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Comparative Analysis of Microbial Communities of Contrasting Soil Types in Different Plant Communities

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Abstract—Microbiomes were analyzed in samples of the major soil types of Russia and Western Kazakhstan region from different plant communities (fallow, forest, agrophytocenosis). The representatives of 42 bacterial and 2 archaeal phyla were identified in the samples, among which the dominant positions were occupied by representatives of ten phyla: nine bacterial (*Actinobacteria* (33.5%), *Proteobacteria* (28.4%), *Acidobacteria* (8.3%), *Verrucomicrobia* (7.7%), *Bacteroidetes* (4.2%), *Chloroflexi* (3.0%), *Gemmatimonadetes* (2.3%), *Firmicutes* (2.1%), *Planctomycetes* (2.0%)) and one archaeal *Crenarchaeota* (2.6%). Data analysis by the methods of multivariate statistics suggests that the taxonomic structure of microbiota is formed under the action of two main factors: the strongest factor is soil acidity, which determines the dynamics of the microbiome at the level of major taxa such as phylum, and the weaker factor is the type of vegetation, which determines the community structure at lower taxonomic level (order, family, genus). Detailed analysis of the samples of podzolic soil in Leningrad Region made it possible to identify bacterial taxa specifically associated both with the type of biome (fallow, forest, agrophytocenosis) and with the specific plant community (specific composition of plant synusia).

Keywords: soil microbiome, high-throughput sequencing, synusiae
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INTRODUCTION

The community of microorganisms inhabiting soil plays a key role in the maintenance of ecological and system functions of the soil. The soil microbiome is a unique resource for different areas of human activities. However, the use and management of the genetic potential of the soil microbiome is impossible without an analysis of environmental factors that influence the microbial community and determine its structure and physiological characteristics. Some of these factors have a strong and well-detected influence on soil microbiota: soil acidity, humidity, salinity, soil texture, redox potential, etc. [1–4].

Plants have a significant impact on the composition and structure of the microbiome via root exudates of different natures and the formation of specifically associated community of rhizosphere microbiome. It was shown [5, 6] that the species diversity and uniformity of plant community influence the taxonomic and functional diversity of the soil microbiome and that the composition of plant communities does not affect so much the alpha diversity of the microbial cenosis but does determine its beta-diversity [7]. However, the influence of vegetation on the soil microbiome is one of the most difficult factors to study. This is due to its variability: spatial (the creation of microniches for soil microorganisms by the root system of a plant), temporal (change in the composition of root exudates at different stages of the life cycle of plants), and taxonomic (the formation of phytocenosis as a labile system of genetically polymorphic species of population that vary in the specificity of the interaction with the components of the soil microbiome).

The influence of plants on soil microbiome was studied by S.P. Kostychev more than 80 years ago. However, due to the complexity of the object (the huge volume and diversity of the soil microbiome, as well as the fact that the most its part is nonculturable), full-fledged research in this field became possible only with molecular genetic methods of analysis, which reached its peak with the appearance of systems for high-throughput sequencing and modern software. However, the composition and structure of soil microbiocenosis are a reflection of the physico-chemical

characteristics of the soil, which must also be considered in analysis of the impact on soil microbiome of such environmental factors as plant community. Therefore, the goal of the present work is to analyze the structure of the microbiomes of the main soil types of Russia with different plant communities by high-throughput sequencing.

MATERIALS AND METHODS

Soil Sampling. In September 2014 a number of expeditions in different regions of Russia were organized, and a representative collection of the main types of soils of Russia, supplemented with samples taken in 2012–2013 in Kazakhstan, was created. The final collection consisted of 93 samples and included the main types (subtypes) of soils: podzolic, sod-podzolic, grey forest, brown, chernozems, and soils of chestnut–solonetz complex and solonchak. The soil samples were selected in both natural plant communities (forests, steppes, and soil of fallow grassland with zonal vegetation) and agrophytocenosis (Table 1). All samples were taken from the upper (humus accumulative) horizon from a depth of 0–15 cm. The main physical-chemical indicators were determined (Tables 2, 3); in the case of the soils of the West Kazakhstan region, special attention was paid to indicators of salinity. Symbols referring to the geographical region of the selection were attributed to the samples (see Table 1).

Analysis of physico-chemical parameters of the soils was made according to generally accepted methods and guidelines: GOST 26423-85 (pH of aqueous extract), GOST 26213-91 (organic matter, %), GOST 26423-85 (total nitrogen, %). The content of mobile forms of phosphorus and potassium in soil samples with pH in excess of 6.5 was determined by Machigin method (GOST 26205-91); in soils with pH values less than 6.5, it was determined by the Kirsanov method (GOST R 54650-2011).

DNA extraction was carried out with the PowerSoil® DNA Isolation Kit (MoBio Laboratories, United States). A Precellys 24 device (Bertin Technologies, France) was used for the mechanical destruction of soil samples. The final DNA concentrations averaged 50 ng/μL. Amplicon libraries of taxonomically significant 16S rRNA gene of bacteria and archaea using universal primers F515 (GTGCCAGCMGCCGCGGTAA) and R806 (GGACTACVSGGGTATCTAAT) for the variable area V4 (approximately 400 bp) containing oligonucleotide identifiers for each sample and supporting sequences were created to conduct taxonomic analysis of the soil microbiome. Pyrosequencing of the nucleotide sequences was performed with the GS Junior (Roche, United States) according to the recommendations of the Roche Company.

Data processing was carried out in the QIIME version 1.8.0 [8]. At the first stage, tags and primers were removed from the read DNA fragments, and the quality of the nucleotide sequences was checked. Primers or homopolymer areas longer than 8 bp were deleted from analysis sequences that had a length less than 200 base pairs (bp) with a quality score less than 25 and contained errors in the barcodes. Chimeric sequences were removed from the library with the use of the ChimeraSlayer module included in the package of QIIME 1.8.0. At the next stage, alignment of the nucleotide sequences was carried out with the PyNast algorithm, and a matrix of genetic distances was constructed.

The grouping of sequences into Operational Taxonomic Unit (OTU) was performed with the uclust algorithm [9] with standard (de novo) settings with a 97% threshold of similarity between sequences, which corresponds to species. Selection of the representative sequences in each OTU group was performed by the most_abundant method. Taxonomic genus identification of sequences was performed with the RDPII database (Ribosomal Database Project, http://rdp.cme.msu.edu/). For all samples the biodiversity of prokaryotic communities was analyzed at the level of beta diversity via mapping of the samples in multidimensional space by principal coordinates analysis (PCoA) of the genetic distances of microbiomes obtained by weighted Unifrac [3]. The significance of statistical differences between the microbiomes in the soil of various plant communities was estimated by means of one-way analysis of variance with post-hoc analysis by the Fisher LSD method in the program STATISTICA 10 Enterprise (www.statsoft.ru). The standard Mantel test with Pearson's correlation coefficient was used to analyze the relation of taxonomic structure with the physico-chemical parameters of the soil.

RESULTS AND DISCUSSION

Data analysis of high-throughput sequencing. In total, the analysis included 271 673 sequences with an average grade of sequences in the sample 2632. Taxonomic analysis revealed the representatives of 42 bacterial and 2 archaeal phyla, among which the dominant positions were occupied by representatives of ten phyla: nine bacterial (*Actinobacteria* (33.5%), *Proteobacteria* (28.4%), *Acidobacteria* (8.3%), *Verrucomicrobia* (7.7%), *Bacteroidetes* (4.2%), *Chloroflexi* (3.0%), *Gemmatimonadetes* (2.3%), *Firmicutes* (2.1%), *Planctomycetes* (2.0%)) and one archaeal *Crenarchaeota* (2.6%), the share of which reached maximum values in the chestnut soils of West Kazakhstan region (6.1%) and sod-podzolic soils in Pskov region (5.5%).

In the context of more detailed taxonomic analysis of the composition of the soil microbiome, the representatives of the 529 families were identified. The composition of bacteria at a given taxonomic level is largely determined by such factors as soil type, sample region, and the nature of the vegetation (Fig. 1).

Table 1. Description of soil sample sites

Type of biome (type of exposure)	Sample ID	Sampling point	Type/subtype of soil (according to the Classification and Diagnostics of Soils, 1977)
Fallow from 1964	PS1	Pskov Oblast. (Pskov Research Institute of Agriculture)	Podzolic/sod-podzolic
Alder outlier	PS2		Same
Arable land	PS3–5		"
Fallow from 1994	BG1–BG15	Leningrad region (Research Institute Belogorka)	"
Forest of temperate zone	BG16–BG30		Podzolic
Arable land	BG31–33		Podzolic/sod-podzolic
Fallow from 1882	KS1–KS3	Voronezh oblast (Stone Steppe Reserve)	Chernozem/typical chernozem
Windbreak	KS4–KS11		Same
Arable land	KS12		"
Fallow	OR1	Orlov oblast (Orlov State Agrarian University)	Gray forest
Fallow	OR2		Chernozem/podzolized chernozem
Arable land	OR3		Gray forest
Arable land	OR4		Chernozem/podzolized chernozem
Windbreak	OR5		Gray forest
Windbreak	OR6		Chernozem/podzolized chernozem
Steppe	KP1	Reserve Kulikovo Pole	Gray forest
Steppe	KP2		Chernozem/podzolized chernozem
Virgin soil	CH1–2	Republic of Kazakhstan, shore of the salty lake Akkol	Solonchak
Virgin soil	CH3		Solonetz
Virgin soil	CH4–CH6		Chestnut soil
Virgin soil	KAZ1	West Kazakhstan region	Solonetz/chestnut solonetz
Virgin soil	KAZ2–3		Chestnut soil/dark chestnut soil
Virgin soil	KAZ4		Solonchak
Virgin soil	KAZ5		Meadow-chestnut
Virgin soil	KAZ6		Chestnut soil/dark chestnut soil
Virgin soil	KAZ7–8		Chestnut soil/light chestnut soil
Virgin soil	KAZ9		Chernozem/south chernozem
Virgin soil	KAZ10		Alluvial/floodplain chestnut
Grass land	KAZ11		Brown/brown solonetzic
Grass land	KAZ12		Chestnut soil/light chestnut soil
Arable land	KAZ13		Chestnut soil
Fallow	KAZ14		Chestnut soil/dark chestnut soil
Fallow	KAZ15		Chestnut soil/dark chestnut soil
Grass land	KAZ16		Meadow-chestnut
Hay field (grass land)	KAZ17		Meadow soil
Arable land	KAZ18		Chernozem/south chernozem
Fallow	KAZ19		Chestnut soil/dark chestnut soil
Fallow	KAZ20		Solonetz/chestnut solonetz
Old-growth forest	KR1–9	Crimea (Nikita Botanical garden)	Brown soil

Table 2. Agrochemical analysis of the studied soil samples (soils of the Russian Federation)

Sample ID	pH_{water}	Total nitrogen, %	Mobile phosphorous, mg/kg	Mobile potassium, mg/kg	Organic matter, %
BG1–BG5	6.26	0.02	362	141	3.02
BG6–BG10	6.33	0.005	278	161	2.63
BG11–BG15	6.26	0.004	268	60	1.75
BG16–BG20	5.90	0.006	34	50	1.75
BG21–BG25	5.54	0.026	69	20	1.66
BG26–BG30	4.74	0.019	91	137	1.56
BG31	6.04	0.043	282	154	2.23
BG32	5.31	0.013	357	127	3.11
BG33	6.18	0.002	347	50	2.27
PS1	7.21	0.002	66	94	2.82
PS2	7.47	0.080	48	280	9.21
PS3	6.06	0.034	194	154	3.78
PS4	5.82	0.004	226	134	3.42
PS5	6.19	0.007	241	84	2.92
KS1–KS3	6.78	0.085	119	330	10.49
KS4	5.87	0.063	5	530	11.48
KS5	6.39	0.084	7	706	12.61
KS6	6.56	0.083	73	962	14.27
KS7	6.98	0.212	9	706	11.72
KS8	7.19	0.039	45	628	10.20
KS9	5.43	0.072	113	922	12.76
KS10	5.87	0.081	39	569	10.60
KS11	5.69	0.169	65	1256	13.59
KS12	6.60	0.115	355	322	7.92
OR1	6.55	0.063	346	267	6.10
OR2	6.94	0.009	386	239	5.92
OR3	6.20	0.010	419	224	4.61
OR4	6.56	0.123	337	153	4.96
OR5	6.70	0.117	383	306	5.42
OR6	6.24	0.007	97	432	5.97
KP1	5.94	0.004	293	141	7.95
KP2	6.60	0.012	365	349	8.39
KR1	7.65	0.091	49	1177	14.15
KR2	8.03	0.086	3	1276	13.20
KR3	7.64	0.073	3	1177	10.76
KR4	7.71	0.070	<1	549	10.40
KR5	7.66	0.081	12	903	12.17
KR6	7.49	0.078	5	824	11.65
KR7	7.86	0.045	39	628	8.90
KR8	7.91	0.145	57	1295	14.22
KR9	7.73	0.102	34	726	10.28

Table 3. Agrochemical analyses of samples of saline soils (Kazakhstan)

Sample ID	C_{org}, %	pH of water extract	Anionic-cationic composition of the aqueous extract , %					Total amount of salts , %
			Cl	SO_4	Ca	Mg	Na	
KAZ1	1.9	8.38	2.49	0.11	0.53	0.62	2.13	0.202
KAZ2	3.6	8.69	3.08	0.04	1.53	0.32	1.59	0.202
KAZ3	3.81	8.84	2.72	0.14	1.34	0.08	2.45	0.226
KAZ4	2.96	8.64	12.55	15.3	15.69	3.24	9.05	1.705
KAZ5	3.25	8.95	0.19	1.05	0.24	0.05	1.44	0.257
KAZ6	2.54	8.06	0.12	1.84	0.61	0.27	1.31	0.272
KAZ7	1.62	9.61	2.63	0.02	1.81	0.77	0.59	0.184
KAZ8	2.05	8.33	0.76	0.05	0.66	0.18	0.46	0.076
KAZ9	3.74	8.37	0.001	0.08	0.003	0.001	0.036	0.16
KAZ10	3.91	8.41	0.05	0.03	0.35	0.01	0.02	0.041
KAZ11	1.04	8.63	0.014	0.007	0.005	0.003	0.003	0.039
KAZ12	1.5	9.11	0.009	0.024	0.005	0.002	0.013	0.065
KAZ13	2.35	8.52	0.004	0.002	0.005	0.002	0.002	0.032
KAZ14	2.67	8.73	0.016	0.007	0.008	0.003	0.004	0.05
KAZ15	2.82	8.52	0.011	0.007	0.008	0.002	0.002	0.038
KAZ16	2.95	8.42	0.009	0.005	0.005	0.003	0.002	0.039
KAZ17	3.09	8.34	0.007	0.002	0.003	0.003	0.003	0.033
KAZ18	2.81	8.31	0.009	0.002	0.01	0.002	0.002	0.049
KAZ19	2.34	8.66	0.025	0.053	0.005	0.003	0.053	0.2
KAZ20	2.45	8.51	0.06	0.005	0.015	0.012	0.016	0.148
CH1	1.17	8.2	25.88	53.38	21.6	3.048	15.92	1.234
CH2	1.17	8.3	4.46	76.13	21.56	1.896	11.18	1.192
CH3	2.05	8.4	1.38	11.23	4.06	0.912	1.334	0.225
CH4	0.98	8.9	0.354	0.192	0.16	0.096	1.173	0.057
CH5	0.78	8.3	0.32	<0.096	0.28	<0.024	0.276	0.029
CH6	1.27	7.2	0.49	0.288	0.12	0.036	0.069	0.014

Influence of soil characteristics on taxonomic structure of soil microbiomes. In the analysis of the connection of soil microbiome with the physico-chemical characteristics of different soil types, the significant correlation values were obtained for pH values of soil ($r = 0.53$–$0{,}56$, $p = 0.001$), potassium ($r = 0.20$–0.21, $p = 0.001$), and samples taken along the gradient of salinity on the shores of salt lake Akkol (Shyngyrlau) with the values of the total content of salts in the soil ($r = 0.60$, $p = 0.001$).

Since the presence in the soil profile of soluble salts is a fairly strong factor influencing the structure of the soil microbiome, the influence of physico-chemical parameters in samples of nonsaline soils (soil samples from the territory of the Russian Federation) were analyzed separately. In this case, there was also a statistically significant correlation of biodiversity of soil microbiome with the content of organic matter in soil ($r = 0.41$–0.45, $p = 0.001$).

The soil acidity mainly affected the content in soil of bacteria from the *Acidobacteria* phylum (representatives of the phylum dominate in acidic sod-podzolic soils of the Leningrad Region with pH values of 4–5; their share in these soils reaches 20%) and *Actinobacteria* abundant in soils with neutral and slightly alkaline pH values (the proportion of representatives of this phylum was maximum in alkaline soils of arid regions Crimea and Kazakhstan and reached 49.9%). In sod-podzolic soils of the temperate zone, acidobacteria from the class *Acidobacteria*-2 and also actinobacteria of the order Actinomycetales and genus *Solibacter* dominated. In the southern regions of Russia, the composition of the microbial community changed with an increase in the hydrothermal ratio and pH value: in chernozem, the number of bacteria from the Solirubrobacteriales order and thermophilic actinobacteria of the Gaiellaceae family increased; in chestnut soils, the percentage of actinobacteria from

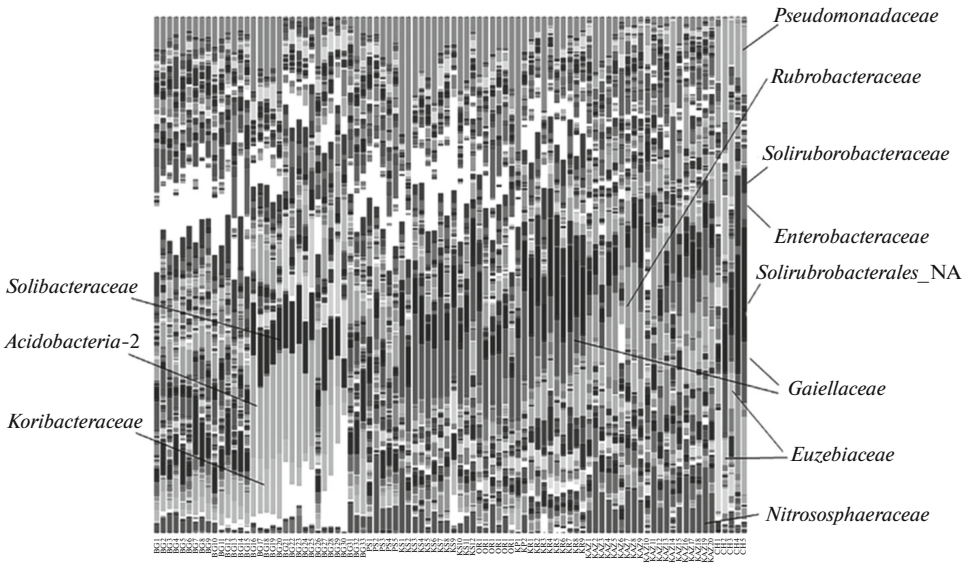

Fig. 1. Taxonomic structure of microbiomes of different soil types with various plant communities at the level of families.

Micrococcales order and *Rubrobacter* genus significantly increased. The samples taken along the gradient of salinity on the shores of salt lake Akkol also formed a distinct group with a predominance of bacteria of the Pseudomonadaceae and Euzebyaceae families (representatives of this family belong to the group of marine actinobacteria) [10] (see Fig. 1).

Differences in the taxonomic structure of microbiomes confirm the data from cluster analysis showing that the separation of clusters is mainly due to the soil type. All of the studied soil types formed separated clusters; chernozem, brown, and gray soils formed clusters with high values of statistical support—jackknife values from 60 to 100% (Fig. 2).

Thus, soil acidity is the most powerful factor in its effects on microbiota (Fig. 3), which determines the dynamics of the microbiome on the level of such taxa as phylum.

Influence of plant communities on the taxonomic structure of the microbiome. According to the data obtained by the methods of multivariate statistics, it can be concluded that a weaker but still significant factor influencing the taxonomic composition of the microbiome is the vegetation type that defines the genus structure of the community. We have identified six major types (groups) of vegetation: (1) woody vegetation of temperate latitudes; (2) woody vegetation of forest-steppe zone (broad-leaved species); (3) shrubs; (4) herbaceous vegetation of the temperate zone; (5) xerophytic vegetation of southern Russia and Kazakhstan; and (6) agrophytocenoses formed by cultivated plants. As can be seen from Fig. 3, each of these groups forms a separate area on the plot; it is worth considering the fact that the vegetation may belong to the category of secondary factors affecting the taxonomic composition of the microbiome. For example, the separation of the group of xerophytic vegetation may result from insufficient soil moisture, and the formation of a group of coniferous forests may be a consequence of the low values of soil acidity (see Fig. 3b).

Therefore, the most appropriate model for determining the effect of vegetation type on the taxonomic composition of the microbiome is an analysis of different plant synusiae in the same soil type in samples with similar values of soil acidity. For these purposes, an analysis of soil samples within various plant synusiae in the Leningrad Region was conducted (Table 4). All samples were divided into three groups according to the type of vegetation: areas with herbaceous vegetation (BG 1–15), forests (aspen, pine, spruce—BG 16–30), and areas with stubbles of agricultural plants (BG 31, 32, 33). In each of the groups characteristic patterns of taxonomic bacterial community were identified (Fig. 4). In the soil microbiome of forest phytocenosis (BG 16–30), the proportion of actinobacteria generally decreased for the families Frankiaceae (0.04% as compared to fallow soil (0.2%, $p < 0.05$) and agrophytocenosis soil (0.4%, $p < 0.05$) and Gaiellaceae (0.8% as compared to the fallow soil (2.8%, $p < 0.05$) and the agrophytocenoses soil (3.8%, $p < 0.05$)), while the proportion of acidobacteria of the Acidobacteriales order (family Koribacteraceae (7.2%, $p < 0.05$) and Acidobacteraceae (6.4%, $p < 0.004$) increased in the microbial community of the forest, which may be due to the acidic reaction of needle litter.

In the fallow-soil microbiocenosis, the proportion of proteobacteria of the families Hyphomicrobiaceae (10.7%, $p < 0.0004$), Bradyrhizobiaceae (4.2%, $p < 0.023$), Bacillaceae (0.8%, $p < 0.028$), and Paenibacillaceae (0.8%, $p < 0.04$) significantly increased. The bacteria Hyphomicrobiaceae and Bradyrhizobiaceae play an important role in the processes of transformation of

Fig. 2. Cluster analysis of the microbiomes of the studied soil samples.

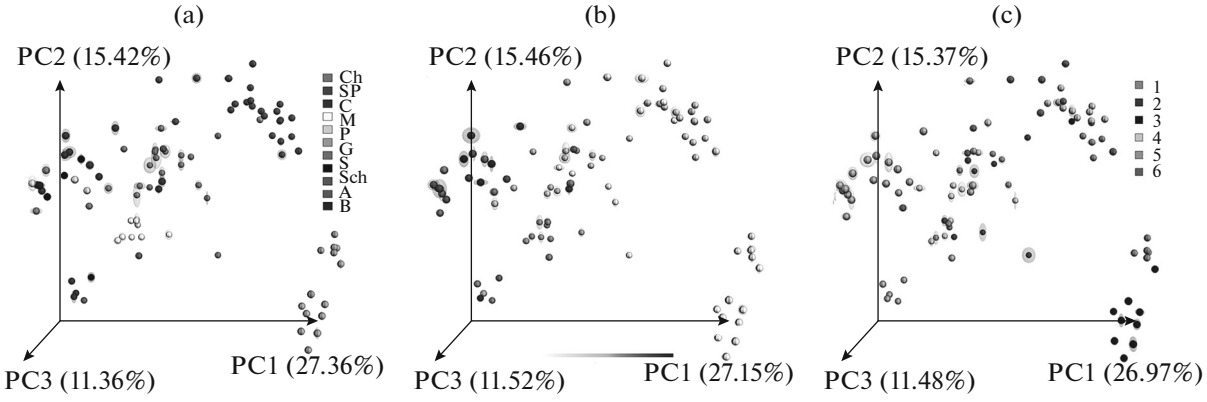

Fig. 3. Analysis of the main coordinates of genetic distances of microbiomes obtained by weighted Unifrac. Grouping of the samples was carried out according to (a) soil type, (b) pH values of the aqueous extract from the soil sample, (c) phytocenosis: Ch—chernozem; SP—sod-podzolic; Cn—chestnut; C—cinnamonic; M—meadow; P—podzolic; G—gray; S—solonetz, Sch—solonchak; A—alluvial; B—brown. (1) shrub, (2) deciduous forest; (3) trees of temperate zone; (4) grass vegetation; (5) xerophytic herbaceous vegetation; (6) agrophytocenosis.

carbon and nitrogen in the soil [11]. The bacteria of the Bacillaceae and Paenibacillaceae families are often found in the rhizosphere of herbaceous plants; many of them are in the group of plant-growth–promoting bacteria (PGPB). Some members of the Paenibacillaceae family have the ability to dissolve phosphates, which may also play a positive role in providing plants with available forms of phosphorus [12].

Table 4. Geobotanical description of studied plant communities in Leningrad oblast

Sampling point	Sample ID	Geobotanical description
Fallow from 1994	BG1–BG5	Catgrass and goldenrod synusia (grass-bush layer: *Dactylus glomerata*, *Solidago virgaurea, Angelica sylvestris, Trifolium pratense, Taraxacum officinale*, *Equisetum pratense;* moss-lichen cover: *Mnium*; bush layer: *Ribes rubrum*). Projective cover 100%.
Fallow from 1994	BG6–BG10	Fireweed–catgrass synusia (grass–bush layer: *Dactylus glomerata*, *Chamerion angustifolium, Taraxacum officinale, Artemisia* sp., *Achillea millefolium*)
Fallow from 1994	BG11–BG15	Part of birch forest with willow (tree layer: *Betula pendula, Salix caprea;* undergrowth*: Quercus robur, Picea abies, Betula pendula;* grass-bush layer: *Dactylus glomerata*, *Solidago virgaurea, Taraxacum officinale, Deschampsia cespitosa*). Projective cover 75%.
Forest	BG16–BG20	Part of aspen forest (tree layer: *Populus tremula, Pinus silvestris,* undergrowth: *Quercus robur, Picea abies, Acer platanoides Sorbus aucuparia, Prunus padus;* grass-bush layer: *Vaccinum vitis-idaea, Veronica chamaedrys, Fragaria vesca, Solidago virgaurea, Athyrium filix-femina, Oxalis acetosella, Maianthemum bifolium, Impatiens noli-tangere, Aegopodium podagraria, Vaccinium myrtillus, Deschampsia cespitosa*)
Forest	BG21–BG25	Part of fir–oxalis–raspberry–goutweed–mnuim forest (*Picea abies*, *Sambucus racemosa*; bush layer: *Rubus idaeus* L., *Veronica chamaedrys, Athyrium filix-femina, Oxalis acetosella, Maianthemum bifolium, Impatiens noli-tangere, Vaccinium myrtillus*; moss-lichen cover: *Mnium, Dicranum polysetum*)
Forest	BG26–BG30	Part of pine–hairy woodrush forest (tree layer*: Pinus silvestris;* undergrowth*: Quercus robur, Picea abies, Sorbus aucuparia, Pinus silvestris;* grass-bush layer*: Solidago virgaurea, Oxalis acetosella, Maianthemum bifolium, Meiampyrum nemorosum, Festuca ovina, Taraxacum officinale, Luzula pilosa, Achillea millefolium, Rumex confertus*)
Arable land	BG31	Crop residues of spring barley (*Hordeum vulgare,* grass-bush layer: *Phleum pretense, Veronica chamaedrys*, *Taraxacum officinale, Matricaria matricarioides, Matricaria chamomilla, Rumex confertus, Plantago major, Capsella bursa-pastoris, Viola tricolor*)
Arable land	BG32	Crop residues of rape (*Brássica napus,* grass-bush layer: *Phleum pretense, Rumex confertus, Dianthus deltoides*)
Arable land	BG33	Crop residues of fall rye (*Secale cereale*, grass-bush layer: *Rumex confertus, Plantago major, Mentha arvensis, Atriplex verrucifera*)

In the agrocenosis soil, the percentage of actinobacteria of the Intrasporangiaceae and Nocardioidaceae families, proteobacteria Haliangiaceae (class *Deltaproteobacteria*), [Kouleothrixaceae] (phylum Chloroflexi), and archaea Nitrosospheraceae significantly increased (see Fig. 4). Cellulosolytic bacteria of the Intrasporangiaceae family were discovered in the rhizosphere community of cultivated plants [13]; bacteria of the Chloroflexi phylum dominated in the bacterial community of cellulosolytic microorganisms in model experiments [14]. It was shown [15] that the use of fertilizers led to an increase of the relative proportion of archaea in the community of microorganisms of typical chernozem in conditions on arable land.

However, the overall microbial community of the agrocenosis soil was not significantly different from the fallow-soil microbiome. For example, in the soils of both agrocenosis and fallow ground, the proportion of the bacterial families Oxalobacteraceae and Comamonadaceae (class *Betaproteobacteria*) increased. It is known from the literature [16, 17] that an increase in bacteria of the *Betaproteobacteria* phylum is often associated with agricultural use of the soil. No significant difference between fallow and arable soils can be a consequence of the fact that the former has still not recovered from anthropogenic influence (age of fallow at the time of sampling was 11 years, while about 20 years are needed to restore the natural physical and chemical parameters of sod-podzolic long-arable soil).

A detailed analysis of the influence of vegetation groups (synusiae) on the soil microbiome in forest and fallow ground was conducted. It was found that synusiae with predominant cat grass and goldenrod had the highest proportion of archaea of the Nitrososphaeraceae family and firmicutes of the Bacillaceae family. On soil with dominance of birch and willow, the proportion of alpha-proteobacteria of the Bradyrhizobiaceae, Sphingomonadaceae, and Rhodospirillaceae

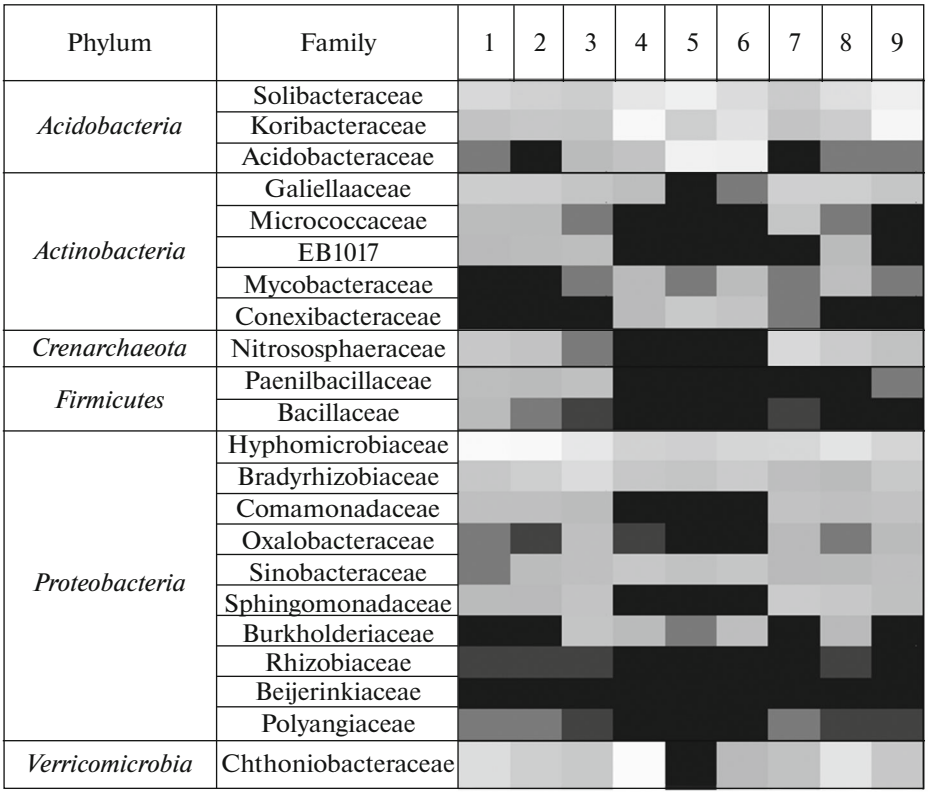

Fig. 4. Structure of the microbiomes of soil samples from Leningrad oblast: (1) Cat grass and goldenrod synusia; (2) fireweed and cat grass synusia; (3) birch and willow outlier; (4) part of aspen forest; (5) part of fir forest; (6) part of pine forest; (7) part of arable land with crop residues of barley; (8) part of arable land with crop residues of rape; (9) part of arable land with crop residues of winter rye. The presented families comprise more than 0.2% of the community.

families; beta-proteobacteria of the Oxalobacteraceae, Comamonadacea, and Burkholderiaceae families; and actinobacteria of the Microbacteriaceae and Frankiaceae families significantly increased. In the soil community of aspen woods the number of bacteria from the Verrucomicrobia phylum, as well as acidobacteria of the Sinobacteraceae, Acidobacteraceae families, actinobacteria of the Conexibacteraceae family, and bacteria of the Caulobacteraceae family (class *Alphaproteobacteria*), increased. The number of the last three taxa (Acidobacteraceae, Conexibacteraceae, and Caulobacteraceae) was maximal in soil microbial cenosis of coniferous woods of fir–oxalis–raspberry-mnuim forests and pine–hairy woodrush synusiae. The maximum content of proteobacteria of the Bejerinkiaceae family (2.2%) was recorded in the region of spruce forests.

The selected plant synusiae can be viewed as a variant of plant succession in the process of overgrowth of anthropogenically transformed soils with the vegetation of the temperate zone: thus, catgrass-goldenrod and fireweed-catgrass synusiae represent the first stage, the birch outlier with willow and the edge of the forest with the dominance of aspen in the tree layer characterize the intermediate (transitional) stage, and the fir forest is a climax state of phytocenosis at the zonal podzolic soil in Leningrad region. Therefore, the identification of character traits in the taxonomic structure of soil microbiomes specifically associated with a particular plant community may also reflect the succession of microbiomes in the process of restoration of anthropogenically disturbed soils.

Thus, in our study, data on the taxonomic structure of the microbiomes of soil samples of different climatic zones with plant communities of natural and anthropogenic origin was obtained. A major determinant of the taxonomic structure was acidity: soils with different pH values of the upper horizon were characterized by different ratios of microbial taxa of the high level (at the level of phyla and classes). The type of plant community plays a subordinate but still significant role in the formation of a specific metagenomic pattern: microbiomes of the soils occupied by herbaceous vegetation were characterized by a generally greater variety than the microbial community of the phytocoenoses with the predominance of tree and shrub vegetation. The differences in the composition of the microbiomes of different vegetation types were also observed for taxa of lower rank.

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