ABS ACTA BIOLOGICA SIBIRICA
A journal on the biodiversity of Siberia and the adjacent lands

Acta Biologica Sibirica 10: 1733–1754 (2024)
doi: 10.5281/zenodo.14523458
http://journal.asu.ru

RESEARCH ARTICLE

Ecological-trophic structure of soil microbial communities in the the middle Ob floodplain

Ellina G. Nikitkina[1], Inna V. Lushchaeva[1], Victor A. Nikitkin[1], Sergey N. Kirpotin[1], Larisa G. Kolesnichenko[1]

1 *National Research Tomsk State University, Tomsk, 634050, Russia*

Corresponding author: Larisa G. Kolesnichenko (klg77777@mail.ru)

Academic editor: R. Yakovlev | Received 11 November 2024 | Accepted 3 December 2024 | Published 21 December 2024

http://zoobank.org/B22B5542-C69C-4289-A425-7BE9C3F5CD4E

Citation: Nikitkina EG, Lushchaeva IV, Nikitkin VA, Kirpotin SN, Kolesnichenko LG (2024) Ecological-trophic structure of soil microbial communities in the the middle Ob floodplain. Acta Biologica Sibirica 10: 1733–1754. https://doi.org/10.5281/zenodo.14523458

Abstract

Soil microbiota plays an integral role in biogeochemical cycles, being used as a key metric of changes and a means of integrated characterization of processes. The paper presents the results of microbiological analysis of soils from the central part of the middle Ob floodplain. The ecological and trophic structure of soil microbial communities was investigated to identify the leading physiological groups of heterotrophic bacteria involved in biogeochemical transformation of organic matter in soil. The relationship of bacteria of different physiological groups with seasonal variations and physical and chemical properties of soils, and the links between bacteria were identified and evaluated. The data obtained can be used to evaluate climate-regulating functions of microbial communities in floodplain soils and assess the potential of the middle Ob floodplain in terms of environmental services and nature management.

Keywords

Floodplain, soils, microbiology, microbial communities, physiological groups of microorganisms, Western Siberia, Ob river

Introduction

The study of functional biodiversity of microorganisms and soil microbial community structures is a crucial field within ecological science. It provides insights into biogeochemical cycles and expands our understanding of biosphere resources.

Soil microorganisms play a pivotal role in biological degradation and soil formation, thereby performing vital engineering functions within the ecosystem (Bossio and Scow 1995; Wardle 1998; Grigoryan et al. 2014; Schuldt et al. 2018; Savich et al. 2019). The study of the temporal dynamics of microbial communities may prove crucial for determining the extent of the release of immobilized labile nutrients and their availability to other ecosystem components (Bauhus and Bart 1995; Diaz-Ravina et al. 1995), including producers (Singh et al. 1989), and for assessing the current status of the soil–plant system (Wardle 1998).

Soil condition is determined by the presence and activity of specific microbial groups, which influence its fertility and degradation (Wardle 1998). Bacterial culture on selective media enables characterization of the composition of syntrophic groups that perform specific functions in natural ecosystems (Yakushev 2015). The functional characterization of microbial communities can be most indicative for assessing biogeochemical processes, since the taxonomic position of bacteria, as a tool for assessing species biodiversity, cannot always be associated with specific ecological functions (Lukina et al. 2020). The concept of functional biodiversity was introduced to acknowledge that the biodiversity components are significant not only for their potential use, but also for the ecosystem functions they provide (Eisenhauer et al. 2019; Lukina et al. 2020; Pacini et al. 2023).

Floodplains are known for elevated microbial activity (Dobrovolsky 1971; Slavnina and Inisheva 1987), and floodplain soils frequently display elevated carbon content attributed to organic matter accumulation (Rinklebe and Langer 2006). Many ecosystem functions (e.g., carbon sequestration, biodiversity conservation, flow regulation) are related to the water regime, which makes floodplain ecosystems and wetlands of paramount importance for the study and prediction of global biogeochemical and ecological processes (Mitsch et al. 2001; Kayranli et al. 2010; Sha et al. 2011; Schlesinger et al. 2013; Argiroff et al. 2017; Janse et al. 2019; Shen et al. 2021).

The Ob River is one of the largest rivers in Russia, and its extensive floodplain is highly dynamic in both space and time (Khromykh et al. 2000), within which biogeochemical processes may be of global character. In addition, meltwater and wastewater accumulate in lotic reservoirs and form an allochthonous component of the floodplain microflora. Hydrologic changes throughout the year can directly determine the soil bacterial composition along with many other factors such as temperature, pH, and nutrient concentration (Unger et al. 2009; Wilson et al. 2011; Moche et al. 2015).

At present, this landscape remains a relevant object of scientific research (Vorobyev et al. 2015; Savichev et al. 2015; Vorobyev et al. 2016; Vorobyev et al. 2019; Shepeleva 2019; Kolesnichenko et al. 2021), yet the last large-scale studies on the microbiological characteristics of soil in the middle Ob floodplain date back to the eighties of the last century (Slavnina and Inisheva 1987) and need some updating with due regard to the above-mentioned dynamics of the landscape.

The study revealed the primary trophic groups of microorganisms involved in nitrogen and carbon cycles in alluvial soils of the middle Ob floodplain. It also evaluated spatial and temporal dynamics of these groups, the relationship with seasonal variations and physical and chemical properties of soils, and the links between the groups.

List of abbreviations: CFU – colony-forming unit; abs. dry soil – absolutely dry soil.

Materials and methods

Study object

The study was conducted in the key sites of the middle Ob floodplain in the Krivosheinsky District, Tomsk Region, at the Kaibasovo Research Station, National Research Tomsk State University (57°24'61"N, 84°18'19"E). The Ob floodplain is divided (Khromykh 1979) into three distinct segments: riparian, central and terrace. For comparative analysis of the microbial content, we used samples from regions adjacent to floodplain lakes located in the central part of the floodplain. This area is flooded by hollow waters most irregularly and unpredictably, it exhibits the greatest ecological plasticity of the species composition of plants and animals, and gas and hydrochemical regimes of the lakes are most variable (Khromykh 1975). The selected objects are shown as sample points in Figure 1 and each one are represented by alluvial sod soils (fluvisols). For calculations, we used the averaged data on soil samples from the organogenic horizon (0–10, 10–20 cm) collected seasonally (winter, spring, summer, and autumn) for 3 years (2019–2021) in compliance with the methodological recommendations (Grigoryan et al. 2014). In 2019, additional samples were taken from the soil profile at depths of 0–10, 20–30, and 50–70 cm.

Statistical analysis (Kruskal-Wallis ANOVA test, $p<0.05$) revealed no significant differences in the elemental composition of soils across the sampling points. Also, no significant differences (Mann-Whitney U-test, $p<0.05$) were found between the elemental composition of soil samples from a depth of 0–10 cm and 10–20 cm, except cadmium ($Z=2.51$, $p=0.01$). The average values of the concentration of chemical elements in samples of alluvial soils of the floodplain of the middle reaches of the Ob River at a depth of 0–10 and 10–20 cm are presented in Table 1.

Figure 1. Maps of key sites (Kaibasovo).

Table 1. Concentration of elements in alluvial sod soils in the middle Ob floodplain, mg/kgh

Elements	depth, cm		Elements	depth, cm	
	0–10	10–20		0–10	10–20
Na	11242.95±600.62	13038.75±1127.87	Cd	0.32±0.01	0.25±0.01
Mg	13753.86±233.17	14033.08±280.28	Sn	2.8±0.07	2.73±0.1
K	16810.91±232	17241.88±250.2	Sb	1.36±0.03	1.37±0.02
Ca	10031.47±455.47	10249.35±387.5	Te	0.02±0	0.02±0
Fe	47152.5±1363.54	47851.09±949.28	Cs	5.78±0.22	5.78±0.15
Li	36.87±1.38	37.15±1.15	Ba	460.97±8.08	459.03±4.41
Be	2.07±0.05	2.11±0.05	La	29.15±0.47	29.6±0.32

Elements	depth, cm		Elements	depth, cm	
	0–10	10–20		0–10	10–20
B	24.18±1.42	24.56±0.51	Ce	54.96±0.78	55.16±0.89
Sc	18.63±0.4	19.23±0.3	Pr	6.93±0.08	7.09±0.06
Ti	4531±19.26	4691.26±104.4	Nd	27.4±0.42	27.77±0.31
V	119.15±3.3	119.95±2.08	Sm	6.09±0.08	6.21±0.07
Cr	101.34±3.27	98.67±1.29	Eu	1.27±0.02	1.29±0.01
Mn	1166.96±17.59	1093.99±64.76	Gd	4.7±0.06	4.68±0.06
Co	18.05±0.34	17.43±0.39	Tb	0.8±0.01	0.8±0.01
Ni	35.09±1.4	34.74±0.97	Dy	4±0.08	4.01±0.04
Cu	42.22±5.56	36.13±0.64	Ho	0.93±0.02	0.93±0.01
Zn	80.72±8.59	72.8±5.27	Er	2.45±0.06	2.45±0.04
Ga	7.56±0.2	7.71±0.18	Tm	0.33±0.01	0.34±0.01
Ge	0.5±0.06	0.52±0.03	Yb	3.02±0.06	3.06±0.06
Se	1.93±0.12	2.07±0.22	Lu	0.39±0.01	0.39±0.01
Rb	92.08±3.13	90.07±2.39	Hf	2.81±0.06	2.81±0.12
Sr	137.07±4.33	144.33±3.22	Ta	0.86±0.02	0.88±0.03
Y	25.87±0.35	26.2±0.22	W	2.69±0.43	2.36±0.3
Zr	112.01±1.49	114.68±3.36	Ед	0.4±0.01	0.4±0.01
Nb	12.2±0.04	12.73±0.21	Pb	21.99±0.87	20.81±0.45
Mo	0.93±0.07	0.89±0.08	Th	10.24±0.36	10.23±0.34
Ag	0.39±0.02	0.42±0.01	U	2.79±0.19	2.72±0.17

Counts of physiological groups of microorganisms

The functional approach to assessment of microbial activity involves individual study of the number and biological activity of each microbial group (Titova and Kozlov 2012) by cultivation on standard selective nutrient media. To assess the contribution of the microbial community of floodplain soils to the nitrogen and carbon cycle, we considered the number of microorganisms that decompose nitrogen-containing organic compounds (ammonifying bacteria); microorganisms that prefer mineral forms of nitrogen (oligonitrophilic bacteria); anaerobic nitrogen-fixing bacteria; nitrifying and denitrifying bacteria; utilizers of nitrogen-free organic matter (amylolytic bacteria); humus-degrading bacteria, oligotrophic bacteria, saccharolytic micromycetes, and cellulolytic aerobic bacteria (Segi 1983; Geltser 1986). For assessment, CFU/g of abs. dry soil on dense selective nutrient substrates was determined, and the most probable number of microorganisms was calculated using the McCredie method (Geltser 1986; Babeva and Zenova 1989) for liquid substrates.

The abundance of ammonifiers was evaluated in fishmeal hydrolyzate broth from the State Scientific Center for Applied Microbiology and Biotechnology. The abundance of amylolytics was evaluated on starch-ammonia agar (SAA): 10 g starch, 2.0 g $(NH_4)_2SO_4$, 1.0 g K_2HPO_4, 1.0 g MgSO4, 1.0 g NaCl, 3.0 g $CaCO_3$, 20 g agar, 1000 ml H_2O_{dist}. Saccharolytic micromycetes were grown in Czapek medium (OOO SPC Biokompas-S, Russia).The abundance of humus-degrading microorganisms was evaluated in Vinogradskogo agar medium for autochthonous microflora: 5 g of K_2HPO_4; 2.5 g of $MgSO_4 \times 7H_2O$; 2.5 g NaCl; 0.05 g $FeSO_4$; 10 ml of ammonium humate (1%); 1000 ml of H_2O_{dist}. Oligotrophs were grown on peat agar prepared as follows: 20 g of soil was poured into 500 ml of tap water and boiled over low heat for 2 h. After being cooled, the extract was filtered and 2% agar-agar was added. Oligonitrophils were cultured on Ashby's Mannitol Agar.

The number of aerobic cellulolytic microorganisms was determined by seeding on Hutchinson-Kleiten agar medium. The number of denitrifiers was determined by the limiting dilution method by culturing on a simple medium for denitrifiers of the following composition (g/l): K_2HPO_4 – 0.5 g, $MgSO_4 \times 7H_2O$ – 0.2 g, KNO_3 – 2.0 g, Rochelle salt ($KNaC_4H_4O_6 \cdot 4H_2O$) – 20.0 g, H_2O_{dist}. The number of nitrifiers was determined by the limiting dilution method in Vinogradsky's liquid medium. 1 liter of medium included: $(NH_4)_2SO_4$ – 2 g; K_2HPO_4 – 1 g; $MgSO_4$ – 0.5 g; $FeSO_4$ – 0.4 g; NaCl – 2 g; $CaCO_3$. The number of anaerobic nitrogen fixers was also determined by the limiting dilution method when cultivated in penicillin bottles in Vinogradsky medium having the following composition: glucose – 20 g, K_2HPO_4 – 1.0 g, $MgSO_4{}^*7H_2O$ – 0.5 g, $CaCO_3$ – 20 g, NaCl – 0 .5 g, $MnSO_4$ – traces, $FeSO_4$ – traces, yeast extract – 10 g, tap water – 1000 ml.

The mineralization coefficient as defined by Mishustin (1956) and the index of pedotrophy as defined by Nikitin (1972) were calculated for each of the selected floodplain soil samples.

Chemical and analytical work on determining the elemental composition of soils was carried out at the Tomsk Regional Center for Collective Use (TR CCU).

Statistical processing and graphical visualization of the experimental data were conducted using the Statistica 7.0 and MS Excel 2016 software. Nonparametric methods (the Kruskal-Wallis ANOVA and median test at $p<0.05$) were employed to identify differences between the samples; correlations were identified by calculating Spearman rank correlation coefficients at $p<0.05$.

Results

Physiological groups of floodplain microorganisms and links between them

The mean total microbial count of zymogenic ammonifying microflora for all the samples was 24.4 million CFU/g of abs. dry soil. It follows from this that the studied samples of floodplain soils can be characterized as being highly enriched with heterotrophic microorganisms (Titova and Kozlov 2012).

The data on the content of soil microorganisms of all physiological groups from five sampling points did not differ, as confirmed by the criterion for evaluation of distribution uniformity (Kruskal-Wallis ANOVA) and the median test data. Significant differences were observed for nitrifying bacteria only (at H=20.09, p=0.0005 for the Kruskal-Wallis test; χ^2=15.25, p=0.0042 for the median test). The general counting results of functional properties of microbial communities in the different points (1–5) of middle Ob floodplain soils are presented in the Table 2.

Ammonifying, oligotrophic, oligonitrophilic and humus-degrading bacteria dominated in all the samples tested. Amylolytic and oligonitrophilic bacteria facilitate the immobilization of mineral forms of nitrogen, which are abundant in soils of the central part of the floodplain. This process is integral to the soil nitrogen cycle (Mishustin 1956; Mishustin 1972; Slavnina et al. 1981; Titova and Kozlov 2012; Reay et al. 2023). Many groups of oligonitrophilic bacteria possess an extensive enzymatic apparatus and are cosmopolitan in their distributions (Titova and Kozlov 2012).

The results showed that the number of humus-destroying bacteria in soil was high, but they were not dominant. This is to be expected under normal conditions of organic matter input, which stimulates the growth of saprotrophic microorganisms typical of non-cultivated soil (Titova and Kozlov 2012). Furthermore, all the samples exhibited elevated number of anaerobic nitrogen-fixing bacteria. The overall number of nitrifying bacteria was low, and in some samples, this group of microorganisms was not identified. A retarded rate of nitrification was also observed in alluvial soils (Slavnina and Inisheva 1987; Khodjimurodova and Raupova 2019).

The proportion of micromycetes in the microbial community of alluvial soils is relatively low, and in cases of prolonged flooding, representatives of this group may even be absent. These assertions are supported by our results. The dominance nonsporulating bacteria can be considered a characteristic feature of soils in the central part of the floodplain (Mekhtiev 1959; Nikitina 1978; Slavnina et al. 1981).

Correlations between separate physiological groups of microbial communities were identified (Spearman rank correlation coefficients at $p<0.05$).

The correlation between the number of amylolytic and ammonifying bacteria (r=0.57) can be attributed to the fact that the primary source of mineral nitrogen for the enzymatic activity of amylolytic bacteria is the metabolic products of ammonifying bacteria. Comparable correlations were reported by other authors (Fomina et al. 2006). A similar pattern in relation to mineral nitrogen can be observed among oligonitrophilic bacteria, which demonstrate a positive correlation with ammonifying bacteria (r=0.87).

A high correlation between oligonitrophilic and humus-degrading bacteria (r=0.93) arises from the similarity of their ecological functions. Oligonitrophilic bacteria can degrade nitrogenous components of humic and fulvic acids. Additionally, the number of oligonitrophilic bacteria demonstrated a positive correlation with the number of oligotrophic bacteria (r = 0.74), as a group of bacteria conditionally differentiated based on their nitrogen consumption patterns (Titova and

Kozlov 2012). The correlation between saccharolytic micromycetes and cellulolytic bacteria (r=0. 68) is due to the involvement of both groups of microorganisms in the complex process of cell wall degradation. High correlation coefficients between nitrifying and denitrifying bacteria (r=0.90) may be due to the mutual arrangement of these microbial groups within the nitrogen cycle.

A substantial number of statistically reliable and positive relationships identified between different physiological groups of microorganisms indicates an effective consortia interaction of the microbiota with regard to the available soil nutrients. Additionally, the results may be due to the rare functional specialization observed among soil bacteria clusters: a microorganism engages in various processes in a targeted manner or through cometabolism (Yakushev 2015); representatives of the same taxonomic and functional units may be accounted in several experiments simultaneously. Synergistic interactions between soil microorganisms ensure consistent mineralization of the organic substance entering soil and utilization of its various components at each stage of the biogeochemical cycle.

Seasonal and profile dynamics of functional microbiological indicators of floodplain soils

Seasonal variations in microbiological indicators of floodplain soils were considered and assessed (Table 3, Fig. 2). The Kruskal-Wallis test demonstrated the response of the content of all physiological microbial groups analyzed, except for saccharolytic micromycetes, and oligotrophic, anaerobic nitrogen-fixing and nitrifying bacteria, to seasonal changes, which is most likely associated with high resistance of these microorganisms to unfavorable environmental changes.

In spring, the activity among all microbial groups sensitive to seasonal changes is relatively low. However, the patterns of seasonal dynamics exhibit notable differences in alluvial meadow soils across other climatic zones (Khodjimurodova and Raupova 2019). In our study, ammonifying bacteria showed decreased abundance in winter and spring; however, in natural and anthropogenically modified soils of Rostov-on-Don, for example, the pattern was reversed (Ivanov and Govortsov 2019).

In general, the seasonal dynamics observed for amylolytic, humus-degrading, and oligonitrophilic bacteria was similar (with summer and winter peaks). Amylolytic, cellulolytic aerobic and denitrifying bacteria showed maximum numbers in summer. At present, there are not enough studies on seasonal dynamics of soil microorganisms during the winter season, which limits the scope for comparison of findings across studies.

The distribution of microorganisms of different physiological groups in the soil profile in June 2019 showed a decreased number of saccharolytic micromycetes, humus-degrading and cellulolytic aerobic bacteria at increased sampling depth (Fig. 3).

Table 2. Functional properties of microbial communities in the middle Ob floodplain soils

Sampling point	Sampling depth, cm	Ammonifying bacteria*	Amylolytic bacteria*	Oligotrophic bacteria*	Saccharololytic micromycetes*	Humus-degrading bacteria*	Cellulolytic aerobic bacteria**	Oligonitrophilic bacteria*	Anaerobic nitrogen-fixing bacteria***	Nitrifying bacteria***	Denitrifying bacteria***	Mineralization coefficient	Index of pedotrophy
		Functional properties of microbial communities from different sampling points											
1	0–10	25.41±1.02	6.48±0.37	8.65±0.45	0.02±0.02	4.61±0.31	105.45±2.14	4.77±0.32	40847.73	29.28	18136.47	1.02	1.11
	10–20	23.87±1.04	26.51±1.25	7.29±0.30	0.02±0.02	8.49±0.58	35.60±1.10	5.83±0.42	46110.56	56.06	24963.88	1.10	1.60
2	0–10	51.35±1.25	11.85±0.54	14.60±0.46	0.06±0.04	8.32±0.48	173.68±2.68	8.63±0.43	36919.10	4851.25	148209.73	0.59	0.72
	10–20	52.21±1.46	5.36±0.33	9.88±0.44	0.03±0.03	3.92±0.24	44.85±1.37	3.81±0.21	65466.13	1031.00	4200.42	0.43	0.89
3	0–10	13.09±0.52	8.04±0.32	11.98±0.43	0.14±0.06	7.33±0.39	60.70±1.79	5.58±0.28	39720.22	193.56	8397.43	1.21	1.25
	10–20	6.00±0.26	6.06±0.23	13.18±0.49	0.02±0.02	2.48±0.19	26.58±1.25	2.22±0.17	51573.65	0.33	16662.87	1.11	1.88
4	0–10	17.67±0.63	6.54±0.33	13.19±0.48	0.11±0.06	7.50±0.30	30.0±1.03	8.24±0.36	92574.99	292.23	23039.16	0.66	1.09
	10–20	9.85±0.39	6.82±0.33	7.49±0.32	0.02±0.02	5.75±0.33	22.22±0.79	3.30±0.24	25211.77	50.88	6993.80	0.60	0.86
5	0–10	20.30±0.69	9.46±0.41	15.95±0.49	0.04±0.02	14.59±0.61	93.75±2.20	10.48±0.39	55622.29	1092.68	22405.18	0.38	0.82
	10–20	10.59±0.37	3.78±0.23	8.16±0.34	0.02±0.01	2.39±0.17	15.08±0.83	4.28±0.27	21639.40	11.76	3536.79	0.45	0.77

Note: * 10^6 CFU/g abs. dry soil; ** 10^3 CFU/g abs. dry soil; ***most probable number of cells/g abs. dry soil.

Table 3. Seasonal variations in functional properties of microbial communities in the middle Ob floodplain soils

Season	Sampling depth, cm	Ammonifying bacteria*	Amylolytic bacteria*	Oligotrophic bacteria*	Saccharolytic micromycetes*	Humus-degrading bacteria*	Cellulolytic aerobic bacteria**	Oligonitrophilic bacteria*	Anaerobic nitrogen-fixing bacteria***	Nitrifying bacteria***	Denitrifying bacteria***	Mineralization coefficient	Index of pedotrophy
		Seasonal variations in functional properties of microbial communities at different times of the year											
Winter	0–10	5.42±0.36	8.82±1.01	19.22±1.57	0.04±0.07	26.12±2.01	not found	11.26±1.21	21060.00	13.00	3948.67	0.59	1.12
	10–20	12.35±1.20	6.64±0.63	11.18±0.95	0.02±0.04	7.84±0.96	not found	8.76±0.92	69233.33	3.87	3066.33	0.80	1.11
Spring	0–10	3.36±0.24	4.73±0.55	10.42±0.69	0.02±0.02	1.85±0.25	3.03±0.27	2.49±0.21	67914.00	192.89	3303.80	1.33	1.76
	10–20	5.86±0.47	2.20±0.30	8.82±0.69	0.01±0.02	1.83±0.25	2.31±0.25	2.41±0.35	21178.00	69.02	310.20	0.64	1.35
Summer	0–10	26.48±0.46	7.66±0.16	12.99±0.23	0.13±0.03	10.47±0.21	219.36±1.3	7.77±0.16	44624.11	994.31	22980.96	0.87	1.03
	10–20	11.77±0.24	15.76±0.40	8.76±0.17	0.03±0.01	6.24±0.19	58.36±0.67	4.49±0.14	32871.84	128.15	16258.64	0.89	1.18
Autumn	0–10	34.01±0.45	10.21±0.23	12.17±0.21	0.05±0.02	5.48±0.15	12.68±0.30	8.19±0.19	68406.60	2151.98	80871.79	0.56	0.82
	10–20	32.15±0.58	5.01±0.14	9.47±0.22	0.02±0.01	2.78±0.09	13.42±0.36	2.72±0.08	49805.69	477.40	10395.51	0.60	1.21

Note: * 10^6 CFU/g abs. dry soil; ** 10^3CFU/g abs. dry soil; ***most probable number of cells/g abs. dry soil.

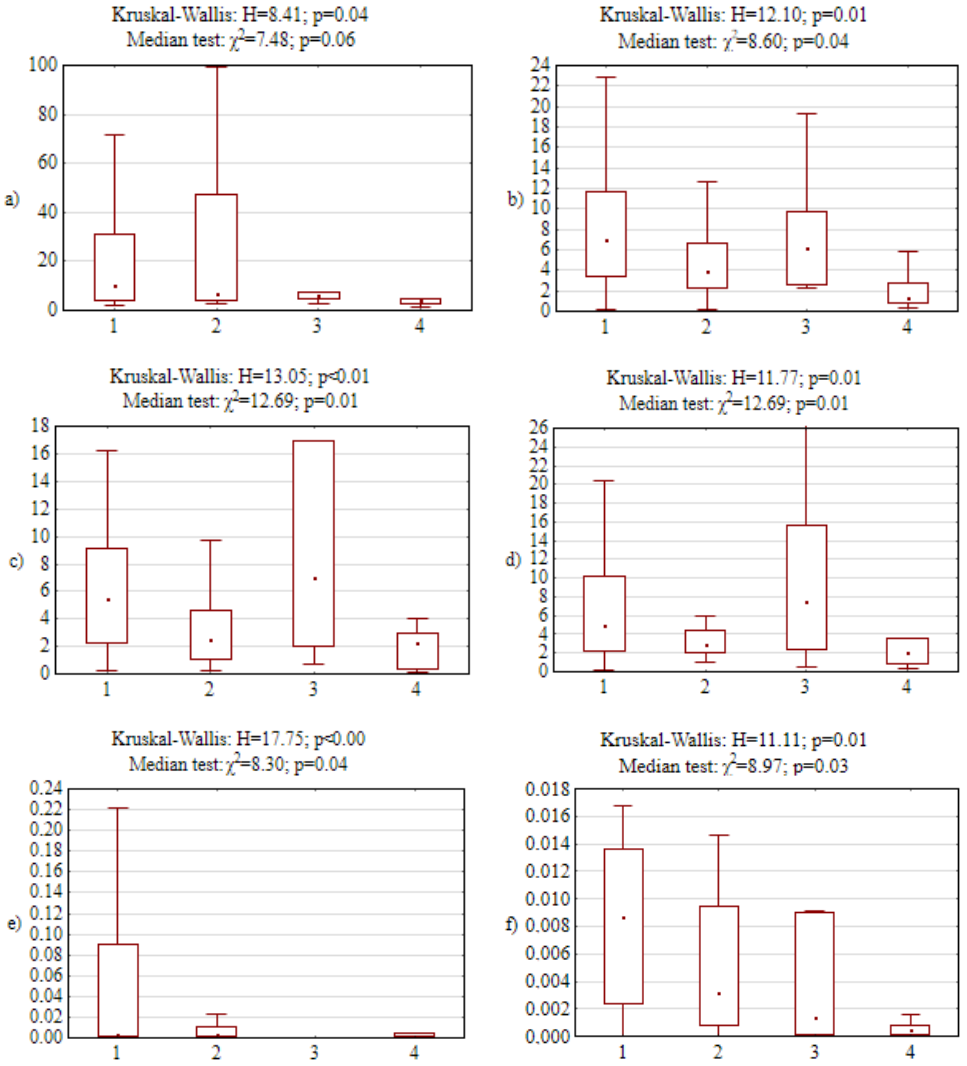

Figure 2. Seasonal variations in the number of microorganisms of different physiological groups, mln CFU/g of abs. dry soil (1 – summer, 2 – autumn, 3 – winter, 4 – spring). Note: a) ammonifying bacteria b) amylolytic bacteria c) humus-degrading bacteria d) oligonitrophilic bacteria e) cellulolytic aerobic bacteria f) denitrifying bacteria (most probable number of cells/g of abs. dry soil).

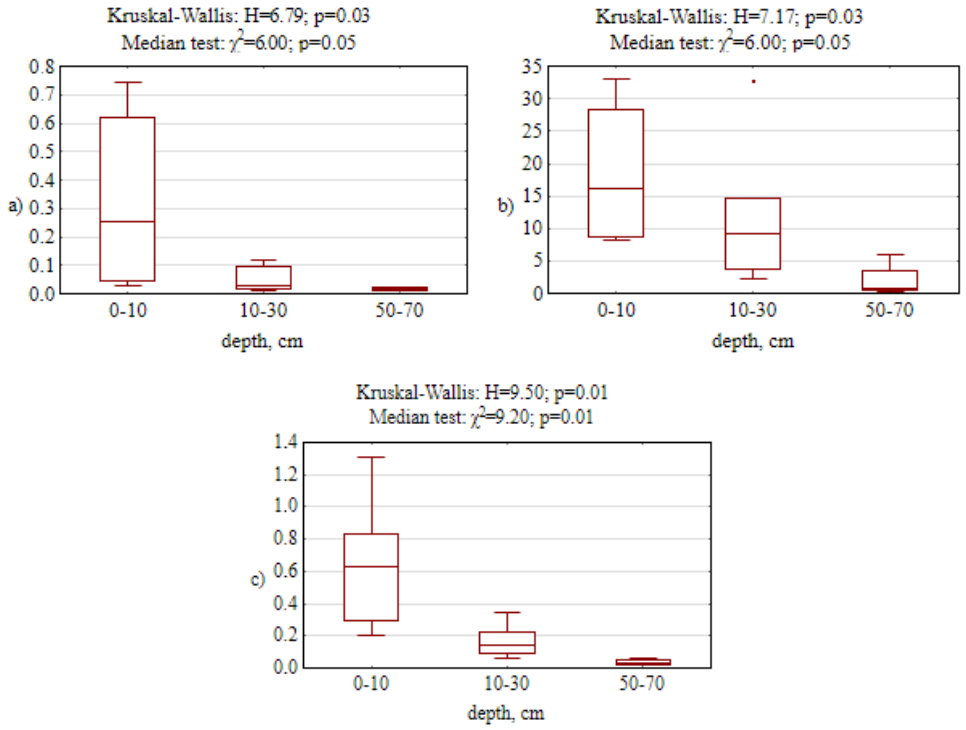

Figure 3. Fluctuations in the average number of microorganisms of different physiological groups (CFU/g of abs. dry soil) at different sampling depths in June 2019. Note: a) saccharolytic micromycetes b) humus-degrading bacteria c) cellulolytic aerobic bacteria.

By September, the profile dynamics shifted and showed a reduced number of saccharolytic micromycetes, amylolytic, oligotrophic, humus-degrading, oligonitrophilic and nitrifying bacteria with increasing sampling depths (Fig. 4a–e). In autumn, soil moisture at greater depths was observed to decrease. The seasonal variations in microbiological activity observed in soil profiles can be attributed to changes in humidity and temperature, the migration of water-soluble compounds derived from plant litter decomposition down the profile, and changes in soil properties (Wardle 1998; Khodjimurodova and Raupova 2019).

The analysis of bacterial distribution in the upper layers of floodplain soils revealed a decrease in the number of saccharolytic micromycetes, humus-degrading, cellulolytic aerobic, oligonitrophilic and denitrifying bacteria with increasing sampling depth (Fig. 5a–d); a similar trend was observed for amylolytic bacteria (Fig. 5e), while the remaining groups of microorganisms demonstrated no depth-dependent changes in numbers. These groups of microorganisms exhibited the greatest sensitivity to changes in conditions associated with increased depths. For comparison, previous studies on the middle Ob River soils did not reveal a reli-

able impact of depths on microbial biomass (Yakutin et al. 2013), although alluvial soils, particularly alluvial meadow soils, show a gradual decrease in soil microbial biomass down the profile (Yakutin et al. 2013, 2014). Decreased microbial biomass at greater depths was reported for floodplain soils of the Kuibyshev Reservoir and for reclaimed alluvial-meadow soils of the Bukhara Oasis (Khodjimurodova and Raupova 2019).

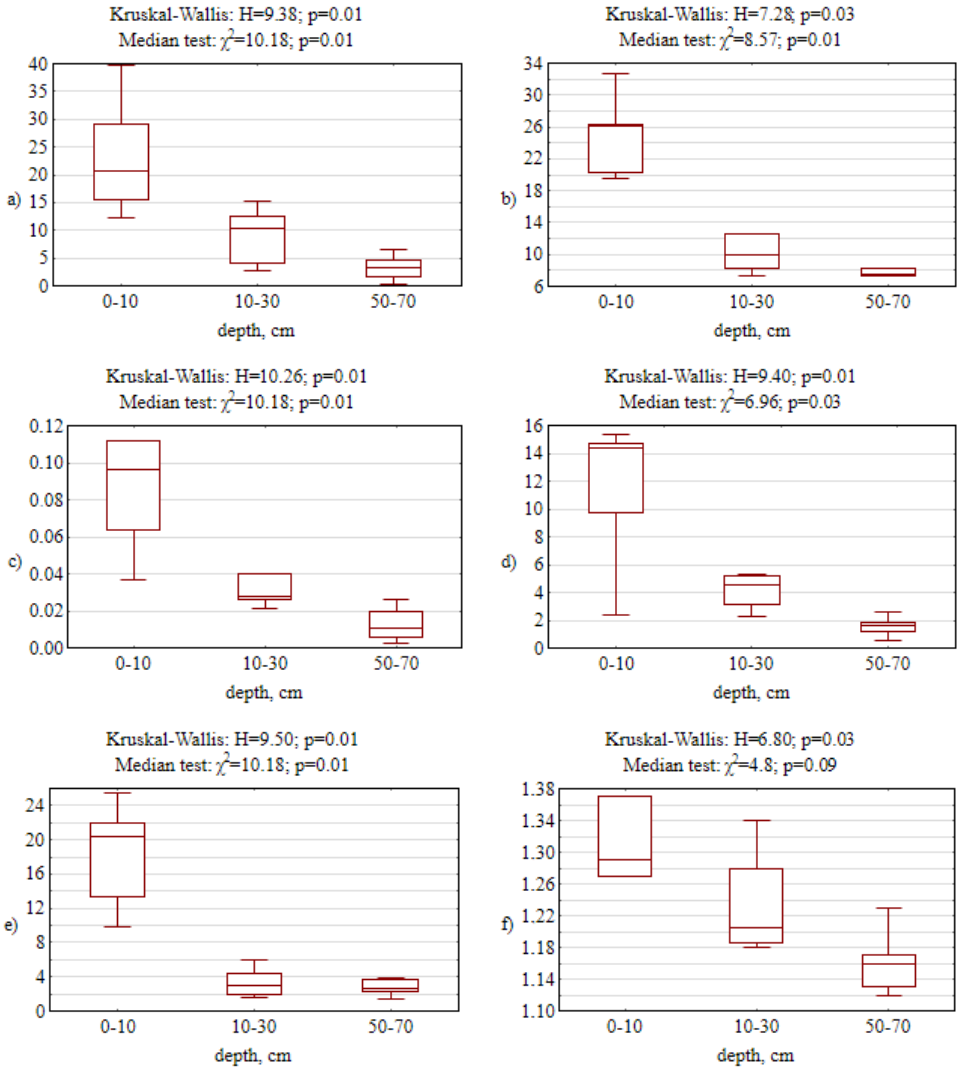

Figure 4. Fluctuations in the average number of microorganisms of different physiological groups (mln CFU/g of abs. dry soil) at different sampling depths in September 2019. Note: a) amylolytic bacteria; b) oligotrophic bacteria; c) saccharolytic micromycetes; d) humus-degrading bacteria; d) oligonitrophilic bacteria; e) nitrifying bacteria (most probable number of cells/g of abs. dry soil).

It is known that oligonitrophilic bacteria are capable of living in environments with scarce nutrient resources, particularly in the upper layers of the soil profile, thereby maintaining the nitrogen balance in this area (Parinkina 1971); in our study, these bacteria were most depth-dependent. Previously, Russian researchers reported a reduced number of amylolytic and ammonifying bacteria in some soils at greater sampling depths, which may depend on the sampling period (Wardle 1998).

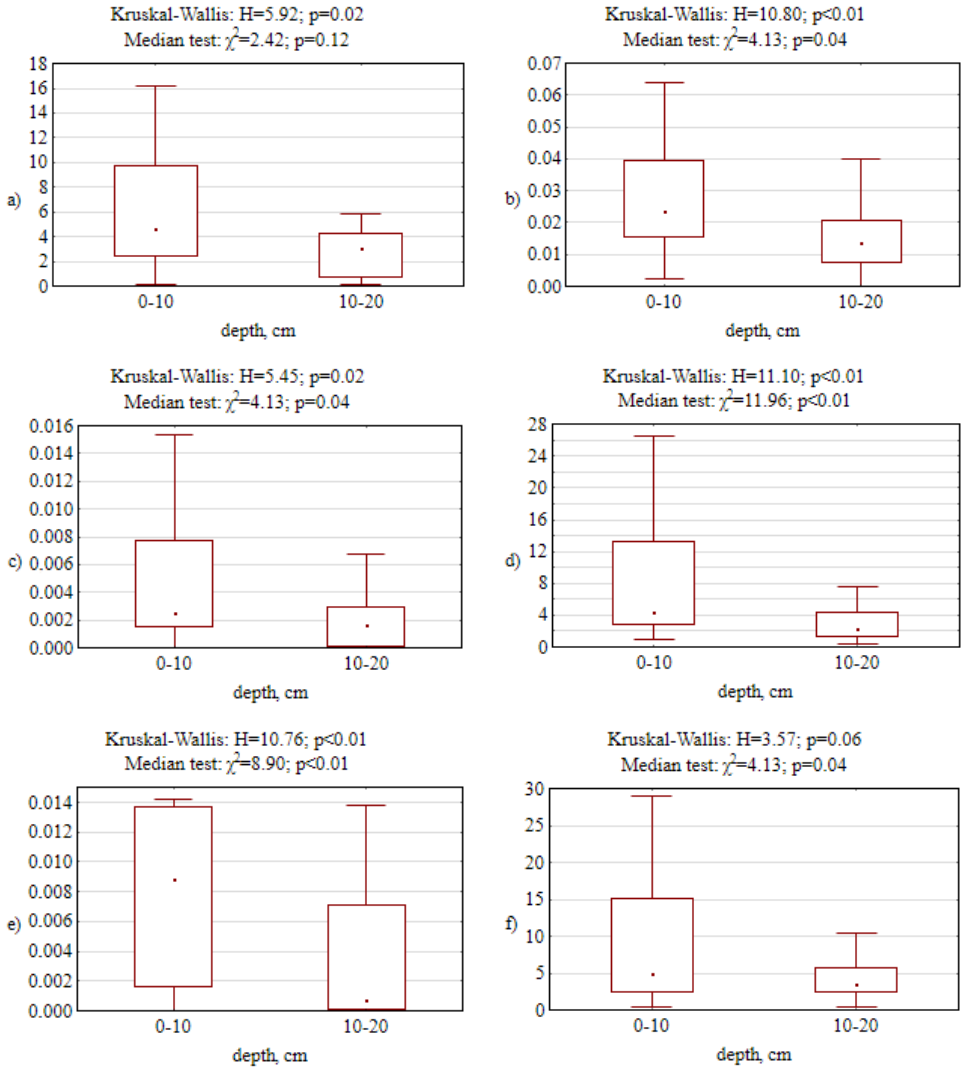

Figure 5. Average number of microorganisms of different physiological groups, mln cells/g of abs. dry soil at sampling depths of 0–10 and 10–20 cm. Note: a) humus-degrading bacteria b) saccharolytic micromycetes c) cellulolytic aerobic bacteria d) oligonitrophilic bacteria e) denitrifying bacteria e) amylolytic bacteria.

No differences in the mineralization coefficient were observed between the upper layers of floodplain soils at different times of the year (Fig. 6a). The mineralization coefficient at 0–10 cm depth exhibited minimal fluctuation throughout the year and varied from 0.6 to 2.1, with the highest value in spring. Coefficients exceeding 1 are considered to be quite high (Titova and Kozlov 2012) and are indicative of elevated ammonia nitrogen levels and intense immobilization processes in the upper layer (0–10 cm) during the spring season. The mineralization coefficient in floodplain soil at 10–20 cm depth exhibited remarkable stability throughout the year. It should be noted that the analysis of the number of amylolytic and ammonifying bacteria did not reveal any seasonal or depth-dependent fluctuations.

Seasonal variations in the index of pedotrophy were studied in the upper layers of floodplain soils at depths of 0–10 and 10–20 cm (Fig. 6b). Significant depth-dependent changes in the index of pedotrophy were observed only in spring and autumn, which can be attributed to the features of the floodplain regime. In spring, the index of pedotrophy at 0–10 cm depth exceeded that at 10–20 cm depth and averaged 1.5, which is the maximum value for all the samples studied. In autumn, the index of pedotrophy increased sharply at 10–20 cm depth (on average, up to 1.3), while in the upper layer it tended to decrease. The decreased index of pedotrophy indicates an increased amount of mobile organic matter in soil (Kontsevaya et al. 2018), which may be associated with the migration of nutrient substrate down the profile (Wardle 1998); intensive accumulation of residues of hard-to-access organic matter is due to the activity of zymogenic microflora. Seasonal variations in the index of pedotrophy were associated mainly with the decreased intensity of ammonification processes in winter and spring (Fig. 2a), since the oligotrophic microflora was insensitive to the seasonal factor.

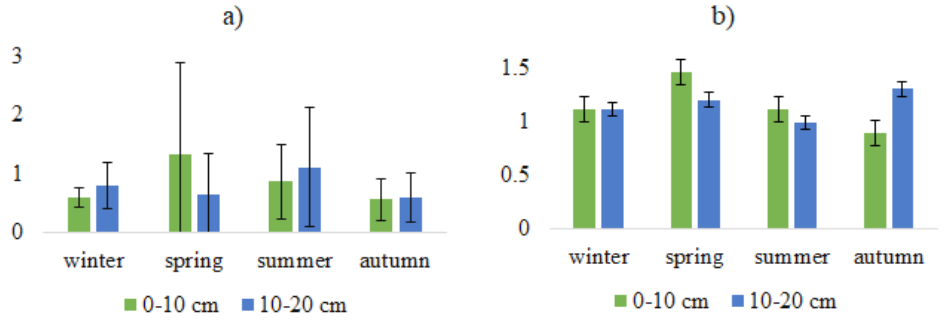

Figure 6. Seasonal variations in functional microbiological indicators at depths of 0–10 and 10–20 cm. Note: a) mineralization coefficient b) index of pedotrophy.

Physical and chemical properties of the studied soils

Higher (5.91 5.94) pH values were found for soils from sampling points 1 and 2, and lower (5.49 5.62) values were observed at points 3, 4 and 5. The pH value in the soil samples demonstrated seasonal stability (with minor deviations towards acidity in spring). The soil samples taken from point 3 showed a twofold higher moisture content compared to other sampling points. Seasonal variations affected the moisture content and showed its virtually twofold increase in winter due to moisture immobilization in the frozen upper layers. Table 4 summarizes the criteria for assessing the distribution uniformity of pH values and relative moisture content depending on the sampling depth (0–10 cm and 10–20 cm), sampling point, and seasonal factor.

Table 4. Criteria for assessing the distribution uniformity of pH values and relative moisture content in floodplain soils depending on the season, sampling point and depth

	pH				Relative moisture content, %			
	Kruskal-Wallis ANOVA		Median Test		Kruskal-Wallis ANOVA		Median Test	
	H	p	χ^2	p	H	p	χ^2	p
Season	2.30	0.51	3.00	0.39	12.52	0.01	7.90	0.05
Sampling point	23.76	<0.01	15.57	<0.01	12.67	0.01	12.05	0.02
Depth	0.87	0.35	0.57	0.45	5.81	0.02	2.42	0.12

Despite the seasonal and spatial physical and chemical differences identified in floodplain soils, the number of microorganisms of the considered physiological groups showed negligible correlations with these indicators. A statistically significant correlation (Spearman's rank correlation at $p<0.05$) was found between pH and the number of saccharolytic micromycetes (r=0.24), ammonifying bacteria (r=0.23) and, accordingly, the mineralization coefficient (r= -0.26) and the index of pedotrophy (-0.38). Soil microbial communities are extremely resistant to drying and wetting of soil (Barnard et al. 2013); however, we found that the number of cellulolytic aerobic (r= -0.26) and ammonifying bacteria (r= -0.27) correlated with the indices of relative moisture content (according to Spearman), and, accordingly, the mineralization coefficient (r=0.43) and the index of pedotrophy (r=0.42), the values of which are partially determined by the latter. The number of detected cellulolytic aerobic bacteria was found to correlate with air temperature (r=0.25).

The pH value and moisture content are considered to be critical for the formation of soil microbial communities (Barnard et al. 2013; Fierer 2017; Banerjee et al. 2015; Banerjee and Siciliano 2012; Blagodatsky and Smith 2012; Gleeson et al. 2010); yet, numerous authors report the complexity and variability of these correlations depending on soil texture, moisture retention, porosity, organic matter content, and depth (Leirós et al. 1999; Rodrigo et al. 1997; Gonçalves and Carlyle 1994).

The effect of soil moisture fluctuations on microbial communities drives the selection of organisms better adapted to these conditions (Rinklebe and Langer 2006; Hackl et al. 2005), which is particularly important for floodplain microbiocenoses (Leontyeva et al. 2005). This may explain the fact that only two of the ten physiological groups of microorganisms considered in this study were sensitive to soil moisture fluctuations, two groups responded to changes in pH values, and only one group responded to air temperature fluctuations.

Conclusion

The floodplain soils of the central part of the middle Ob River are extremely rich in heterotrophic microorganisms.

The spatial variability of the microbiological indicators of floodplain soils within the studied territorial context was not high, despite the identified differences in the soil pH values and relative moisture content. Floodplain soils at the sampling points exhibited similar physiological activity of bacteria. Ammonifying, humus-degrading, oligotrophic and oligonitrophilic bacteria were most abundant in the soil samples.

Different physiological groups of microorganisms showed numerous statistically significant positive correlations, which is likely due to the functional cosmopolitan nature of most soil bacteria.

The highest values of the total microbal numbers were observed in summer, whereas the lowest values were found in spring. The seasonal dynamics of ammonifying, amylolytic, humus-degrading, cellulolytic aerobic, oligonitrophilic and denitrifying bacteria in floodplain soils was identified and assessed. Oligotrophic, anaerobic nitrogen-fixing, nitrifying bacteria and saccharolytic micromycetes were most resistance to seasonal variations.

Changes in the profile distribution were revealed for microorganisms of various physiological groups during the summer–autumn low-water period, and some of them were sensitive to sampling depth. Saccharolytic micromycetes, oligonitrophilic and denitrifying bacteria exhibited the highest sensitivity to increased sampling depth and inhabited mostly the upper layers of floodplain soils. At 0–10 cm depth, the mineralization coefficient reached its maximum in spring, and at 10–20 cm depth, it remained stable throughout the year. The indices of pedotrophy at different sampling depths differed significantly only in spring and autumn, which may be attributed to the features of the floodplain regime and the migration of nutrient substrate down the profile.

Acknowledgement

The work was carried out with the support of state assignment of the Ministry of Science and Higher Education of the Russian Federation (project No. FSWM-2020-0019) (field research), №FSWM-2023-0005 (office and statistical processing of material) and the Russian Science Foundation №23-16-00218 (conceptualization, writing and editing of the main text).

References

Argiroff WA, Zak DR, Lanser CM, Wiley MJ (2017) Microbial Community Functional Potential and Composition Are Shaped by Hydrologic Connectivity in Riverine Floodplain Soils. Microbial Ecology 73: 630–644. https://doi.org/10.1007/s00248-016-0883-9

Babeva IP, Zenova GM (1989) Soil biology: Textbook. Moscow State University Press, Moscow, 336 pp. [In Russian]

Banerjee S, Helgason B, Wang L, Winsley T, Ferrari BC, Siciliano SD (2015) Legacy effects of soil moisture on microbial community structure and N_2O emissions. Soil Biology and Biochemistry 95: 40–50. https://doi.org/10.1016/j.soilbio.2015.12.004

Banerjee S, Siciliano S (2012) Spatially tripartite interactions of denitrifiers in arctic ecosystems: activities, functional groups and soil resources: denitrifier spatial patterns in arctic soils. Environmental Microbiology 14: 2601–2613. https://doi.org/10.1111/j.1462-2920.2012.02814.x

Barnard RL, Osborne CA, Firestone MK (2013) Responses of soil bacterial and fungal communities to extreme desiccation and rewetting. ISME Journal 7(11): 2229–2241. https://doi.org/10.1038/ismej.2013.104

Bauhus J, Barthel R (1995) Mechanisms of carbon and nutrient release and retention within beech forest gaps. The role of microbial biomass. Plant and Soil 168(169): 585–592. https://doi.org/10.1007/BF00029372

Blagodatsky S, Smith P (2012) Soil physics meets soil biology: Towards better mechanistic prediction of greenhouse gas emissions from soil. Soil Biology and Biochemistry 47: 78–92. https://doi.org/10.1016/j.soilbio.2011.12.015

Bossio DA, Scow K (1995) Impact of Carbon and Flooding on the Metabolic Diversity of Microbial Communities in Soils. Applied and Environmental Microbiology 61(11): 4043–4050. https://doi.org/10.1128/aem.61.11.4043-4050.1995

Diaz-Ravina M, Acea MJ, Carballas T (1995) Seasonal changes in microbial biomass and nutrient flush in forest soils. Biology and Fertility of Soils 19: 220–226. https://doi.org/10.1007/BF00336163

Dobrovolsky GV (1971) River floodplains as landscapes of high life density and intensive soil-forming process. In: Biological productivity and cycles of chemical elements in plant communities. Nauka, Leningrad, 226–231. [In Russian]

Eisenhauer N, Schielzeth H, Barnes AD, Barry KE, Bonn A, Brose U, Bruelheide H, Buchmann N, Buscot F, Ebeling A, Ferlian O, Freschet GT, Giling DP, Hättenschwiler S,

Hillebrand H, Hines J, Isbell F, Koller-France E, König-Ries B, de Kroon H, Meyer ST, Milcu A, Müller J, Nock CA, Petermann JS, Roscher C, Scherber C, Scherer-Lorenzen M, Schmid B, Schnitzer SA, Schuldt A, Tscharntke T, Türke M, van Dam NM, van der Plas F, Vogel A, Wagg C, Wardle DA, Weigelt A, Weisser WW, Wirth C, Jochum M (2019) A multitrophic perspective on biodiversity-ecosystem functioning research. Advances in Ecological Researches 61: 1–54. https://doi.org/10.1016/bs.aecr.2019.06.001

Fierer N (2017) Embracing the unknown: disentangling the complexities of the soil microbiome. Nature Reviews Microbiology 15(10): 579–590. https://doi.org/10.1038/nrmicro.2017.87

Fomina NV, Sorokin GA, Demidenko ND (2006) Ecological and microbiological monitoring of soil in a forest nursery in Krasnoyarsk Krai. Bulletin of the Krasnoyarsk State Agrarian University 10: 146–153. [In Russian]

Geltser YG (1986) Biological diagnostics of soils. Moscow State University Press, Moscow, 78 pp. [In Russian]

Gleeson D, Müller C, Banerjee S, Ma W, Siciliano S, Murphy D (2010) Response of ammonia oxidizing archaea and bacteria to changing water filled pore space. Soil Biology and Biochemistry 42–10: 1888–1891. https://doi.org/10.1016/j.soilbio.2010.06.020

Gonçalves JLM, Carlyle JC (1994) Modelling the influence of moisture and temperature on net nitrogen mineralization in a forested sandy soil. Soil Biology and Biochemistry 26(11): 1557–1564. https://doi.org/10.1016/0038-0717(94)90098-1

Grigoryan BR, Koltsova TG, Sungatullina LM (2014) Methodological recommendations for assessing the soil and ecological status of agricultural lands for compliance with the requirements of organic farming. Kazan, 52 pp. [In Russian]

Hackl E, Pfeffer M, Donat C, Bachmann G, Zechmeister-Boltenstern S (2005) Composition of the microbial communities in the mineral soil under different types of natural forest. Soil Biology and Biochemistry 37(4): 661–671. https://doi.org/10.1016/j.soilbio.2004.08.023

Ivanov FD, Govortsov AV (2019) Seasonal dynamics of the number of microorganisms in natural and anthropogenically transformed soils of Rostov-on-Don. In: Proceedings of the VIII scientific and practical conference with international participation. Genetics is the fundamental basis of innovations in medicine and breeding, Rostov-on-Don (Russia), September 2019. Southern Federal University Publishing House, Rostov-on-Don–Taganrog, 121–123. [In Russian]

Janse HJ, van Dam AA, Hes EM, de Klein JJM, Finlayson CM, Janssen ABG, van Wijk D, Mooij WM, Verhoeven JTA (2019) Towards a global model for wetlands ecosystem services. Current Opinion in Environmental Sustainability 36: 11–19. https://doi.org/10.1016/j.cosust.2018.09.002

Kayranli B, Scholz M, Mustafa A, Hedmark A (2009) Carbon storage and fluxes within freshwater wetlands: a critical review. Wetlands 30: 1–124. https://doi.org/10.1007/s13157-009-0003-4

Khodjimurodova N, Raupova NB (2019) Microbiological activity of old irrigated and newly irrigated meadow-alluvial soils. Bulletin of Science and Practice 5(3): 27–33. [In Russian]

Khromykh VS (1975) Structure and qualitative assessment of the Middle Ob floodplain landscapes within the boundaries of Tomsk Region. PhD Thesis, Novosibirsk, Russia. [In Russian]

Khromykh VS, Kostenko EA, Ogorodnikov AV (2000) The role of soil in the dynamics of floodplain landscapes In: Modern problems of soil science in Siberia. Vol. 1: Proceedings of the International scientific conference dedicated to the 70th anniversary of the formation of the Department of Soil Science, Tomsk State University. Tomsk (Russia), 149–153. [In Russian]

Khromykh VS (1979) Natural zoning of the Middle Ob floodplain. Issues of Siberian geography. Tomsk 12: 69–86. [In Russian]

Kolesnichenko YY, Kolesnichenko LG, Vorobyev SN, Shirokova LS, Semiletov IP, Dudarev OV, Vorobyev RS, Shavrina U, Kirpotin SN, Pokrovsky OS (2021) Landscape, Soil, Lithology, Climate and Permafrost Control on Dissolved Carbon, Major and Trace Elements in the Ob River, Western Siberia. Water 13: 31–89. https://doi.org/10.3390/w13223189

Kontsevaya II, Daineko NM, Zyablitsky KO, Minina AV (2018) Effect of the microbial preparation PoliFunKur on agronomically useful groups of soil microorganisms in corn crops. Bulletin of Science and Practice 4(9): 96–102. [In Russian]

Leirós M, Trasar-Cepeda C, Seoane S, Gil-Sotres F (1999) Dependence of mineralization of soil organic matter on temperature and moisture. Soil Biology and Biochemistry 31(3): 327–335. https://doi.org/10.1016/S0038-0717(98)00129-1

Leontyeva MS, Dobrovolskaya TG, Pochatkova TN (2005) Effect of floodplain regime on the taxonomic structure of soil bacterial complexes. Bulletin of Moscow University (Series 17. Soil Science) 1: 36–39. [In Russian]

Lukina NV, Geraskina AP, Gornov AV, Shevchenko N, Kuprin AV, Chernov TI, Chumachenko SI, Shanin VN, Kuznetsova AI, Tebenkova DN, Gornova MV (2020) Biodiversity and climate-regulating functions of forests: current issues and research prospects. Issues of Forest Science 3(4): 1–90. http://dx.doi.org/10.31509/2658-607x-202141k-60

Mekhtiev SY (1959) Some data on the study of various soils of Moldova. Microbiology 25(5): 31–38. [In Russian]

Mishustin EN (1956) Microorganisms and soil fertility. Academy of Sciences Press, Moscow, 342 pp. [In Russian]

Mishustin EN (1972) Microorganisms and agricultural productivity. Nauka, Moscow, 343 pp. [In Russian]

Mitsch WJ, Day JW, Gilliam WJ, Groffman PM, Hy D, Randall GW, Wang N (2001) Reducing nitrogen loading to the Gulf of Mexico from the Mississippi River Basin: strategies to counter a persistent ecological problem. Bioscience 51(5): 373–388. https://doi.org/10.1641/0006-3568(2001)051[0373:rnlttg]2.0.co;2

Moche M, Gutknecht J, Schulz E, Langer U, Rinklebe J (2015) Monthly dynamics of microbial community structure and their controlling factors in three floodplain soils. Soil Biology and Biochemistry 90: 169–178. https://doi.org/10.1016/j.soilbio.2015.07.006

Nikitin BA (1972) Method for determining humus content in soils. Agrochemistry 3: 123–125. [In Russian]

Nikitina VG (1978) Microflora and biochemical activity of floodplain soils of the Lower Irtysh. In: Lower Irtysh Valley. Current status of the natural environment. Irkutsk, 81–89. [In Russian]

Nikitina ZI (1991) Microbiological monitoring of terrestrial ecosystems. Nauka, Novosibirsk, 222 pp. [In Russian]

Pacini GC, Bruschi P, Ferretti L, Santoni M, Serafini F, Gaifami T (2023) FunBies, a model for integrated assessment of functional biodiversity of weed communities in agro-ecosystem. Ecological Modelling 486: 1–24. https://doi.org/10.1016/j.ecolmodel.2023.110529

Parinkina OM (1971) On the microbiological characteristics of some soils of Western Taimyr. In: Biogeocenoses of the Taimyr tundra and their productivity. Nauka, Leningrad, 32–35. [In Russian]

Rafailova EA, Tukhbatova RI, Pankova AV, Alimova FK (2009) Microflora of periodically flooded soils on the example of Bolshoy Mansur Island. Water: chemistry and ecology 4: 18–22. [In Russian]

Reay MK, Loick N, Evershed RP, Muller C, Cardenas ML (2023) Moisture effects on microbial protein biosynthesis from ammonium and nitrate in an unfertilised grassland. Soil Science and Soil Biology 184: 109–114. https://doi.org/10.1016/j.soilbio.2023.109114

Rinklebe J, Langer U (2006) Microbial diversity in three floodplain soils at the Elbe River (Germany). Soil Biology and Biochemistry 38(8): 2144–2151. https://doi.org/10.1016/j.soilbio.2006.01.018

Rodrigo A, Recous S, Neel C, Mary B (1997) Modelling temperature and moisture effects on C–N transformations in soils: comparison of nine models. Ecological Modelling 102(2–3): 325–339. https://doi.org/10.1016/S0304-3800(97)00067-7

Savich VI, Mosina LV, Norovsuren J, Sidorenko OD, Anikina DS (2019) Microbiological activity of soils as a factor of soil formation. International Agricultural Journal 1: 38–42. https://doi.org/10.24411/2587-6740-2019-11010 [In Russian]

Savichev OG, Tokarenko OG, Pasechnik EY, Nalivaiko NG, Ivanova EA, Nadeina LV (2015) Microbiological composition of river waters in the Ob' basin (West Siberia) and its associations with hydrochemical indices. IOP Conference Series: Earth and Environmental Science 27(1): 12–35. https://doi.org/10.1088/1755-1315/27/1/012035

Schlesinger WH, Bernhardt ES (2013) Biogeochemistry: an analysis of global change. Elsevier, New York, 672 pp. https://doi.org/10.1016/C2012-0-01654-7

Schuldt A, Assmann T, Brezzi M, Buscot F, Eichenberg D, Gutknecht J, Härdtle W, He JS, Klein AM, Kühn P, Liu X, Ma K, Niklaus PA, Pietsch KA, Purahong W, Scherer-Lorenzen M, Schmid B, Scholten T, Staab M, Tang Z, Trogisch S, von Oheimb G, Wirth C, Wubet T, Zhu CD, Bruelheide H (2018) Biodiversity across trophic levels drives multifunctionality in highly diverse forests. Nature Communications 9: 1–10. https://www.nature.com/articles/s41467-018-05421-z

Segi Y (1983) Methods of soil microbiology. Kolos, Moscow, 296 pp. [In Russian]

Sha C, Mitsch WJ, Mander Ü, Lu J, Batson J, Zhang L, He W (2011) Methane emissions from freshwater riverine wetlands. Ecological Engineering 37: 16–24. https://doi.org/10.1016/j.ecoleng.2010.07.022

Shen R, Lan Z, Rinklebe J, Nie M, Hu Q, Yan Z, Fang C, Jin B, Chen J (2021) Flooding variations affect soil bacterial communities at the spatial and inter-annual scales. Science of The Total Environment 759(10): 143–471. https://doi.org/10.1016/j.scitotenv.2020.143471

Shepeleva LF (2019) Structure and dynamics of meadow communities of the Middle Ob. Tomsk State University Publishing House, Tomsk, 348 pp. [In Russian]

Singh JS, Raghubansh AS, Singh RS, Srivastava SC (1989) Microbial biomass acts as a source of plant nutrients in dry tropical forest and savanna. Nature 338(6215): 499–500.

Slavnina TP, Inisheva LI (1987) Biological activity of soils of Tomsk region. Tomsk State University Publishing House, Tomsk, 216 pp. [In Russian]

Slavnina TP, Pashneva GE, Kakhatkina MI, Tazynbaev MG (1981) Soils of the Middle Ob floodplain, their meliorative status and agrochemical characteristics. Tomsk State University Publishing House, Tomsk, 227 pp [In Russian]

Titova VI, Kozlov AV (2012) Methods for assessing the functioning of soil microbiocenosis involved in the organic matter transformation. Nizhny Novgorod Agricultural Academy, Nizhny Novgorod, 64 pp. [In Russian]

Unger M, Kennedy AC, Muzika R-M (2009) Flooding effects on soil microbial communities. Applied Soil Ecology 42(1): 1–8. https://doi.org/10.1016/j.apsoil.2009.01.007

Vorobyev SN, Kirpotin SN, Vorobyeva TE, Kolesnichenko LG, Izerskaya LA (2016) Alluvial soils of the Ob River floodplain and their significance in the formation of geochemical flow from western Siberia. Riparian Zones: Characteristics, Management Practices and Ecological Impacts 1: 263–288.

Vorobyev SN, Pokrovsky OS, Kirpotin SN, Kolesnichenko LG, Shirokova LS, Manasypov RM (2015) Flood zone biogeochemistry of the Ob River middle course. Applied Geochemistry 63: 133–145. https://doi.org/10.1016/j.apgeochem.2015.08.005

Vorobyev SN, Pokrovsky OS, Kolesnichenko LG, Manasypov RM, Shirokova LS, Karlsson J, Kirpotin SN (2019) Biogeochemistry of dissolved carbon, major, and trace elements during spring flood periods on the Ob River. Hydrological Processes 33(1): 1579–1594. https://doi.org/10.1002/hyp.13424

Wardle DA (1998) Controls of temporal variability of the soil microbial biomass: A global-scale synthesis. Soil Biology and Biochemistry 30(13): 1627–1637. https://doi.org/10.1016/S0038-0717(97)00201-0

Wilson JS, Baldwin DS, Rees GN, Wilson BP (2011) The effects of short-term inundation on carbon dynamics, microbial community structure and microbial activity in floodplain soil. River Research and Applications 27: 213–225. https://doi.org/10.1002/rra.1352

Yakushev AV (2015) Integral structural-functional method for characterizing microbial populations. Soil Science 48(4): 429–446. https://doi.org/10.1134/S1064229315040110

Yakutin MV, Andrievsky VS, Shepelev AI (2014) Features of changes in the zoomicrobiological complex during the natural evolution of floodplain soils of the middle Ob. Bulletin of Surgut State University 2(4): 74–79. [In Russian]

Yakutin MV, Andrievsky VS, Shepelev AI (2013) Use of soil-biological methods in monitoring floodplain ecosystems in the middle Ob region. Interexpo Geo-Siberia 2: 1–6. [In Russian]