

## Soil microorganisms

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### SOILS OF CHERNEVAYA TAIGA OF WESTERN SIBERIA — MORPHOLOGY, AGROCHEMICAL FEATURES, MICROBIOTA

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## Abstract

The soils of Chernevaya taiga are unique in terms of high fertility that was formed not as a result of agricultural practices, but due to the combination of a huge volume of biotic and abiotic resources. This area was able to preserve its "pre-agricultural" level of fertility overtime by avoiding the negative consequences of long-standing agricultural usage. Comprehensive analysis of all related properties within the framework of a metagenomic study and identification of microbial drivers of fertility can become the basis for innovative technologies aimed to increase the productivity of soils and crops. In this work, for the first time were obtained data on the taxonomic structure and features of the microbiota of soils in the Chernevaya taiga and identified taxa, the number of which significantly increases with the transition from the mature zonal soil to the soil of Chernevaya taiga. Analysis of soil samples collected during expeditionary surveys in 2019 showed that the soils in the Western Siberia (Novosibirsk, Tomsk, Kemerovo, and Altai regions) portion of the Chernevaya taiga are texture-differentiated dark gray soils (clay loam and silt clay varieties confined to the deluvial cover of the Holocene and Late Pleistocene) that were formed as a result of a unique combination of geogenic and bioclimatic conditions. These soils are not affected by the permafrost in winter timers and are supplied with enough moisture to precipitate rapid mineralization of litter material and the fixation of mineral nutrients in the upper humus layer of the soil profile. The accumulation of nutrients is an essential property of the soils of the Chernevaya taiga associated with the phenomenon of gigantism and extremely high levels of plant productivity. The soils of Chernevaya taiga contain the maximum amount of carbon in organic compounds compared with soils of oligotrophic habitats (9.85% versus 2.74%). The levels of actual soil fertility in the soils of the Chernevaya taiga are several times higher than in the soils of adjacent biotopes (the maximum content of the exchange forms of phosphorus and potassium is 702 and 470 mg/kg), which, when compared to oligotrophic forests, are poor in terms of agrochemical fertility (the maximum content of the exchange forms of phosphorus and potassium is 113 and 18 mg/kg), do not have a pronounced humus profile and are either gray-humus (Umbrisol) or Podzol types according to substantive-profile classification of Russian soils. The diversity of microorganisms in the studied soils varies depending on the trophic regime of the ecosystem. The soils of the Chernevaya taiga are characterized by an increased diversity of the microbial community (estimated

by the Shannon index), as well as by presence of phyla *Nitrospirae* and *Thaumarchaeota*, that, however, are not dominant. Phyla *Proteobacteria*, *Verrucomicrobia*, *Actinobacteria*, *Acidobacteria*, *Planctomycetes*, *Firmicutes* appeared to be common for all studied soils.

Keywords: soil ecological functions, Chernevaya taiga, microbial communities, NGS, fertility factors, Western Siberia

The global dominance of humanity in the biosphere is determined primarily by agriculture development, which covers more than half of the Earth's land area. It leads to fundamental changes in the environment and climate [1], food and energy shortages, loss of biodiversity and ecosystem stability, and natural water pollution [2-5]. More than 60% of all land changes in the period from 1982 to 2016 are related to human activity, which indicates the controlling role of humanity in the development of the Earth [6]. The problems caused by the anthropogenic transformation of the soil cover and the ecological soil functions are among the most important in the current century [7]. Modern humanity is obliged to preserve and protect the soil since soil resources are the basis of food and environmental security of nations. Long-term use of soils in agricultural production has many negative consequences for soil properties, including organic matter degradation (including dehumidification), increased greenhouse gas emissions, and diversification of its emission products, changes in the acid-base composition of the soil, soil depletion, etc. [8-10]. The use of agricultural technologies (plowing and loosening, application of mineral and organic fertilizers, etc.) significantly changes the biogeochemical cycles, including those involving soil microorganisms. The general trend of these changes is manifested in a decrease in the soil ability to provide agricultural plants with the necessary amount of mineral nutrition elements and nitrogen. In this regard, the agroecosystem cannot function effectively without the introduction of additional doses of nutrients in the form of fertilizers [10].

The introduction of fertilizers into the agroecosystem is accompanied by the emergence of new problems, namely, the significant removal of elements from the agroecosystem with surface and subsurface water runoff [11-13]. Moreover, the return of agriculture from fertilizer application decreases over time [14], and with an increase in the doses of applied nitrogen, the efficiency of its retention by the agroecosystem decreases [13]. These unavoidable processes can be slowed down if a sufficient pool of microbial biomass is created in the soil, which can accumulate elements of mineral nutrition and nitrogen of organic origin in the periods between harvesting and planting of crops. Moreover, some biogeochemical mechanisms that make it possible to retain some of the nitrogen introduced with fertilizers in ecosystems for decades, even under the conditions of existing agricultural practices, are known [15]. It means that the problem caused by a decrease in the effectiveness of fertilizers during their long-term use will be solved by technologies that help maintain and realize the soil fertility potential.

In our opinion, the necessary pool of microbial biomass can be formed bionically, by using models of natural microbiota that can maintain the highest possible biological productivity of vegetation in humid autonomous landscapes as a basis due to the sufficient closure of the biological cycle of substances in the system. In the conditions of the percolative regime, it is ensured by maintaining the cycle volume of mineral nutrition elements. The composition of such a microbiota should develop evolutionarily with a gradual increase in the volume of the biological cycle due to the constant exogenous supply of fertilizers in the case of their weathering and nitrogen in the process of nitrogen fixation. The factors that disrupt these events, by "breaking" the evolutionary cycles, include global natural and anthropogenic cataclysms, catastrophic fires, and plowing. The use of microbiota could become one of the directions of biological soil reclamation, which is extremely important for the agricultural landscapes of Russia [16].

The soils of Chernevaya taiga are a clear example of the key ecological functions of the edaphotope associated with fertility and forest-growing properties. Its study is important for understanding the phenomenon of high soil fertility. The unique combination of soil formation factors in Chernevaya taiga triggers the drivers of intensive soil formation and the circulation of elements. It should be noted that at present, practically no such ecosystems are left in the moderate climate. As a rule, the forest ecosystems of Europe are either located on the place of former agricultural land or were located on their periphery and experienced a powerful influence of the pyrogenic factor [17]. Primary undisturbed ecosystems, which are extremely productive and maximally biogeochemically intensive bioinert formations, should be sought within the barrier-rain landscapes of Siberia.

The main areal of Chernevaya taiga is located in the altitude range of approximately from 200 to 700-800 m on the western, windward macroslopes of the mountains and foothills of the south of Western Siberia. Chernevaya taiga belongs to the type of barrier-rain landscapes and is characterized by a complex of features [26-31]: fir and aspen are dominants in the stand; the grass layer formed by Siberian tallgrass species is well-developed; large shrubs are present in the underwood; the synusia of ground leafy mosses is poorly represented, the epiphytic bryoflora is quite rich; the flora is represented by a complex of relatively thermophilic nemoral species; the spring synusia of ephemeroids is strongly developed; in winter, a deep snow cover is formed (from 80 cm to 2 m or more), due to which the soils do not freeze, which is not typical for the continental climate of the taiga of Western Siberia; there is no stratified ground litter, the decomposition time of the litter is less than 2 years; the number of earthworms is one of the highest in Russia, in general, mesofauna activity is high, including the winter period. Due to the above factors and the soil features of Chernevaya taiga, its bio-productivity in comparison with other zonal types of ecosystems of the temperate zone is maximum.

The tallgrass Chernevaya taiga in the foothills and mountains of southern Siberia is one of the largest preserved massifs of tallgrass forests in Russia. Tallgrass forests are also typical for the Far East. In general, within the taiga zone, tallgrass forests have been preserved in the form of isolated areas, for example, in the Cis-Ural region and on the western slopes of the Urals, on the plains of Western Siberia, in places that have been least exposed to fires and the effects of traditional nature management [21, 22]. The least disturbed areas of tallgrass forests meet the definition of climax ecosystems according to both phytocenotic and soil criteria. The annual litter of tallgrass rapidly decomposes, which over time leads to the accumulation of mineral elements in the humus horizon [18] and supports an active biological cycle of substances, heterogeneity of the intra-cenotic environment, and high biodiversity. The water and climatic conditions and the specific hydrophysical characteristics of the respective soils probably contribute to the stabilization of plant food elements in the soil profile.

The choice of tallgrass forests as a bionic model is associated with the fact that they were the least exposed to exogenous disturbances in the past [19, 20]. In biogeographic studies, it is shown that exogenous disturbances lead to the structure simplification (spatial, species) of communities [23]. There is a point of view that the modern zonal ecosystems of the southern, middle, and northern taiga are seral series of vegetation restoration after exogenous disturbances — fires, logging, plowing, in other words, during demutation shifts [20]. Almost all of these forests are litter-bearing, with a predominance of green mosses, small-grass and low-bush species. Among them, only boreal-nemoral tallgrass forests are considered by some authors as relatively fully corresponding to the final stage of autogenic succession [24].

The given point of view on the nature of boreal forests is debatable, but it well emphasizes the isolation of tallgrass forests. Despite the name, Chernevaya taiga actually differs significantly from the actual taiga, boreal ecosystems in terms of species and coenotic composition, nutrient status, and biogeochemistry. Chernevaya taiga is considered by most researchers as a sub-nemoral, or hemiboreal, ecosystem, that is, it belongs to another class of ecosystems than the boreal forest (the taiga itself) [25].

The uniqueness of the soils of Chernevaya taiga is in exceptionally high fertility, realized at the expense of internal biotic and abiotic resources, and the preservation of microbiota that is not affected by agricultural practices. The soils of Chernevaya taiga show some features, in particular, high forest growth activity with a general low accumulation of humus (effective fertility) [26], and an unusually high rate of decomposition of plant residues [27]. The analysis of such a complex of related properties in the framework of metagenomic research is a serious fundamental task. The result of its solution and the identification of microbial drivers of fertility can be innovative technologies to increase the productivity of soils and crops.

To study the soil microbiota, high throughput sequencing is used [28, 29], which makes it possible to identify components of microbial communities, including uncultivated ones, with previously inaccessible accuracy. It has become clear that the soil microbiota (especially the rhizospheric microbiota) plays an important role in plant nutrition and protection from biotic and abiotic stresses, which is why special attention is currently being paid to the analysis of rhizospheric communities of microorganisms [30].

It is obvious that the phenomenon of high soil fertility in Chernevaya taiga cannot be limited only by agrochemical and agrophysical parameters and must be associated with the characteristics of the soil microbiota. It can also be expected that studies of this potential source of new economically significant strains (for example, cellulolytic microorganisms, producers of antibiotics, and a variety of biologically active molecules) typical for the studied ecosystem will go beyond the limits of soil and agricultural microbiology. However, no data on the soil microbiota of Chernevaya taiga have been available so far.

This paper is the first one dedicated to characterization of the taxonomic structure of prokaryotic microbiota of the Chernevaya taiga soil. It is shown that the differences between the mature zonal soil and the soil of Chernevaya taiga are most likely determined at levels below the phylum. Taxa, the number of which significantly increases in the soil of Chernevaya taiga, were identified. These are predominantly unclassified prokaryotes. Among the identified microorganisms, the order *Chthoniobacterales* is of particular interest, the first representative of which was isolated only recently.

One of the major goals of this study is to determine the main morphological, agrochemical features, and taxonomic composition of the soil microbiota of Chernevaya taiga in Western Siberia in comparison with soils associated with oligotrophic ecosystems of pine forests on sandy soil-forming substrates.

*Materials and methods.* In the second half of July 2019, expeditionary surveys of soils have been conducted in the Tomsk, Kemerovo, and Novosibirsk Regions, as well as in the Altai. The objects of the study were four soil profiles (different variants of Chernevaya taiga in the Salair and Kuznetsk–Alataus areals), as well as two soils from relatively oligotrophic habitats associated with ancient Aeolian sand massifs covered with pine forests. The southern variants of the studied soils were represented by the following objects: N1 (Dark Gray Soil of Chernevaya taiga, Altai Territory; 54.14070°N, 84.9495°E), N2 (Dark Humus Luvisol, grass pine forest, erosion valley, Novosibirsk Region; 54.37083°N, 82.4393°E), N3 (Gray Humus Soil on aeolian sandy loams under oligotrophic coniferous forest

ecosystem, Novosibirsk Region; 54.40810°N, 82.18420°E); northern variants — T1 (dark gray soil in a tallgrass fir-aspen forest with a shrinking fir stand, Tomsk Region; 56.30693°N, 85.47063°E), T2 (Sod-Podzolic Soil, tallgrass broad grass birch-fir post-logging Chernevoy forest, Kemerovo Region; 55.88619°N, 86.00433°E), T3 (Sod-Eluvial Sandy Loam Soil under the oligotrophic ecosystem of mixed pine forest with an admixture of larch, Tomsk Region, coordinates: 56.48106°N, 84.79860°E).

The soil texture was analyzed according to Kaczynski with pyrophosphate peptization of microaggregates (the sedimentation method). The content of organic carbon and nitrogen was determined using an elemental analyzer (EURO EA-3028-HT, EuroVector S.p.A., Italy; resource center Chemical Analysis and Materials Research Centre of the St. Petersburg State University Research Park). The pH of the water extract was measured at a ratio of 1:2.5, when the pH of the water suspension was below 7.0. The pH of the salt suspension was measured at the same ratio. Mobile compounds of phosphorus and potassium were determined by the Kirsanov method modified by CINAO (GOST R 54650-2011. National standard of the Russian Federation. Soils), exchangeable ammonium — by the CINAO method (GOST 26489-85. State standard of the USSR. Soils), nitrates — by the ionometric method (GOST 26951-86. State standard of the USSR. Soil).

Basal respiration as an indicator of the biological metabolic activity of soils was measured according to the description [37] in closed chambers, taking into account the amount of CO<sub>2</sub> emitted over 7 days by the titration method.

The soil temperature regime was recorded with an automatic device for monitoring climatic parameters SAM-SM (Institute of Monitoring of Climatic and Ecological Systems SB RAS, Russia).

DNA for metagenomic analysis was isolated from soil samples using the NucleoSpin Soil kit (Macherey-Nagel GmbH & Co. KG, Germany) following the manufacturer's instructions.

Preparation of libraries for high throughput sequencing included amplification of the target fragment of the variable V4 region of the 16S rRNA gene using universal primers (515F — 5'-GTGCCAGCMGCCGCGGTAA-3'/806R — 5'-GGACTACVSGGGTATCTAAT-3') [31] together with linkers and unique barcodes. Polymerase chain reaction (PCR) was performed on a T100 Thermal Cycler device (Bio-Rad Laboratories, USA) in 15  $\mu$ l of a reaction mixture containing 0.5 units of Q5® High-Fidelity DNA Polymerase (New England BioLabs, USA), 1X Q5 Reaction Buffer, 5 pmol of each of the primers, 3.5 mM dNTP (Evrogen, Russia) and 1-10 ng of the DNA matrix. The PCR program included a denaturation stage at 94 °C — 1 min, product amplification for 35 cycles (94 °C — 30 s, 50 °C — 30 s, 72 °C — 30 s), and final elongation at 72 °C — 3 min. Further sample preparation and sequencing were performed following the Illumina protocol (16S Metagenomic Sequencing Library Preparation) on the Illumina MiSeq instrument (Illumina, Inc., USA) using the MiSeq Reagent Kit v3 (600 cycles) with two-way reading (2×300 n) (Illumina, Inc., USA).

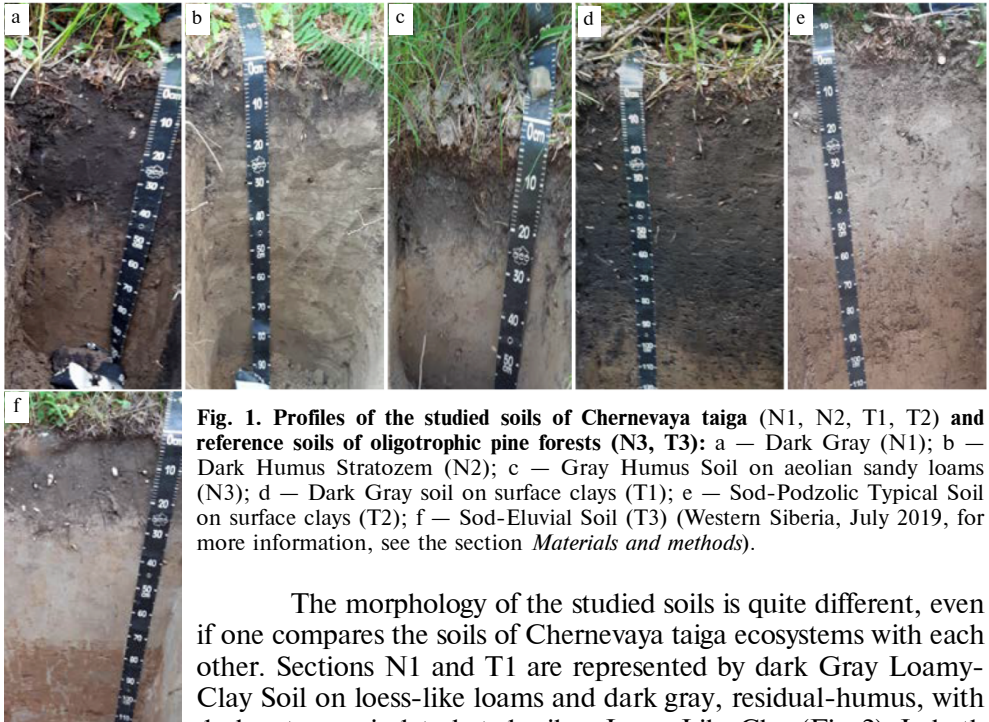
Preprocessing of the received data included removal of service sequences using the Cutadapt program [32], as well as denoising, combining paired reads, and deleting chimeras using the Dada2 package [33] implemented in the R software environment. The taxonomic classification of the obtained amplicon sequence variants was also performed using release SILVA 132 database (<https://www.arb-silva.de/documentation/release-132/>) containing data for the SSU rRNA genes [34]. Further processing, including the construction of a phylogenetic tree using the SEPP algorithm [35], the calculation of  $\alpha$ - and  $\beta$ -diversity, was performed within the QIIME2 package [36], and the plugins implemented in it. The diversity indices reflecting the actual predicted species richness (Chao1),

the degree of evenness according to Shannon and dominance according to Simpson were taken into account to assess the  $\alpha$ -diversity,

The packages phyloseq [37] and DESeq2 [38] were used to identify differentially abundant taxa. Based on the results of the performed analysis, a sub-sample of phylotypes was formed, the change in the abundance of which is significant at  $\alpha \leq 0.1$  (taking into account the Benjamini-Hochberg correction).

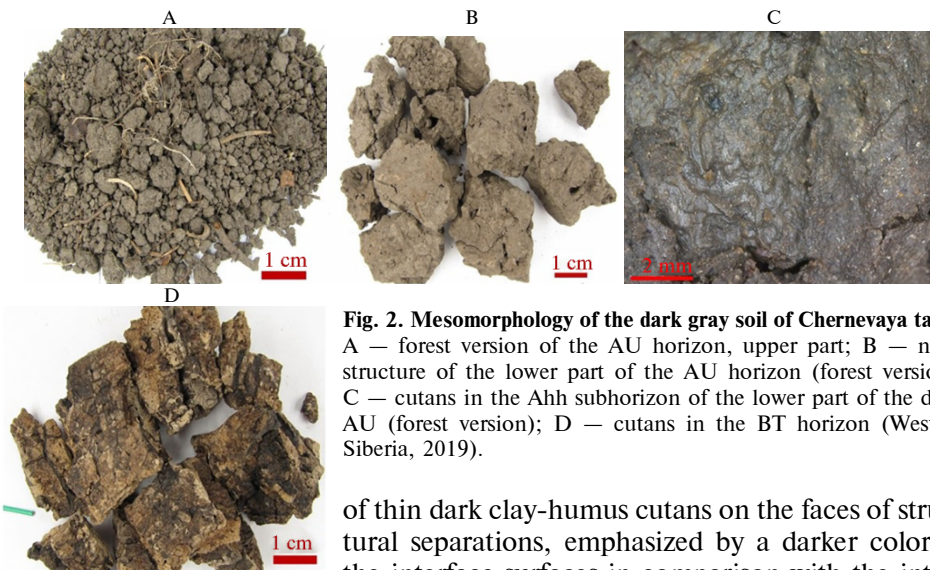
The total organic carbon and nitrogen content, soil basal respiration, and agrochemical parameters were measured in 3-fold analytical repetition and presented as mean ( $M$ ) and standard errors of the mean ( $\pm$ SEM). The soil texture was evaluated in one repetition. To assess the correlation ratio between the parameters of soil availability of nutrients, Spearman's correlation coefficient  $r$  was calculated. The significance of the differences between the indicators for the soils of Cherevaya taiga and oligotrophic habitats was evaluated by one-way analysis of variance (one-way ANOVA). The taxonomic structure of soil microbiota samples was analyzed in 4 independent repetitions.

**Results. Morphology and analytical characteristics.** The morphological characteristics and texture of the soils of the selected sites (Fig. 1) are presented in Table 1. The studied sections had covered the main components of the biodiversity of Cherevaya taiga, represented on the surface clays by such contrasting variants as dark gray and sod-podzolic soils [39].



**Fig. 1. Profiles of the studied soils of Cherevaya taiga (N1, N2, T1, T2) and reference soils of oligotrophic pine forests (N3, T3):** a — Dark Gray (N1); b — Dark Humus Stratozem (N2); c — Gray Humus Soil on aeolian sandy loams (N3); d — Dark Gray soil on surface clays (T1); e — Sod-Podzolic Typical Soil on surface clays (T2); f — Sod-Eluvial Soil (T3) (Western Siberia, July 2019, for more information, see the section *Materials and methods*).

The morphology of the studied soils is quite different, even if one compares the soils of Cherevaya taiga ecosystems with each other. Sections N1 and T1 are represented by dark Gray Loamy-Clay Soil on loess-like loams and dark gray, residual-humus, with dark cutans, wind-turbated soil on Loess-Like Clay (Fig. 2). In both soils, there is a well-developed deep dark humus horizon, which has a more complex structure in T1, which is associated with signs of residual humus formation, namely, a decrease in lightness on the Munsell scale in Fig. 1 (see Table 1). This horizon in both soils is characterized by a well-developed three-dimensional lumpy structure, which is gradually replaced by prismatic and nutty-prismatic separations (Fig. 2, A, B). The dark humus horizon in the first case passes into a subeluvial stratum with signs of the EL eluvial horizon in the form of separate small morphons. In the second case, the dark humus horizon is replaced by the flow-humus horizon Ahh, which is characterized by an increased moisture content, the presence



**Fig. 2. Mesomorphology of the dark gray soil of Chernovaya taiga:** A — forest version of the AU horizon, upper part; B — nutty structure of the lower part of the AU horizon (forest version); C — cutans in the Ahh subhorizon of the lower part of the deep AU (forest version); D — cutans in the BT horizon (Western Siberia, 2019).

of thin dark clay-humus cutans on the faces of structural separations, emphasized by a darker color of the interface surfaces in comparison with the intra-surface mass.

### 1. Morphological characteristics, the color of soil horizons, the skeletal and fine soil content in the studied soils of Chernovaya taiga (Western Siberia, 2019)

Depth, cm	Horizon	Munsell color code	Skeletal content, %	Fine soil content, %
N1, Dark Gray Soil (Altai Region)				
0-10	O	10 YR 3/1	No data	No data
10-20	AU	10 YR 4/1	11	89
20-30	AU	10 YR 4/1	12	88
30-40	BEL	10 YR 6/2	18	82
40-50	BEL	10 YR 6/2	21	79
60-80	BI	5 YR 6/3	19	81
80-100	BC	5 YR 6/3	21	79
N2, Dark Humus Stratozem (Novosibirsk Region)				
0-2	O	10 YR 3/1	No data	No data
2-10	AU	10 YR 4/1	22	78
10-20	RU	5 YR 2.5/1	11	89
30-40	RU	5 YR 2.5/1	0	100
60-70	RU	5 YR 2.5/1	0	100
80-90	C	7.5 YR 8/1	0	100
N3, Gray-Humus Soil on aeolian sandy loams (Novosibirsk Region)				
0-3	O	10 YR 4/1	No data	No data
3-15	AY	7.5 YR 8/1	6	94
20-30	AC	7.5 YR 8/1	4	96
40-50	C	7.5 YR 8/1	2	98
T1, Dark Gray Soil (Tomsk Region)				
0-1	O	10 YR 4/1	No data	No data
1-15	AU	10 YR 4/1	19	81
15-30	AU	10 YR 4/1	18	82
35-55	Ahh	10 YR 3/3	19	81
70-110	BTtur	5 YR 4/6	21	79
T2, Sod-Podzolic Soil (Kemerovo Region)				
0-3	AY	7.5 YR 6/1	93	7
3-17	EL	5 YR 7/1	25	75
20-30	BEL	5 YR 7/1	18	82
30-40	BT	5 YR 4/6	21	79
40-50	BT	5 YR 4/5	22	78
60-70	BT	5 YR 4/5	23	77
80-90	BCi	5 YR 6/3	5	95
105-120	BCi	5 YR 6/3	10	90
T3, Sod-Eluvial Soil (Tomsk Region)				
0-3	O	10 YR 4/1	No data	No data
10-20	AY	7.5 YR 8/1	5	95
40-50	EL	5 YR 7/1	2	98
50-60	BT	5 YR 4/6	1	99
60-80	BT	5 YR 4/6	1	99

Note. N1, N2, T1, T2 — soils of Chernovaya taiga, N3, T3 — reference soils of oligotrophic pine forests.

Dark Gray Soils are not widely distributed in Chernevaya taiga. They have not been previously described for the low-mountain part, although the authors' studies have shown that there is a high probability of meeting them in the lower parts of the slopes, in hollows, that is, in places with additional moisture. Apparently, the fact that such soils are not mentioned in the works of other authors on Chernevaya taiga is due to the insufficient geographical knowledge of this region. The two examined profiles, N1 and T1, differ in the features of the lower part of the deep dark-humus horizon. In the N1 profile, eluvial morphons appear, which is associated with active subsurface runoff in low-mountain terrain, when in this part there is no accumulation, but the concentration of flows and the removal of a fine fraction, which is enriched with humus. A relative accumulation of skeletal, a dusty fraction that has light tones happens in this place. Such morphons indicate the evolution of this soil towards the dark humus butterburs, which are widely distributed in the foothill sub-taiga of Western Siberia (Prialtayskaya soil province), where they occupy a reduced position in micro-, less often in mesorelief. In the T1 profile, the Ahh subhorizon is isolated in the lower part of the deep AU horizon. It is the second humus horizon bearing signs of illuvial transformation, which is diagnosed by dark humus-clay cutans on the interface surfaces (see Fig. 2, C). Clay cutans settle due to the slow flow of the topwaters (which is confirmed by a series of field observations in spring and late summer) in the conditions of hollows that drain the gentle slopes relative to the flat terrain of the northern part of the studied area of Chernevaya taiga. Below in the textural horizon, the composition of the cutans is preserved, but their thickness and abundance increase (see Fig. 2, D).

The soils of points N2 and T2 are represented by the next stage of nutrient status, that is, not Dark Gray Soils, but Stratozem and Sod-Podzolic ones, both of which are also typical for Chernevaya taiga. The Dark-Humus Medium-Loamy Stratozem on stratified loams (slide-rocks) is located in the erosional valley of the Karakan River under a grassy pine forest with the presence of aconite. Sod-Podzolic Medium Loam on loess-like loam is located in the post-logging aspen-birch-fir tallgrass forest of Chernevaya taiga.

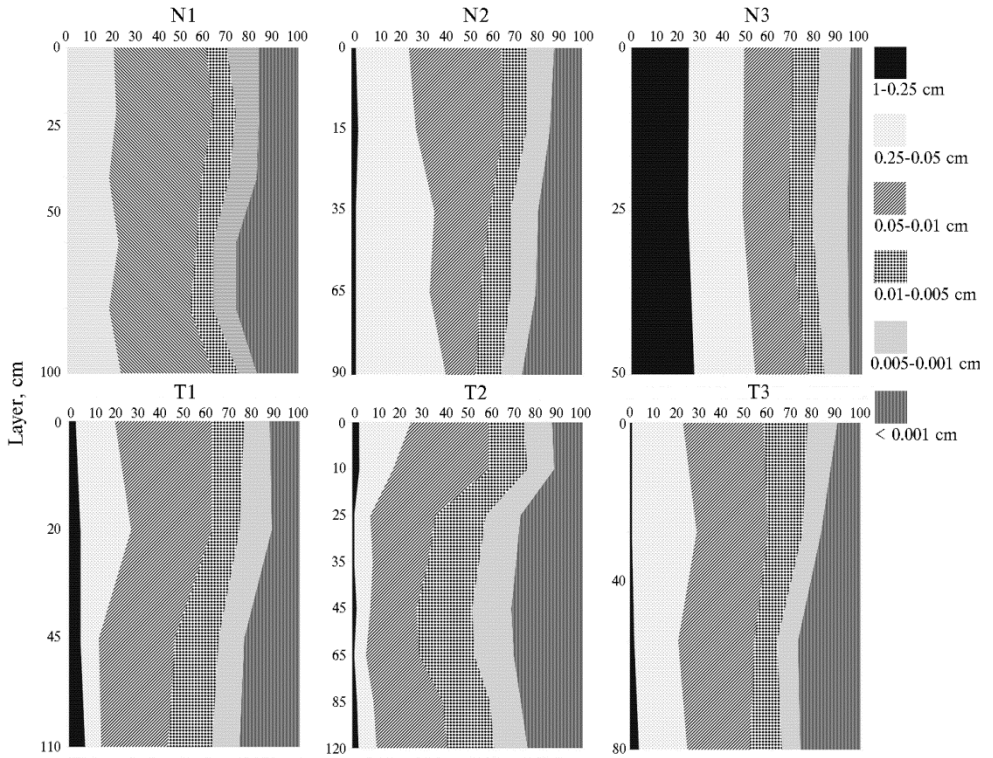
The soils of points N3 and T3 (reference soils of oligotrophic pine forests) are represented by relatively oligotrophic variants since in their origin they are associated with light soil-forming rocks and pine forests: N3 – Gray-Humus Sandy Loam on aeolian sandy loam in the grass-pine brake-sedge forest, T3 – Sod-Eluvial Sandy Loam under the oligotrophic ecosystem of mixed-grass pine forest with an admixture of larch. At the same time, within the T3 point, there are plant species typical for the Chervoy forest: *Cacalia hastata* L., *Aconitum septentrionale* (Koelle) Korsh., *Milium effusum* L. However, their abundance and viability are significantly lower than in the studied Chervoy forests. The soil profiles of Chernevaya taiga are usually more differentiated by the content of silt and physical clay compared to the soils of the oligotrophic variants (Fig. 3), which indicates the intensive development of eluvial processes.

Thus, it can be seen that the type of soil and its profile organization largely correspond to the type of forest. Thus, Chernevaya taiga is not formed on soils confined to sandy rocks with light soil texture. Forests of Chernevaya taiga are confined to either dark gray or Sod-Podzolic Soils with a pronounced binomial structure of the soil profile, loam-clay soil texture.

Chemical analysis showed a gradual decrease in the profile distribution of carbon and nitrogen (Table 2), which is in principle typical for texture-differentiated and gray-humus soils. The highest content of organic carbon and nitrogen is typical for the upper organomineral horizons of the soils of Chernevaya taiga, and it is precisely for dark gray soils, which indicates their maximum trophicity. The



soils of oligotrophic habitats have, on average, the lowest humus content. Approximately the same patterns apply to the total nitrogen content. The ratio of carbon to nitrogen [40] indicates an average or high nitrogen content of the soil. The studied soils are close to neutral or slightly acidic, which is typical for texture-differentiated soils. At the same time, the soils of oligotrophic habitats are more acidic, which is associated with less buffering of sandy loam fine soil compared to loam [41]. The intensity of basal respiration was generally higher in oligotrophic soils (points N3 and T3), and the profiles — in the bedding horizons.



**Fig. 3. Profile diagrams of the soil texture of the studied soils:** N1, N2, T1, T2 — soils of Chernevaya taiga, N3, T3 — reference soils of oligotrophic pine forests (Western Siberia, 2019). For a description of the soil samples, see the section *Materials and methods* and Table 1.

## 2. Carbon and nitrogen content, acidity, and basal respiration of the studied soils ( $n = 3$ , $M \pm SEM$ , Western Siberia, 2019)

Code, depth, cm	C, %	N, %	C/N	pH of the extract		Basal respiration, mg of CO <sub>2</sub> /(100 g of soil · day)
				water	saline	
N1 0-10	4.76±0.23	0.37±0.05	12.81	6.56	5.82	0.022±0.003
N1 10-20	3.22±0.17	0.27±0.04	11.57	6.13	5.20	0.019±0.002
N1 20-30	2.40±0.17	0.18±0.03	13.00	6.02	4.69	0.013±0.002
N1 30-40	2.25±0.10	0.17±0.03	12.88	5.85	4.64	0.021±0.002
N1 40-50	1.41±0.07	0.11±0.02	12.71	5.44	4.89	0.021±0.002
N1 60-80	0.45±0.05	0.06±0.02	8.14	6.30	4.53	0.020±0.004
N1 80-100	0.24±0.04	0.05±0.01	5.42	6.39	4.57	0.028±0.003
N2 0-2	2.14±0.21	0.16±0.01	13.51	6.95	5.96	0.062±0.001
N2 2-10	2.02±0.19	0.15±0.01	13.59	7.35	No data	0.047±0.009
N2 10-20	0.23±0.04	0.03±0.01	6.45	7.22	No data	0.037±0.008
N2 30-40	0.16±0.04	0.03±0.01	5.68	7.09	No data	0.040±0.002
N2 60-70	0.15±0.02	0.03±0.01	5.18	6.81	5.70	0.041±0.004
N2 80-90	0.46±0.09	0.05±0.01	8.44	6.65	5.65	0.041±0.004
N3 0-3	2.70±0.21	0.17±0.03	15.46	6.70	6.20	0.051±0.004
N3 3-15	0.21±0.04	0.03±0.01	7.49	5.93	5.52	0.029±0.007
N3 20-30	0.05±0.02	0.02±0.01	2.85	6.06	4.91	0.045±0.008
N3 40-50	0.03±0.05	0.01±0.01	6.00	6.39	5.38	0.052±0.007

T1 0-1	9.85±0.28	0.62±0.04	15.66	6.59	6.32	0.206±0.006
T1 1-15	3.46±0.25	0.28±0.05	12.31	5.96	5.14	0.048±0.007
T1 15-30	2.37±0.20	0.31±0.02	7.67	5.93	4.71	0.041±0.004
T1 35-55	1.84±0.12	0.14±0.02	12.73	5.28	4.69	0.043±0.001
T1 70-110	0.76±0.09	0.08±0.02	9.00	5.97	4.86	0.048±0.001
T2 0-3	3.97±0.42	0.37±0.02	10.75	6.72	6.16	0.071±0.007
T2 3-17	1.38±0.12	0.14±0.03	9.44	5.33	4.82	0.053±0.002
T2 20-30	0.56±0.07	0.06±0.02	8.08	5.70	4.38	0.028±0.003
T2 30-40	0.38±0.07	0.04±0.01	7.89	5.17	4.26	0.053±0.008
T2 40-50	0.47±0.09	0.07±0.01	6.98	6.03	4.25	0.059±0.008
T2 60-70	0.29±0.04	0.05±0.01	6.30	5.61	4.17	0.055±0.007
T2 80-90	0.20±0.04	0.04±0.01	4.98	5.86	4.30	0.052±0.008
T3 0-3	2.41±0.31	0.20±0.03	12.24	6.96	6.17	0.078±0.001
T3 10-20	0.36±0.08	0.04±0.02	8.62	5.16	4.40	0.053±0.003
T3 40-50	0.07±0.02	0.02±0.01	3.57	5.18	4.54	0.042±0.003
T3 50-60	0.09±0.02	0.03±0.01	3.26	5.69	4.66	0.057±0.004
T3 70-110	0.07±0.01	0.03±0.01	2.25	5.73	4.69	0.063±0.007

One-way ANOVA:

p &lt; 0.04      p &lt; 0.03

p &lt; 0.04

Note. N1, N2, T1, T2 — soils of Chernevaya taiga, N3, T3 — reference soils of oligotrophic pine forests.

### 3. Agrochemical parameters of the studied soils ( $n = 3$ , $M \pm SEM$ , Western Siberia, 2019)

Code, depth, cm	P, mg/kg	K, mg/kg	N-NH <sub>4</sub> , mg/kg	N-NO <sub>3</sub> , mg/kg
N1 10-20	343±21	319±25	11.14±2.15	15.57±1.53
N1 20-30	357±24	266±17	4.33±0.23	10.07±0.58
N1 30-40	702±34	217±14	2.76±0.22	8.59±0.41
N1 40-50	460±22	71±6	0.73±0.06	5.37±0.32
N1 60-80	605±23	133±8	0.41±0.07	5.37±0.42
N1 80-100	682±45	120±8	0.41±0.04	4.97±0.41
N2 0-2	255±20	198±11	10.23±0.97	14.53±1.01
N2 2-10	210±13	174±12	5.42±0.23	11.24±0.85
N2 10-20	178±11	125±8	0.41±0.05	9.54±0.41
N2 30-40	223±11	114±8	0.32±0.04	4.51±0.31
N2 60-70	200±15	95±8	0.25±0.03	7.54±0.52
N2 80-90	210±13	152±11	0.95±0.08	8.56±0.45
N3 3-15	113±8	195±16	0.57±0.05	7.11±0.40
N3 20-30	131±9	71±5	0.49±0.04	4.56±0.25
N3 40-50	243±12	58±4	0.73±0.05	4.03±0.14
T1 1-15	234±15	470±45	7.32±0.54	8.59±0.61
T1 15-30	166±10	355±32	2.20±0.04	7.52±0.45
T1 35-55	231±16	262±22	1.06±0.08	8.19±0.35
T1 70-110	373±16	186±14	0.49±0.05	6.71±0.50
T2 3-17	79±7	200±29	12.69±0.89	18.93±0.33
T2 20-30	76±7	106±15	1.79±0.09	9.66±0.12
T2 30-40	107±8	62±6	0.65±0.05	6.98±0.15
T2 40-50	104±7	98±8	BLD	7.25±0.40
T2 60-70	82±5	142±12	0.24±0.03	12.89±0.60
T2 80-90	87±5	151±14	BLD	9.40±0.10
T2 105-120	184±6	160±12	BLD	8.46±0.20
T3 10-20	44±5	106±11	0.09±0.01	12.21±0.98
T3 40-50	97±9	18±2	0.16±0.02	8.05±0.14
T3 50-60	319±22	22±2	0.08±0.02	6.31±0.50
T3 70-110	234±24	71±3	0.16±0.03	8.32±0.32

One-way ANOVA

p &lt; 0.05

p &lt; 0.04

p &lt; 0.04

p &lt; 0.03

Note. N1, N2, T1, T2 — soils of Chernevaya taiga, N3, T3 — reference soils of oligotrophic pine forests. BLD — below limit of detection.

The distribution of available forms of phosphorus in the soil profiles was inhomogeneous. Thus, there is a first maximum in the humus horizon, as well as a second maximum in the illuvial formation (Table 3). This distribution is typical for potassium, although sometimes the second maximum is just below the illuvial formation. As for the ammonium and nitrate forms of nitrogen, they are concentrated mainly in the upper horizons. At the same time, the predominance of nitrate forms of nitrogen in soils is typical.

The values of the Spearman's correlation coefficient calculated for the soils of Chernevaya taiga and oligotrophic habitats (Table 4) revealed in the studied

soils a negative correlation between the content of phosphorus and potassium, as well as phosphorus and ammonium and nitrate forms of nitrogen. This correlation was more pronounced in the soils of Chernevaya taiga, which indicates a higher degree of nutrient status in comparison with the soils of oligotrophic habitats. The correlation coefficients for potassium and other compared elements had positive values, and their values were higher for the soils of Chernevaya taiga. The accumulation of total nitrogen correlates well with the accumulation of potassium and nitrate nitrogen. For total nitrogen and ammonium nitrogen, no close relationships were found.

**4. Spearman's correlation coefficients ( $r$ ,  $p = 0.05$ ) for agrochemical indicators of the studied soils (Western Siberia, 2019)**

Indicator \ Indicator	P	K	N-NH4	N-NO3	C	N
Soils of Chernevaya taiga (N1, N2, T1, T2)						
P	1	-0,75	-0,37	-0,27	-0,48	-0,55
K	-0,75	1	0,78	0,69	0,17	0,20
N-NH4	-0,37	0,78	1	0,93	-0,06	-0,003
N-NO3	-0,27	0,69	0,93	1	0,08	0,11
C	-0,48	0,17	-0,06	0,08	1	0,98
N	-0,55	0,20	-0,03	0,11	0,98	1
reference soils of oligotrophic pine forests (N3, T3)						
P	1	-0,36	0,24	-0,67	-0,17	-0,10
K	-0,36	1	0,19	0,45	0,40	0,46
N-NH4	-0,24	-0,19	1	-0,71	-0,03	-0,04
N-NO3	-0,67	0,45	-0,71	1	0,35	0,37
C	-0,17	0,40	-0,03	0,35	1	0,98
N	-0,10	0,46	-0,04	0,37	0,98	1

Thermal monitoring conducted for the Dark Gray Soil (T1) showed that during the winter period (2019–2020), the soil practically did not freeze. Negative temperatures (from  $-1$  to  $0$  °C) began to penetrate the soil in early November, reaching a depth of 30 cm by the end of December, after which the zero level (temperatures from  $+0.1$  to  $-0.1$  °C) slowly fell to a depth of 40 cm by mid-February. Within these depths, a great constancy of temperatures was observed in winter. Only in the first centimeters from the surface, the temperature could fall below  $-0.1$  °C, but not reaching  $-2$  °C. In the summer, the soil warmed up to  $+12$  °C to a depth of 50 cm, and the maximum temperature detected was  $+16$  °C at the depth of 10 cm. It is probably due, among other reasons, to the high humidity of the soil.

It should be noted that Chernevaya taiga is characterized by unusually high biological productivity of all components of the ecosystem. No other autonomous landscapes in Siberia can compete with Chernevaya taiga either in terms of the volume of “living matter” or in terms of the intensity of its impact on geogenic and microclimatic factors. According to available data, the mass of annual ground litter of plants is about 55–63 c/ha of dry matter per year, and the biomass is expressed in the following figures: phytomass – up to 4000 dt/ha, zoomass (herpetoria and pedobionts) – 4–8 dt/ha, the biomass of soil-dwelling microorganisms – 80–90 dt/ha [42]. In forests of Chernevaya taiga, tallgrass supplies 28–30 dt/ha of the total annual amount of ground litter of 55–63 dt/ha of dry matter. The content of nitrogen and ash elements in the litter of the grassy layer is significantly higher than in the material of the wood litter (the ash content of the grassy layer is 11.3%, and the ash content of the wood layer is 3.4%, the amount of nitrogen is 2.4 and 1.6 %, respectively) [26]. The tree layer, which has a huge phytomass, returns annually to the biological cycle a disproportionately small amount of ash elements and nitrogen – almost 3–4 times less than their annual intake to the soil surface when the grass stands die off. Phytomass reserves in Chernevaya taiga are 1.5–2 times higher than in the lowland southern taiga of

Western Siberia, nitrogen reserves are 2-2.5 times higher, calcium reserves are 1.4-1.8 times higher, and the annual intake of Ca with litter is 4 times higher [41]. It is known about the study, according to which the content of phosphorus in the soils of Chernevaya taiga is 879-1042 mg/kg [43]. Let us note that it corresponds to the upper range typical for other ecosystems of the Earth's biosphere (including rainforests of the tropical and temperate zones). It has been reported that in terms of the number of actinomycetes and spore-forming forms of bacteria, these soils are close to some steppe soils, black soils, while they are characterized by small absolute and relative numbers of fungi [33].

The rate of litter cycle in Chernevaya taiga is 1-1.5 years [44]. The litter consists of several fractions that differ in the decomposition rate (the lowest is in the needles of fir and cedar, birch leaves, the fall of branches, and the bark of shrubs and trees). The tallgrass fall is labile, decomposing in a year. The absence of litter, the retention of mineral substances from leaching in a humid climate, and the powerful development of tallgrass give the biological cycle some "tropical" features. That's why Chernevaya taiga is also called "Siberian tropics".

Another feature of Chernevaya taiga is that the total content of calcium in the soil-forming rocks (loess-like clays) in a layer of 1 m is 3300 dt/ha [44]. This amount of calcium passes through the biological cycle in less than 6-7 thousand years. Therefore, in the absence of a reliable recycling mechanism, for which tallgrass parcels are responsible, Chernevaya taiga could not exist. This is what can be observed in the southern part of the forest zone of Western Siberia, where recycling mechanisms were disrupted by forest fires.

The most common component of the soil cover of Chernevaya taiga is texture-differentiated soils (Podzolic, Sod-podzolic, and Light Gray). The trend of the Holocene evolution of these soils consisted of the depletion of the root zone by silt and the periodic mixing of the soil mass by treefalls. At present, within the average depth of the root systems of the main forest-forming plants – fir and aspen, a relatively homogeneous horizon EL or AEL has been formed, with a thickness of 45 to 80 cm, under which the BT horizon lies. Performed measurements of the depths of the tree-fall hollows of fir and aspen in Chernevaya taiga showed that their average depth in normal humid conditions was 51 cm, in case of water-logging – 40 cm. At the same time, no significant differences in the depth of the aspen and fir hollows were detected. Such a soil structure corresponds to the definition of the climax profile of forest soil and indicates the absence of significant exogenous disturbances that interrupted the steady flow of generations of tree species.

The soil cover of Chernevaya taiga is a phenomenon of high-altitude differentiation of landscapes on the mountain macroslopes of southern Siberia, open to western moist air currents. In the mountains and foothills of Chernevaya taiga, there is an upper limit of distribution, above which in the area of medium-mountain terrain, mountain Podzolic Soils, Eluvozem – Pseudopodzolic Soils without an illuvial horizon [42], and Brown Soils [45] dominate in soil profiles. A geographically common feature for all soils of Chernevaya taiga is the presence of well-structured strata, light in the soil texture, with high-quality water-physical properties, represented in the studied soils by the AY, AEL, EL, AU, Ahh horizons. Below these horizons, there is always a water-resistant horizon, whether it is the surface loams and clays transformed into the BT horizon, or the debris-weathering crust and the deeper dense R horizon. The presence of such a binomial structure favors the formation of topwaters and longer retention of moisture, which in the conditions of the sub-boreal belt and high differentiation of the relief supports the possibility of the existence of tallgrass communities with sufficient

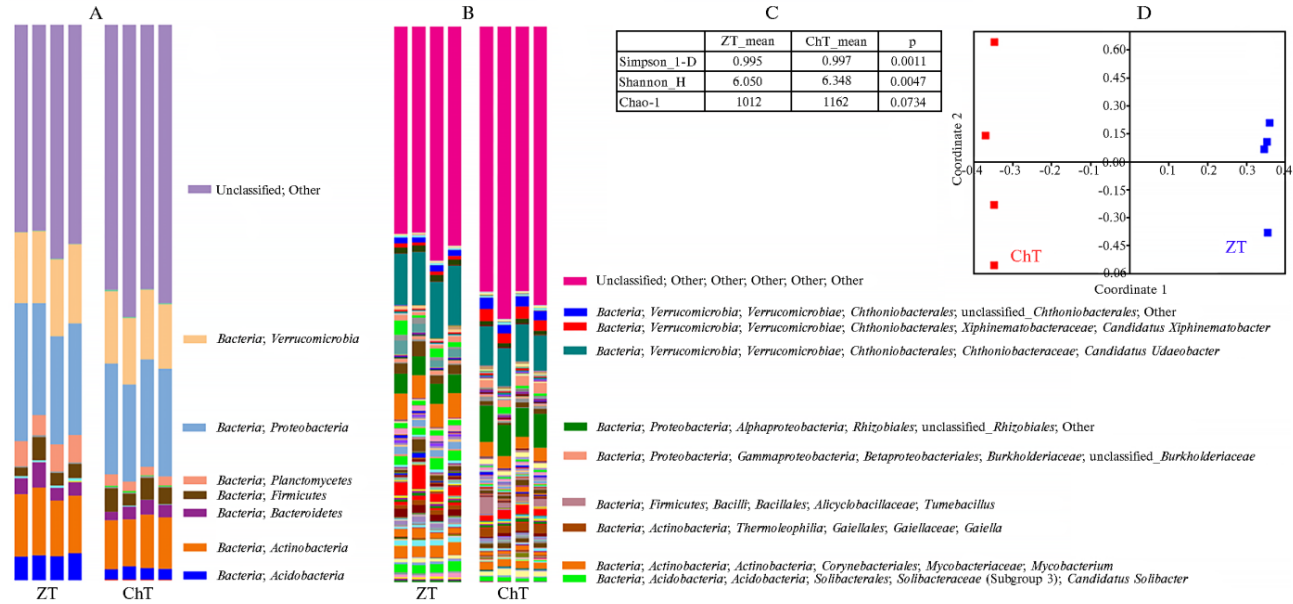
moisture supply in the dry season. Outside of such a binomial structure of soils, the functioning of tallgrass ecosystems is impossible, tallgrass will be replaced by mixed grasses or sedge phytocenoses. In spring and the rainy season, the presence of a well-structured half-meter thick layer contributes to the infiltration of moisture, which is why a favorable air regime is always maintained in the upper root horizon, which contributes to the favorable functioning of root systems. It is also proved by the fact that at the oligotrophic point N3, where there was no water-resistant horizon, there were no tallgrass herbaceous species in the community, and at the point T3, there were these species, since the presence of the horizon D at this point contributes to a favorable water regime, although the lack of nutrient status of the habitat does not allow tallgrass species to maintain their phytocenotic positions.

In the studied soils, the cutan complexes were also very different. Dark Gray Soils that occupy concave slopes have a better-formed cutan complex than Sod-Podzolic Soils.

The two main wood edificators of Chernevaya taiga are Siberian fir *Abies sibirica* Ledeb. and aspen *Populus tremula* L. When moving to the north, climbing into the mountains, in the lower parts of the slopes, aspen may give dominance to birch (*Betula pendula* L.). Chernevaya taiga ecosystems are closely related to Sod-Podzolic Ultra-Deep-Lit Soils, which are changed throughout the areal. As it has been already noted, the most significant are not the soils themselves, but their eluvial horizons in the presence of the underlying water-resistant horizon, as evidenced by the wide distribution of eluvial reservoirs in the mountains.

Soils with a strong eluvial profile dominate not only in the soil profiles of Chernevaya taiga but are also developed on the well-drained plains of Western Siberia [46-49]. The Ultra-Deep Podzolic Soils of the plain, as well as the mountains, are characterized by the spread of fir forests or forests dominated by fir. As it is noted [50], the coefficient of association of fir phytocenoses with Sod-Podzolic Soils is 1.0. During the expeditionary survey, it was confirmed that the fir had a deeply penetrating root system (a large number of anchor roots concentrated in the thickness of 1 m), it reacted to the nature of moisture, and in waterlogged areas, the root distribution becomes surface. With fir, cedar (*Cedrus* Trew, 1757, nom. cons.), which also has a deep root system, dominates as well. During the Holocene period, when the fir formation occupied territories with Deep-Podzolic Soils, there was repeated inversion of the soil layer during treefalls, as evidenced by a complex of signs of treefall disturbances. During successions of wind-turbated soils, the processes that cause eluvial cleavage and lessivage increase [51, 52], which leads to textural differentiation. It can be assumed that where the conditions for deep treefall (with the involvement of a thickness of up to 1 m) were more favorable, the formation of more deeply eluviated soils occurred. The strengthening of eluviation was undoubtedly favored by vigorous intra-soil erosion, which enhances the morphogenetic effect of treefalls.

High humus content is generally typical for Dark Gray Soils [53]. At the same time, the Dark Gray Soils under our study were characterized by a humus profile developed in depth, which indicates their high fertility. The humus content was slightly lower in Sod-Podzolic Soils and even lower in Gray-Humus and Sod-Podzols of oligotrophic pine forests, which corresponds to the literature data [54]. In the studied soils, no eluvial-illuvial differentiation of humus profiles was observed, which is more typical for texture-differentiated soils than for alpha humus soils [55]. According to our data, the acidity of the soils, was quite consistent with their nature and was increased in the case of Gray-Humus and Sod-Podzolic Soils, which is associated with the type of plant litter (pine) and the light soil texture of the soil-forming rocks.



**Fig. 4.** Taxonomic structure of the microbiota of the mature zonal taiga soil (ZT) and Chernevaya taiga soil (ChT) at the level of phyla (A) and genera (B); diversity indices (C) and the results of the  $\beta$  diversity analysis (principal coordinate analysis, Bray-Curtis distances) (D) (Western Siberia, 2019) are presented.

The dissociation of the illuvial profiles of various nutrition elements is due to the unequal mobility of their forms in the soil environment [55]. The very presence of the second maximum is associated with the role of the eluvial type of soil formation in the formation of biologically active reserves of nutrients in various parts of the soil profile. The predominance of nitrate forms of nitrogen, which are easily accessible to plants (especially in the upper horizons), indicates the important role of nutrient intake from the litter.

Thus, the Dark-Gray Soils of Chernevaya taiga represent a peculiar variant of texture-differentiated soils, which differ from their European counterparts from non-Chernevoy forests by the development of the humus profile and the increased content of fertilizer elements, which contributes to the formation of a special nutrient status with a pronounced phenomenon of gigantism. At the same time, there is a decrease in the degree of morphochromatic differentiation of soil profiles due to the impregnation of humus substances.

Characteristics of the taxonomic structure of soil microbiota. The analysis of the taxonomic structure of the soil prokaryotic microbiota of the mature zonal soil and the soil of Chernevaya taiga, performed in four replications, showed that at the level of prokaryotic phylum, both soils had a similar structure and contained representatives of 15 phyla typical for soil microbial communities. Among them, *Proteobacteria*, *Verrucomicrobia*, *Actinobacteria*, *Acidobacteria*, *Planctomycetes*, and *Firmicutes* dominated, and the proportion of unclassifiable microorganisms was also very high (Fig. 4, A).

A much finer structure can be identified at the genus level (see Fig. 4, B), from which become obvious that the differences between soils are most likely due to differences between taxa of a lower rank than phyla. The revealed dominants of the soil microbiota are typical for the majority of natural soils of the temperate zone [56], which includes the boreal type of soils and forests. The presence of acidobacteria is typical of soils with a slightly acidic reaction of the environment [38], which is one of the characteristics of the studied taiga soils. Representatives of the phylum Firmicutes can participate in the decomposition of organic alkyl fragments of forest litter, which also occurs in the studied soils, where there is a residual accumulation of well-humified organic matter. *Actinobacteria* can also take part in the degradation of plant polymers, which confirms the high intensity of the biological cycle in the forest ecosystems of Chernevaya taiga and the rapid mineralization of low-molecular components of soil organic matter. Representatives of *Verrucomicrobia* indicate the presence of an intense zoogenic (possibly coprogenic) factor in soil formation, which was also confirmed by the results of our morphological study of soils.

The analysis of the diversity indices (see Fig. 4, C) showed that there was no significant difference in the number of identified taxa between the soils, but according to the Simpson and Shannon indices [57], it can be seen that there are, although small, but significant differences in the parameters due to both evenness and richness of diversity. The total effect can be seen in the analysis of  $\beta$  diversity (see Fig. 4, D), where a clear differentiation between the microbiota of the mature zonal soils and the soils of Chernevaya taiga is visible.

It is clear that possible differences in the taxonomic structure of the microbiotas of the mature zonal soil and the soil of Chernevaya taiga are most interesting to identify prokaryotic taxa, presumably associated with high fertility. As a result of the analysis, taxa were identified, the number of which significantly increases during the transition from the mature zonal soil to the soil of Chernevaya taiga. The total part of such taxa was 5.6% in the mature zonal soil and 32.2% in the soil of Chernevaya taiga. Table 5 shows a list of the identified taxa of the genus rank, grouped at the level of prokaryotic orders, showing a significant increase

in the number during the transition from the mature zonal soil to the soil of Chernevaya taiga.

More than half of the differentially presented taxa belong to unclassified prokaryotes, as, indeed, in the entire original microbiota. However, among the taxa that have been identified, there are several very interesting ones. In Table 5, taxa are sorted by abundance in the soil of the Chernaya taiga. This list is dominated by genera of the orders *Rhizobiales*, *Chthoniobacterales*, *Bacillales*, *Myxococcales*, each of which potentially has some connection with soil fertility, although it is difficult to prove it. Nevertheless, the order *Rhizobiales* can undoubtedly be associated with soil, mainly symbiotic, nitrogen fixers. *Bacillales* and *Myxococcales*, as well as the listed *Chitinophagales*, may be related to the decomposition of organic matter.

**5. Taxa that increase in abundance during the transition from the mature zonal soil (ZT) to the soil of Chernevaya taiga (ChT), grouped at the level of prokaryotic orders (Western Siberia, 2019)**

Phylum	Order	Taxon abundance, %		Magnification degree	Number of genera
		ZT average	ChT average		
Unclassified		3.085	18.616	6.0	138
<i>Proteobacteria</i>	<i>Rhizobiales</i>	0.648	3.193	4.9	11
<i>Verrucomicrobia</i>	<i>Chthoniobacterales</i>	0.581	2.744	4.7	7
<i>Firmicutes</i>	<i>Bacillales</i>	0.120	1.456	12.1	7
<i>Proteobacteria</i>	<i>Myxococcales</i>	0.289	1.266	4.4	10
<i>Actinobacteria</i>	<i>Propionibacterales</i>	0.199	0.772	3.9	5
<i>Bacteroidetes</i>	<i>Chitinophagales</i>	0.044	0.686	15.5	5
<i>Actinobacteria</i>	<i>Gaiellales</i>	0.106	0.451	4.3	2
<i>Acidobacteria</i>	<i>Pyrimonadales</i>	0.131	0.382	2.9	1
<i>Actinobacteria</i>	<i>Micromonosporales</i>	0.106	0.304	2.9	2
<i>Planctomycetes</i>	<i>Pirellulales</i>	0.034	0.255	7.6	2
<i>Actinobacteria</i>	<i>Frankiales</i>	0.012	0.200	16.9	1
<i>Verrucomicrobia</i>	unclassified_ <i>Verrucomicrobiae</i>	0.053	0.197	3.7	2
<i>Actinobacteria</i>	<i>Microtrichales</i>	0.014	0.171	12.5	2
<i>Actinobacteria</i>	<i>Corynebacterales</i>	0.012	0.160	13.5	1
<i>Actinobacteria</i>	<i>Solirubrobacterales</i>	0.044	0.153	3.5	2
<i>Proteobacteria</i>	<i>Steroidobacterales</i>	0.005	0.147	29.3	1
<i>Actinobacteria</i>	unclassified_ <i>Actinobacteria</i>	0.005	0.146	26.8	1
<i>Verrucomicrobia</i>	<i>Pedosphaerales</i>	0.026	0.139	5.4	1
<i>Proteobacteria</i>	<i>Xanthomonadales</i>	0.018	0.106	5.8	2
<i>Actinobacteria</i>	<i>Micrococcales</i>	0.018	0.094	5.3	1
<i>Gemmatimonadetes</i>	<i>Gemmatimonadales</i>	0.024	0.090	3.7	1
<i>Bacteroidetes</i>	<i>Flavobacteriales</i>	0.004	0.073	19.7	1
<i>Actinobacteria</i>	unclassified_ <i>Actinobacteria</i>	0.010	0.066	6.9	1
<i>Planctomycetes</i>	<i>Isosphaerales</i>	0.019	0.063	3.3	1
<i>Planctomycetes</i>	<i>Tepidisphaerales</i>	0.008	0.063	7.6	1
<i>Actinobacteria</i>	<i>Streptosporangiales</i>	0.004	0.059	14.9	1
<i>Actinobacteria</i>	<i>Streptomycetales</i>	0.014	0.046	3.3	1

The order *Chthoniobacterales* noted in this list is quite interesting: only recently the first representative of this order was isolated in culture [58], and its genome was sequenced [59]. This taxon is interesting not only because it belongs to the phylum *Verrucomicrobia*, the ecological significance of which (especially in soil communities) has become apparent recently, but also because its “talking” name has some connection with the topic of this study since it comes from the Greek word χθών (earth, soil) and is used in ancient mythological and modern philosophical discourse to refer to “chthonic” creatures and essences that represent the primeval natural power of the earth. Certainly, it is not necessary to take this circumstance too clearly, but it is impossible not to pay attention to it since this taxon is one of the dominant ones, presumably related to the soil fertility of Chernevaya taiga. In any case, the taxonomic and functional composition of a specific component of the soil microbiota of Chernevaya taiga can become a source of new knowledge about the mechanisms of formation and maintenance of soil fertility.

Noteworthy is the actual absence of Archaeal phyla in mature zonal soil,



while the phylum *Thaumarchaeota* (0.1%) is represented in the soil of the Chernevaya taiga.

Thus, our data have clarified the morphological organization, taxonomic position, thermal regime, and texture of the soils of Chernevaya taiga of Western Siberia. It has been found that the soils of the Chernevaya taiga of Western Siberia mainly belong to the division of texture-differentiated soils, of Sod-Podzolic, Gray, and Dark Gray Soil types with clay loam and silt clay soil texture of soil-forming material. These soils are formed in unique combinations of geogenic and bioclimatic conditions, not affected by the permafrost in winter, supplied with moisture to precipitate the rapid mineralization of the litter material and the fixation of mineral nutrients in the upper humus layer of the soil profile. The accumulation of biophilic elements is the most important property of the soils of Chernevaya taiga, which is associated with the phenomenon of gigantism and extremely high plant productivity. Located in adjacent biotopes on light soil-forming material, the soils of oligotrophic forests are poor in terms of agrochemical fertility, do not have a pronounced humus profile, and belong either to the gray humus or to the Al-Fe humus and sod-eluvial variants. At the level of prokaryotic phyla, both soils have a similar structure and contain representatives of 15 phyla typical for soil microbial communities. In general, the taxonomic composition of the microbial phyla corresponds to that in moderately moist soils of the temperate zone. The differences between soils are most likely due to differences between taxa of the rank lower than phyla. The diversity of microorganisms in the studied soils varies depending on the nutrient regime of the ecosystem. The number of phylotypes in soil samples of Chernevaya taiga is increased in comparison with oligotrophic habitats. The soils of Chernevaya taiga are characterized by a greater variety of microbial communities according to the Shannon index, as well as the presence of the phyla *Nitrospirae* and *Thaumarchaeota*, which are not present in the soils of oligotrophic habitats. The Actinobacteria phylum, which is one of the prokaryotic dominants, provides a high intensity of the biological cycle in the forest ecosystems of Chernevaya taiga and rapid mineralization of low-molecular components of soil organic matter. Thus, the soils of Chernevaya taiga have a specific microbiota and the corresponding microbial drivers of soil processes responsible for the productivity of these soils. They are a unique component of the boreal ecosystems of Western Siberia, which allows gaining new knowledge about the mechanisms of increased soil productivity with a unique combination of bioclimatic and geogenic factors.

## REFERENCES

1. Vitousek P.M., Mooney H.A., Lubchenco J., Melillo J.M. Human domination of Earth's ecosystems. *Science*, 1997, 277(5325): 494-499 (doi: 10.1126/science.277.5325.494).
2. Clark C. M., Tilman D. Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature*, 2008, 451(7179): 712 (doi: 10.1038/nature06503).
3. Diaz R.J., Rosenberg R. Spreading dead zones and consequences for marine ecosystems. *Science*, 2008, 321(5891): 926-929 (doi: 10.1126/science.1156401).
4. Marques A., Martins I.S., Kastner T., Plutzer C., Theurl M.C., Eisenmenger N., Huijbregts M.A.J., Wood R., Stadler K., Bruckner M., Canelas J., Hilbers J.P., Tukker A., Erb K., Pereira H.M. Increasing impacts of land use on biodiversity and carbon sequestration driven by population and economic growth. *Nature Ecology and Evolution*, 2019, 3(4): 628-637 (doi: 10.1038/s41559-019-0824-3).
5. Tilman D. Biodiversity and environmental sustainability amid human domination of global ecosystems. *Daedalus*, 2012, 141(3): 108-120 (doi: 10.1162/DAED\_a\_00166).
6. Song X.-P., Hansen M.C., Stehman S.V., Potapov P.V., Tyukavina A., Vermote E.F., Townsend J.R. Global land change from 1982 to 2016. *Nature*, 2018, 560(7720): 639-643 (doi: 10.1038/s41586-018-0411-9).

7. Foley J.A., DeFries R., Asner G.P., Barford C., Bonan G., Carpenter S.R., Chapin F.S., Coe M.T., Daily G.C., Gibbs H.K., Helkowski J.H., Holloway T., Howard E.A., Kucharik C.J., Monfreda C., Patz J.A., Prentice I.C., Ramankutty N., Snyder P.K. Global consequences of land use. *Science*, 2005, 309(5734): 570-574 (doi: 10.1126/science.1111772).
8. Davidson E.A. The contribution of manure and fertilizer nitrogen to atmospheric nitrous oxide since 1860. *Nature Geoscience*, 2009, 2(9): 659-662 (doi: 10.1038/ngeo608).
9. Guo J.H., Liu X.J., Zhang Y., Shen J.L., Han W.X., Zhang W.F., Christie P., Goulding K.W.T., Vitousek P.M., Zhang F.S. Significant acidification in major Chinese croplands. *Science*, 2010, 327(5968): 1008-1010 (doi:10.1126/science.1182570).
10. Gomiero T. Soil degradation, land scarcity and food security: Reviewing a complex challenge. *Sustainability (Switzerland)*, 2016, 8(3): article № 281 (doi: 10.3390/su8030281).
11. Kopittke P.M., Menzies N.W., Wang P., McKenna B.A., Lombi E. Soil and the intensification of agriculture for global food security. *Environment International*, 2019, 132: article № 105078 (doi: 10.1016/j.envint.2019.105078).
12. Di H.J., Cameron K.C. Nitrate leaching in temperate agroecosystems: sources, factors and mitigating strategies. *Nutrient Cycling in Agroecosystems*, 2002, 64(3): 237-256 (doi: 10.1023/A:1021471531188).
13. Sebito M., Mayer B., Nicolardot B., Pinay G., Mariotti A. Long-term fate of nitrate fertilizer in agricultural soils. *Proceedings of the National Academy of Sciences of the United States of America*, 2013, 110(45): 18185-18189. (doi: 10.1073/pnas.1305372110).
14. Wang Y., Ying H., Yin Y., Zheng H., Cui Z. Estimating soil nitrate leaching of nitrogen fertilizer from global meta-analysis. *Science of the Total Environment*, 2019, 657: 96-102 (doi: 10.1016/j.scitotenv.2018.12.029).
15. Tilman D., Cassman K.G., Matson P.A., Naylor R., Polasky S. Agricultural sustainability and intensive production practices. *Nature*, 2002, 418(6898): 671-677 (doi: 10.1038/nature01014).
16. Castellano M.J., David M.B. Long-term fate of nitrate fertilizer in agricultural soils is not necessarily related to nitrate leaching from agricultural soils. *Proceedings of the National Academy of Sciences of the United States of America*, 2014, 111(8): E766 (doi: 10.1073/pnas.1321350111).
17. Kalinicheva E.Yu., Pol'shakova N.V., Kolomeichenko A.S. *Vestnik Orlovskogo gosudarstvennogo agrarnogo universiteta*. 2017, 3(66): 121-128 (in Russ.).
18. Ramankutty N., Foley J.A. Estimating historical changes in global land cover: Croplands from 1700 to 1992. *Global Biogeochemical Cycles*, 1999, 13(4): 997-1027 (doi: 10.1029/1999GB900046).
19. Kryshnyaya S.V. *Vestnik Sakhalinskogo muzeya*, 2011, 17: 338-356 (in Russ.).
20. Bobrovskii M.V. *Lesnye pochvy Evropeiskoi Rossii* [Forest soils of the European Russia]. Moscow, 2010 (in Russ.).
21. Smirnova O.V., Lugovaya D.L., Prokazina T.S. *Uspekhi sovremennoi biologii*, 2013, 2: 164-177 (in Russ.).
22. Smirnova O.V., Shashkov M.P., Korotkov V.N., Shirokov A.I. *Priroda*, 2008, 12: 20-24 (in Russ.).
23. Smirnova O.V., Aleinikov A.A., Smirnov N.S., Lugovaya D.L. *Priroda*, 2014, 2: 54-63 (in Russ.).
24. Tishkov A.A. *Voprosy geografii*, 2012, 134: 15-57 (in Russ.).
25. *Monitoring biologicheskogo raznoobraziya lesov Rossii: metodologiya i metody* /Otvetsvennyi redaktor A.S. Isaev [Monitoring of forest biological diversity in Russia: methodology and methods. A.S. Isaev (ed.)]. Moscow, 2008 (in Russ.).
26. Taranov S.A. V kn.: *Lesnye pochvy gornogo okaimleniya yugo-vostoka Zapadnoi Sibiri (Vostochnyi Altai, Gornaya Shoriya, Salair)* /Otvetsvennyi redaktor R.V. Kovalev [In: Forest soils of mountain bordering in the southeast of Western Siberia (Eastern Altai, Gornaya Shoria, Salair)]. Novosibirsk, 1974: 75-132 (in Russ.).
27. Babenko A.S., Nefed'ev P.S., Nefed'eva Yu.S. *Vestnik Tomskogo gosudarstvennogo universiteta*, 2009, 319:182-185 (in Russ.).
28. Fierer N., Strickland M.S., Liptzin D., Bradford M.A., Cleveland C.C. Global patterns in belowground communities. *Ecology Letters*, 2009, 12(11): 1238-1249 (doi: 10.1111/j.1461-0248.2009.01360.x).
29. Delgado-Baquerizo M., Oliverio A.M., Brewer T.E., Benavent-González A., Eldridge D.J., Bardgett R.D., Maestre F.T., Singh B.K., Fierer N. A global atlas of the dominant bacteria found in soil. *Science*, 2018, 359(6373): 320-325 (doi: 10.1126/science.aap9516).
30. Lundberg D.S., Lebeis S.L., Paredes S.H., Yourstone S., Gehring J., Malfatti S., Tremblay J., Engelbrekton A., Kunin V., del Rio T.G., Edgar R.C., Eickhorst T., Ley R.E., Hugenholtz P., Tringe S.G., Dangl J.L. Defining the core *Arabidopsis thaliana* root microbiome. *Nature*, 2012, 488: 86-90 (doi: 10.1038/nature11237).
31. Bates S.T., Berg-Lyons D., Caporaso J.G., Walters W.A., Knight R., Fierer N. Examining the global distribution of dominant archaeal populations in soil. *The ISME Journal*, 2011, 5: 908-917 (doi: 10.1038/ismej.2010.171).
32. Martin V. Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet journal*, 2011, 17(1): 10-12 (doi: 10.14806/ej.17.1.200).
33. Callahan B.J., McMurdie P.J., Rosen M.J., Han A.W., Johnson A.J.A., Holmes S.P. DADA2: High-resolution sample inference from Illumina amplicon data. *Nature Methods*, 2016, 13: 581-

34. Quast C., Pruesse E., Yilmaz P., Gerken J., Schweer T., Yarza P., Peplies J., Glöckner F.O. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Research*, 2013, 41(D1): D590-D596 (doi: 10.1093/nar/gks1219).
35. Janssen S., McDonald D., Gonzalez A., Navas-Molina J.A., Jiang L., Xu Z.Z., Winker K., Kado D.M., Orwoll E., Manary M., Mirarab S., Knight R. Phylogenetic placement of exact amplicon sequences improves associations with clinical information. *mSystems*, 2018, 3: e00021-18 (doi: 10.1128/mSystems.00021-18).
36. Bolyen E., Rideout J.R., Dillon M.R., Bokulich N.A., Abnet C.C., Al-Ghalith G.A., Alexander H., Alm E.J., Arumugam M., Asnicar F., Bai Y., Bisanz J.E., Bittinger K., Brejnrod A., Brislawn C.J., Brown C.T., Callahan B.J., Caraballo-Rodríguez A.M., Chase J., Cope E.K., Da Silva R., Diener C., Dorrestein P.C., Douglas G.M., Durall D.M., Duvallet C., Edwardson C.F., Ernst M., Estaki M., Fouquier J., Gauglitz J.M., Gibbons S.M., Gibson D.L., Gonzalez A., Gorlick K., Guo J., Hillmann B., Holmes S., Holste H., Huttenhower C., Huttley G.A., Janssen S., Jarmusch A.K., Jiang L., Kaehler B.D., Kang K.B., Keefe C.R., Keim P., Kelley S.T., Knights D., Koestler I., Kosciolek T., Kreps J., Langille M.G.I., Lee J., Ley R., Liu Y.X., Loftfield E., Lozupone C., Maher M., Marotz C., Martin B.D., McDonald D., McIver L.J., Melnik A.V., Metcalf J.L., Morgan S.C., Morton J.T., Naimey A.T., Navas-Molina J.A., Nothias L.F., Orchanian S.B., Pearson T., Peoples S.L., Petras D., Preuss M.L., Pruesse E., Rasmussen L.B., Rivers A., Robeson M.S., Rosenthal P., Segata N., Shaffer M., Shiffer A., Sinha R., Song S.J., Spear J.R., Swafford A.D., Thompson L.R., Torres P.J., Trinh P., Tripathi A., Turnbaugh P.J., Ul-Hasan S., van der Hoof J.J.J., Vargas F., Vázquez-Baeza Y., Vogtmann E., von Hippel M., Walters W., Wan Y., Wang M., Warren J., Weber K.C., Williamson C.H.D., Willis A.D., Xu Z.Z., Zaneveld J.R., Zhang Y., Zhu Q., Knight R., Caporaso J.G. Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. *Nature Biotechnology*, 2019, 37: 852-857 (doi:10.1038/s41587-019-0209-9).
37. McMurdie P.J., Holmes S. phyloseq: An R package for reproducible interactive analysis and graphics of microbiome census data. *PLoS ONE*, 2013, 8(4): e61217 (doi: 10.1371/journal.pone.0061217).
38. Love M.I., Huber W., Anders S. Moderated estimation of fold change and dispersion for RNA-seq data with DESeq2. *Genome Biology*, 2014, 15(12): 550 (doi: 10.1186/s13059-014-0550-8).
39. Loiko S.V., Geras'ko L.I., Kulizhskii S.P., Amelin I.I., Istigechev G.I. *Pochvovedenie*, 2015, 4: 410-423 (doi: 10.7868/S0032180X15040061) (in Russ.).
40. Orlov D.S., Sadovnikova L.K., Sukhanova N.I. *Khimiya pochv* [Soil chemistry]. Moscow, 2005 (in Russ.).
41. Bazilevich N.I., Titlyanova A.A. *Biologicheskii krugovorot na pyati kontinentakh: azot i zol'nye elementy v prirodnykh nadzemnykh ekosistemakh* [Biological circulation on five continents: nitrogen and ash elements in natural above-ground ecosystems]. Novosibirsk, 2008 (in Russ.).
42. Trofimov S.S. *Ekologiya pochv i pochvennye resursy Kemerovskoi oblasti* [Ecology of soils and soil resources of the Kemerovo region]. Novosibirsk, 1975 (in Russ.).
43. Achat D.L., Bakker M.R., Augusto L., Derrien D., Gallegos N., Lashchinskiy N., Milin S., Nikitich P., Raudina T., Rusalimova O., Zeller B., Barsukov P. Phosphorus status of soils from contrasting forested ecosystems in southwestern Siberia: effects of microbiological and physico-chemical properties. *Biogeosciences*, 2013, 10: 733-752 (doi: 10.5194/bg-10-733-2013).
44. Loiko S.V., Bobrovskii M.V., Amelin I.I. *Materialy dokladov Vserossiiskoi nauchno-prakticheskoi konferentsii «Chelovek i priroda — vzaimodeistvie na osobo okhranyaemykh prirodnykh territoriyakh», posvyashchennoi Godu osobo okhranyaemykh prirodnykh territorii i Godu ekologii (Novokuznetsk, 27-30 sentyabrya 2017 goda)* [Proc. All-Russ. Conf. «Man and nature — interaction in protected natural areas»]. Novokuznetsk, 2017: 81-96 (in Russ.).
45. Smolentsev B.A., Smolentseva E.N. *Vestnik Tomskogo gosudarstvennogo universiteta. Biologiya*, 2020, 50: 6-27 (doi: 10.17223/19988591/50/1) (in Russ.).
46. Korsunov V.M. V sbornike: *O pochvakh Sibiri* [In: About the soils of Siberia]. Novosibirsk, 1978: 122-131 (in Russ.).
47. Korsunova T.M., Korsunov V.M. V sbornike: *Genezis i geografiya lesnykh pochv* [In: Genesis and geography of forest soils]. Moscow, 1980: 85-104 (in Russ.).
48. Korsunov V.M., Vedrova E.F., Ignat'eva L.N. V sbornike: *Pochvy zony KATEKa* [In: Soils of the KATEK zone]. Krasnoyarsk, 1981: 99-113 (in Russ.).
49. Korsunov V.M., Vedrova E.F. V sbornike: *Geografiya i kartografiya lesnykh pochv* [In: Geography and cartography of forest soils]. Novosibirsk, 1982: 66-88 (in Russ.).
50. Gorozhankina S.M., Konstantinov V.D. *Geografiya taigi Zapadnoi Sibiri* [Geography of the taiga of Western Siberia]. Novosibirsk, 1978 (in Russ.).
51. Vasenev I.I., Targul'yan V.O. *Vetroval i taezhnoe pochvoobrazovanie (rezhimy, protsessy, morfogenez pochvennykh suksessii)* [Windfall and taiga soil formation (modes, processes, morphogenesis of soil successions)]. Moscow, 1995 (in Russ.).
52. Vasenev I.I. *Pochvennye suksessii* [Soil successions]. Moscow, 2008 (in Russ.).

53. Urusevskaya I.S., Khokhlova O.S., Sokolova T.A. *Pochvovedenie*, 1992, 8: 22-37 (in Russ.).
54. Ponomareva V.V. *Teoriya podzoloobrazovatel'nogo protsessa. Biokhimicheskie aspekty* /Pod redaktsiei M.M. Kononova [The theory of the podzol formation process. Biochemical aspects. M.M. Kononov (ed.)]. Kazan', 1964 (in Russ.).
55. Ponomareva V.V., Plotnikova T.A. *Gumus i pochvoobrazovanie (metody i rezul'taty izucheniya)* [Humus and soil formation (methods and results of the study)]. Leningrad, 1980: 222 (in Russ.).
56. Pershina E.V., Ivanova E.A., Korvigo I.O., Chirak E.L., Sergaliev N.H., Abakumov E.V., Provorov N.A., Andronov E.E. Investigation of the core microbiome in main soil types from the East European plain. *Science of the Total Environment*, 2018, 631-632: 1421-1430 (doi: 10.1016/j.scitotenv.2018.03.136)
57. Rozenberg G.S. *Byulleten' Samarskaya Luka*, 2007, 16(3-21): 581-584.
58. Sangwan P., Chen X., Hugenholtz P., Janssen P.H. *Chthoniobacter flavus* gen. nov., sp. nov., the first pure-culture representative of subdivision two, *Spartobacteria classis* nov., of the phylum *Verrucomicrobia*. *Applied and Environmental Microbiology*, 2004, 70(10): 5875-5881 (doi: 10.1128/AEM.70.10.5875-5881.2004).
59. Kant R., van Passel M.W., Palva A., Lucas S., Lapidus A., Glavina del Rio T., Dalin E., Tice H., Bruce D., Goodwin L., Pitluck S., Larimer F.W., Land M.L., Hauser L., Sangwan P., de Vos W.M., Janssen P.H., Smidt H. Genome sequence of *Chthoniobacter flavus* Ellin428, an aerobic heterotrophic soil bacterium. *Journal of Bacteriology*, 2011, 193(11): 2902-2903 (doi: 10.1128/JB.00295-11).