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SOIL BIOLOGY

# Taxonomic Structure of Bacterial Communities of Rhizospheric Soil under Bogs' Plants

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**Abstract**—For the first time, the ratio of large taxa and the genera spectrum of the prokaryotic community of the rhizosphere soil under typical plants of bogs were studied using high-throughput sequencing. The predominance of Acidobacteria and Alpha-proteobacteria and a low proportion of other taxa (less than 10%) were established. Representatives of the phyla Acidobacteria and Actinobacteria, as well as the class Alpha-proteobacteria class predominated among the 24 bacterial genera found. Common bacterial genera were identified in rhizospheric soil under plants and surface layers of peat. Representatives of most of these bacteria are adapted to grow in an acidic environment at low temperatures and consume various sugars, polysaccharides, aromatic compounds, and organic and amino acids. Bacteria of the genera *Cytophaga* and *Acidothermus*, widely distributed in bacterial communities, are capable of cellulose destruction, while representatives of the genus *Occallatibacter* utilize chitin and bacteria of the genus *Nocardia* consume humic substances and lignin.

*Keywords:* bogs, plants, rhizospheric soil, bacterial communities, phyla, spectrum of genera, bacterial functions, high-performance pyrosequencing, metabarcoding of 16S rRNA gene

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## INTRODUCTION

Despite the fact that the bacterial communities of peat soils has been studied for more than half a century, there are still many questions that microbiologists have yet to answer. The main ones are: which bacterium taxa prevail in peat bogs, and what are their ecological functions in this specific habitat, where microbial destruction is blocked by high water cut, low temperature and low acidity, anaerobiosis, and a high content of sphagnols toxic to bacteria? To answer these questions, the methods for assessing bacterial diversity should be improved. The development of these methods is considered in detail in our review, which analyzes the work of Russian and foreign microbiologists over the past 20 years [3]. The example of peat soils has shown how ideas about the diversity of these soils' bacterial communities have changed with the development of methods ranging from the traditional classical cultural to molecular biological. The current stage is characterized by the use of molecular methods of analysis, allowing investigation of bacterial diversity directly in situ, bypassing the stages of cultivation on nutrient media.

Analysis of bacterial phylogenetic diversity by molecular biological methods demonstrated that bogs are one of the most favorable natural habitats for acidobacteria. They survive in peatlands using various heteropolysaccharides that are released as a result of the destruction of sphagnum and other plant residues. At the same time, they are active at low temperatures and in an acidic environment, which is typical for bogs [32]. Planctomycetes is one of the dominant groups of bacteria in the upper layers of sphagnum bogs in the boreal zone [6, 16, 25]. The review of Dedysh [15] provides a list of all currently known genera of acidobacteria, planctomycetes, and methylobacteria found in sphagnum bogs in Russia and other countries. The use of molecular methods makes it possible to identify a wide range of representatives of the methanogenic community of sphagnum bogs. Archaea of the families Methanomicrobiaceae, Methanocarpusculaceae, and Methanoplanaceae were detected in the upper layers of the peat core, while archaea of the genus *Methanosarcina* were detected in the deeper anoxic layers of peat [40]. The importance to use the high-throughput sequencing method for reconstructing the phylogenetic diversity of prokaryotic communities was demonstrated by the example of the studying the upper layers of the peat bog in Yaroslavl oblast. [36].

The aim of this work was to identify the bacterial diversity of rhizospheric soil under three species of typical bog plants using the method of high-throughput sequencing (16S rRNA gene metabarcoding) and compare the results obtained with the literature data regarding the ratio of taxa and the diversity of bacterial

genera in peat bogs obtained using different molecular biological methods.

## MATERIALS AND METHODS

The studies were carried out on the permanent trial plot of West Dvina Peatland-Forest Station of Institute of Forest Science of the Russian Academy in Tver oblast. Analyzed peatland under dwarf shrubs–cottongrass–sphagnum pine forest is the part of typical oligotrophic swamp massif Sosvyatskoe. In June 2018, rhizospheric soil samples were collected under plants typical of this phytocenosis: wild rosemary (*Ledum palustre* L.), hare's-tail cottongrass (*Eriophorum vaginatum* L.), and bottle sedge (*Carex rostrata* Stokes). Plants were collected at four points 50–100 m apart; they were carefully dug up and the soil was shaken off from the roots onto paper sheets. An averaged soil sample was obtained by mixing those taken at four sites. Soil samples were packed in sterile plastic bags, cooled, and delivered to the laboratory for further analysis on the same day.

The taxonomic diversity of the prokaryotic soil community was studied using high-throughput sequencing of V3–V4 hypervariable regions of the 16S rRNA gene. Total DNA was extracted using PowerSoil DNA Isolation Kit (MO BIO, USA) according to the manufacturer's recommendations. Amplification of the 16S rRNA gene fragments were carried out using degenerate primers PRK341F (CCTACGGGRBGCASCAG) and PRK806R (GGACTACYVGGGTATCTAAT) complementary to the sequences of both bacteria and archaea. The PCR fragments obtained were purified using QIAquick columns according to the manufacturer's protocol and each of them was dissolved in 50 μL of TE buffer. The amount of material obtained was sufficient for further analysis. Hypervariable fragments of the 16S rRNA gene were analyzed by high-throughput sequencing using Illumina Miseq sequencing platform. The runtime was 39 h and 8 million paired ends were read. After the sequencing, files with forward and reverse reads from both ends of the DNA were formed, which were a textual description of the primary structure of linear macromolecules in the form of a sequence of monomers. Data was processed using QIIME 1.9.1 automated algorithm, including merging forward and reverse reads, removing technical sequences, filtering sequences with low average quality of sequencing accuracy for each individual nucleotide (quality <Q20), filtering chimeric sequences, aligning reads to reference sequences of 16S rRNA genes, and distributing sequences by taxonomic units based on Silva database (release 132). The operational taxonomic unit (OTU) classification algorithm with an open-reference OTU and similarity threshold of 97% was used.

## RESULTS

The bacterial communities of rhizospheric soil under plants were represented by the following phyla: Proteobacteria, Acidobacteria, Actinobacteria, Verrucomicrobia, Bacteroidetes, Planctomycetes, Cyanobacteria, Firmicutes, Chloroflexi, and WPS-2 (Fig. 1). In total, these phyla composed 96–99% of the bacterial community.

Shares of Proteobacteria (35–49% of the total number of sequences) and Acidobacteria (28–39%) were the largest in microbiomes. Representatives of the Actinobacteria and Verrucomicrobia composed no more than 10% of the total number of sequences. The share of other groups (Bacteroidetes, Planctomycetes, Cyanobacteria, Firmicutes, Chloroflexi and uncultured bacterial WPS-2 candidate phylum) was low and ranged of 1 to 3%. Proteobacteria in microbiomes belonged to three classes: α-Proteobacteria, γ-Proteobacteria, and δ-Proteobacteria. Among them, representatives of α-Proteobacteria predominated (22–42% of the total number of sequences). Shares of γ-Proteobacteria and δ-Proteobacteria ranged from 5 to 8% and 2 to 7%, respectively. In rhizospheric soil under wild rosemary, the share of alpha-proteobacteria was maximum. It was twice as much as shares of bottle sedge and cotton grass. In contrast, the share of acidobacteria was higher in soil under bottle sedge and cotton grass.

Analysis of the bacterial community of the peat layer (0–5 cm) of peat bogs in Yaroslavl oblast by high-throughput sequencing revealed a similar ratio of most main taxa (Fig. 1) [36]. The share of planctomycetes was the only exception. In the surface peat layer and in the rhizospheric soil under plants, it composed 6 and 1%, respectively. The results of the study of the bacterial communities of the sphagnum-lichen bog in the subarctic zone of Russia (Yamalo–Nenetsky Avtonomny Okrug) were similar to those given above [1]. The predominance of acidobacteria and alpha-proteobacteria and a gradual decrease in the proportion of actinobacteria, gamma-proteobacteria and verrucomicrobia were revealed.

Thus, bacterial communities of the upper layers of peat bogs, regardless of their geographical location, and rhizospheric soil under bog plants, are characterized by the predominance of acidobacteria and alpha-proteobacteria.

Analysis of the taxonomic composition of bacterial communities at the genus level in rhizospheric soil under the studied plants revealed representatives of 24 genera. The maximum number of genera was detected among alpha-proteobacteria and actinobacteria (6) as well as acidobacteria (5). In other phylums, only one or two genera were found (Table 1).

Alpha-proteobacteria in the studied substrates were represented by the genera *Bradyrhizobium*, *Roseiarcus*, *Nitrobacter*, *Pseudolabris*, *Acidocella*, and *Telmatospirillum*. Bacteria of the genera *Rhizobium* and *Bradyrhizo-*

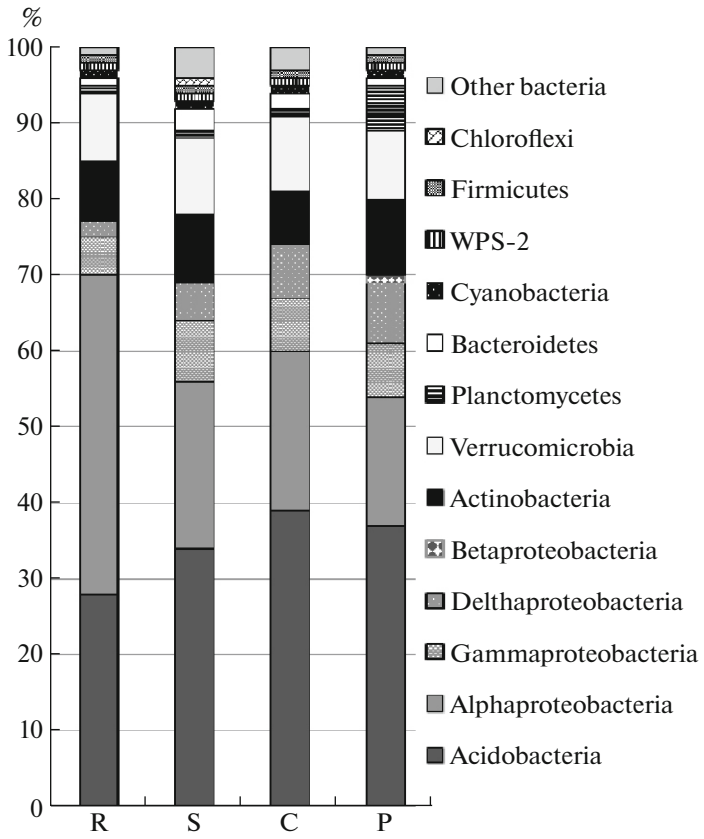


**Fig. 1.** The taxonomic structure (at the phylum level) of the bacterial communities of the rhizosphere soil under plants and in the surface layer (0–5 cm) of the bog: B is rosemary, O is sedge, P is cottongrass, and T is peat (according to [36]).

*bium* are known to form nodules on the roots of legumes. However, in recent years, bacteria of the genus *Bradyrhizobium*, which are not capable of nodule formation and do not contain nitrogen-fixation genes, have been isolated from soils in Europe and Japan [19, 41]. The functions of these bacteria are reduced to the degradation of aromatic compounds and denitrification. The genus *Bradyrhizobium* was considered as a subdominant in the work [12], in which bacterial communities in an alpine sphagnum bog in Austria were studied. Bacteria of the genus *Roseiarcus* were isolated for the first time from methanotrophic communities of the acidic sphagnum bog and described as a novel genus and a novel family Roseiarcaceae of the order Rhizobiales of the class Alpha-proteobacteria [22]. These bacteria contain bacteriochlorophyll and grow consuming certain sugars and organic acids under microaerophilic conditions. Bacteria of the genus *Nitrobacter* are typical nitrite oxidizers found in most soils and water bodies. Bacteria of the genus *Pseudolabris* were first isolated from red soil in Taiwan and described as a novel genus and species *Pseudolabris taiwanensis* [20]. Bacteria of this genus do not utilize sugars and use only acetate, fumarate, and lactate. They differ from the most closely related genus *Labrys* mainly in the composition of fatty acids.

The genus *Acidocella* has been described as a result of the transfer of two species of the genus *Acidiphilum* (*A. facilis* and *A. amynolitica*) to the novel genus *Acidocella* [21]. Bacteria of this genus were isolated from different acid soils and acidic thermal springs, as well as as dominants from living sphagnum. They are obligate acidophilic organisms that grow at $pH_{sal}$ of 2.5 to 6.0 using various aromatic compounds (benzoic acid, phenol, naphthalene), as well as on certain sugars. Some strains are resistant to heavy metals (cadmium, nickel, copper, zinc) [12]. Bacteria of the genus *Telmatospirillum* are facultative anaerobic acid-tolerant components of the methanogenic community isolated from the Siberian mesotrophic bogs [38]. Under aerobic conditions, they can grow as chemoorganotrophs utilizing glucose and certain organic acids, while, under anaerobic conditions, they grow as autotrophs using hydrogen and carbon dioxide. Thus, among detected alpha-proteobacteria, representatives of three genera were capable of degradation of various aromatic compounds, while others use sugars, organic acids, and amino acids.

Bacteria of the class Gamma-proteobacteria were represented in rhizospheric soil under the studied

**Table 1.** The spectrum of bacterial genera found in rhizospheric soil under plants of bogs

| Taxon | | | Plant | | |
|---|---|---|---|---|---|
| Class | Family | Genus | wild rosemary | bottle sedge | hare's-tail cottongrass |
| Alphaproteobacteria | Bradyrhizobiaceae | *Bradyrhizobium* | + | + | + |
| | Roseiarcaceae | *Roseiarcus* | + | + | + |
| | Xanthobacteraceae | *Nitrobacter* | – | + | – |
| | | *Pseudolabris* | – | – | + |
| | Acetobacteraceae | *Acidocella* | + | + | + |
| | Magnetospirillaceae | *Telmatospirillum* | + | + | – |
| Gammaproteobacteria | * | *Acidibacter* | + | + | + |
| Acidobacteria | Acidobacteriaceae | *Occallatibacter* | + | + | + |
| | | *Acidicapsa* | + | – | – |
| | | *Granulicella* | + | + | + |
| | | *Acidipila* | – | – | + |
| | Solibacteraceae | *Bryobacter* | + | + | – |
| Actinobacteria | Mycobacteriaceae | *Mycobacterium* | + | – | – |
| | Acidothermaceae | *Acidothermus* | + | + | + |
| | Nocardiaceae | *Nocardia* | + | – | – |
| | | *Rhodococcus* | – | + | – |
| | Conexibacteriaceae | *Conexibacter* | + | + | + |
| | | *Solirubrobacter* | + | – | – |
| Verrucomicrobia | Opitutaceae | *Opitutus* | + | + | + |
| | Chtoniobacteracea | *Chtoniobacter* | + | + | + |
| Planctomycetes | Planctomycetaceae | *Aquisphaera* | + | + | + |
| | | *Singulisphaera* | + | – | – |
| Bacteroidetes | Sphingobacteriaceae | *Mucilaginibacter* | + | + | – |
| | | *Cytophaga* | – | + | – |

Plus (+) means taxon was detected; minus (–) means taxon was not found; asterisk (*) means no family, no order.

plants by one genus *Acidibacter* (Table 1). Representatives of this genus were first isolated from a lake formed on abandoned mine in Spain [17]. They are moderate acidophiles that can grow utilizing hexoses, disaccharides, and some other organic compounds. Their particular characteristic is resistance to high concentrations of iron and aluminum and the ability to oxidize iron under strictly anaerobic conditions.

Acidobacteria revealed included representatives of five genera: *Occallatibacter*, *Acidicapsa*, *Granulicella*, *Acidipila*, and *Bryobacter*. Bacteria of the genus *Occallatibacter* were first isolated from the floodplain soil in Namibia and described as a new genus containing two species *O. ripars* and *O. savannae* [18]. These are acid-tolerant bacteria that use various sugars and polysaccharides for growth. They are capable of hydrolyzing pectin and chitin, but not starch and cellulose. Other representatives of acidobacteria (found only under wild rosemary) were representatives of aerobic, acidophilic genus *Acidicapsa* isolated from the sphagnum bog and described as a novel genus [24]. Their preferred substrates are sugars, pectin, galacturonic, and glucuronic acids. Bacteria of the genus *Granulicella* were also first isolated from acidic sphagnum bogs and described as a novel genus including four species [31]. These are acidophilic psychrotolerant bacteria that can use various sugars and polysaccharides, including pectin, xylan, starch, lichenan, but not cellulose and chitin. Bacteria of the genus *Acidipila* (identified under cottongrass) were first isolated from acidic soils in Japan and described as a novel genus (species *A. rosea*) [30]. Representatives of this genus are acidophilic chemoorganotrophic bacteria that can use various sugars, as well as peptone, gluconic acid, and some amino acids. The bacteria of the genus *Bryobacter* were first isolated from the sphagnum bog and described as a novel genus and species *B. aggregatus* [26]. They are acid tolerant bacteria that can use some polysaccharides, sugars, and organic acids.

Thus, the description of the genera of acidobacteria suggests that all of their representatives are capable of degradation of pectin and other polysaccharides, the use of most sugars, some organic acids, amino acids, and aromatic compounds. Acidobacteria of only one genus *Occallatibacter* can decompose chitin.

In rhizospheric soil under plants, six genera of actinobacteria were found: *Acidothermus*, *Mycobacterium*, *Nocardia*, *Rhodococcus*, *Conexibacter*, and *Solirubrobacter* (Table 1). Bacteria of the genus *Acidothermus* were first isolated from acidic thermal springs and described as a novel genus and species *A. cellulolyticus* [28]. Bacteria of this genus were also isolated from forest soils along with other cellulolytic bacteria when searching for producers of enzymes necessary for cellulose degradation [39], as well as from desert soils in Mongolia [7]. Bacteria of the genus *Mycobacterium* were detected in soils as saprotrophic and environmentally significant microorganisms, despite the fact that pathogens predominate among representatives of this genus For example, bacteria of the genera *Mycobacterium* and *Streptomyces* were isolated as subdominant from the permafrost peaty soils in Yakutia [5]. Fast-growing saprotrophic representatives of the genus *Mycobacterium* were found in soils contaminated with polycyclic aromatic hydrocarbons [27]. It is known that microbial preparations containing different types of hydrocarbon-oxidizing mycobacteria are used for the restoration of oil-contaminated soils. The bacteria of the genera *Nocardia* and *Rhodococcus* are typical inhabitants of soils and rhizospheres of different plants [4]. The specific functions of nocardia in the soil have been described by Tepper [10] and Manucharova [9]. A study of the physiological and biochemical properties of various species of the genus *Nocardia* demonstrated that they are capable of slow degradation of humic acid and related compounds (aromatic and nitrogen-containing heterocyclic compounds). The authors pay attention to the specificity of the enzymatic machinery of nocardia, which is characterized by the absence of many types of proteinase, amylase, invertase, and some other hydrolytic enzymes. This feature limits the possibility of the participation of these organisms in the conversion of fresh organic residues and determines their use of the most stable decomposition products: hydrocarbons, lignin, and soil humic substances.

Actinobacteria of the genus *Rhodococcus* are capable of oxidizing high molecular weight *n*-alkanes and complex organochlorine compounds that are difficult to biodegrade including benzene, toluene, naphthalene, polychlorinated biphenyls, and some herbicides. The predominance of bacteria of the genus *Rhodococcus* was detected in urban soils, especially in those that were contaminated with oil and polychlorobiphenyls [8]. Certain strains of Rhodococcus are currently used for the production of bacterial preparations applied for bioremediation of oil-contaminated soils.

Bacteria of the genus *Conexibacter* were first isolated from forest soils in Italy and described as a novel genus and species *C. woesei* [29]. Bacteria of this species grow at $pH_{sal}$ 7–7.5 and temperature of 28–37°C. Another species, *C. arvaliswas*, was described later [35]. Its representatives were isolated from agricultural soil in Japan. In contrast to the type species *C. woesei*, bacteria of this species are able to grow in the pHsal range of 5 to 10 and at a temperature of 5 to 37°C. Bacteria of this species use various sugars and some organic acids as carbon sources, hydrolyze gelatin and esculin, and reduce nitrates.

Actinobacteria of the genus *Solirubrobacter* (found under wild rosemary) were isolated for the first time from an earthworm burrow in agricultural soil and described as a novel genus and species *Solirubrobacter pauli* [37]. Bacteria of this species use various sugars and some amino acids (alanine, lysine, arginine), and do not utilize alcohols. Thus, among actinobacteria found in rhizospheric soil under raised bog plants, the genera, representatives of which are capable of degrading complex polymers and polycyclic aromatic hydrocarbons, were identified.

Under the studied species of bog plants, two genera (*Opitutus* and *Chthoniobacter*) belonging to the phylum Verrucomicrobia were identified (Table 1). Bacteria of the genus *Opitutus* were isolated for the first time from rice paddy soil and described as a novel genus and species *Opitutus terrae* [14]. These bacteria are obligate anaerobes that can use various mono-, di- and polysaccharides, but cannot grow utilizing alcohols or amino and organic acids. Propionate, acetate, hydrogen, and ethanol are the main products of their metabolism and they also can reduce nitrates. Bacteria of this genus were also detected in the surface layers of a raised peat bog in Yaroslavl oblast [36]. Representatives of the genus *Chthoniobacter* were first isolated from soil under clover and ryegrass in Australia and described as a novel genus and species *Chthoniobacter flavus* [34]. Bacteria of this species are aerobes, grow utilizing plant polysaccharides, but are not able to grow consuming amino acids, organic acids, and alcohols; i.e., they use the same substrates as the bacteria of the genus *Opitutus.*

Planctomycetes in rhizospheric soil under the studied plants were represented by two genera: *Aquisphaera* and *Singulisphaera* (Table 1). Bacteria of the genus *Aquisphaera* were first isolated from the sediment of an aquarium with fresh tap water and described as a novel genus and species *A. giovannonii* [11]. These are budding aerobic heterotrophic bacteria that grow at pHsol 7.5–8.5 and a temperature of 30–35°C. They assimilate sugars, organic acids, amino acids and are able to decompose starch, gelatin, and peptone. Planctomycetes of the genus *Singulisphaera* were isolated from acidic sphagnum bogs in the Yaroslavl oblast and described as a novel genus and species *S. acidiphila* [23]. They are budding cocciform bacteria, aerobes

capable of growth under microaerobic conditions, moderate acidophiles growing at a pH of 4.2–7.5 and a temperature of 4–33°C. Bacteria of this species use many sugars and some amino acids, can hydrolyze pectin, gelatin, xylan, and lichenan. Thus, both genera of planctomycetes are hydrolyzers and typical copiotrophs, which are active in a wide range of pH and temperature. The detection of bacteria of the genus *Singulisphaera*, which were isolated for the first time from the peat bog, in the rhizospheric soil under bog plants, was entirely appropriate, while the detection of the genus *Aquisphaera* was, perhaps, accidental.

Bacteria of the phylum Bacteroidetes were represented in the studied substrates by the genera *Mucilaginibacter* and *Cytophaga*. Bacteria of the genus *Mucilaginibacter* were isolated for the first time from the acidic sphagnum bog in Siberia and described as a novel genus and two species *M. paludis* and *M. gracilis* [33]. They are organotrophic aerobic and facultative anaerobic acid- and psychrotolerant bacteria growing in a wide range of $pH_{sal}$ 4.5–10 and temperatures of 4–37°C. Preferred substrates for these microorganisms are sugars (they ferment glucose and sucrose), but they can also decompose starch, pectin, xylan, laminarine and some other polysaccharides (but not cellulose and chitin). Bacteria of the genus *Cytophaga*, described in 1929 by S.N. Vinogradskii as active cellulolytic microorganisms, were subsequently found in various types of soils, detritus, and rhizosphere of many plants. In the peat bog, their share was 19% of the total number of bacterial taxa in the surface layer and 10–12% at a depth of 10–50 cm [2].

It is practically impossible to compare the genus composition of a bacterial community in rhizospheric soil with that obtained by authors who studied the bacterial complexes of peat by a similar method (sequencing of the 16S rRNA gene), since such studies are not numerous and mainly devoted to the study of individual groups: methanogens, methylotrophs, and acidobacteria. Nevertheless, it was possible to find common genera in the studied soil under plants and in the surface layers of raised peat bogs shown in various literature, but these data are not enough to reveal clear differences. It is necessary to study the bacterial complexes of rhizoplans, phylloplans of bog plants, peat horizons using modern methods, since this work has not yet been performed. However, at the level of higher bacterial taxa, such work was carried out [13]. For example, 46 samples of different samples of vascular plants, mosses and lichens of sphagnum bogs in Austria were analyzed. Based on different indices, including alpha diversity, it was found that there are no significant differences in bacterial diversity between different plant species. Several genera of bacteria that were detected in this work corresponded to those found in rhizospheric soil: *Aquisphaera*, *Singulisphaera* (Planctomycetes), *Acidocella* (Alpha-proteobateria), *Chtoniobacter*, and *Opitutus* (Verrucomicrobia).

## CONCLUSIONS

The use of high-throughput sequencing (metabarcoding of the 16S rRNA gene) in rhizospheric soil under typical plants of bogs made it possible to characterize the presence and ratio of large bacterial phyla and to reveal the predominance of acidobacteria and alpha-proteobacteria in the bacterial communities. The revealed regularities in the structure of bacterial phyla and classes for rhizospheric soil are similar to those established for the surface layers of peat bog. In this work, a wide spectrum of bacterial genera (24) from different phylums and classes, many of which are described only in recent years, was revealed and analyzed, including those that are inherently resistant to artificial culture. Most bacteria from the genera found are acid-tolerant and grow in a wide temperature range. Many representatives of these genera are copiotrophs that utilize various sugars, organic acids, amino acids, alcohols, and aromatic compounds. Bacteria of only four genera were capable of hydrolysis to utilize compounds that are resistant to the activity of other bacteria. Bacteria of the genera *Cytophaga* and *Acidothermus* are able to degrade cellulose; *Occallatibacter* are able to hydrolyze chitin, while *Nocardia* may utilize humic substances. That makes sense, considering the very low degree of decomposition of high peat, which includes sphagnols, which are the most difficult for degradation and toxic to bacteria. An analysis of the causes of the slow decomposition of *Sphagnum* peat is given in our collective monograph [2].

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## COMPLIANCE WITH ETHICAL STANDARDS

*Conflict of interests*. The authors declare that they have no conflicts of interest.

*Statement on the welfare of animals*. This article does not contain any studies involving animals performed by any of the authors.

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