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First data on total and carbon cycling microbial diversity of the key reference soils of the "Ladoga" carbon measurement supersite

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Abstract

The "Ladoga" carbon supersite is part of the All-Russian carbon monitoring national system, it is located in the Boreal coniferous forest zone, and work is underway here to implement measures to control the emission of greenhouse gases. This study reports data on the total and carbon-associated diversity of the soil microbes of reference soils. We obtained 729 amplicon sequence variants from 35 soil samples. Total diversity is represented by 11 phyla of bacteria and 1 phylum of methanogenic archaea (for Histosol). Carbon-cycling bacteria diversity is represented by six phyla (*Actinobacteriota*; *Proteobacteria*; *Acidobacteriota*; *Bacteroiodota*; *Firmicutes*; and *Verrucomicrobiota*). The dominant carbon-cycling bacteria in the studied soils are *Actinobacteriota* and *Proteobacteria*. The analysis of α- and β-diversity allowed us to identify three clusters of microbiota different in taxonomic composition — these are topsoil of Podzol and subsoil of Podzol (statistically significant ($p < 0.05$) differences in abundance for *Proteobacteria* and *Verrucomicrobiota* were revealed). Histosol is distinguished in a separate cluster of microbial diversity; it differs from Podzol in the abundance of carbon-cycling bacteria by *Proteobacteria* and *Bacteroiodota* ($p < 0.0001$). Further studies of the soil microbiome of the "Ladoga" carbon supersite should be focused on the study of functionally specialized groups of carbon and nitrogen cycle microbes and their ecosystem functions.

Keywords: carbon supersite, soil microbiota, 16S rDNA amplicon sequencing, high-throughput sequencing, Podzol, Histosol.

Introduction

Soil microorganisms play an important role in the global biosphere-atmosphere carbon cycle (Naylor et al., 2020; Vasar et al., 2022; Wu et al., 2024). Bacteria play a major role in the decomposition of organic matter of mortmass from dead plants, animals, and fungi (Barbato et al., 2022; Baldrian, López-Mondéjar, and Kohout, 2023; Wu et al., 2024). Various phyla of the soil core microbiota are involved in the processes of carbon transformation in terrestrial ecosystems (Morten Dencker et al., 2019; Varsadiya, Urich, Hugelius, and Bárta, 2021; Xue et al., 2023; Wu et al., 2024). Currently, several important phyla are identified as responsible for organic matter recycling processes: *Actinobacteriota, Proteobacteria, Cyanobacteria, Acidobacteriota, Myxococcota, Bacteroiodota, Firmicutes, Verrucomicrobiota, Bdellovibrionota* (Xue et al., 2023). These bacterial phyla are divided into functional groups based on their metabolic processes in nutrient

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transformation differences that may influence soil organic carbon (SOC) storage and soil organic matter transformation processes (Jeewani et al., 2020; Naylor et al., 2020; Fu et al., 2022). It is crucial to understand the performance of the carbon cycle at the micro-level in the context of global climate change (Schimel and Schaeffer, 2012; Domeignoz-Horta et al., 2020; Naylor et al., 2020). In Russia, a network of carbon measurement supersites (hereinafter "carbon supersite") has been organized to study climate-related processes of carbon cycle transformation in terrestrial and aquatic ecosystems. Carbon supersites will cover all climatic and ecological zones on the territory of Russia and will conduct (and are already conducting) research aimed at fundamental and applied tasks necessary to combat climate change on the planet (Abakumov, Polyakov, and Chukov, 2022). Studies of soil microbiota at carbon supersites have so far not received enough attention. Therefore, the purpose of this work is to obtain the first data on the taxonomic composition of the microbiome of reference soils of the "Ladoga" carbon supersite (Leningrad region). In addition, using statistical and bioinformatics methods, we aim to assess the α- and β-diversity of soil microorganisms and to detect the abundance of important phyla as responsible for soil organic carbon cycling processes.

Materials and methods

Soil survey and main study area settings

The area of the "Ladoga carbon" supersite is located in the Leningrad Region (Fig. 1), Voeikovo settlement (59.948001N, 30.717330E). The territory belongs to the Boreal coniferous (southern taiga) forest zone (FAO, 2012) with a Warm-summer Humid Continental (Dfb) Climate (Peel, Finlayson, and McMahon, 2007). An average annual temperature is +5.6 °C and an average annual precipitation is 707 mm (Suleymanov et al., 2023). The relief is composed of fluvioglacial sediments of the Valdai glaciation and is represented by Esker and Kame formations (Makarova et al., 2023). Dominant vegetation types in projective cover are: *Pinus sylvestris*, *Vaccínium myrtíllus*, *Vaccíniumvítis-idaéa*, *Athyrium filix-femina* — at high elevation; *Betula pendula*, *Calamagrostis arun-dinacea*, *Sphagnum platyphyllum*, *Vaccíniumvítis-idaéa* — at peatlands (Makarova et al.,

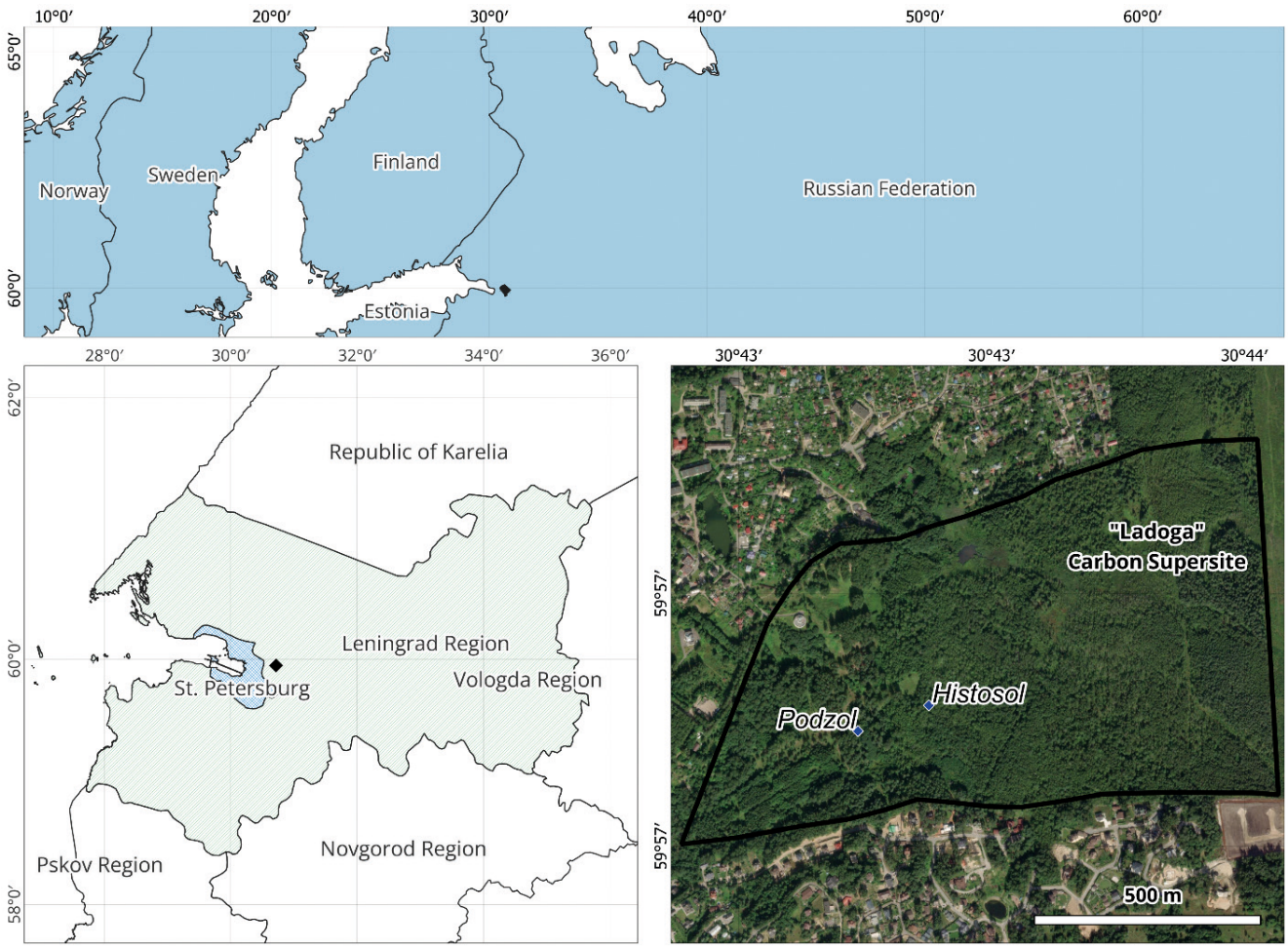


Fig. 1. Location of the "Ladoga" carbon measurement supersite on a global (black markers) and regional scale. Blue markers indicate the sampling locations for the corresponding soils.

2023; Suleymanov et al., 2023). The dominant soils (according to WRB (2022) classification) are Entic Podzols, Folic Podzols, Hortic/Plaggic Podzols (on the territory of old fields) and different types of Histosols (Fibric, Hemic, Sapric) (Makarova et al., 2023; Polyakov et al., 2023; Suleymanov et al., 2023). Samples for microbiological analysis were collected from the two most common soils in the area (without obvious anthropogenic impact) — Folic Podzol (Oi-Oe (0–2 cm) — AhE (2–13 cm) — Bs (13–34 cm) — BC/C (34–100 cm)) and Fibric Histosol (He (0–50 cm) — Ha (50–… cm)). The chemical properties of these soils are described in details in (Makarova et al., 2023; Polyakov et al., 2023; Suleymanov et al., 2023). Basic chemical properties: Folic Podzol — pH_{water} 5.6 — 6.0, SOC — 7.5 % in Oi-Oe horizon; 3.3 % — in AhE horizon; in deeper horizons 0.6 — 0.2 %. Fibric Histosol — pH_{water} 4.7 — 5.3 in He horizon; 3.7 — 4.1 in Ha horizon; SOC — 38–47 % in profile (Polyakov et al., 2023; Abakumov et al., 2024). Samples for microbiological analysis were taken from each soil horizon. After sampling, all soil samples were transported at +4 °C and stored at –20 °C.

DNA Extraction

The total soil DNA was extracted by using the protocol described in (Pinaev et al., 2022). Quality control was carried out by PCR and agarose gel electrophoresis. The sequencing of the V4 variable region of the 16S rRNA gene was performed on the Illumina MiSEQ sequencer (Illumina, San Diego, CA, USA) at the Centre for Genomic Technologies, Proteomics and Cell Biology (ARRIAM, Russia), using the primers 515f (GTGCCAGCMGCCGCGGTAA) and 806r (GGACTACVSGGGTATCTAAT) (Caporaso et al., 2011).

Bioinformatics analysis

The general processing of sequences was carried out in R 4.0 (R Core Team, 2013), using dada2 (v. 1.28.0) (Callahan et al., 2016) and phyloseq (v. 1.44.0) (McMurdie and Holmes, 2013) packages, according to the author's choice of working pipeline. The 16S rDNA amplicon sequences were processed according to the dada2 pipeline. Sequences were trimmed by length (minimum 280 bp for forward and 210 bp for reverse reads) and quality (absence of N, maximum error rates maxEE were 2 for both forward and reverse reads). Amplicon sequences variants (ASVs) were determined according to the dada2 algorithm, and chimeric ASVs were removed by the "consensus" method. The taxonomic annotation was performed by the naive Bayesian classifier (provided in the dada2 package, default settings), with the SILVA 138 database (Quast et al., 2012) used as the training set; phyla names were corrected according to LPSN (Parte et al., 2020). The α–diversity (observed ASV and Simpson indices) and β-diversity (Bray — Curtis distance) metrics were calculated using "phyloseq" and "vegan" (Oksanen et al., 2018) packages. The NMDS ordination of Bray — Curtis distances were drawn using the "phyloseq" package. The PERMANOVA analysis was carried out using the "vegan" package.

Results and discussion

After the bioinformatic processing was completed, 729 ASVs from 35 samples were obtained. The minimum read count per library was 1244, maximum 12787, mean — 3444. After rarefaction for α-diversity analysis depth of sequencing was 1244 sequences per sample.

Major phyla observed were *Proteobacteria*, *Actinobacteria*, and *Bacteroidetes* followed by *Acidobacteria*, *Verrucomicrobia*, *Planctomycetes*, *Gemmatimonadetes*, *Euryarchaeota,* and *Firmicutes* (Fig. 2A). According to the bar graphs, the relative abundance of phyla in Podzol reflects the differences between topsoil (Oi-Oe and AhE horizons) and subsoil (Bs and BC/C horizons). For the first two horizons of topsoil (Oi-Oe and AhE) of Podzol the dominance of representatives of the *Proteobacteria* phyla (40.9 — 56.5 %) is noted. Samples from deeper parts of the soil section (Bs) demonstrated the high values of the phyla *Gemmatimonadetes* (18.5 — 30.2 %). For parent material (BC/C), the absence of *Verrucomicrobia* (1.0 — 3.3 %) and lower values of *Gemmatimonadetes* (3.7 — 14.5 %) are noticeable. The bacteria phylum's typical for Podzols include the phyla *Proteobacteria* (mainly *Rhodoplanes* and *Xanthomonadales*), *Acidobacteria*, *Actinobacteria*, *Bacteroidetes* (Evdokimova et al., 2020; Manucharova et al., 2021; Trifonova et al., 2021). It is shown in Fig. 2B that in topsoil (Oi-Oe and AhE horizons) among *Proteobacteria* phyla nitrite-oxidizing bacteria *Nitrobacter* — chemoautotrophic organisms related to nitrification processes are especially abundant (Laffite et al., 2020). The proportion of *Verrucomicrobia* phyla decreases further down the Podzol profile (Oi-Oe — 6.5 ± 3.3 %; AhE — 8.1±2.2 %; Bs — 3.1 ± 1.2 %; BC/C — 1.2 ± 1.6 %) since these phyla are cosmopolitans of the rhizosphere (Bünger et al., 2020) and are related to soil fertility conditions (Dash, Nayak, Pahari, and Nayak, 2020). The high abundance of *Gemmatimonadetes* (25.5 ± 4.2 %) in the Bs horizon is explained by the genesis of this horizon, it is well drained since it is composed of fine sands, while the phyla of *Gemmatimonadetes* shows good adaptation to the conditions of low moisture (Singh et al., 2023). Therefore, *Gemmatimonadetes* abundance decreases (8.9 ± 3.6 %) in more humid parent material (BC/C horizon). In subsoil close to parent material (BC/C) an increase in the abundance of *Actinobacteria* in the total microbiome pool was observed (31.5 ± 6.4 %), among this phylum an increase

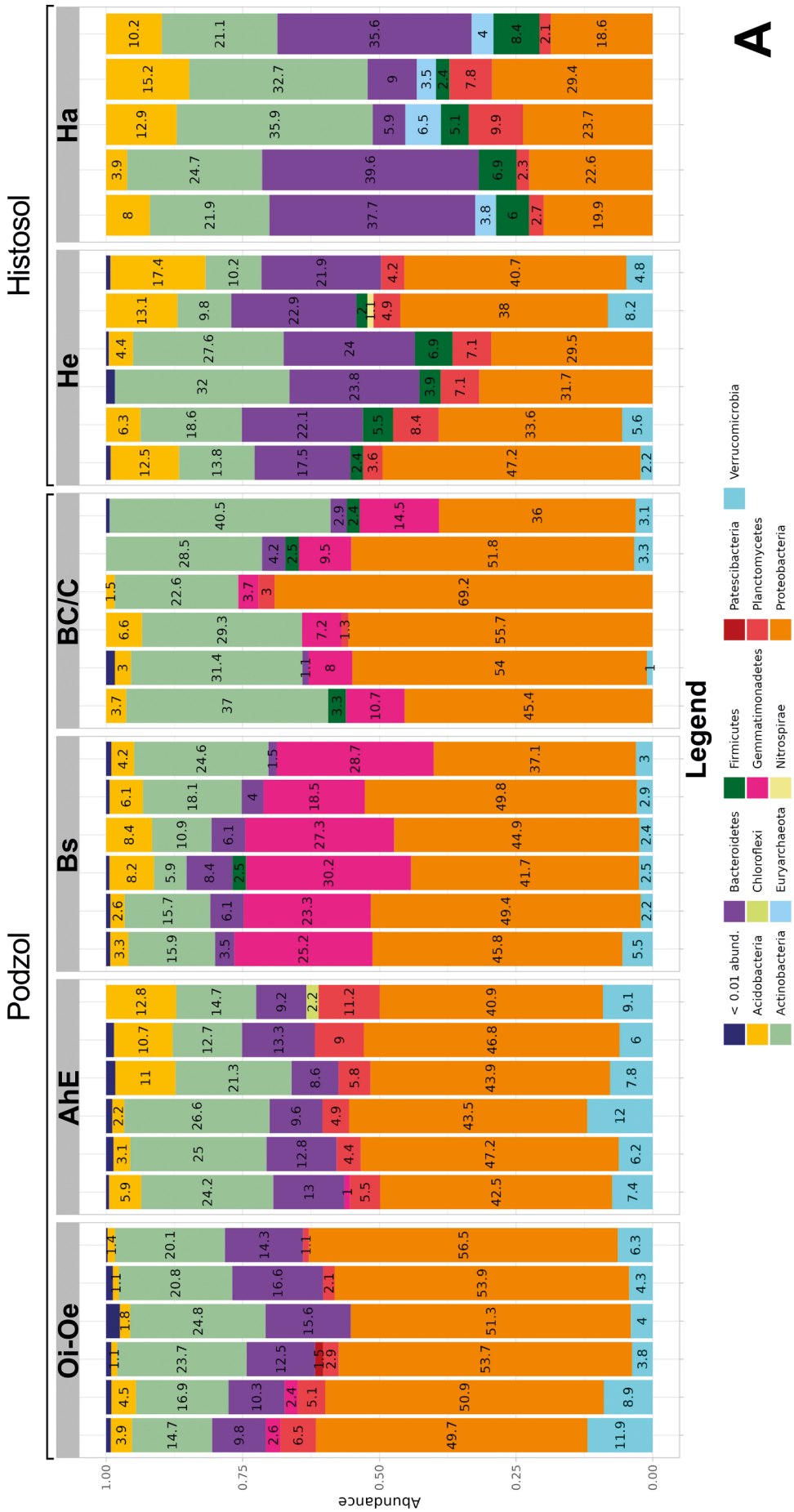
in the abundance of *Mycobacterium* — environmental nontuberculous mycobacteria was observed. According to Glickman et al. (2020), the growth of *Mycobacterium chimaera* is inhibited in the presence of a mineral form of aluminum hydroxide and manganese-containing mineral. The increased abundance of *Mycobacterium* can be linked to the processes of illuviation of Al-Fe compounds across the soil profile and beyond its limits, which is typical for Podzols in this region.

The major bacteria found in peat soils are *Proteobacteria* (Tsitko et al., 2014; Christiansen, Green, Fryirs, and Hose, 2022), *Acidobacteria* (Rakitin et al., 2022), *Chloroflexi* (Christiansen, Green, Fryirs, and Hose, 2022), *Verrucomicrobia* (Aksenov et al., 2021), also the presence of *Bacteroidetes* and *Actinobacteria* (Serkebaeva, Kim, Liesack, and Dedysh, 2013), *Planctomycetes* (Kulichevskaya, Pankratov, and Dedysh, 2006) is noted. As for Histosols microbiota (Fig. 2A), there is a high abundance of *Bacteroidetes* (He — 20.2 ± 0.4 %; Ha — 25.2 ± 16.2 %), as well as the presence of *Firmicutes* and *Planctomycetes* in each sample. In addition, for the peat deposit (Ha horizon), it is possible to note the presence of representatives of the phylum *Euryarchaeota* (2.6 ± 2.3 %), which are methanogenic archaea.

From the total microbiome diversity, the abundance of bacterial phylum working in carbon cycling was isolated (Fig. 2B). The diversity of the carbon cycling phylum was recalculated as a proportion of the total abundance. The bacteria working for carbon cycling were identified as *Actinobacteriota*; *Proteobacteria*; *Acidobacteriota*; *Bacteroiodota*; *Firmicutes*; *Verrucomicrobiota* (*Cyanobacteria*, *Myxococcota* and *Bdellovibrionota* were not included as they were < 0.01 % of the total abundance). *Proteobacteria* and *Acidobacteriota* phyla hold a significant part of the whole abundance among carbon cycling bacteria in Pozdol. A paired comparison of phylum abundance using Sidak multiple comparisons tests showed that there are not many significant similarities in bacterial abundance for carbon cycling. In the topsoil of Podzol, there were statistically significant differences in abundance for *Proteobacteria* ($p < 0.01$) and *Acidobacteriota* ($p < 0.001$). In the subsoil of Podzol, statistically significant differences in abundance were found only for *Actinobacteriota* ($p < 0.0001$). Among the phylum of carbon-cycling bacteria in Histosol, the dominant phyla were *Actinobacteriota*, *Proteobacteria,* and *Bacteroiodota*. The differences in the abundance of *Proteobacteria* phylum ($p < 0.05$) between He and Ha horizons were statistically significant.

According to the one-way ANOVA (Fig. 3A, B), for all observed ASVs ($Df1 = 5$, $Df2 = 29$, $F = 2.6715$, $p < 0.01$), Simpson ($Df1 = 5$, $Df2 = 29$, $F = 5.049$, $p < 0.01$) and Shannon ($Df1 = 5$, $Df2 = 29$, $F = 3.6097$, $p < 0.01$) indices, the soil horizon was a significant predictor of α-diversity. Data on α-diversity of the soil microbiomes showed that Podzol is completely different from Histosols in terms of microorganism biodiversity. Thus, the highest number of ASVs was in the Oi-Oe horizon of the Podzol from the monitored site. The lowest number of ASVs was found in the parent material, particularly on the BC/C horizons, which is in accordance with the fact that in-depth microbial biodiversity decreases. The richness of topsoil samples was presumably higher than that of subsoil. The Histosol samples had the lowest value of richness, according to the observed ASV index. It was significantly lower than the ones obtained from the He horizon, but mostly both peat sections had lower richness in comparison with Podzol samples. A significant difference in evenness (according to the Simpson index) has been discovered between the Histosol and Podzol, as well as between different horizons of the Podzol soil profile (especially between topsoil and subsoil). In general, the highest evenness was characterized for the topsoil samples, whereas lower horizons had moderate values. The α-diversity for the carbon cycle phylum's (Fig. 3C, D) is similarly distributed. Podzol and Histolos are statistically different ($F = 30.43$. $DF1 = 5$, $DF2 = 198$, $p < 0.0001$). Statistically significant differences in microbial diversity at carbon cycle phylum's between topsoil (Oi-Oe and AhE horizons) and subsoil (Bs and BC/C horizons) of Podzol were also found ($F = 9.20$ $DF1 = 5$, $DF2 = 132$, $p < 0.0001$).

Taxonomic diversity of soil microbiome is strongly related to chemical properties and soil regimes (Philippot et al., 2024). The soils we investigated are variable in genesis and in physicochemical properties. Podzols are characterized by lower content of SOC and they are more drained. Histosols are characterized by high moisture and high content of organic carbon. We have previously noted that the core phyla of the microbial community for both soils are *Proteobacteria*, *Actinobacteria*, and *Bacteroidetes*. However, the lower-level differences in the taxonomic composition of the microbial community are probably associated with the genesis of the soils and their physicochemical properties (Evdokimova et al., 2020; Rakitin et al., 2022). The β-diversity analysis also revealed differences between samples in a defined manner. The association of the taxonomic composition of the microbiome with soil physicochemical properties should also be investigated, but we are already able to identify similar microbiome clusters based on β-diversity analysis (Fig. 3). The results of the NMDS (beta-diversity, calculated using Bray — Curtis distances) are presented in Fig. 3E, F. According to this data, the topsoil samples of Podzol had a unique microbial composition, clustered in NMDS, in their own, partly diverse, clusters. Samples from Bs and BC/C horizons were also grouped in clusters, but much clearer ones. At the same time, samples from the Histosol clustered NMDS, but each in its unique group. According to the PERMANOVA, the soil


A
Podzol
Histosol
Oi-Oe
AhE
Bs
BC/C
He
Ha
Abundance
1.00
0.75
0.50
0.25
0.00
Legend
< 0.01 abund.
Acidobacteria
Actinobacteria
Bacteroidetes
Chloroflexi
Euryarchaeota
Firmicutes
Gemmatimonadetes
Nitrospirae
Patescibacteria
Planctomycetes
Proteobacteria
Verrucomicrobia

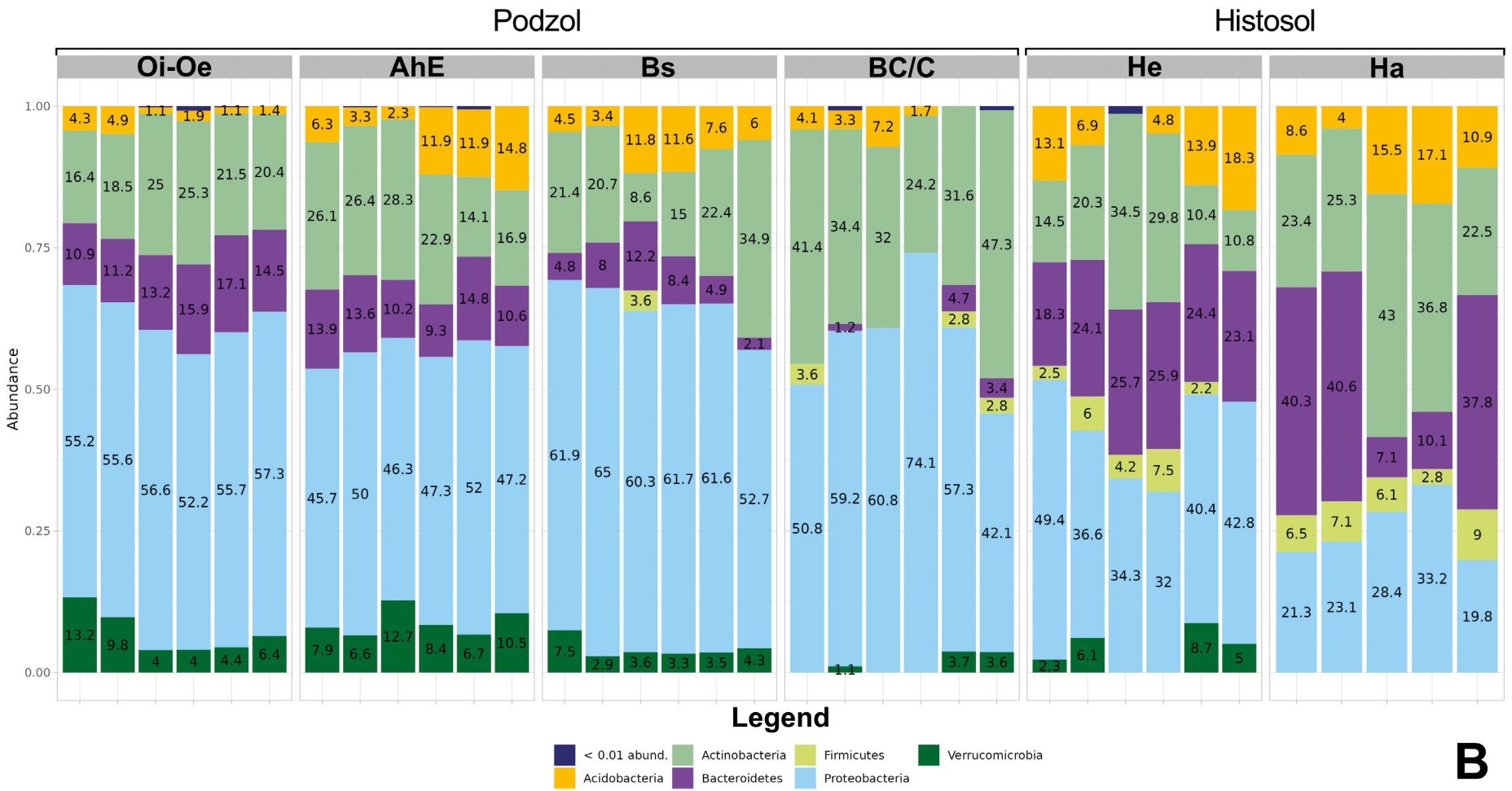


Fig. 2. A — Total relative abundance of microorganism's phyla for each soil horizon of Podzol and Histosol (n = 6); B — Relative abundances of carbon cycling phyla (Xue et al., 2023).

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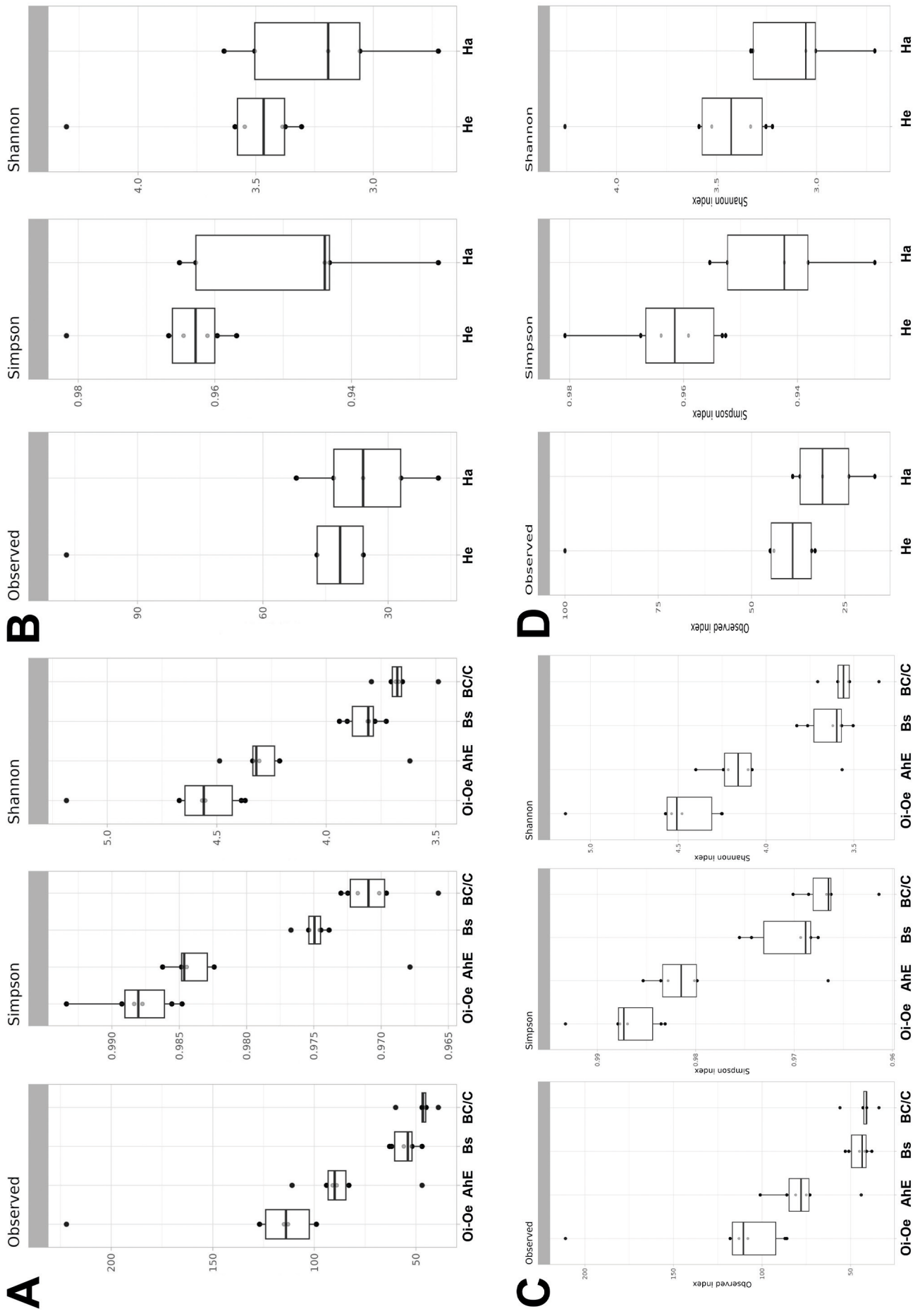
A
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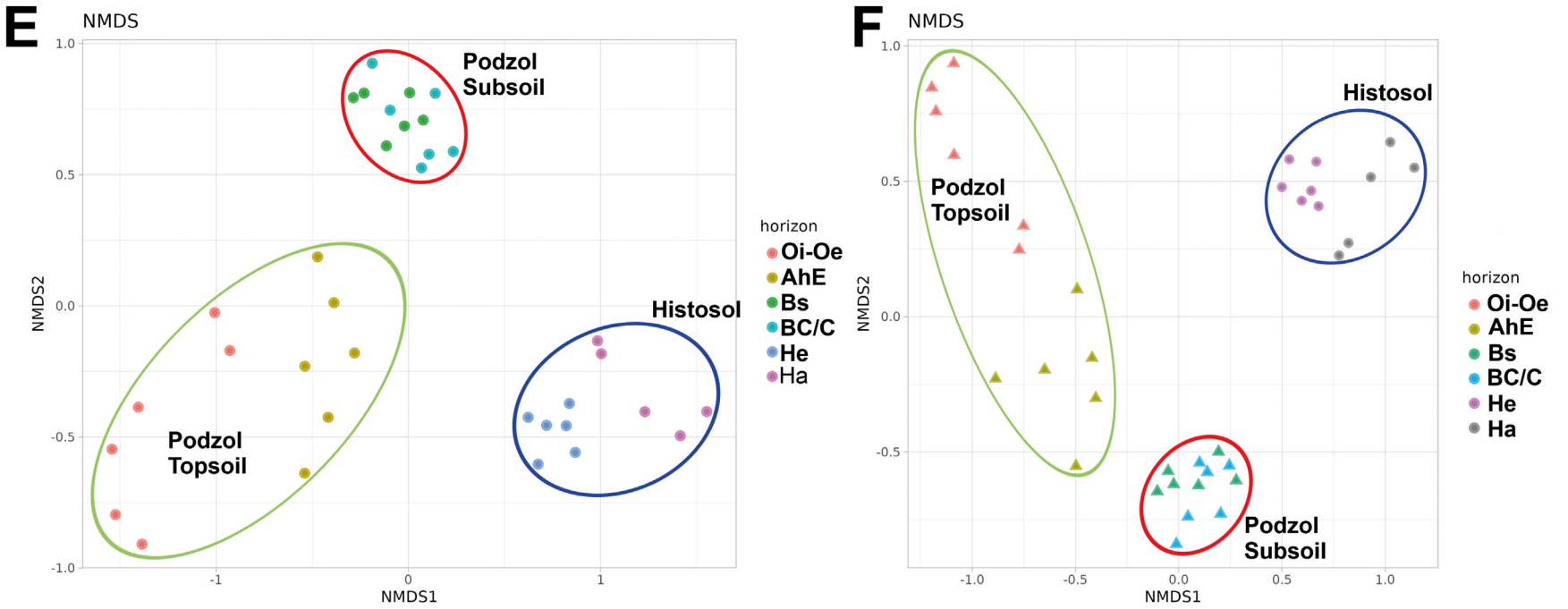

Fig. 3. The α-diversity indices of total relative abundance for each soil horizon A — for Podzol, B — for Histosol (observed ASVs, Simpson and Shannon indices). The α-diversity indices of relative abundance for carbon cycle phyla for each soil horizon C — for Podzol, D — for Histosol (observed ASVs, Simpson and Shannon indices). The β-diversity multivariate analysis by non-metric multidimensional scaling using Bray — Curtis dissimilarity E — of total relative abundance, F — for carbon cycle phyla.

horizon was a significant factor of β-diversity (Df1 = 5, Df2 = 29, F = 8.1903, $p < 0.001$) for the Bray — Curtis distances. Therefore, according to β-diversity, it is possible to categorize the studied soils into three different groups (for total and carbon cycle phylum's relative abundance) in terms of microbial diversity: 1 — topsoil of Podzol (Oi-Oe and AhE horizons); 2 — subsoil of Podzol (Bs and BC/C horizon); 3 — Histosol (He and Ha horizon).

Conclusions and outlook

Microbial diversity analysis identified 729 unique ASVs from 35 soil samples. A total of 11 phyla of bacteria and 1 phylum of archaea were identified. The dominant bacterial phyla in Podzol and Histosol are *Proteobacteria* and *Actinobacteria*. The presence of a certain phylum and genus is associated with the features of soil genetic horizons: *Nitrobacter* — associated with the topsoil (Oi-AhE horizons) of Podzol; *Verrucomicrobia* — more often found in the topsoil, as they are cosmopolitans of the rhizosphere; *Gemmatimonadetes* — which are adapted to low moisture, found in the drained horizon Bs composed by sands. For Histosol, a higher abundance of *Firmicutes* was found and methanogenic archaea (*Euryarchaeota*) were identified in the deep Ha horizon. The total microbial diversity can be separated into three independent clusters: topsoil of Podzol; subsoil of Podzol; and Histosol. Although the list of phyla is common for both reference soils, we observe statistically significant differences in relative abundance between these two soils, and between parts of the soil profile (especially in Podzol). The main differences in microbiological diversity are related to the different genesis of reference soils: Podzols — these are post lithogenic soils with organo-mineral matrix, where biogenic accumulation and recycling of organic matter occurs mainly in topsoil. Histosols are organogenic soils composed of previously accumulated organic matter (peat) of various degrees of decomposition. In addition, these two soil types differ significantly in soil regimes (water, air, and thermal), so we found microorganisms associated with soil horizons with different parameters (e. g.: methanogenic archaea (*Euryarchaeota*), which were found in the waterlogged and anaerobic horizon of Ha of Histosol). Of the prominent phylum of carbon cycle bacteria were identified: *Actinobacteriota*; *Proteobacteria*; *Acidobacteriota*; *Bacteroiodota*; *Firmicutes*; and *Verrucomicrobiota*, which are clustered similarly. The highest abundance among carbon cycling bacteria was revealed for *Actinobacteriota*, *Proteobacteria* in Podzol *Actinobacteriota*, *Proteobacteria*, and *Bacteroiodota* in Histosol. Statistically significant differences in the phylum abundance of carbon cycle bacteria between the two soils were found between *Proteobacteria* and *Bacteroiodota* ($p < 0.0001$). Further research should be focused on studying functional groups related to carbon and nitrogen cycling in the bacterial communities and identifying their ecosystem functions for different reference soils of the "Ladoga" carbon supersite.

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