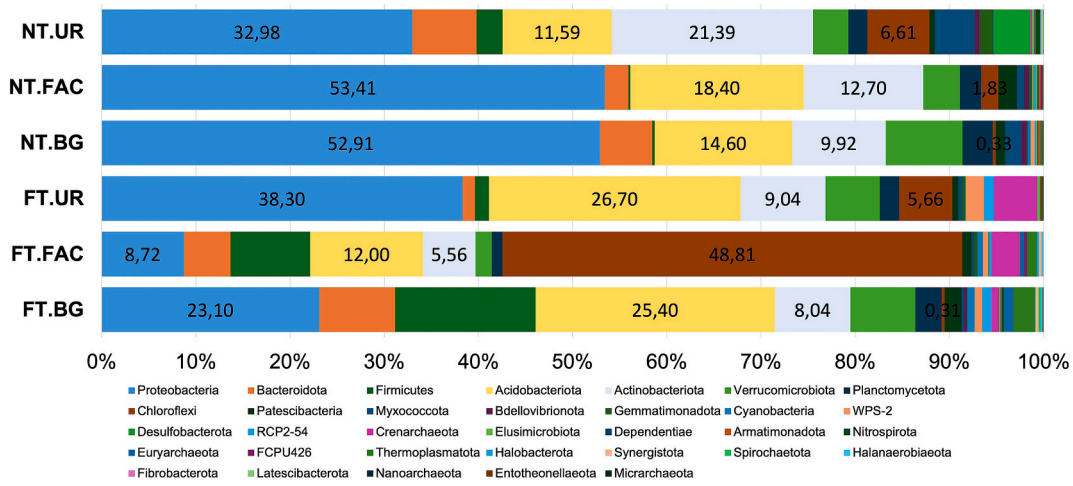

Fig. 5. Bacterial taxonomic structure of soil microbiome at a phylum level in urban (NT.UR – Apatity, FT.UR – Murmansk), industrially polluted (NT.FAC – AL, FT.FAC – CU-NI) and background soils (NT.BG, FT.BG).

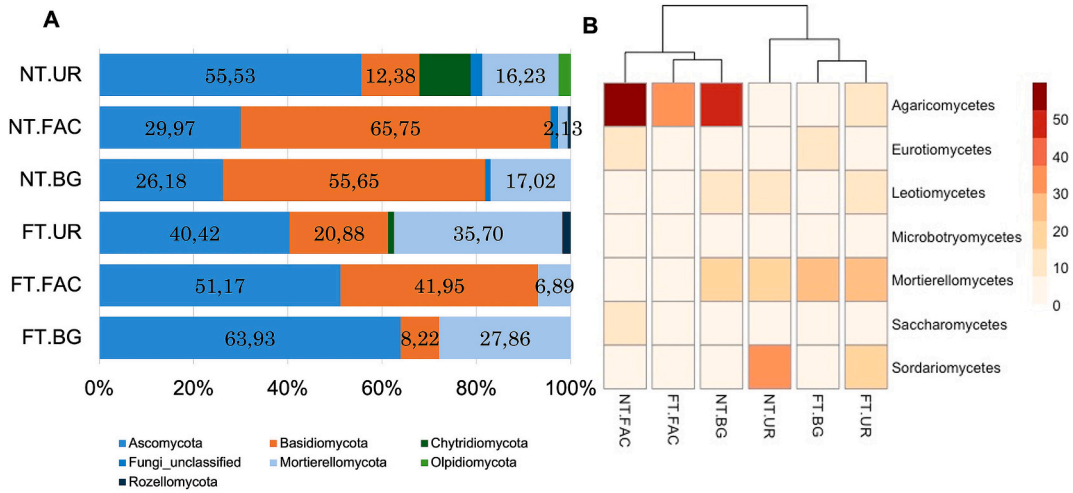

Fig. 6. Fungal taxonomic structure of soil microbiome at a phylum level (A) and distribution of the dominant fungal classes (B). Clustering analysis based on the computation of the pairwise Bray – Curtis dissimilarity matrix.
Urban soils (NT.UR – Apatity, FT.UR – Murmansk), industrially polluted soils (NT.FAC – AL, FT.FAC – CU-NI) and background soils (NT.BG, FT.BG).

trend, with its highest abundance in urban soils (9 % in Murmansk and 21 % in Apatity). Acidobacteriota exhibited a similar trend in Murmansk, with decreasing abundance from urban (27 %) to background (25 %) to industrially polluted soils (12 %). However, in Apatity, the abundance of Acidobacteriota decreased in the order of industrially polluted (18 %), background (14 %), and urban soils (12 %).

Across all sites, a total of 7 fungal phyla were detected, including unclassified fungi (Fig. 6A). The most abundant phyla were Ascomycota (26–64 %), Basidiomycota (8–65 %), and Mortierellomycota (2–35 %). The highest fungal diversity was observed in the urban soils of Apatity, where Chytridiomycota (11 %) and Olpidiomycota (2.5 %) were exclusively detected. In industrially polluted soils near both smelters, the relative abundance of Mortierellomycota decreased, while the abundance of Basidiomycota increased. The dominant fungal classes across all soil samples were Agaricomycetes (Basidiomycota), Mortierellomycetes (Mortierellomycota), and Sordariomycetes (Ascomycota) (Fig. 6B). Interestingly, Mortierellomycetes exhibited a distinct spatial pattern, being prevalent in urban and background soils, with abundance decreasing from north to south. However, this class was almost absent in soils near the industrial smelters. In contrast, Sordariomycetes were characteristic of urban soils, exhibiting high abundance. Agaricomycetes, although the most abundant class overall, were predominantly associated with contaminated soils near the smelters and background soils near Apatity.

Fungal communities were primarily composed of soil-dwelling taxa, with a slightly lower proportion of plant-associated fungi (Fig. 7A). Most identified taxa were saprotrophs, and their relative abundance was lowest near CU-NI. Urban soils exhibited the greatest diversity of fungal functional groups (8–11 groups), compared to industrially polluted soils (5–6 groups). Cluster analysis based on Euclidean distance revealed that the functional groups in contaminated soils near the CU-NI and AL smelters were most similar (Fig. 7B).

Venn diagram analysis revealed that 33–39 % of bacterial OTUs were shared across all samples, with the highest percentage of unique OTUs (20–25 %) found in the background soils (Fig. 8A, B). In contrast, only 6–7 % of fungal OTUs were shared among all samples, with the highest percentage of unique OTUs (35–38 %) occurring in the urban soils of both cities (Fig. 8C, D).

3.5. *Impact of ecosystem variables and chemical parameters on the abundance and composition of microbial communities*

To assess the influence of environmental factors on the variability in microbial community structure, we performed a multivariate analysis of variance (MANOVA). The type of anthropogenic impact significantly influenced the abundance of bacterial and fungal genes (explaining 34 % and 41 % of the variance, respectively), as well as the biomass of prokaryotes and actinomycetes (explaining 69 % and 35 % of the variance, respectively). Fungal biomass was more strongly influenced by ecosystem type (16 % of variance explained) than other factors. The type of anthropogenic disturbance (industrial vs. urban) was the primary driver of microbial community variability. In contrast, neither the bioclimatic zone (forest-tundra vs. northern taiga) nor vegetation cover had a significant effect on the measured microbial parameters (Fig. S3).

We used factor analysis to assess the influence of anthropogenic activities on the physicochemical and microbiological properties of the soil and to identify the main factors shaping microbial communities (Zhang et al., 2019; Gomez-Brandon et al., 2022; Cong et al., 2023). The Kaiser-Meyer-Olkin (KMO) criterion (0.68) confirmed the sampling adequacy for factor analysis, exceeding the recommended threshold of 0.5. The first two principal components explained 64 % of the total variance in the measured soil properties (Fig. 9A).

Principal component analysis was used to identify the main factors influencing the variability in soil physicochemical and microbiological properties. The first principal component (PC1) explained 39 % of the total variance and was associated with urbanization. This component correlated with total carbon, nitrogen, pH, and the abundance of bacterial and fungal genes and bacterial biomass. The second principal component (PC2) explained 25 % of the total variance and was associated with industrial pollution, correlating with the concentrations of potentially toxic elements (Co, Cu, Ni). Among the microbiological parameters, archaeal gene abundance was most strongly associated with this component. PCA identified three distinct clusters of sampling locations (Fig. 9B). Background soils occupied an intermediate position between urban and industrially impacted soils, which formed distinct and non-overlapping clusters. Urban soils exhibited lower variability in chemical and microbiological properties compared to industrially polluted soils, likely reflecting the more heterogeneous nature of industrial pollution. These results demonstrate that the type of

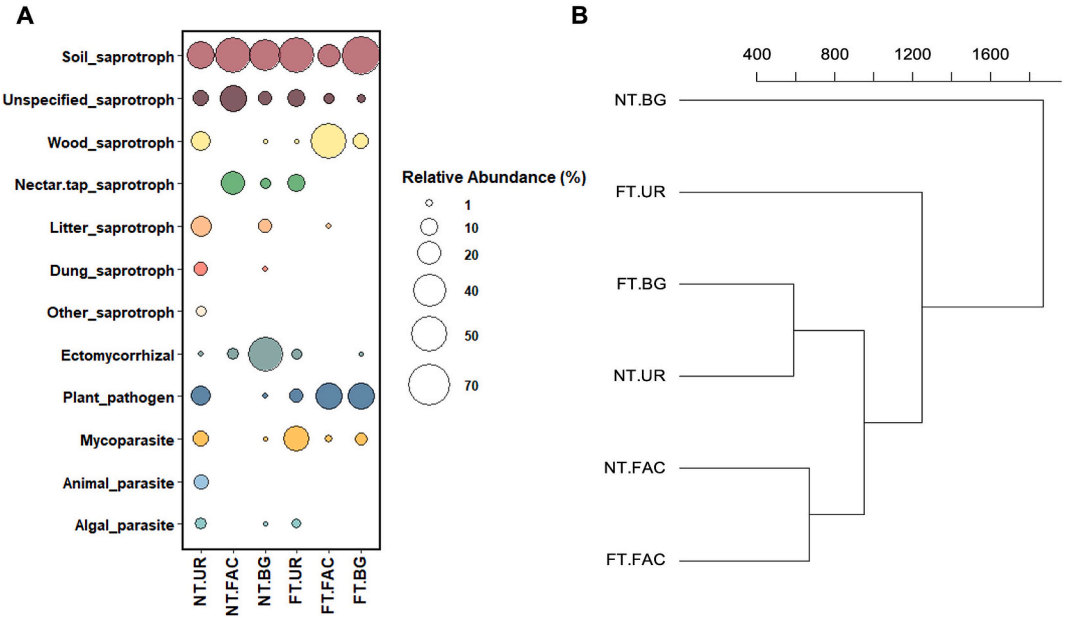

Fig. 7. Relative abundance of OTUs (%) assigned to the functional groups in the soil fungi (A) and cluster analysis (B) in urban (NT.UR – Apatity, FT.UR – Murmansk), industrially polluted (NT.FAC – AL, FT.FAC – CU-NI) and background soils (NT.BG, FT.BG).

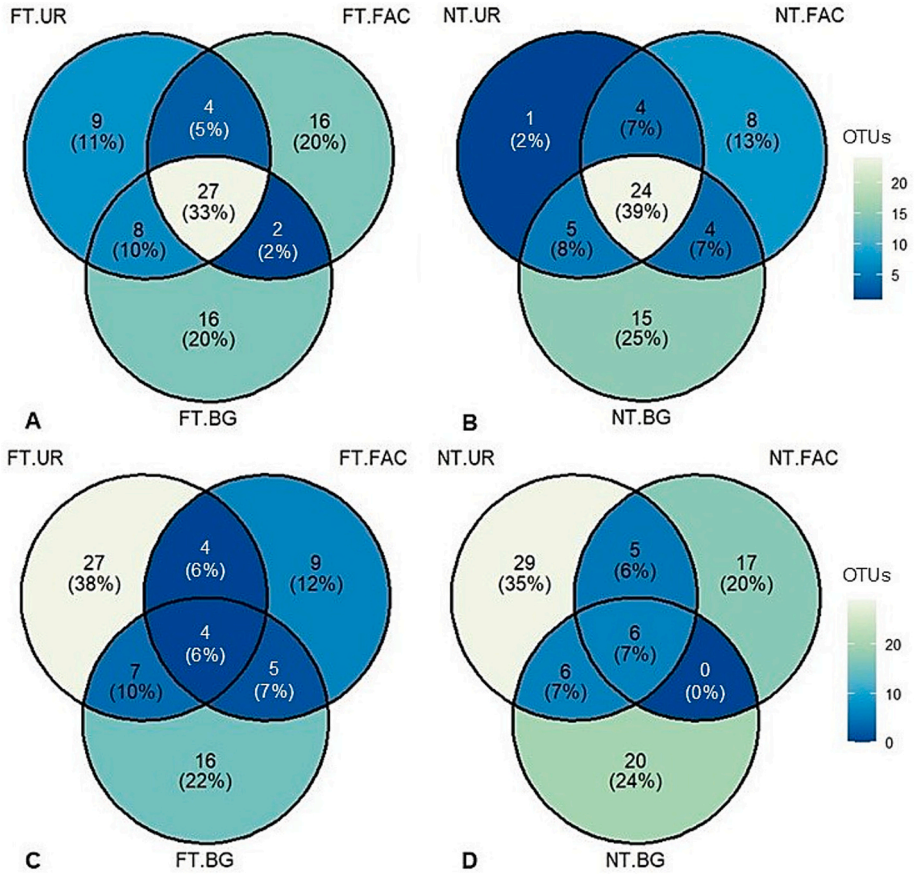

Fig. 8. Venn diagrams illustrating the number of unique and shared bacterial (AB) and fungal (CD) OTUs in urban (NT.UR – Apatity, FT.UR – Murmansk), industrially polluted (NT.FAC – AL, FT.FAC – CU-NI) and background soils (NT.BG, FT.BG).
FAC – AL, FT.FAC – CU-NI) and background soils (NT.BG, FT.BG).

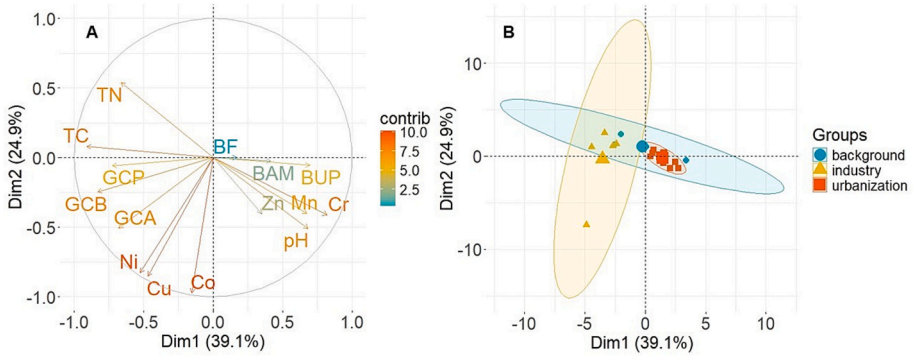

Fig. 9. Factor analysis using principal component analysis (PCA) (A) and individuals factor map (B). Note: GCB - genes copies of bacteria, GCA - genes copies of archaea, GCF - genes copies of fungi, BUP - biomass of unicellular prokaryotes, BAM - biomass of actinomycete mycelium, BF - biomass of fungi.

anthropogenic activity was a major driver of microbial community structure and function.

4. Discussion

4.1. The effect of industrial emissions on soil microbial properties

The impact of pollution on ecosystem stability is complex and can manifest in contrasting ways. Pristine, non-stressed ecosystems are considered more stable since surviving in polluted environments requires significant metabolic investment, reducing the resilience of organisms to additional stressors (Stone et al., 2001). Conversely, stressed ecosystems can develop tolerance to specific pollutants, enhancing their stability. This tolerance may be positively correlated with pollutant concentration, leading to increased resistance over time (Demoling and Bååth, 2008). Studies on microbial communities in metal-contaminated environments have revealed a range of responses, including: sensitivity (e.g. decrease in microbial biomass and enzyme activities, as well as shifts in microbial community composition); resistance or tolerance (minimal or negligible effects); resilience (initial impacts followed by adaptation and recovery to a new stable state in chronically polluted soils) (Rajeev et al., 2021; Wang et al., 2007). Soil microbial communities can be affected not only by direct metal pollution, but also by changes in edaphic parameters (Liu et al., 2012; Deng et al., 2015) and

vegetation cover (Thion et al., 2012; Bourceret et al., 2016). Jiang et al. (2020) showed that loss of biodiversity caused by heavy metals did not affect microbial functional stability, but soil organic matter and C/N were crucial factors governing microbial functional stability. Vegetation cover can shape microbial diversity by stimulating some microbial populations, plant root exudates could modify HM speciation, mobility, and availability in the rhizosphere (Wenzel, 2009). There is an effect of plants on soil microbial biomass and diversity because vegetal litter or residues bring complex organic matter into soils (Cébron et al., 2015) and also pose the question of selection or diversification of microorganisms.

Our findings demonstrate that industrial pollution significantly alters soil microbial communities in the Arctic. In industrially impacted soils, we observed a decrease in bacterial gene copy numbers, accompanied by a reduction in both taxonomic and functional diversity. While fungal gene abundance increased in these soils, fungal diversity (taxonomic and functional) was also diminished. These shifts in microbial community structure and function have important implications for ecosystem processes. Reduced microbial diversity can lead to decreased efficiency of nutrient cycling and organic matter decomposition, potentially affecting soil health, plant growth, and overall ecosystem stability. Furthermore, the altered microbial community composition in polluted soils may favor the spread of resistance genes through horizontal gene transfer. This could contribute to the emergence of resistant pathogens or disrupt the delicate balance within microbial ecosystems.

Emissions from CU-NI had a greater impact on the soil microbial community than those from AL. This was evident in the shifts in microbial community structure at both the group and taxon level. The higher toxicity of CU-NI emissions, which have a destructive effect on soil and vegetation, leading to the formation of industrial barrens, likely contributes to this difference (Kozlov and Zvereva, 2007; Slukovskaya et al., 2021). Interestingly, fungi appeared to be more resilient to industrial pollution than other microbial groups. This was evidenced by an increase in fungal biomass and gene abundance near both the AL and CU-NI smelters. This observation is consistent with previous studies demonstrating the higher tolerance of soil fungi to heavy metals compared to bacteria (Rajapaksha, 2011; Oyewole et al., 2019).

Emissions from the industrial plants significantly influenced the structure of both prokaryotic and fungal biomass. We observed a marked increase in the proportion of actinomycete mycelium and a corresponding decrease in the proportion of unicellular prokaryotes near both smelters. This pattern is consistent with previous studies demonstrating a shift towards filamentous growth forms in prokaryotes under environmental stress (Peciulyte and Dirginciute-Volodkiene, 2009; Cimermanova et al., 2021; Sun et al., 2023). In the fungal community, we observed an increased proportion of spores and a decreased proportion of mycelium along the pollution gradient, coupled with a reduction in the number of large fungal propagules. These changes suggest that industrial emissions induce stress in the fungal community (Korneykova et al., 2021b, 2023a). Interestingly, we also found an increase in archaeal gene abundance near both smelters. In the area impacted by CU-NI, archaea constituted 40 % of the microbial community at distances of 16 km or greater. This suggests that archaea, a relatively understudied group of soil microorganisms, may possess a remarkable ability to persist and function in anthropogenically disturbed soils, exhibiting significant adaptability to pollution stress (Li et al., 2017; Hemmat-Jou et al., 2018; Krzmarzick et al., 2018; Yang et al., 2022).

While the structure of fungal communities was similar between the two industrial sites, the composition of bacterial communities differed. Proteobacteria dominated near AL, while Chloroflexi were prevalent near CU-NI. The dominance of Proteobacteria near AL may reflect their metabolic versatility; these bacteria can utilize a wide range of organic substrates for carbon and energy (Bouskill et al., 2010), enabling them to thrive in diverse and challenging environments (Chejara et al., 2021). The prevalence of Chloroflexi near CU-NI is likely due to their inherent resistance to heavy metals, as documented in previous studies (Lopez et al., 2017).

In the fungal community, two phyla, Ascomycota and Basidiomycota, accounted for 93–95 % of the total abundance. The increased proportion of these taxa in contaminated soils aligns with observations from other studies in boreal forest ecosystems (Mikryukov et al., 2021). This shift may indicate a decline in soil health and quality (Semenov et al., 2022; Yang et al., 2023). Furthermore, we observed a suppression of the Mortierellomycota phylum near both smelters, consistent with our previous findings (Korneykova and Nikitin, 2021) and those of other researchers (Nordgren et al., 1983; Torres-Cruz et al., 2018; Guo et al., 2023). The high abundance of Agaricomycetes near both the CU-NI and AL smelters may be attributed to their enhanced ability to tolerate and mitigate the effects of heavy metals (Robinson et al., 2021).

4.2. *The effect of urbanization on soil microbial properties*

Urban ecosystems are shaped by a complex interplay of environmental factors and human activities, resulting in highly heterogeneous soils. The structure of soil microbial communities was mainly influenced by soil pH, nitrogen availability, organic carbon content, temperature, and redox status (Cederlund et al., 2014). However, urban environments also introduce unique factors such as land-use history, management of urban green infrastructure, grass cover density, and plant litter thickness, all of which contribute to soil heterogeneity. This inherent diversity and spatial variability, coupled with varying levels of anthropogenic impact, can make it challenging to distinguish urban soils from natural soils based solely on parameters such as taxonomic and functional diversity and microbial biomass (Korneykova et al., 2023a, 2023b). The predominance of bacterial gene copies in the microbial community is a common feature of anthropogenically disturbed soils, as evidenced by our findings and previous studies (Korneykova et al., 2021a, 2021b, 2022; Korneykova and Nikitin, 2021). This bacterial dominance is also characteristic of other Arctic regions (Nikitin et al., 2022). Archaeal gene number was an order of magnitude lower than that of bacteria, likely reflecting the more specialized and restricted ecological niches typically occupied by archaea (Baker et al., 2020). Fungi represented a minor component of the soil microbiome in our study, consistent with observations in other polar regions (Korneykova et al., 2021a, 2021b, 2022, 2023a).

The number of all microbial groups in the urban and industrial soils of our study exceeded that found in previous Arctic studies (Korneykova et al., 2021a; Korneykova et al., 2023a; Nikitin et al., 2022). This suggests that urban and industrial environments may support higher microbial abundance than more pristine Arctic regions, and that microbial abundance generally decreases with increasing latitude. However, fungi were an exception to this pattern. The abundance of fungal genes in our study was an order of magnitude lower than that reported for the Franz Josef Land archipelago (Nikitin and Semenov, 2022). This finding supports the hypothesis that fungi may play an increasingly important role in ecosystems experiencing more extreme climatic conditions (Cox et al., 2016).

Interestingly, we observed a contrasting pattern in microbial abundance between the two cities. In Murmansk, the abundance of all microbial groups was lower in urban soils compared to the more southern city of Apatity. This observation aligns with the general trend of decreasing microbial abundance with increasing latitude, a pattern often observed in natural ecosystems (Dobrovolskaya et al., 2015; Cox et al., 2016). However, in the background soils, the abundance of microbial genes was higher in Murmansk than in Apatity. This difference may be attributed to the characteristics of the Murmansk background soil, which had higher carbon content and lower pHw, as well as potentially lower levels of industrial pollution in the Murmansk area compared to Apatity (Evdokimova et al., 2013). In Apatity, we observed a significant increase in the abundance of microbial genes in urban soils compared to the background soil. This likely reflects the greater diversity of ecological niches available in urban environments due to the variety of

substrates and land uses (Fu et al., 2022; Korneykova et al., 2022). However, in Murmansk, the abundance of microbial genes was lower in urban soils compared to the background. This contrasting pattern may be attributed to the higher number of industrial enterprises and differences in vegetation cover in Apatity compared to Murmansk. Both pollution and vegetation are key factors influencing microbial communities in urban soils (Menefee and Hettiarachchi, 2017; Saltan et al., 2020).

Anthropogenic impacts extend beyond quantitative changes in microbial communities, affecting the morphology of soil microorganisms as well. Mycelium, the primary component of fungal biomass, is a key indicator of fungal viability and overall health (Polyanskaya et al., 2012, 2020; Dobrovolskaya et al., 2015). In our study, the proportion of mycelium in Apatity soils did not exceed 25 %, and in Murmansk soils, it reached only 35 %, suggesting significant stress on the fungal community (Nikitin et al., 2020). Fungi in urban soils were predominantly present as spores, further supporting this conclusion. The dominance of small spores, thin mycelium, and the near absence of large propagules across all urban sites provide additional evidence of stress in the fungal community (Nikitin et al., 2020; Korneykova et al., 2021a). Although large spores were occasionally observed in urban soils, suggesting the presence of localized favorable microsites for fungal development (Polyanskaya et al., 2012), their overall scarcity highlights the challenges faced by fungi in these environments.

In the prokaryotic community, the proportion of actinomycete mycelium was higher in background soils compared to urban soils, indicating the sensitivity of this group to urban pollution (Cimermanova et al., 2021). Furthermore, the high proportion of small, unicellular bacteria in urban soils suggests a high level of stress in the prokaryotic community (Lysak and Lapygina, 2018). Urban soils exhibited increased bacterial taxonomic diversity, the development of unique fungal communities, and an expansion of functional diversity. These findings are consistent with previous research highlighting the potential for urban environments to promote microbial diversity (Zhao et al., 2013; Whitehead et al., 2022; Scholier et al., 2023). This enhanced microbial diversity in urban soils has important implications for ecosystem resilience. Increased taxonomic and functional diversity leads to functional redundancy, where multiple species can perform similar ecological roles. This redundancy buffers against disturbances and enhances resistance to pollutants (Griffiths and Philippot, 2013). Furthermore, higher diversity increases the likelihood of species survival and recolonization after disturbances, promoting the restoration of key ecosystem functions such as nutrient cycling and organic matter decomposition. Diverse microbial communities also possess greater potential for adaptation and evolutionary responses to fluctuating environmental conditions. This continuous selection for stress-tolerant microbes enhances the resilience of urban ecosystems.

The bacterial community in the background soils was dominated by Proteobacteria and Acidobacteriota. These phyla, along with Actinobacteriota, are also typical for urban soils across various bioclimatic zones (Gomez-Brandon et al., 2022; Sazykina et al., 2022). The bacterial communities in the urban soils of both Murmansk and Apatity exhibited a similar structure in terms of the dominant phyla. The fungal community was dominated by three phyla, with a notable increase in the relative abundance of Mortierellomycota in urban soils. This observation aligns with previous research highlighting the prevalence of Mortierellomycetes in urban environments (Crous et al., 2021; Whitehead et al., 2022). *Mortierella* species are globally distributed and play a vital role in the ecology of urban green spaces, often serving as indicators of soil health and ecosystem function (Delgado-Baquerizo et al., 2021; Zhang et al., 2021).

4.3. Contrasting effects of urbanization and industrial activity

Urbanization and industrial activity exerted distinct and often contrasting effects on soil microbial communities. Opposite trends were observed for many parameters, highlighting the specificity of each type of anthropogenic impact. For instance, near industrial enterprises, we observed an increase in the relative abundance and gene copy number of archaea, as well as an increase in the proportion of actinomycetes within the microbial community. Conversely, in urban soils, these microbial groups were suppressed. Fungi displayed resilience to industrial emissions, as evidenced by increased abundance near the smelters; however, the taxonomic and functional diversity of fungal communities declined. Bacteria were suppressed near industrial facilities, showing a decrease in gene copy number and taxonomic and functional diversity. In urban soils, conversely, bacteria thrived, exhibiting increased taxonomic and functional diversity. In cities, an increase in the taxonomic and functional diversity of all microbial groups was also observed, likely due to the presence of additional niches for their development.

The taxonomic composition of microbial communities differed significantly between urban and industrially contaminated soils. Urban soils exhibited a typical bacterial community structure for various bioclimatic zones, with Proteobacteria, Actinobacteriota, and Acidobacteriota as the dominant phyla (Li et al., 2022, 2023; Lin et al., 2022; Ma et al., 2022). In Apatity, Proteobacteria show similar abundance in industrially polluted and background soils but a decrease in urban soils. This trend suggests that Proteobacteria in Apatity can adapt to certain industrial pollutants, possibly using them as energy sources due to their metabolic versatility. In contrast, urban soils may introduce stressors like urban-specific contaminants or physical disturbances, creating less favorable conditions for Proteobacteria. In Murmansk, Proteobacteria abundance declines progressively from urban to background to industrially polluted soils. This suggests that industrial pollutants in Murmansk are likely more toxic or disruptive to Proteobacteria populations than those in Apatity. Members of the phylum Acidobacteria are abundant and widespread across soils but are considered oligotrophic bacteria, thriving in low-nutrient environments. Observed differences suggest that Acidobacteriota respond to pollution and environmental stressors based on local soil chemistry, pollution types, and other factors, which vary between Murmansk and Apatity. Their tolerance for pollution in Apatity compared to Murmansk may be due to specific pollution characteristics that impact Acidobacteriota differently in each location.

Soils contaminated by the copper-nickel smelter displayed a striking shift in bacterial community composition, with Chloroflexi comprising 49 % of the total abundance. This dominance of Chloroflexi is likely attributable to their remarkable resistance to heavy metals, particularly copper. Recent research has highlighted the influence of copper contamination on the abundance of metal resistance genes (MRGs) in soil bacteria (Li et al., 2022), with Chloroflexi emerging as a key phylum harboring these genes. This is likely due to their high tolerance to metal stress and their ability to thrive in low-nutrient conditions, which are characteristic of contaminated soils. Furthermore, Chloroflexi may actively contribute to metal detoxification processes (Liu et al., 2021), further explaining their prevalence in these impacted environments. This pattern is consistent with the broader observation that metal-tolerant bacteria, such as Chloroflexi, tend to dominate in heavily polluted areas as more sensitive species decline (Zhao et al., 2019).

The observed increase in Actinobacteriota abundance in urban soils may provide functional advantages to these ecosystems. Many Actinobacteria produce carotenoid pigments, which enhance their resistance to harsh environmental conditions, including cold stress, enabling them to thrive in extreme environments (Fong et al., 2001). This may explain their prevalence in the urban soils of Murmansk and Apatity, which experience long winters and significant temperature fluctuations. Moreover, Actinobacteria are known for their ability to degrade hydrocarbons, pesticides, and aromatic compounds, contributing to environmental detoxification by removing various pollutants (Galiulin et al., 2010).

The fungal community was dominated by three phyla: Ascomycota, Basidiomycota, and Mortierellomycota. Ascomycota and Basidiomycota

are recognized as key components of microbial communities in metal (loid)-contaminated soils (Li et al., 2023). Microorganisms can absorb bioavailable fractions of heavy metals and metalloids, influencing microbial community structure and function (Zhen et al., 2019). The effects of these heavy metal ions on microbial biochemistry and metabolism can be complex, ranging from beneficial to harmful depending on their concentration and the specific metals involved.

In our study, the proportion of filamentous fungi (Basidiomycota) increased significantly in industrially contaminated soils, reaching 42 % in Murmansk and 66 % in Apatity. This increase suggests that Basidiomycota, along with Ascomycota, play a crucial role in the adaptation and function of microbial communities in metal(loid)-contaminated environments (Chen et al., 2012, 2014). Principal component analysis revealed distinct patterns in microbial community structure between urban and industrially impacted soils. Industrially contaminated soils exhibited greater variability in chemical and microbiological parameters compared to urban soils, while background soils occupied an intermediate position between these two groups. Bacterial communities were more homogeneous in composition across all studied areas, with 30–35 % of OTUs shared among all samples. This suggests that bacterial communities are less sensitive to anthropogenic disturbance and the specific type of impact. In contrast, fungal communities were more sensitive, with only 6–7 % of OTUs shared among all samples. Urban soils harbored the most distinct and diverse fungal communities, exhibiting lower similarity to both background and industrially impacted soils.

4.4. Study limitations

Spatial and temporal variability of soil microbiological parameters presents challenges in drawing definitive conclusions from the data. The inherent heterogeneity of soil microbiological properties may obscure broader patterns of pollution impact. Sampling along a gradient of pollution from industrial plants in various directions from the emission source could help capture the spatial heterogeneity more effectively, accounting for factors like wind patterns, vegetation cover, and soil characteristics. Furthermore, the study was limited by the lack of consideration of annual and seasonal dynamics. Investigating microbial properties across different timeframes would provide a deeper understanding of how microbial communities respond to varying types and intensities of anthropogenic stressors. Future studies should aim to incorporate this temporal aspect to better grasp the complex functioning of soil microbial communities under long-term industrial pollution. Conducting studies at a limited number of sites (2 industrial and 2 urban) is also a study limitation. There are other industrial plants and urban sites in the study area, however we focused on the largest cities and the most impactful industrial enterprises.

5. Conclusion

This study demonstrates the sensitivity of Arctic soil microbial communities to anthropogenic pressures associated with urban and industrial development. While both urbanization and industrial activities alter the structure and functioning of soil microbial communities, they do so in distinct ways, with varying consequences for soil health. Industrial emissions suppress microbial abundance and reduce the taxonomic and functional diversity of soil microbial communities. The severity of the impacts varied depending on the source and the specific chemical composition of the emissions. Near the copper-nickel smelter, significant detrimental effects on microbial biomass and community structure were observed within 16 km of the emission source. Similarly, negative impacts were observed within 1.5 km of the aluminum smelter.

The effect of urbanization on the soil microbiome is more complex. In polluted and disturbed urban sites, the proliferation of opportunistic or pathogenic species can pose risks to urban vegetation and human health. However, in the constructed soils of urban green infrastructure, we observed an increase in the abundance of bacterial genes, including those involved in key metabolic pathways. This enrichment has the potential to improve nutrient cycling, organic matter decomposition, and the degradation of pollutants. Urban soils also exhibited increased taxonomic and functional diversity of microbial communities, likely contributing to their adaptability to anthropogenic stressors and environmental changes. However, this increased diversity and functional capacity could also lead to unintended consequences. Shifts in dominant microbial pathways could alter nutrient cycling, potentially increasing greenhouse gas emissions or causing nutrient imbalances.

While this study did not fully elucidate the roles of specific functional groups and keystone species within the various niches of these anthropogenic landscapes, our findings demonstrate that land-use change has a greater impact on soil microbial communities than bioclimatic conditions. Specifically, the shift from natural ecosystems to either urban or industrial land use had a more pronounced effect on microbial community structure and function than the differences between the forest-tundra and northern taiga zones. This finding has important implications for land-use planning in the Arctic. As urban and industrial development continue to expand in the region, understanding the consequences of these land-use changes for soil microbial communities is crucial for sustainable land management. By considering the impacts on soil microbes, we can develop strategies to mitigate negative effects and promote the ecological functions that support healthy and resilient Arctic ecosystems.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Korneykova Maria reports financial support was provided by RUDN University. Korneykova Maria reports a relationship with RUDN University that includes: employment. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geodrs.2024.e00890.

Data availability

No data was used for the research described in the article.

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