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RESTORATION OF SOIL MICROBIOME IN VARIOUS SOIL HORIZONS AFTER CROWN AND SURFACE WILDFIRES

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❀ Fires have a strong effect on soil microbiome, and the mechanisms of soil restoration after fires are currently not well understood. This study describes the characteristics of microbial communities in the Psamment Entisol soils of pine forests in the city of Togliatti after forest crown and surface fires. Geochemistry, soil respiration and microbial community structure via *16S* rRNA gene sequencing were studied in different soil horizons. Both crown and surface fires resulted in the variations of microbial diversity and shifts in taxonomic composition. There is a tendency to an increase in the proportion of representatives from phyla *Actinobacteria* and *Gemmatimonadetes* for soil samples recovering after fires. An increase in the proportion of bacteria (*Micrococcaceae*, *Blastocatellaceae*) associated with the degradation of substances formed after combustion also has been shown. The research has shown that the crown fire has a smaller effect on the soil microbiome than the surface fire, the largest changes in the microbiome structure were found in the intermediate horizon. At the same time, differences in the structure of the soil microbiome between horizons are intensified after exposure to the soil of a surface fire.

❀ **Keywords:** wildfire; soil microbiome; *16S* rRNA.

ВОССТАНОВЛЕНИЕ ПОЧВЕННОГО МИКРОБИОМА В РАЗЛИЧНЫХ ПОЧВЕННЫХ ГОРИЗОНТАХ ПОСЛЕ ВЕРХОВОГО И НИЗОВОГО ЛЕСНЫХ ПОЖАРОВ

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❀ Пожары оказывают сильное влияние на почвенный микробиом, при этом механизмы восстановления почвы после пожаров в настоящее время недостаточно изучены. В данном исследовании дана характеристика микробных сообществ в серогумусовых почвах сосновых лесов г. Тольятти после верхового и низового пожаров. Было проведено филотипирование микробных сообществ по гену *16S* рРНК в различных почвенных горизонтах. Как верховой, так и низовой пожары привели к изменению разнообразия в таксономическом составе почвенного микробиома. Для проб почв, восстанавливающихся после пожаров, была показана тенденция к увеличению доли представителей типов *Actinobacteria* и *Gemmatimonadetes*. Также было показано увеличение доли бактерий (*Micrococcaceae*, *Blastocatellaceae*), связанных с деградацией веществ, образующихся после сгорания. Настоящее исследование показало, что верховой пожар оказывает меньшее влияние на микробиом почвы, чем низовой, при этом наибольшие изменения в структуре микробиома были обнаружены в промежуточном горизонте почвы. Было показано увеличение различий в структуре почвенного микробиома между горизонтами после воздействия на почву низового пожара.

❀ **Ключевые слова:** лесные пожары; почвенный микробиом; *16S* рРНК.

INTRODUCTION

Forest fires have the most severe and complex impact on the ecosystem, with both direct and indirect impact on the soil. After a wildfire, the soil's chemical composition changes radically, as the amount of available nitrogen and carbon decreases due to their direct burnout. After pyrogenesis, a layer of ash is generated in the soil, which in turn affects the pH (the soil becomes acidic) and degree of nitrogen availability [1, 2]. The death of the vegetation cover affects the rhizosphere microbiome. According to reports, wildfire significantly reduces the biodiversity of the soil microbiome, whereas the shift in diversity is noted primarily in the upper soil layer that is directly exposed to heating. In addition, heat exposure reduces the biomass of microorganisms. At the same time, the composition of the microbiome changes, and fungi begin to predominate in the soil, which are less resistant to heating than bacteria (bacterial endospores can survive the significant heating of the soil) [3], and spore-forming Gram-positive bacteria begin to prevail [4]. Soil microbiome changes persist for a long period — for years and even decades [5].

The soil microbiome plays a significant role in the restoration of the postfire ecosystem. The role of the Actinobacteria phylum is especially prominent, and the role of its representatives from the *Arthrobacter* and *Streptomyces* genera in the restoration of nitrogen balance in postpyrogenic soils has been revealed [6]. In addition to their participation in the nitrogen cycle, many Actinobacteria representatives are active parts of the rhizosphere and can stimulate plant growth.

This study focused on the soil microbiome changes after a forest fire in the vicinity of Togliatti (Russia, Samara region). The studied sampling points have already been described by a team of authors both from a geochemical standpoint and from the standpoint of studying the soil's functional activity [7]. Forest fires cause significant changes in the physical and chemical characteristics of the upper soil layer, and changes in the micromorphological structure of the upper soil horizons and the accumulation of combustion products in the pyrogenic horizons occur. In this case, the parameters characterizing the state of the microbiome (basal respiration and mycelial length of fungi and actinomycetes) approach the indicators close to the control already 2 years after a forest fire [7]. The study aimed to analyze the compositional changes in the soil microbiome using phylotyping methods for the 16S rRNA gene using Illumina (USA) next-generation sequencing technologies.

The literature described several studies of soil microbiome changes using phylotyping for 16S rRNA after forest fires, both within several weeks after a forest fire [7, 8] and during longer chronoseries [9, 10]. A laboratory approach to studying the microbiome adaptation to pyrogenic carbon is also of interest [4]. Unfortunately, data on the study of the soil microbiome after pyrogenic exposure are incomplete and often contradictory, which may be associated with the differences in the type of soil studied and the geography of the studies. The differences in the work methodology should also be taken into account.

This study aimed to identify the groups of microorganisms associated with the degradation of substances formed after combustion and the structural changes in the soil microbiome during soil recovery after various types of forest fires in different soil horizons using Illumina sequencing technologies.

MATERIALS AND METHODS

Soil samples were taken 2 years after extensive forest fires in 2010 from a pine forest of the Samara region near the city of Tolyatti (53°29′43.80″N, 49°20′56.44″E, 179 m above sea level). These soils were formed on sandy alluvial dunes and classified as gray-humus soils. Samples were taken from three points, namely, in the forest affected by a surface fire, in the forest affected by a crown fire, and at the control point. As a control, identical gray-humus soils under a pine forest, located in the nearest zone not affected by forest fires, were studied. Three soil sections were made at each point under study. Samples were taken from soil sections 1 to 1.2 m deep from the soil horizons of AY (5–15 cm), AC (15–25 cm), and C (25–70 cm). The soil profiles were described, and the samples were taken for microbiome and chemical analyses in triplicate.

The physical and chemical analysis of the soil was conducted according to the method described previously in detail [7]. DNA was isolated using the developed method [11] with glass beads of various

diameters as an abrasive material. The soil sample was destructed on a Precellys 24 homogenizer (Bertin Technologies, France). The purity of the isolation and the amount of DNA isolated were tested by electrophoresis in 1% agarose in 0.5× TAE buffer. The average DNA concentration in the sample was 50 ng/ml. The purified DNA preparations were used for quantitative polymerase chain reaction (PCR) and preparation of amplicon libraries (primers F515 5′GTGCCAGCMGCCGCGGTAA-3′ and R806 5′GGACTACVSGGGTATCTAAT-3′ [12]) according to the instructions for the sequencing protocol supplied by Illumina. Sequencing and primary data processing were performed on an Illumina MiSeq device at the Genomic Technologies and Cell Biology Center for Collective Usage of the All-Russian Scientific Research Institute of Agricultural Sciences. For quantitative PCR, primers were used for three groups of microorganisms, namely, bacteria EUB338 (ACTCCTACGGGAGGCAGCAG) and EUB518 (ATTACCGCGGCTGCTGG) [13], archaea ARC915f (AGGAATTGGCGGGGGAGCAC) and ARC1059r (GCCATGCACCWCCTCT) [14], and fungi ITS1f (TCCGTAGGTGAACCTGCGG) and 5.8S (CGCTGCGTTCTTCATCG) [15]. The qPCRmix-HS SYBR kit (Evrogen, Russia) was used to prepare the reaction mixture according to the manufacturer's instructions. A series of 10-fold dilutions of 16S fragments of *Escherichia coli* and *Helicobacter pylori* and *ITS1 Saccharomyces cerevisiae* were used as standards. The measurements were performed on a CFX96 amplifier (Bio-Rad, Germany) according to the following protocol: 95 °C for 3 min and then 40 cycles at 95 °C for 20 s, 50 °C for 20 s, and 72 °C for 20 s. Each sample was presented in triplicate.

The sequenced 16S rRNA gene sequences were processed using the R [16] and QIIME2 [17] software packages. Rstudio [18] was used as a development environment for R. For the initial processing of raw sequences, the dada2 package was used [19], which obtained more reproducible and accurate results due to the use of denoizing algorithms, rather than clustering of phylotypes, in contrast to more classical approaches [20]. The taxonomic affiliation of phylotypes was determined using the RDP classifier based on the Silva 132 database [21]. The phylogenetic tree was constructed in the QIIME2 software environment using the SEPP package [22]. For some analyses, data normalization was performed using the rarefaction algorithm in the QIIME2 software environment during the analysis of α-diversity according to the basic recommendations of the developers. The normalization was performed by variance stabilizing transformation in the DESeq2 package [23] to compare the relative abundance of phylotypes in the samples. The analysis of α-diversity (QIIME2) and β-diversity was carried out (for the analysis of β-diversity, the communities were compared to the construction of a matrix of their similarities/differences using the weighted and unweighted UniFrac and Bray–Curtis algorithms). The reduction of the dimension of the similarity/difference matrices during data visualization for the study of β-diversity was performed using nonmetric multidimensional scaling (NMDS). PERMANOVA [24] presented in the form of the adonis2 function as part of the vegan package [25] was used as the statistics of sample separation in the analysis of β-diversity. The influence of the physical and chemical parameters of the soil on the composition of the microbiome was also determined using the Mantel test (vegan). For this purpose, we compared the matrices constructed from the Bray–Curtis distances using the Pearson correlation with 9999 permutations. The R phyloseq [26], ggplot2 [27], ggpubr [28], dplyr [29], and tibble [30] packages were also used for data postprocessing and visualization.

The DESeq2 package was used as a tool to search for the relative representation between phylotypes. The prenormalized data were tested using the Wald test, and the Benjamini–Hochberg procedure was used to adjust the significance, and the threshold was 10% to filter out insignificant changes and the two times change in relative representation. To formalize the selection of the most significantly changing families, we used the random forest classifier (randomForest package [31], with 1000 trees) based on the DESeq2 package results (using the $\log_2$ fold-change parameter).

The analysis of the minor components of the conditionally rare taxa (CRT) community was performed using the SimpleRareToPrev.R script with a representation threshold of 0.001 and a *b*-value (a measure of binomial distribution) of 0.9 [32].

RESULTS

Analysis of the diversity of microbial communities

From 36 samples from 587,362 sequences, 8096 phylotypes were obtained. About 79.4% of them were identified to the family and 47.1% of the total number of phylotypes were identified to the genus. About 15% of the studied phylotypes were found in two or more samples. These phylotypes represented the majority of the amplicon library (77% of the total number of sequenced nucleotide sequences). The number of common phylotypes for the control site and surface fire was much less than for control and crown fire. At the same time, in the microbiome of the lower horizon, the core part was larger in terms of both the number and representation of common phylotypes. The results revealed that, under the influence of stressful conditions on the microbiome, both the relative number (from 40.1% for control to 13.9% for surface fire) and the absolute number (116 OTU-33 OTU) of phylotypes of the core microorganisms significantly decreased.

In the analysis of α-diversity (Table 1) using various methods of assessing the richness of species (total number of phylotypes and Faith's phylogenetic diversity index) and evenness (Simpson's inverse index, Shannon's index, and Faith's index), a decrease in diversity in the AC horizon of surface fire (except for phylogenetic diversity) and an increase in diversity in the middle horizon during a crown fire were noted. In addition, there was a significant increase in the richness of species and a decrease in evenness in the upper soil horizons after a crown fire.

Also, for the AC horizon during a surface fire, a decrease in the minor component was shown (the proportion of phylotypes with a relative proportion of <0.01% decreased from 49% to 35%). In particular, the middle AC horizon was characterized by a sharp change in the frequencies of abundance of the minor phylotypes when comparing their distribution at the control point and samples of the surface fire (Fig. 1). In the communities, there was a significant fluctuation in the frequencies of the minors, and this component was analyzed separately. To obtain additional information on the minor component change, a subgroup of CRT minor phylotypes (phylotypes with proportion that did not exceed 1%; the binomial distribution coefficient for samples was >0.9) was identified for each soil horizon. Then, 429 CRT for horizon C, 523 CRT for AC, and 1144 CRT for AY were obtained. When analyzing the constructed Bray–Curtis distances by the Mantel test for CRT and non-CRT phylotypes, a strong correlation was obtained for all horizons under study (AY: $R^2 = 0.7$, $p = 0.001$; AC: $R^2 = 0.8$, $p = 0.001$; C-AC: $R^2 = 0.82$, $p = 0.001$).

Table 1

Results of α-diversity analysis

Soil horizon and sampling point	No. phylotypes	Simpson	Shannon	Faith PD
AY, control	591 ± 14	8.2 ± 0.1	8.2 ± 0.1	52.9 ± 2.9
AY, crown fire	755 ± 93	7.3 ± 0.4	7.3 ± 0.4	44.9 ± 6.6
AY, surface fire	468 ± 25	7.5 ± 0.1	7.5 ± 0.1	50.6 ± 5.3
AC, control	582 ± 49	7.7 ± 0.1	7.7 ± 0.1	50.1 ± 3.9
AC, crown fire	755 ± 93	8.3 ± 0.1	8.3 ± 0.1	68.7 ± 5.2
AC, surface fire	468 ± 25	7.5 ± 0.1	7.5 ± 0.1	48.9 ± 3.4
C, control	499 ± 29	7.9 ± 0.1	7.9 ± 0.1	57 ± 3.5
C, crown fire	499 ± 20	7.8 ± 0.1	7.8 ± 0.1	50.5 ± 1.4
C, surface fire	394 ± 35	7.5 ± 0.4	7.5 ± 0.4	49.5 ± 4

Note. Shannon, Shannon's index; Simpson, Simpson's diversity inverse index; Faith PD, Faith's phylogenetic diversity index.

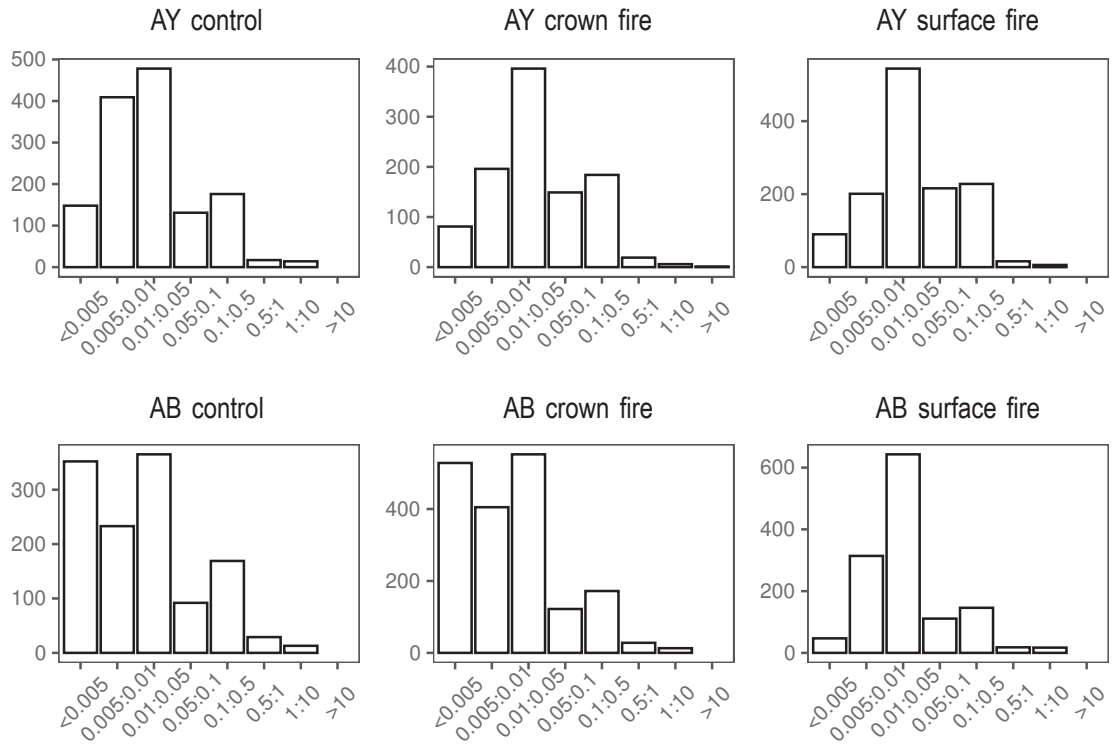

Fig. 1. Distribution of the representation of phylotypes by their frequencies. The abscissa represents the intervals of the relative representation of phylotypes (percentage of the total number of phylotypes in the sample), and the ordinate is the median number of phylotypes for a given range

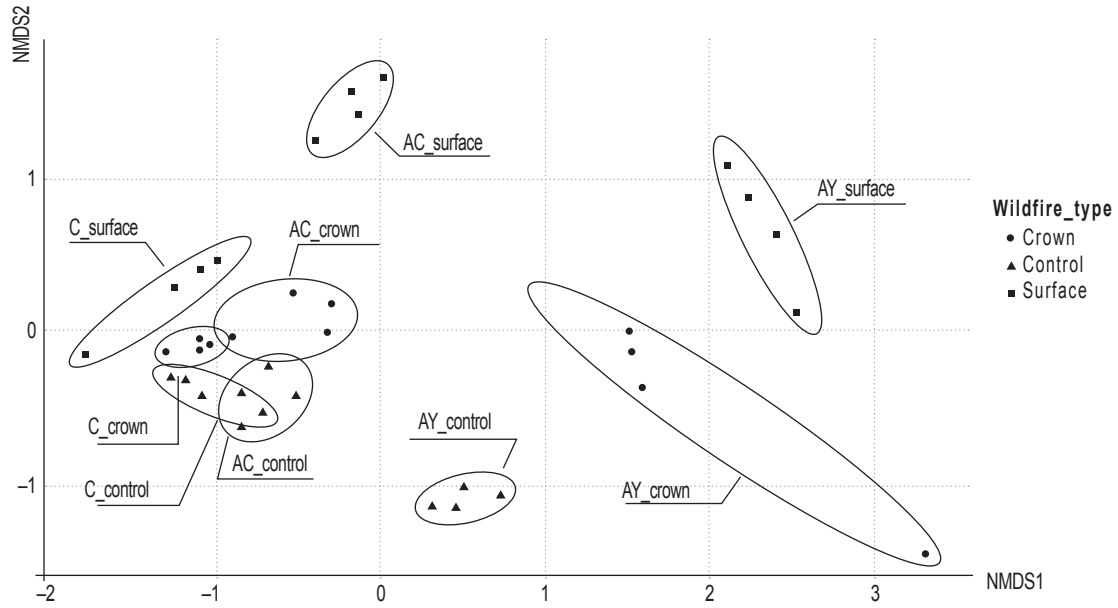

Fig. 2. Ordination of NMDS according to the distance of Bray – Curtis β-diversity of soil microbiome. The shape of the markers is the type of wildfire, and the figure captions are the horizon and the sampling point

In the analysis of β-diversity (Fig. 2) for each horizon, all microbiomes at all sampling points (control, point of surface fire, and point of crown fire) were significantly different. At the same time, using weighted metrics (taking into account the proportion of the phylotype in the community), the AC horizon stood out sharply (Bray–Curtis: $R^2 = 0.68$, $p_{adj} = 0.001$; weighted UniFrac: $R^2 = 0.71$, $p_{adj} = 0.002$; unweighted UniFrac: $R^2 = 0.3$, $p_{adj} = 0.002$).

Assessment of the number of microorganisms using real-time PCR

The control point was characterized by a significant (five to eight times) decrease in the number of analyzed groups of microorganisms from the upper soil horizons to the lower ones (Fig. 3). In the control samples, bacteria predominated in the communities, followed by archaea, and then fungi ranked third. Approximately the same picture was noted for the crown fire, although it was shown that the total number of microorganisms at the point of the crown fire decreased. The surface fire was characterized by a sharp decrease in the number of archaea in all horizons (13 times) and an insignificant decrease in bacteria (2 times), whereas the number of fungal ribosomal operons in the AY and C horizons did not significantly differ from the control. There were significant changes in the intermediate horizon AC during soil restoration in a surface fire. The total number of microorganisms in it is lower than in the underlying maternal horizon, and the number of ribosomal operons of archaea decreased by 70 times compared to the control.

Physical and chemical parameters of the soil and diversity of the microbial community

According to the Mantel test results (Table 2), a strong significant correlation was noted between the soil microbiome structure and the content of nitrites and substrate-induced respiration in the soil. A weaker correlation was noted for basal respiration and potassium content in soil.

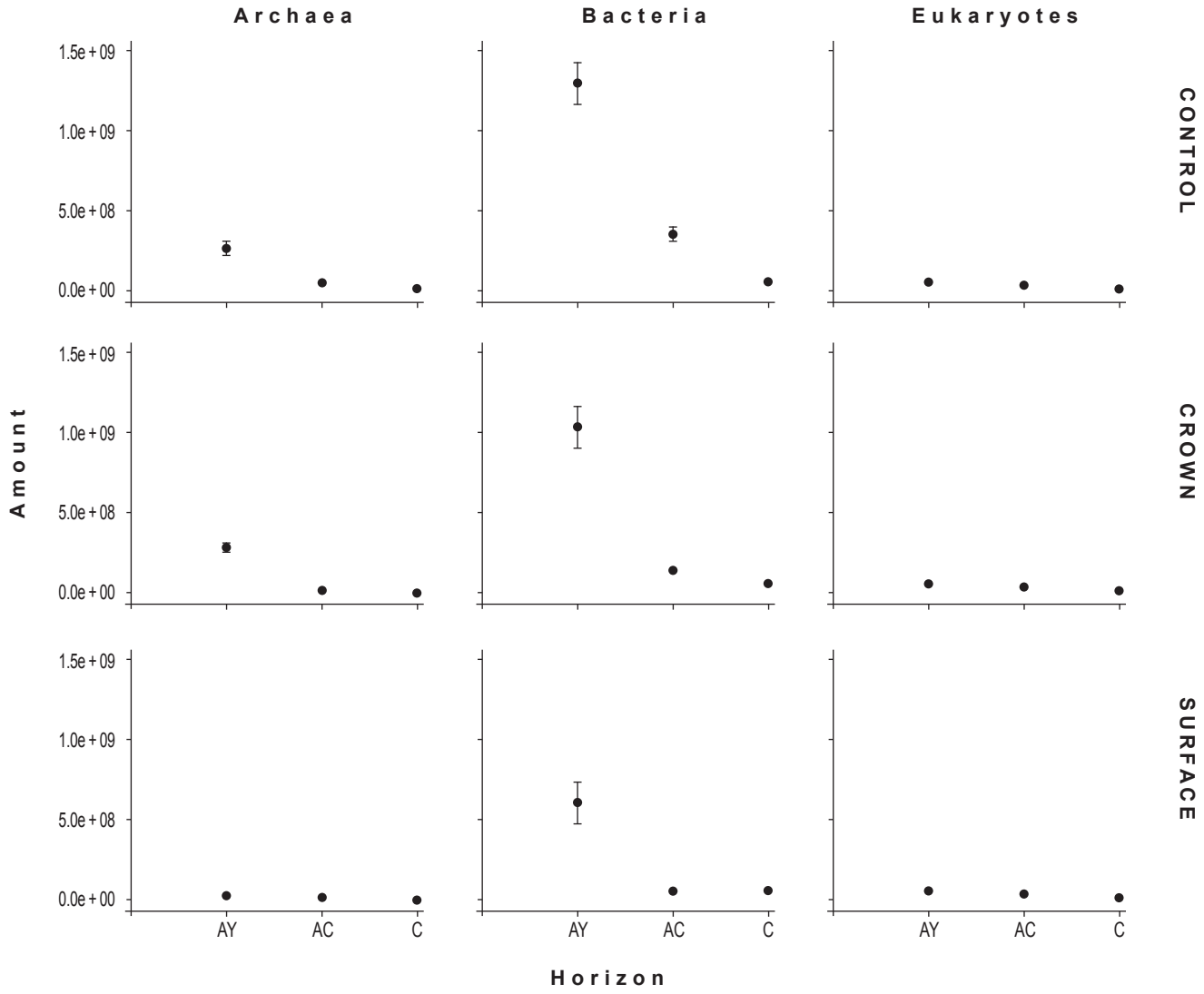

Fig. 3. Real-time PCR. Vertical lines represent the number of ribosomal operons; the mean error is noted

For the dominant systematic groups, the Mantel test was also performed for the geochemical parameters most influencing the microbiome (Table 3). Significant differences between the study groups were found in the correlation of the microbial community and pH and the correlation to the nitrite level in the soil. In contrast to the major bacterial phyla, the β-diversity of archaea does not correlate with the level of nitrates in the soil and demonstrates a strong significant correlation only with the level of substrate-induced respiration in the soil.

Taxonomic structure analysis

The predominant phyla in the studied samples for the upper horizon AY were the phyla *Proteobacteria* (40%), *Acidobacteria* (13.7%), *Actinobacteria* (13.6%), and *Bacteroidetes* (11.9%). For the AC horizon, they were the phyla *Proteobacteria* (36.5%), *Acidobacteria* (18.8%), *Actinobacteria* (12.3%), and *Bacteroidetes* (11.3%). In the AY horizon, in a crown fire, the representatives of *Acidobacteria* ($p_{adj} = 0.004$), *Alphaproteobacteria* ($p_{adj} = 0.026$), *Thaumarchaeota* ($p_{adj} = 8.4 \times 10^{-8}$), and *Bacteroidetes* ($p_{adj} = 0.044$) decreased significantly, the proportion of Actinobacteria ($p_{adj} = 0.0028$) increased significantly from 7.2% to 22.2%, and the proportion of the phylum Gemmatimonadetes increased ($p_{adj} = 3.6 \times 10^{-4}$). In the AC horizon, the proportions of *Bacteroidetes* ($p_{adj} = 0.025$) and *Thaumarchaeota* ($p_{adj} = 7.6 \times 10^{-11}$) decreased, and the proportions of *Acidobacteria* ($p_{adj} = 0.005$), *Planctomycetes* ($p_{adj} = 2.2 \times 10^{-4}$), *Deltaproteobacteria* ($p_{adj} = 0.003$), and *Gemmatimonadetes* ($p_{adj} = 3.4 \times 10^{-9}$) increased.

After a surface fire in the AY horizon, the proportion of the representatives of the phyla *Alphaproteobacteria* ($p_{adj} = 0.006$), *Thaumarchaeota* ($p_{adj} = 0.07$), and *Bacteroidetes* ($p_{adj} = 0.02$) decreased, and the proportions of *Cyanobacteria* ($p_{adj} = 0.006$) and *Gemmatimonadetes* ($p_{adj} = 0.04$) increased.

Table 2

Mantel test results for all samples

Parameter	R^2	p
pH	0.36	0.05
C	−0.14	0.6
N	−0.16	0.75
P_2O_5	0.15	0.37
K_2O	0.43	0.04
NH_4	−0.12	0.72
NO_3	0.67	0.02
Basal respiration	0.44	0.02
Substrate-induced respiration	0.6	0.002

Table 3

Mantel test results for the major taxonomic groups (large bacterial phyla and archaea)

Parameter	*Arhaea*		*Actinobacteria*		*Acidobacteria*		*Verrucomicrobia*		*Proteobacteria*		*Firmicutes*	
	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p
pH	−0.13	0.32	0.38	0.4	0.28	0.1	0.29	0.12	0.43	0.02	0.53	0.01
K_2O	0.4	0.19	0.49	0.01	0.35	0.08	0.32	0.16	0.4	0.01	0.53	0.01
NO_3	0.31	0.11	0.81	0.001	0.56	0.02	0.5	0.03	0.7	0.01	0.83	0.01
Basal respiration	0.37	0.16	0.49	0.003	0.44	0.02	0.46	0.04	0.35	0.04	0.5	0.03
Substrate-induced respiration	0.6	0.02	0.6	0.001	0.57	0.004	0.58	0.01	0.51	0.003	0.6	0.005

In the middle AC horizon, after a surface fire, the proportions of *Thaumarchaeota* ($p_{adj} = 0.014$), *Patescibacteria*, *Firmicutes*, and *Chloroflexi* decreased, and the proportions of *Alphaproteobacteria* ($p_{adj} = 0.047$), *Deltaproteobacteria* ($p_{adj} = 0.001$), *Actinobacteria* ($p_{adj} = 2.1 \times 10^{-8}$), *Planctomycetes* ($p_{adj} = 0.018$), and *Nitrospirae* ($p_{adj} = 0.003$) increased.

In the middle AC horizon at the point of the surface fire, compared to the control point, 152 phylotypes mainly related to the phyla Proteobacteria (31.6%), Acidobacteria (17.7%), Actinobacteria (16.8%), and Bacteroides (15.8%) increased significantly, and 267 phylotypes from the phyla Proteobacteria (30.1%), Acidobacteria (21.8%), Actinobacteria (10.9%), and Bacteroidetes (10.9%) decreased. In the upper horizon, 337 phylotypes from the phyla Proteobacteria (29.5%), Acidobacteria (16.5%), Actinobacteria (14%), and Bacteroidetes (11.2%) significantly increased, and 156 phylotypes from the phyla Proteobacteria (32.3%), Acidobacteria (23.2%), Bacteroidetes (14.8%), and Actinobacteria (7%) decreased.

After a crown fire, a smaller number of phylotypes changed than in a surface fire. In the middle horizon, 77 phylotypes increased and 100 phylotypes decreased. In the upper horizon AY, after a crown fire, 77 phylotypes significantly increased and 100 phylotypes decreased. At the same time, a strong asymmetry was noted in the distribution among representatives of Actinobacteria, as the number of Actinobacteria that increased in the upper horizon after a crown fire was more than twice the number of those that decreased. According to the above data, during a surface fire, the same tendency was noted for the upper soil horizon.

Despite the apparent similarity in the bacterial community changes in crown and surface fires, analysis of individual phylotypes revealed significant differences. Based on the comparison results of the control areas and those after a wildfire, using the random forest classifier, the most significantly changing families were identified based on the DESeq2 package results.

Compared to the control in the crown fire in the upper horizon AY, there was a decrease in the proportion of representatives of the TRA3-20 families of the Gammaproteobacteria class (widely represented unidentified minor phylotypes), the Rhizobiaceae division from the Xanthobacteraceae families (numerous unidentified phylotypes, identified phylotypes by the genera *Bradyrhizobium*, *Rhodoplanes*, and *Tardiphaga*; the major phylotypes Seq4, 1.2% in control; $p_{adj} = 0.0012$), and the Rhizobiales Incertae group.

For a surface fire in the upper horizon, the proportion of the *Rhizobiales Incertae* group also decreased, whereas some minor representatives of the *Xanthobacteraceae* family (Rhodoplanes, Seq274, Pseudolabris, etc.), in contrast to a crown fire, increased significantly in their representation.

For the upper horizon of postpyrogenic points, especially for the surface fire, the proportion of representatives of the *Nitrososphaeraceae* family of the phylum *Thaumarchaeota decreased*, although this family was represented by a large number of unidentified phylotypes with one dominant (Seq1, 3.9% at the control point). At the same time, minor phylotypes of *Nitrososphaeraceae* did not show significant changes between the points studied.

After the surface and crown fires in the upper horizon, the increase in major families from the phyla described above occurred, namely Actinobacteria (families Micrococcaceae and Microbacteriaceae) at the crown fire point and Actinobacteria (families Microbacteriaceae, Thermomonosporaceae, and Mycobacteriaceae), *Bacteroidetes* (*Flavobacteriaceae*), and *Chloroflexi* (*Caldilineaceae*) at the surface fire point. A sharp increase in two phylotypes, *Micrococcus* (absent in the control, 0.55% at the point of the crown fire) and *Pseudarthrobacter* (0.1 and 9.6%, respectively), was especially characteristic of a crown fire.

The middle horizon AC of postpyrogenic points, as well as the upper horizon, was also characterized by a decrease in the proportion of representatives of Xanthobacteraceae and *Rhizobiales Incertae*. For the point of crown fire, the proportion of representatives of the family *Nitrososphaeraceae* of the phylum *Thaumarchaeota* also decreased. In the middle horizon of the surface fire, Seq1 also decreased its abundance ($p_{adj} = 0.01$), but another phylotype, unique for the given specimen, appeared (Seq164, the proportion in the AC horizon of the surface fire is 1.02%).

The points of crown and surface fires were also characterized by a decrease in the proportion of the Myxococcaceae family (Actinobacteria). In addition, the proportions of *Solirubrobacteraceae (Actinobacteria*) and *Nitrososphaeraceae* decreased at the point of the crown fire. At the point of surface fire, *Gaiellaceae* (*Actinobacteria*; major phylotype *Gaiella*; $p_{adj} = 0.0004$, 1.05% in control), *Pyrinomonadaceae* (*Acidobacteria*, major phylotype RB41; 10.3% at the control point, 2.7% at surface fire), *Anaerolineaceae* (*Chloroflexi*, several minor phylotypes and UTCFX1; $p_{adj} = 6.9 \times 10^{-9}$, 0.56% for the AC layer), BSV26 (minor phylotype of the phylum *Bacteroidetes*), *Saprospiraceae* (*Bacteroidetes,* order Chitinophagales, multiple minor phylotypes and unidentified major phylotype Seq46; 1.32 in the control horizon AC, $p_{adj} = 1.8 \times 10^{-6}$), *Saprospiraceae* (*Bacteroidetes*, multiple minor phylotypes), and *Bacillaceae* (*Firmicutes*, genus *Bacillus*; $p_{adj} = 0.0004$) decreased.

At points after the fire, an increase in the *Sphingobacteriaceae* family was noted, represented by phylotypes of two genera, *Mucilaginibacter* and *Pedobacter*; in addition to this family, during surface and upper fires, other families did not significantly increase their proportion together relative to the control point.

For the AC horizon of the crown fire, there was an increase in representatives of the families *Ilumatobacteraceae* (*Actinobacteria*, multiple minor phylotypes), Mycobacteriaceae (genus *Mycobacterium*, one of the major phylotypes; $p_{adj} = 0.0015$), Gemmatimonadaceae (multiple minor phylotypes), *Solibacteraceae* (minor phylotypes and increase in the major phylotype *Bryobacter*; $p_{adj} = 0.06$), WD2101 (Planctomycetes, multiple minor phylotypes), and *Opitutaceae* (*Verrucomicrobia*, multiple minor phylotypes; the major phylotype of the phylum Verrucomicrobia, family *Chthoniobacteraceae*, *Candidatus Udaeobacter* did not change significantly; 0.69). For a surface fire, there was an increase in the families Microbacteriaceae (Actinobacteria, with significant growth in the upper horizon), SC-I-84 (Gammaproteobacteria, minor phylotypes), env.OPS_17 (minor phylotypes of the order Sphingobacteriales), Blastocatellaceae [Acidobacteria, multiple phylotypes, and unidentified phylotype Seq69 is especially characteristic, which is noted only in the AC (2.38%) and C (0.26%) horizons of the surface fire], and Rhizobiaceae [genera *Ensifer* ($p_{adj} = 0.0015$)), *Allorhizobium* ($p_{adj} = 0.0015$), *Mesorhizobium* ($p_{adj} = 0.0015$), and *Aminobacter* ($p_{adj} = 0.0015$)].

DISCUSSION

In the analysis of the general structure of the microbial community, its biodiversity, and the core structure of the pyrogenic soil, its special aspects were revealed. In the soil after a forest fire, the core component decreased due to an increase in the diversity of the minor component of the microbiome, characteristic of postpyrogenic horizons. This was especially pronounced in the AC horizon and least noticeably in the C horizon. Both the absolute number of core phylotypes and their relative abundance decreased. The literature presented a widespread view that the part of the microbiome, represented by minor phylotypes, is metabolically active and sensitive to environmental changes [34, 35].

In the analysis of β-diversity, a strong difference was found in the results for the weighted metrics (weighted UniFrac and Bray–Curtis distance) and the method that did not take into account the representation of individual phylotypes (unweighted UniFrac), which was especially pronounced in the middle soil horizon after a surface fire. Perhaps this was due to a decrease in the minor component in these samples. To confirm this theory, taxa related to the CRT were identified. The literature presented conflicting data on this group [32, 33], although some studies reported that, in the absence of stressful conditions, the CRT structure does not differ from the rest [33]. We have shown a strong correlation between the CRT and non-CRT components of the soil microbiome, which does not enable to suggest any pronounced role of the CRT component of the soil in a fire, and it does not imply that individual members of this group cannot play an important role in soil restoration after exposure to a stress factor, such as forest fire.

In the analysis of the taxonomic composition changes based on 16S rRNA amplicons, in most studies, the depth of analysis was limited only by the phylum level. Moreover, if several years have passed after the fire, in some cases, the difference in the taxonomic structure between the points affected by the forest fire and the control points is not traced

(2 years after the forest fire [1]), although significant changes are noted in shorter chronoseries even at such high levels. In two studies, 3 years [9] and 7 years [37] after the forest fire, changes were revealed at the phylum level, which was possibly related to the 3 years' case with the slow rate of soil recovery studied in a subarctic climate. In the studies mentioned above, in which more than 1 year has passed after a forest fire, there was an increase in the phyla Actinobacteria and Gemmatimonadetes [9] as well as AD3 and Gemmatimonadetes [31]. Studies of the taxonomic composition of soil microbiome at an earlier period after a forest fire were presented in the literature [7, 8], whereas changes in the taxonomic composition were often opposite of the later trends (for example, the increase in the proportion of *Firmicutes*, *Betaproteobacteria*, and *Bacteroidetes* was characteristic of rapid colonization).

In the study on the inoculation of soil microbiome under laboratory conditions in the soil with pyrogenic carbon content [5], there was a stable increase in the representatives of the phyla *Gemmatimonadetes* and *Actinobacteria* (*Myxococcaceae*). We have shown an increase in the total proportion of the representatives of the phylum Gemmatimonadetes in the AY horizon of postpyrogenic points and AC horizon of the crown fire. Apparently, we can associate the increase in this group to the soil microbiome's response to pyrogenic carbon. At a lower taxonomic level, we were unable to reveal significant changes, as in the studied samples 114 phylotypes from this phylum were identified, representing a minor component of the soil microbiome that was extremely variable at the studied points, which complicates the statistical analysis of this group that presumably plays an important role in soil reamidation after forest fires.

The increase in the proportion of the phylum Actinobacteria, as noted in the AY horizon of the crown fire and the AC horizon of the surface fire, was much more controversial. The response of actinomycetes to soil restoration varied greatly both at the family level and at the level of individual phylotypes. At the same time, the literature showed an important role of individual representatives of actinomycetes in the remediation of postpyrogenic soils (for representatives of the genus *Arthrobacter* of the family Micrococcaceae [9]), in good agreement with literature data on the possibility of degradation by various actinomycetes (*Mycobacterium* and *Rhodococcus*) of a wide range of oxidized organic compounds, including cyclopyrenes formed as a result of combustion [38, 39]. There was a rapid increase in the AY horizon of the crown fire of the phylotype of the genus *Pseudoarthobacter* and other members of the family Micrococcales, which was associated with their possible participation in the degradation of combustion products. The characteristic increase in the postpyrogenic soil of such actinomycetes as *Solirubrobacter*, *Myxococcus*, and *Mycobacterium*, as described in the literature, showed in our data ambiguous changes depending on the horizon and the point of study.

After the forest fire, the representatives of the phylum Traumarhaeota decreased considerably. The literature [34] showed that these microorganisms were associated with free ammonium oxidation in the soil. According to the literature [32], *Nitrososphaera* was inversely correlated with the presence of Xanthobacteraceae in soil in agrocenoses, as they are antagonists in the nitrogen cycle. Our study showed a rapid decrease in both *Nitrososphaera* and Xanthobacteraceae and other representatives of *Rhizobiales* in postpyrogenic soils. The decrease of the *Rhizobiales* group did not occur in the upper soil horizons after a surface fire. At the same time, the correlation between the Bray–Curtis distance for *Rhizobiales* and the level of nitrites did not differ from the average values for all other microorganisms ($R = 0.5467$, $p = 0.02$), indirectly indicating that the number of *Rhizobiales* did not depend directly on the level of available nitrogen, and the reaction was more complex. Apparently, despite the decrease in the level of available nitrogen after the fire, the structure of plant-microbial interactions in the soil was also disturbed, leading to a decrease in *Rhizobiales* in some soil horizons.

There was a change in the postpyrogenic soil of specific marker groups of microorganisms associated with the biodegradation of complex organic compounds and bioremediation of soils contaminated with heavy metals. Thus, in the AC horizon of the surface fire, a rapid increase in Blastocatellaceae associated with the biodegradation of complex organic compounds was noted [41, 42]. Phylum Planctomices (the most typical family is WD2101) also increased its proportion in postfire points [43]. Representatives of this phylum were noted as the in-

habitants of complex biotopes that can metabolize a whole range of polymers. In the upper horizons, there was a decrease in the representatives of the TRA3-20 families (described earlier in the literature as typical representatives of the core microbiome for soil communities and mines contaminated with heavy metals [44]) and SC-I-84 [44–46] (increase in mines with a high content of heavy metals and in arable soil), which is difficult to interpret unequivocally.

Despite the proximity of the β-diversity values for the upper soil horizon after all types of fires ($R^2 = 0.24$, $p = 0.03$), changes in the soil that occurred during surface and crown fires had different effects on the soil, as determined according to the microbiome's reaction, which was previously noted in the differences in the representation of taxa of microorganisms. The change in the median horizon AC revealed this difference with the most contrast. Apparently, the impact of a crown fire on the soil was largely limited by the action of combustion products entering the soil, leading to an increase in the groups of microorganisms associated with the metabolism of pyrogenic carbon (Gemmatimonadetes and Pseudoarthobacter). In a surface fire, due to the temperature effect, a complex change in soil microaggregates occurred, which possibly changed the physical and chemical properties of the soil. The disturbance of the rhizosphere, which is more clearly manifested during a surface fire, was also noticeable.

In the upper horizon AY, the soil acidified during surface fires (7.2–6.5) and crown fires (7.2–6.1). In the middle horizon AC, during a surface fire, significant alkalization occurred (5.5–6.6). Also, the pH increased after pyrogenesis in the lower layer. According to the literature [3], although pH is the most important factor determining the soil community's structure, we could not reveal this dependence using the Mantel test for the entire dataset. Most likely, this was because the pH in the samples differed insignificantly and unevenly. Acidification of the upper horizon under the influence of fire in the study area was generally uncharacteristic for postpyrogenic soils and rather an exception. In the short-term dynamics for this dataset, alkalization, a characteristic of postpyrogenic soils, was noted [3, 7]. At the same time, considering the influence of the ecological factors on individual phyla, we revealed both a strong correlation (Firmicutes and Proteobacteria) between the soil microbiome structure and pH and a lack of correlation (Acidobacteria and Archaea). The correlation between the level of soil respiration and the structure of the microbial community was quite natural and expected. At the same time, there was a correlation between the level of nitrites, but not ammonium, and the total nitrogen content in the soil, which most likely depended on the degree of availability of nitrogen compounds for microorganisms in the postpyrogenic soil. Also, the results obtained on the correlation of nitrites and the soil microbiome structure can be associated with a lower solubility of nitrites, in contrast to ammonium compounds, devoid of such a clear distribution pattern in the soil as for nitrites.

Our data demonstrated tendencies similar to those in the literature in changes in the soil microbiome taxonomic structure after a forest fire. An increase in the proportion of taxa associated with the degradation of substances formed after combustion was revealed. Our study presented that a crown fire has a lesser effect on the soil microbiome than a surface fire. In addition, there was a considerable dependence of the obtained data on the studied soil horizon. The community changed significantly after a surface fire in the intermediate layer AC compared to the upper and lower horizons in both the representation of individual groups of microorganisms and the qualitative change in the soil microbiome structure.

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