



Article

The Characterization of Biodiversity and Soil Emission Activity of the "Ladoga" Carbon-Monitoring Site

Evgeny Abakumov ¹, Timur Nizamutdinov ^{1,*}, Darya Zhemchueva ¹, Azamat Suleymanov ^{1,2,3}, Evgeny Shevchenko ⁴, Elena Koptseva ^{1,5}, Anastasiia Kimeklis ^{1,6}, Vyacheslav Polyakov ¹, Evgenia Novikova ¹, Grigory Gladkov ^{1,6} and Evgeny Andronov ^{1,6}

- ¹ Department of Applied Ecology, Faculty of Biology, St. Petersburg State University, 199034 Saint Petersburg, Russia; e.abakumov@spbu.ru (E.A.); daryapearl13@gmail.com (D.Z.); a.suleymanov@spbu.ru (A.S.); e.koptseva@spbu.ru (E.K.); a.kimeklis@spbu.ru (A.K.); v.polyakov@spbu.ru (V.P.); e.novikova@spbu.ru (E.N.); grgladkov@arriam.ru (G.G.); e.andronov@arriam.ru (E.A.)
 - ² Laboratory of Soil Science, Ufa Institute of Biology, Ufa Federal Research Centre, Russian Academy of Sciences, 450054 Ufa, Russia
 - ³ Department of Environmental Protection and Prudent Exploitation of Natural Resources, Ufa State Petroleum Technological University, 450064 Ufa, Russia
 - Center for Diagnostics of Functional Materials for Medicine, Pharmacology, and Nanoelectronics,
 - St. Petersburg State University, 199034 Saint Petersburg, Russia; e.shevchenko@spbu.ru
 ⁵ Department of Vegetation Science and Plant Ecology, St. Petersburg State University,
 - 199034 Saint Petersburg, Russia All-Russia Research Institute for Agricultural Microbiology (ARRIAM), 196608 Saint Petersburg, Russia
 - Correspondence: t.nizamutdinov@spbu.ru or timur_nizam@mail.ru

Abstract: The global climate crisis forces mankind to develop carbon storage technologies. "Ladoga" carbon monitoring site is part of the Russian climate project "Carbon Supersites", which aims to develop methods and technologies to control the balance of greenhouse gases in various ecosystems. This article shows the condition of soil and vegetation cover of the carbon polygon "Ladoga" using the example of a typical southern taiga ecosystem in the Leningrad region (Russia). It is revealed that soils here are significantly disturbed as a result of agrogenic impact, and the vegetation cover changes under the influence of anthropogenic activity. It has been found that a considerable amount of carbon is deposited in the soils of the carbon polygon; its significant part is accumulated in peat soils ($60.0 \pm 19.8 \text{ kg} \times \text{m}^{-2}$ for 0–100 cm layer). In agrogenically disturbed and pristine soils, carbon stocks are equal to 12.8 ± 2.9 kg × m⁻² and 8.3 ± 1.3 kg × m⁻² in the 0–100 cm layer, respectively. Stocks of potentially mineralizable organic matter (0–10 cm) in peat soils are 0.48 ± 0.01 kg × m⁻²; in pristine soils, it is 0.58 ± 0.06 kg × m⁻². Peat soils are characterized by a higher intensity of carbon mineralization $9.2 \pm 0.1 \text{ mg} \times 100 \text{ g}^{-1} \times \text{day}^{-1}$ with greater stability. Carbon in pristine soils is mineralized with a lower rate -2.5 ± 0.2 mg × 100 g⁻¹ × day⁻¹. The study of microbial diversity of soils revealed that the dominant phyla of microorganisms are Actinobacteria, Bacteroidetes, and Proteobacteria; however, methane-producing Archaea-Euryarchaeota-were found in peat soils, indicating their potentially greater emission activity. The results of this work will be useful for decision makers and can be used as a reference for estimating the carbon balance of the Leningrad region and southern taiga boreal ecosystems of the Karelian Isthmus.

Keywords: boreal ecosystems; carbon measurement supersites; soil and vegetation associations; SOC stock; soil carbon mineralization; soil microbiota

Citation: Abakumov, E.;

Nizamutdinov, T.; Zhemchueva, D.; Suleymanov, A.; Shevchenko, E.; Koptseva, E.; Kimeklis, A.; Polyakov, V.; Novikova, E.; Gladkov, G.; et al. The Characterization of Biodiversity and Soil Emission Activity of the "Ladoga" Carbon-Monitoring Site. *Atmosphere* **2024**, *15*, 420. https://doi.org/10.3390/ atmos15040420

Academic Editor: Dezhong Yang

Received: 22 February 2024 Revised: 23 March 2024 Accepted: 25 March 2024 Published: 28 March 2024



Copyright: © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/).

1. Introduction

Carbon polygons (or Carbon Supersites) is a climate project focused on the creation of a network of special monitoring sites in Russia to develop and test carbon balance control technologies, as well as the implementation of climate projects related to the accounting of climate-active CO₂ deposition fluxes [1]. The network of carbon polygons covers different types of terrestrial and aquatic ecosystems, including agroecosystems with relief, vegetation, and soil cover structures representative of the territory. Currently, there are 18 Carbon Supersites in Russia with a total area of more than 39 thousand hectares [2]. In addition, based on Carbon Supersites, it is planned to organize "Carbon Farms", which are areas where active carbon sequestration takes place. Carbon sequestration is planned to be used to organize afforestation, irrigate previously drained peatlands, and use conservation farming technologies. According to recent estimates, the global soil organic carbon sequestration potential is 2–5 Gt CO₂ × year⁻¹. The main contribution to soil protection and carbon sequestration is achieved by avoiding forest conversion and through reforestation (1.2 $CO_2 \times year^{-1}$) and biochar application (1.1 Gt $CO_2 \times year^{-1}$) for quality and fertilization enhancement in temperate regions [3]. According to the latest estimates, the CO_2 absorption potential for carbon polygons and farms in Russia is 3700 ± 1900 Kt $CO_2 \times$ year⁻¹. The "Ladoga" carbon polygon is located in the Leningrad Region in the boreal coniferous forests zone; it has not yet entered the global network, but research is already actively underway [4-6].

Soil organic carbon (SOC) has an important role in the global carbon cycle, sequestering significant volumes of carbon that would otherwise be emitted to the atmosphere as CO₂ [7,8]. The global soil carbon stock is 3.2 times the size of the atmospheric pool and 4 times the size of the biotic carbon pool [9]. There are different estimates that about 20% of the world pedosphere carbon stocks are accumulated on the territory of Russia; for the 0–100 cm layer, it is from 285 to 364 Pg SOC under the global carbon stocks of 1417–1824 Pg SOC in the one-meter layer [10–12]. For the 30 cm soil layer on the territory of Russia, the major part of carbon stocks is accumulated in mineral soil horizons -62%; the rest falls on organogenic soil horizons as follows: 20% – peat of wetland soils; 9% – peat of semihydromorphic soils; 9%—carbon of litter [12]. In addition, significant stocks of organic carbon in Russia are concentrated in terrestrial phytomass, which is 38.8 Pg C or 7.2% of the global carbon stocks of terrestrial phytomass estimated at 550 Pg [10,11]. Losses of soil organic carbon result from various factors; at the global level, the main factor in the reduction of world stocks of SOC is global climate warming [13]. At the local level, SOC losses are associated with various anthropogenic factors, the main ones being the increase in the area of agricultural land and deforestation [14]. The conversion of natural ecosystems to agricultural land has resulted in a loss of 116 Gt of carbon in a two-meter layer of soil over the last 60 years [15]. The loss of carbon from forest degradation and deforestation is up to 15% of anthropogenic carbon emissions [16]. Therefore, in the framework of the implementation of the Russian Carbon Supersites project, a qualitative and quantitative assessment of soil carbon stocks and emission potential of soils at each of the monitoring sites is mandatory [11].

For the territory of the "Ladoga" Carbon Supersite, initial assessments of soil organic matter stabilization rate and carbon stocks in the 0–10 cm layer based on remote sensing data [4,6] were performed earlier, and a project concept for its functioning was developed [5]. The vegetation cover on the territory of the monitoring site was described in a fragmentary sense [5]. In this reference, the purpose of this study was to conduct a comprehensive study of soils and vegetation of the "Ladoga" Carbon Supersite. The research tasks included the following: (1) field studies and morphometric characterization of soils and vegetation cover of various landscape positions; (2) calculation and assessment of SOC content and potentially mineralizable organic carbon stocks in different soils; (3) determination of degree organic matter mineralization rate in different soils and landscape positions; (4) analysis of taxonomic composition of soil microbiota.

2. Materials and Methods

2.1. Geography, Climate, Topography, and Parent Material

The territory of the "Ladoga" carbon polygon is located in the northern part of the Leningrad Region on the territory of the Koltushskaya Upland between St. Petersburg and Lake Ladoga in the southern taiga (boreal coniferous forests) forest zone of the humid continental (Hemiboreal) climate (Dfb). Winters are long but soft (average January temperature is -10 °C), and summers are warm and comparatively short (average July temperature is 16–17 °C) with total annual precipitation of 550–850 mm [17]. The primary forests are secondary, post-agricultural, post-harvest pine forests with an admixture of small-leaved and mixed vegetation. The anthropogenic load on the territory is expressed in the growing recreational load, plowing of kames slopes, active development of territories, and quarry sand mining [17].

The Koltushskaya Upland is an example of a hilly (kame) relief of water-glacial accumulation with hill heights up to 80 m and isolated thermokarst hollows. The relief was formed 10–12 thousand years ago in the process of melting and retreat of the Valdai glaciation [18]. A significant area of the upland is occupied by agricultural land [17]. The kames in the central part of the upland form a hilly drained plateau. The edge of the upland passes into a staggered abrasion escarpment (areas of which have a strong recreational load). The upland passes into waterlogged terraces and plains. The upland is composed of lake-glacial and water-glacial (fluvioglacial) noncarbonate sediments. Soil forming occurs on lightly sorted medium-grained sands and sandy loams with the rare presence of crystalline rock fragments of various degrees of fossilization; thin interlayers of light loamy material are also noted [19,20]. Postglacial sediments are represented by modern peats, which are formed via overgrown and waterlogged closed basins [18]. Podzol type of soil formation is predominant on sands and sandy loams under the conditions of kame relief [21]. Most soils are classified as Podzols according to the WRB classification [22]. Bog (peat) soils are distributed under conditions of excessive moistening.

2.2. Field and Laboratory Studies

The study was organized in a representative area of the Koltushskaya Upland near Voeikovo village (territory of the "Ladoga" carbon polygon), and the kame uplands and their different slopes, as well as adjacent inter-kame waterlogged depressions, relief depressions, and accumulative terraces (Figure 1) were studied. A total of 15 soil profiles were plotted to characterize the spatial features of soil formation on the territory. The classification of soils was determined according to the Russian Field Soil Identifier [23]. Morphological investigations took into account the latest suggested changes to the Russian Soil Classification described in the works of N. B. Khitrov and M. I. Gerasimova [24,25]. Vegetation description was carried out at five key sites using standard methods [26].

Chemical analysis of samples was carried out according to standard methods. pH_{water} and pH_{salt} (1 N KCl) suspensions were determined at a soil/solution ratio of 1:2.5 (pH/OPP/Temp Tester Milwaukee Mi106 (Milwaukee, USA). Bulk density was determined using the cutting ring method by drying undisturbed soil samples to constant weight at 105 °C. Total carbon was determined using a LECO TruSpec® Micro (LECO, Cleveland, OH, USA) CHNS elemental analyzer at the SPBU Science Park. The content of total carbon was equated to the SOC since no evidence of carbonates was observed in the soils. SOC stocks were calculated taking into account soil stoniness and excluding the litter horizon. Particle size distribution was determined by the sedimentation method with pyrophosphate peptization [27,28].

The cumulative value of C-CO₂ production was established by scaling the amount of C-CO₂ at each measurement term to the sum for the previous terms. The amount of C-CO₂ was determined by the closed-chamber method, capturing CO₂ with 0.1 N NaOH solution. Concentrations were determined by titration using 0.05 N HCl solution, with prior fixation of CO₂ using 1 N BaCl₂. During the whole incubation period (175 days), the moisture

content of the samples was held at 25% of the weight (at room temperature). Before the start of the experiment, air-dry soil samples were pre-incubated for 10 days at 25% moisture content. Potentially mineralizable organic carbon (C_{pm}) at the time of incubation was calculated by approximating the cumulative curves with the first-order kinetics equation. More details on the methodology can be found in the works of V.M. Semenov [29,30].



Figure 1. Elevation map and sampling locations of "Ladoga" carbon supersite.

To describe the taxonomic composition of the soil microbiota, DNA was isolated according to the protocol described in [31]. Quality control was performed by PCR and electrophoresis in agarose gel. Sequencing of the V4 variable domain of the 16S rRNA gene was performed on an Illumina MiSEQ sequencer (Illumina, San Diego, CA, USA) at the Center for Genomic Technologies, Proteomics, and Cell Biology (ARRIAM, Russia) using primers 515f (GTGCCAGCMGCCGCGGCGGTAA) and 806r (GGACTACVSGGG-TATCTAAT) [32].

Total sequence processing was performed in R 4.3.0 [32], using dada2 (v. 1.28.0) [33] and phyloseq (v. 1.44.0) [34] packages according to the author's choice of working pipeline. The 16S rDNA amplicon sequences were processed according to the dada2 pipeline. Sequences were cut for their length (minimum 260 bp for forward and 208 bp for reverse reads) and quality. ASVs were determined using the dada2 algorithm, and chimeric ASVs were removed using the "consensus" method. The taxonomic composition was performed using a naive Bayesian classifier (provided in the Dada2 package, default settings), with the SILVA 138 database [35] used as a training sample; Phyla titles were corrected according to LPSN [36].

3. Results and Discussion

The territory of Koltushskaya Upland has been repeatedly subjected to anthropogenic transformation. Several centuries ago, during the Novgorod Principality, the "wild" vegetation (coniferous forests with admixtures of small-leaved species) was reduced and turned into agricultural land. With the beginning of the period of decline of the Novgorod Principality, most of the developed territories went into a fallow state and were overgrown with secondary forests dominated by pine with an admixture of birch, aspen, and some other unpretentious species [18]. The second stage of development of the territory of Koltushskaya Upland can be dated back to the end of the 19th century when the suburban areas of St. Petersburg were actively developed due to the increase in the number and density of the population of St. Petersburg province. However, the overall agrogenic and anthropogenic impact on the landscapes of Koltushskaya Upland decreased due to territorial separation and the small-scale contouring of peasant farms [37]. During the Great Patriotic War, the area was also severely damaged, as the Koltushskaya Upland had an important strategic location. Even tens of years later, the microrelief traces branching the lines of trenches, which began to play a role in the redistribution of thaw water and precipitation, became ecological niches for wetland plants [18].

The secondary forests of the Koltushskaya Upland were actively reforested again in the postwar period and developed for agriculture. Vegetable growing and forage farming were actively developed. Agricultural development led to the invasion of some vegetation species (e.g., Heracleum sosnowskii and H. mantegazzianum). According to 1966 data, the most actively plowed (or turned into hayfields) were flat slopes and plateau-like areas of relief, which partially preserved thickets of grey alder (Alnus glutinosa) and birch-aspen small woods. On the tops of kame hills and abrupt slopes, pine-birch and pine-heath forests were preserved [38]. Active agricultural development of the territory (plowing and grazing) in combination with hilly terrain on sandy soils resulted in the rapid degradation of the soil and vegetation cover of the territory. The processes of water erosion intensified, and thin podzolic soils were intensively washed away, leading to the migration of material rich in organic matter and mineral fertilizers into the adjacent water basins, which intensified the processes of their eutrophication. The collapse of the USSR and the crisis years of the 1990s also changed the face of Koltushskaya Upland; most agricultural facilities closed down and the recently developed areas began to fallow again. A new stage of secondary succession began; grass cover was restored in pasture meadows, and its species composition was enriched with weedy and meadow species (Tripleurospérmum inodórum, Matricaria discoidea, Fragária vesca, Campanula rotundifolia, Scorzoneroides autumnalis, Viola canina, Viola tricolor, Vícia crácca, Diánthus deltoídes, Glechóma hederácea, Veronica chamaedrys, Stellaria graminea, Saponaria officinalis, Knautia arvensis, Silene viscaria, Euphorbia virgata, etc.). Meadows bordering forest vegetation were actively overgrown with pine, birch, or aspen. Arable lands were overgrown with birch and aspen stands, while willow and alder were also found under conditions with excessive moisture. The rapid growth of forest vegetation (especially coniferous vegetation) contributed to the loss of soil fertility and activation of secondary podzolization processes [18].

Currently, the Leningrad Region is a large agro-industrial region, and anthropogenic impact affects most of its natural ecosystems due to the extensive anthropogenic disturbance of natural soil and vegetation cover that occurs everywhere. Railroad and highway construction, drainage ditches, embankments, and quarry development lead to the rupture of various genetic links between different components of natural ecosystems. The following types of anthropogenically modified soil cover patterns are identified for the soil cover structure of the Leningrad Region: tree logging; forest reclamation; forest fire control measures; recreational forest; postwar; agroforest; forest nurseries; agrogenic; agromeliorative; postagrogenic; recreational and park; pipe-line and power-line; urbanized; agrourbanized (horticultural); road (highways and railways); mining pits and quarries. Each type of anthropogenically modified landscape is characterized by corresponding changes in the natural soil cover and the structure of natural phytocenoses. Anthropogenic activity is also associated with an increase in the natural diversity of soils and changes in their resource potential [39,40]. Vsevolozhsky District of the Leningrad Region (where most of the Koltushskaya Upland is located and the carbon polygon "Ladoga" is situated) has an area of 3055.11 km², with a population density of 154.88 people × km⁻², and there are 280 settlements in the district, 4 of which are cities. The density of highways is 162 km × 1000 km⁻². The area of agricultural land is estimated as 5–9% of the total land area of the district, of which 41% is abandoned land; 41% is arable land; 12% is fodder land; 6% is perennial plantations [41]. At present, the ecosystems of the Koltushskaya Upland, besides the agricultural load, are affected by the building development of territories and growing recreational load, as well as mining (sand and gravel quarries) of minerals [42,43]. Relatively undisturbed ecosystems are preserved only in the territory of the natural park of regional significance and UNESCO World Heritage Site "Koltushkie Vysoty" (in Russian—*Konmyuckue выcomы*) with an area of 1211.6 ha and in the territory adjacent

to the Voeikov State Geological Observatory with an area of 150.6 ha. Despite the protected status of these areas, there have been repeated dry grass fires due to the ever-increasing intensity of recreational use of these areas.

The "Ladoga" carbon monitoring site is located in a lowland plain with kame hills and plateau-like relief. The kame uplands are occupied by birch-pine forests (Figure 2A). Pines range in diameter from 14 cm to 58 cm. Tree heights are 20–21 m. Birches are 32–61 cm in diameter. The height of trees is also 18–20 m. Crown closure is 0.7. The regeneration of species is predominantly oak, which indicates the nemoralization of the flora. There are 15 oaks in the 0.5–1.0 m size class and 1 oak in the size class of up to 0.5 m and 1 oak 1.8 m high.



Figure 2. Vegetation at the "Ladoga" carbon polygon. (**A**) Kame hills; (**B**) flat slopes and plateaulike relief areas; (**C**) abandoned fields and vegetable gardens; (**D**) inter-kame depressions; (**E**) relief depressions and accumulative terraces.

Undergrowth is well pronounced, predominantly rowan. The height of rowan trees averages 2.5–3.5 m. The undergrowth includes one *Padus avium* (1.4 m) and one *Frangula alnus* (1.3 m). The cover of the herbaceous shrub layer is 90%. The dominant species is May lily of the valley (*Convallaria majalis*). All other species have significantly lower coverage: *Melampyrum pretense* – 5%, *Avenella flexuosa* – 3%, *Veronica officinalis* – 2%, *Galium boreale* – 1%, *Calamagrostis epigeios* – 1%, *Rubus saxatilis* – 1%, and *Agrostis tenuis* – 1%. Some grasslands and forest species have been recorded with less than 1% coverage: *Knautia arvensis*, *Hieracium umbellatum*, *Festuca ovina*, *melica nutans*, *Campanula patula*, *Melampyrum nemorosum*, *Dactylis glomerata*, *Galium mollugo*, *Vaccinium vitis-idaea*, *Vaccinium myrtillus*, *Solidago virgaurea*, and *Pteridium pinetorum*.

Pine dominance is related not only to the climatic peculiarities of the territory but also to soil parameters. The tops of kame hills and abrupt slopes are characterized by sod-podbur (Table 1 CP1, CP9). The thickness of the gray humus (sod) horizon is 10–15 cm; in section CP1, the gray humus horizon is weakly podzolized, and complete horizon E is not distinguished. The soils are acidic, with the minimum value of pH in the gray humus (sod) horizon. The content of SOC is maximum in the litter horizon and gray humus horizon and sharply decreases down the profile.

N⁰	Horizon	Thickness, cm	pH _{water}	pH_{salt}	Bulk Density, g × cm ⁻³	SOC, %	Soil Photo
Podzolized sod-podbur on fluvioglacial sediments							
	(Entic Podzol)						
	О	0–2	5.9	5.2	0.8	7.54	
	AYe	2–13	5.6	4.5	0.9	3.33	
CP1	BF	13–34	5.9	4.7	1.5	0.62	and the state of
	BC	34–45	5.9	5.3	1.4	0.19	
	С…	45	6.0	4.9	1.6	0.17	R
		Sc	d-podbur on f	luvioglacial se	ediments		
			(Ent	ic Podzol)			
CP9	Ο	0–2	-	-	0.3	16.65	Ccm
	AY	2–15	4.7	4.1	1.0	2.25	- 10 -
	BHF	15–27	5.0	4.2	1.3	1.15	- 20 -
	С…	27–	4.9	4.4	1.1	0.56	- 40 -

Table 1. Main soil characteristics of soils attached to the tops of kame hills and their abrupt slopes.

The particle size distribution of the soils attached to the kame tops and abrupt kame slopes is fine-sandy and sandy loam (Figure 3A,B). The fine-sandy and coarse-dusty fraction (up to 70% and up to 36%) dominates the soil texture. The percentage of physical clay (<0.01 mm) in the fine soil does not exceed 10% in the AY horizons and is significantly decreased in the underlying horizons. The dominance of pine in the first level is associated with the poverty of such light soils and their low parameters of natural fertility and weak water-holding capacity [18].

The flat slopes of kames and their plateau-like tops are occupied by secondary grassbirch forests (Figure 2B). The crown closure is 0.8–0.85, the tree height is 18–21 m, and the trunk diameter is 17–27 cm. Undergrowth is rare, with *Acer platanoides* at 0.5–3.5 m, *Populus tremula* at 2 m, *Pinus sylvestris* at 0.5 m, and *Quercus robur* at 0.8 m. The undergrowth is diverse in the species but quite sparse. The following species were recorded in the shrub stand: *Padus avium, Corylus avellana, Salix caprea, Viburnum opulus, Alnus incana, Sorbus aucuparia,* and *Swida sericia*. The projective coverage of the grassy layer is 40–45%, which is represented by the following species: *Calamagrostis canescens*–10%; *Agrostis tenuis*– 15%; *Dactylis glomerata*–7%; *Poa pratensis*–3%; *Veronica chamaedrys*–1%; *Calamagrostis arundinacea*–1%; *Rubus saxatilis*–<1%; *Moehringia trinervia*–<1%; *Solidago virgaurea*– <1%; *Geranium palustre*–<1%; *Convallaria majalis*–1%; *Stellaria media*–<1%; *Galium mollugo*–1%; *Geum urbanum*–<1%; *Vicia sepium*–<1%; *Chamaenerion angustifolium*–1%; *Melampyrum pretense*–<1%. Mosses are rare, with a coverage of not more than 3–5%, and the following was noted: *Pleurozium schreberi*.

Soils on the flat slopes of kames are predominantly postagrogenic (agrozems) of small and medium plowing layers with a thickness of postagrogenic horizon AYpa up to 27 cm (Table 2), which is clearly distinguished by smooth boundary and abrupt transition to underlying horizons. Strongly disturbed postpyrogenic soils with abundant charcoal inclusions were also noted (section CP4). The soils are acidic, the pH_{water} of the postpyrogenic horizon is not higher than 5.3, and pH_{salt} in similar horizons is 3.7–4.6. SOC content in postagrogenic horizons 1.22–4.33% down the profile is much lower. The exception is the gray humus postpyrogenic soil (section CP4) in which SOC distribution is heterogeneous and determined by the presence of anthropogenic artifacts (charcoal).

Nº	Horizon	Thickness, cm	pH _{water}	pH_{salt}	Bulk Density, g × cm ⁻³	SOC, %	Soil Photo
Medium plowed post-agricultural illuvial-iron agrozem on fluvioglacial sediments							
(Plaggic Podzol (Arenic))							
	0	0–1	5.6	5.4	0.3	16.15	10
	O/AO	1–8	5.0	4.3	0.3	5.08	20
CP3	AYpa	8–30	4.4	4.2	1.4	1.22	- 40
CIU	BFff	30–50	4.8	4.5	1.2	0.59	- 59 -
	BCff	50-80	5.3	4.5	1.2	0.45	- 70 -
	C…g,ff	80-100	4.8	4.4	1.3	0.54	- 00 -
		Gray humus	postpyrogenia	c soil on compa	acted sandy loam		
			(An	ithrosol)			-Om.
	О	0–2	5.2	5.0	0.4	16.63	- 10
CP4	AYpyr	2–30	4.2	3.7	1.0	2.96	- 40
CI4	RYR	30–70	4.4	3.8	0.9	3.95	- 20 - 10 - 10
	C∵ff	70–100	4.4	4.1	1.0	1.46	
	Si	mall plowed postagr	ogenic illuvial	-iron agrozem	on fluvioglacial se	diments	
(Plaggic Podzol (Arenic))							
	0	0–2	-	-	0.5	20.96	10-
	AYpa	2–10	5.3	4.6	0.7	2.84	- 20 -
CP8	BF	10-15	5.2	4.3	1.1	0.47	- 50 -
CIU	BC	15–35	5.2	4.5	1.2	0.36	
	BCff	35–70	5.2	4.7	1.3	1.11	
	C··	70-80	5.0	4.6	1.1	0.31	
Medium plowed illuvial-iron postagrogenic agrozem on fluvioglacial sediments							
			(1 laggie 1 v	ouzor (/ irenie)	/		000
	AYpa	0–27	4.6	4.1	0.9	1.78	10
CP12	BF	27–50	4.9	4.2	1.1	0.72	40 - 5⊖ - 30 -
							- 59
	C∵ff	50-85	4.7	4.3	1.4	0.60	
Medium plowed illuvial-iron postagrogenic agrozem on fluvioglacial sediments							
			(Plaggic Po	odzol (Arenic))			
	O AV	0-1	-	-	0.2	41.77	10
	АҮра	1-24	3.9	3.8	1.1	4.33	- 20 -
CP10	БЕ	24-45	4.8	4.3	1.2	0.84	- 50 -
CITO	BH BC#	45-55	4.6 4 E	4.3	1.2	0.95	-B. Manuer
	DCII Cuff	33-70 70	4.3 1 Q	4.3 1 1	1.3 1 <i>1</i>	0.47	
	C11	/0	4.7	4.4	1.4	0.37	and the second

Table 2. Main soil characteristics of soils attached to flat kame slopes and their plateau-like peaks.

Abandoned fields and vegetable gardens are covered by fallow fern-grass-ruderal meadows (Figure 2C). Vegetation is irregular, with many species of weedy-ruderal and

weedy-meadow groups. The invasive species *Solidago anadensis* has been found. This vegetation is combined with ferns *Athyrium filix-femina* and *Dryopteris carthusiana*. The total vegetation cover on the site is 100%. Grass stand height is considerable, which is up to 1.4– 1.6 m (taking into account generative organs), and the main growth height of vegetative mass is 0.6–0.8 m. The most abundant species are as follows: *Dactylis glomerata*—17%; *Athyrium filix-femina*—15%; *Salamagrostis epigeios*—12%; *Dryopteris carthusiana*—10%; and *Solidago anadensis*—15%. The rather abundant species are as follows: *Urtica dioica*—7%; *Chamaenerion angustifolium*—5%; and *Vicia cracca*—5%. The low-coverage species are as follows: *Vicia sepium*—3%; *Agrostis teuis*—3%; and *Artemisia vulgaris*—1%. *Scrophullaria nodosa, Lathyrus pratensis*, and *Bunias orientalis* were observed with less than 1% cover.



Figure 3. Profile of particle size distribution (%) by genetic horizons for several of the soil profiles. (A) CP1, (B) CP9, and (C) CP14. BS—bound sand, S—sandy loam, and SL—light loam [28].

Postagrogenic soils under meadow grassland vegetation are characterized by a greater thickness of agro-transformed horizon compared to agrozems on flat kame slopes (Table 3). Soils are classified as agrozemes of medium or deep plowing with a thickness of the AYpa horizon; they are also acidic (pH_{water} 4.6–4.9; pH_{salt} 3.9–4.3). SOC content is maximum on the surface of the post-agricultural horizons, ranging narrowly from 1.72 to 2.03 %. The particle size distribution (Figure 3C) is dominated by coarse dust fraction (0.05–0.01 mm) throughout the profile, with the maximum content found in the BF horizon (53 %) and the minimum in the AYpa horizon (43 %). The content of physical clay also increases with depth, from 19% at the surface to 23 % in the parent material. Probably, there is an enrichment of the profile with fine material due to its removal from the topsoil.

N⁰	Horizon	Thickness, cm	pHwater	pH_{salt}	Bulk Density, g × cm ⁻³	SOC, %	Soil Photo
	De	ep plowed post-agri	cultural illuvia	l-iron agrozem	ı on fluvioglacial s	ediments	
			(Plaggic Pc	odzol (Arenic))			
	0	0–1	-	-	0.15	16.82	0mm = 10 = 1
CP5	АҮра	1-40	4.9	4.3	1.2	1.93	= 20 ; 3459 = 30 .
010	BFff	40–60	5.0	4.5	1.3	0.60	- 40 - 58
	C…g,ff	60–75	5.1	4.6	1.2	0.53	- 50 - - 70 -
	Me	dium plowed illuvia	l-iron postagro	genic agrozen	n on fluvioglacial s	sediments	
		-	(Plaggic Po	dzol (Arenic))			
			× 00				
	АҮра	0–30	4.8	4.0	1.1	1.72	= 10 :
CP13	BF	30–60	5.0	4.5	1.1	0.64	-32-
	C··	60–80	5.3	4.6	1.4	0.51	- 60 - - 70 -
	De	ep plowed post-agrie	cultural illuvia	l-iron agrozem	n on fluvioglacial s	ediments	
			(Plaggic Po	dzol (Arenic))			
	AYna	0-45	4.6	39	1.3	2.03	10 T
CP14	mpu	0 10	1.0	0.9	1.0	2.00	20-
	BF	45–65	4.9	4.3	1.0	1.04	20
	C…ff	65–85	5.1	3.8	1.3	0.51	- 28 - 60 - - 70 - 100 -

Table 3. Main soil characteristics of soils attached to abandoned fields and vegetable gardens.

Boggy birch forests occupy the inter-kame depressions (Figure 2D). The height of trees is 12–14 m, with a trunk diameter of 22–25 cm. Stand regeneration is rare. The following trees were recorded: *Alnus glutinosa*-2.5 m; *Acer platanoides*-2.3 m; *Quercus robur*-1.6 m. The undergrowth is medium-dense. In the shrub tier, there are *Frangula alnus*, *Salix aurita*, *Salix cinerea*, and *Viburnum opulus*. The average height of the shrub tier is 2.0–3.5 m. The herbage is high, up to 1.5–1.6 m, and rather dense; the projective cover of the herbage tier is 75–80%. In the herb tier, the following species coexist: *Lysimachia vulgaris*-12%; *Filipendula ulmaria*-20%; *Equisetum palustre*-15%. The following species are quite abundant *Viola palustris*-15%; *Geum rivale*-3%; *Deschampsia cespitosa*-10%; *Equisetum palustre*-1%; *Cirsium palustre*-1%; *Crepis paludosa*-<1%; *Luzula pilosa*-<1%; *Galium palustre*-1%; *Scirpus sylvaticus*-2%; *Potentilla erecta*-<1%; *Ranunculus acris*-<1%; *Maianthemum bifolium*-<1%; *Scutellaria galericulata*-1%; *Dryopteris carthusiana*-1%.

The wetlands are occupied by intrazonal peaty-perennial eutrophic soils (Table 4). The degree of peat decomposition is about 50% in all studied profiles; large undecomposed roots and wood remains have been found.

Nº	Horizon	Thickness, cm	pH _{water}	pH_{salt}	Bulk Density,	SOC, %	Soil Photo
			Peat-perent	nial eutrophi	c soil		
			(H	Histosol)	e son		
	TE1	0–10	5.2	4.9	0.2	38.40	
	TE2	10-20	5.3	4.6	0.3	41.96	
CP2	TE3	20-30	4.7	4.6	0.2	46.35	
	TE4	30-50	4.1	3.5	0.2	43.81	
	TT	50	3.7	3.3	0.2	40.49	
			Peat-peren	nial eutrophi	c soil		
			- (H	Histosol)			
CP6	TE1	0–15	4.4	3.9	0.1	36.54	0 m = 10
	TE2	15–30	4.1	3.8	0.15	44.51	- 20 - - 50 - - 30 -
			Peat-perent	nial eutrophi	c soil		
	(Histosol)						
CP7	TE1	0–15	4.7	4.3	0.1	41.29	Dem 10
	TE2	15–30	4.8	4.3	0.15	46.19	- 30
CP15	TE1	0–20	4.8	3.8	0.2	48.82	10
	TE2	20–40	5.1	4.0	0.1	51.54	- 50 -
	TE3	40-50	4.9	3.9	0.1	48.94	- S2 - - 60 -
	TT	50-80	5.1	4.0	0.1	51.44	- 70 -

Table 4. Main soil characteristics of soils attached to inter-kame wetland depressions of relief.

As a general rule, water starts to seep out of the section walls from a depth of 30–50 cm, but near old drainage ditches the section can be deepened to 80–100 cm (section CP15). The peat-perennial soils are overmoistened, characterized by high acidity with SOC content everywhere above 35% and reaching 51.5%. Soils are formed due to the waterlogging of secondary forests, and the bog nutrition is mixed, resulting from atmospheric precipitation and due to the lateral runoff of groundwater from the slopes of kames.

Relief depressions and accumulative terraces are occupied by wet grass lowland bogs (Figure 2D). The vegetation is very close, and the total projective cover is 100%. Grass stand height is 1.6–1.8 m. The vegetation cover is dominated by the following: *Typha latifolia*—15%; *Filipendula ulmaria*—40%; *Lysimachia vulgaris*—20%; *Equisetum palustre*—12%; *Scirpus sylvaticus*—7%. Coverage of other species does not exceed 1–2%: *Elytrigia repens, Impatiens perviflora, Crepis paludosa, Impatiens glandulifera,* and *Geum rivale*. Mosses are rare, and *Brachythecium sp.* was noted.

Under the semi-hydromorphic conditions of accumulative terraces, dark humus gleyey soils are formed (Table 5) with poorly differentiated profiles with the inclusion of large organic residues (roots, branches). From a depth of 40 cm, the localized spots of gley around roots are noted. These soils are slightly acidic with a relatively high SOC content of 5–6%, the concentration of which slightly varies with depth.

					Bulk Density,		
N⁰	Horizon	Thickness, cm	pHwater	pH_{salt}	g × cm ⁻³	SOC, %	Soil Photo
Dark humus gley soil							
			(His	tic Gleysol)			
CP11	AU1	0–20	4.7	4.0	0.7	5.62	
	AU2	20-40	4.9	4.1	0.8	6.57	
	AUg1	40-60	4.7	4.4	0.8	4.66	
	AUg2	60-80	5.0	4.4	0.3	6.18	

Table 5. Main soil characteristics of soils attached to relief depressions and accumulative terraces.

The structure of the vegetation cover of the study area has a wide spatial heterogeneity, which is explained by the long history of agricultural development of these places, which continues at present; the shallow contour of land use is a characteristic feature of farming in the southern part of the Karelian Isthmus [43]. In general, we can actualize the data of V.K. Pestryakov [44] on the dominance of lightened pine and secondary herbaceous pine-birch forests on light parent material of the territory of the Karelian Isthmus since we have described birch-pinerowan-landish forests in places with conditionally undisturbed stands. However, there is still an opinion that the presence of pine forests in the kame uplands is an extrazonal phenomenon, as well as the black alder forests previously described in the lowlands of the Koltushskaya Upland [45,46]. O.G. Chertov noted that spruce forests (heather, lingonberry, etc.) and pine forests dominate on basic cation-rich sands of heavily drained plains and slopes of different genesis [47]. The presence of oak in the undergrowth may indicate the nemoralization (shift in plant species list from boreal to sub-boreal type) of the flora, but it may also be related to its invasion from the territories of neighboring households, as "cultural" plants were repeatedly observed in the whole territory of the study area.

Anthropogenically initiated changes in the natural look of the Karelian Isthmus ecosystems were noted by V.K. Pestryakov [44]. The reclamation measures initiated by human activity led to changes in the natural processes of ecogenesis on most of the Karelian Isthmus and the territory of the Koltushskaya Upland in particular. Exodynamic changes are expressed in the formation of burned areas, shrublands and wetlands, and secondary small-leaved forests in place of former forests, which were previously described in this paper [44]. Changes in natural phytocenoses were preceded by anthropogenically initiated changes in the soil cover of the Koltushskaya Upland. Zonal soils of podzol type in the process of agricultural development were transformed into agrozems. After they transitioned to a fallow state, they were occupied by synanthropic vegetation species. Analyzing the early works devoted to the soils of the North-West and Leningrad region [20,44], we can conditionally distinguish four main groups of soils on Koltushsky heights: 1forest soils of podzol type on automorphic landscapes; 2-soils of semi-hydromorphic landscapes; 3-peat soils of hydromorphic landscapes; 4-anthoropo-, agrogenically modified soils on different types of landscapes characterized by the peculiarity of vegetation cover. Postagrogenic soils of the Karelian Isthmus are separately marked in the Red Book of Soils of the Leningrad Region, as they preserve footprints of past agricultural development and are the memory of the landscape [48].

Some authors connect the peculiarities of soil formation with an eluvial–illuvial differentiated profile on lake-glacial and fluvioglacial deposits with their automorphous position and richness of parent material, and the intensity of podzol process with the thickness and composition of the litter; earlier, this fact was also described in the work of V.V. Ponomareva [8,40]. High acidity (especially in the lower part of organogenic horizons) of sandy soils is associated with a flushing water regime and active removal of organic compounds from the litter horizon down the profile [20,49]. The authors also note that the particle size distribution of these soils is dominated by coarse (1–0.25 mm) and fine (0.25– 0.05 mm) sands, which is confirmed by our data (Figure 1A,B). The light particle size distribution of sandy soils of pine forests of the middle taiga (Karelia Republic), which was similar in terms of genesis, was also noted in the [50]. During the agricultural development of sandy soils, the profile is enriched with more finely dispersed dusty-clay material and its filtration down the profile occurs [44].

Forest and arable soils of the Karelian Isthmus rather stably preserve SOC stocks due to their relatively high soil organic matter content and soft local soil climatic regime [44]. Based on the data given in the monograph, we calculated that the 0–10 cm layer of podzolized sandy soils of the Karelian Isthmus (without taking into account the litter horizon O) is $1.7 \text{ kg} \times \text{m}^{-2}$, and in the 0–100 cm layer, $3.6 \text{ kg} \times \text{m}^{-2}$ of carbon is stored; in sod-podzolic soils in the 0–10 cm layer, the SOC stock is $2.5 \text{ kg} \times \text{m}^{-2}$; in the 0–100 cm layer, the SOC stock is 7.8 kg \times m⁻². Some data on the SOC stocks of podzolic sandy soils of the central and northern parts of the Karelian Isthmus are also given there; they vary from 6.9 to 7.2 kg × m⁻² in the 0–100 cm layer. In the cultivated sod–weak–podzolic gleyey soils (classified as agrozem medium plowed postagrogenic illuvial-iron gleyey according to Russian soil taxonomy) of the central and southern parts of the Karelian Isthmus, carbon stocks on dusty stratified sandy loam measure $4.7 \text{ kg} \times \text{m}^{-2}$ in the layer 0–10 cm and $12.4 \text{ kg} \times \text{m}^{-2}$ in the layer 0–100 cm. The data on SOC stocks in the 0–70 cm layer of humus-peaty soils are also given there, measuring at $40.6 \text{ kg} \times \text{m}^{-2}$. Previously, studies of SOC stocks in the 0–10 cm soil layer were already conducted for this area by spatial modeling using remote sensing data, but these studies were conducted without taking into account the genesis of soils and the degree of their anthropogenic disturbance [6]. It was shown that in a plot or carbon polygon of more than 150 ha, SOC stocks in the 0–10 cm layer varied from 1 to more than 9 kg \times m⁻² [6]. According to our data (Figure 4), when conditionally dividing the studied soils into undisturbed (podzol), postagrogenic (agro), and bog (peat) soils, SOC stocks in the 0–10 cm layer are not statistically different between undisturbed sod-podbur and postagrogenic agrozems. For the 0–10 cm layer, the following SOC stock values were found: sod-podburs -2.7 ± 0.7 kg × m⁻²; postagrogenic agrozems -2.5 ± 1.1 kg × m⁻²; peat $soils - 5.7 \pm 1.6 \text{ kg} \times \text{m}^{-2}$.



Figure 4. SOC stocks in 0–10 cm (A) and 0–100 cm (B) layers (excluding litter horizon). Pozdol—profiles CP1 and CP9; agro—CP3,5,8,10,12,13,14; peat—CP2,6,7,11,15. Ord. one-way ANOVA: ns—not significant; *-p < 0.05; **-p < 0.01; ***-p < 0.001; ****-p < 0.001.

For the 0–100 cm layer, the following values of stocks were obtained: sod-podbur – $8.3 \pm 1.3 \text{ kg} \times \text{m}^{-2}$; postagrogenic agrozems – $12.8 \pm 2.9 \text{ kg} \times \text{m}^{-2}$; peat soils – $60.0 \pm 19.8 \text{ kg} \times \text{m}^{-2}$. Thus, the largest carbon stocks for soils of the "Ladoga" carbon polygon are observed in peat-perennial eutrophic soils due to the active accumulation of plant residues and peat formation. Hydromorphic conditions and a low degree of humification lead to the deposition of soil organic matter. Carbon stocks in soils of taiga forests at automorphic

positions are related to the dominants of forest composition, species richness of vegetation cover, stand age, and history of nature use in the territory [50,51]. Soils of middle and north taiga pine forests in Karelia and the Karelian Isthmus are characterized by a low carbon stock (10 kg × m⁻² including litter in the 0–50 cm layer) compared to spruce and birch forests (12.5 and 13.8 kg × m⁻² for the same layer). For the Karelian Isthmus, past agricultural activities are also the cause of carbon accumulation in post-agricultural soil horizons, but the carbon stocks in litter and illuvial horizons remain low, which does not lead to a significant increase in carbon stocks (Figure 4) in post-agricultural soils in the territory of the Koltushskaya Upland [51].

Organic carbon stocks, their stability, and their resistance to biodegradation depend on climate, vegetation type, and land use [29,52]. Taking into account that the studied area of the Koltushskaya Upland is the base for the operation of the "Ladoga" carbon polygon, it is important to assess not only carbon stocks in soils but also the ability of organic matter to support ecological and biological functions of soil [30]. One of the methods for assessing the sequestering potential of soil is to determine the stocks of potentially mineralizable (biologically active) carbon [53]. As a result of the approximation of cumulative C-CO₂ production curves (Figure 5A) obtained from incubation for 175 days, the initial parameters of potentially mineralizable carbon (C_{pm}) content in anthropogenically undisturbed soils were calculated (Table 6). In the gray humus podzolized horizon AYe of the sodpodbur horizon, the C_{pm} content = 502.5 ± 104.6 mg × 100 g⁻¹, which is 15.1 ± 3.1% of the SOC. Thus, the C_{pm} stock in the 0–10 cm layer for podzolized sod-podbur is equal to 0.48 ± 0.01 kg × m⁻².



Figure 5. (**A**) Cumulative curves of C-CO₂ emission by different soils. (**B**) Intensity of soil respiration by different soils during various periods of incubation. CP1—podzolized sod-podbur; CP2—peatperennial eutrophic soil. Measurements were carried out for horizons AYe and TE1 (n = 3).

In the TE1 horizon of peat-perennial eutrophic soil, the $C_{pm} = 3394.7 \pm 380.3 \text{ mg} \times 100 \text{ g}^{-1}$ or $8.8 \pm 0.9\%$ of the SOC. C_{pm} stock in the 0–10 cm layer of peat-perennial eutrophic soil is equal to $0.58 \pm 0.06 \text{ kg} \times \text{m}^{-2}$. Peat soils are characterized by higher mineralization intensity compared to sod-podbur (9.2 ± 0.1 vs. 2.5 ± 0.2 mg × 100 g⁻¹ × day⁻¹) and a higher degree of organic matter stability. However, there is evidence that the size and structure of the mineralizable organic matter pool of peat soils are controlled by the temperature regime and water content [53,54].

Parameter	Podzolized Sod-Podbur (n = 3)	Peat-Perennial Eutrophic Soil (n = 3)				
SOC, mg × 100 g ⁻¹	3330	38400				
C _{pm} , mg × 100 g ⁻¹	502.5 ± 104.6	3394.7 ± 380.3				
Cpm, % of SOC	15.1 ± 3.1	8.8 ± 0.9				
Mineralization constant (k), day ⁻¹	0.005 ± 0.001	0.003 ± 0.001				
Mineralization intensity (IM), mg ×	25 ± 0.2	0.2 + 0.1				
100 g ⁻¹ × day ⁻¹	2.5 ± 0.2	9.2 ± 0.1				
Stability Index (SI)	5.8 ± 1.3	10.4 ± 1.3				
Note: $IM = C_{pm} \times k$, $IS = (SOC - C_{pm})/C_{pm}$ [54].						

Table 6. Potentially mineralizable organic matter content and mineralization characteristics of anthropogenically undisturbed soils of the "Ladoga" carbon polygon.

Soil carbon pools are sensitive to microbial diversity in soil [55,56]. Soil bacteria and fungi are directly involved in the carbon cycle, and their necromass is the main carboncontaining component contributing to the stable SOC pool [57]. Currently, some phyla of microorganisms involved in carbon cycling are distinguished according to their functional groups [57]. For example, *Acidobacteria* can decompose complex carbon substrates; *Prote-obacteria*, *Cyanobacteria*, *Euryarchaeota*, *Crenarchaeota*, and *Chlorophyta* can fix carbon; methanogenic Archaea during the process of anaerobic decomposition of organic matter can produce methane [56].

In our study of soils of automorphic landscapes (Figure 6, CP1), the dominant bacterial phyla are *Proteobacteria* and *Actinobacteria*, with *Bacteroidetes*, *Acidobacteria*, *Verrucomicrobia*, *Planctomycetes*, and *Gemmatimonadetes* somewhat less represented. Statistically significant differences in the abundance of *Acidobacteria* and *Proteobacteria* were found between the litter (O) and sod (AYe) soil horizons.



Figure 6. Taxonomic composition of soil microbial community (left) in surface and subsurface soil horizons. Results of pairwise comparison of abundance (right) of identified taxa between horizons. (Ord. one-way ANOVA: **-p < 0.01; ***-p < 0.001; ***-p < 0.001).

The dominance of phylum *Proteobacteria* (mainly *Rhodoplanes* and *Xanthomonadales*), *Acidobacteria*, *Actinobacteria*, and *Bacteroidetes* in the total microbiome pool is typical for podzolic soils [58–60]; other bacterial phyla may also be present, but the above mentioned are most common.

For soils on hydromorphic positions (peaty-perennial eutrophic soil), Proteobacteria, Bacteroidetes, Actinobacteria were the most dominant. Significantly lower abundance was detected for Euryarchaeota, Acidobacteria, Verrucomicrobia, and Nitrospirae. The methanogenic Archaea – Euryarchaeota – were identified in the deep part of the profile. Verrucomicrobia, as cosmopolitans of the rhizosphere, were identified in the surface soil horizons [61]. In addition, a low abundance of Nitrospirae phyla was found in the upper part of the soil profile. According to previously published data, the main bacterial phyla characteristics of peat bog soils are Proteobacteria, Acidobacteria, Chloroflexi, and Verrucomicrobia [62-65]; some studies also noted the presence of Bacteroidetes, Actinobacteria [66], and Planctomycetes [67]. Globally, forest soils represent an important biological sink of atmospheric CH4-they dominate the total soil CH4 uptake (20-45 Tg CH4 yr-1) on land and thereby play an important role in modulating the increasing atmospheric CH₄ concentration [68]. Since methane emissions are primarily produced by methanogenic archaea, a group of microorganisms thrive in anaerobic environments, such as natural wetlands and tundra, rice paddies, ruminants, landfills, and sediments [69]. For example, certain types of bacteria, such as acetoclastic methanogens and hydrogenotrophic methanogens, are known to be key players in the methane production process [70]. More than 70% of annual CH₄ emission is biogenic CH4 originating from the activity of methanogens [71]. The territory of the Leningrad Region is a significant peat area where investigation of methane fluxes is crucial for understanding its global contribution to climate change in the region. In our monitoring site specifically, as representatives of Euryarchaeota, a huge phylum of methanogens constitutes the majority of archaeal clones in peat samples. It was previously thought that *Euryarchaeota* only lived in extreme environments (in terms of temperature, salt content, and/or pH), but later it was shown that *Euryarchaeota* also live in moderate environments, such as low-temperature acidic environments [72]. The activity of archaea in our research site will contribute to methane production, which has implications for climate change due to methane's potent greenhouse gas effect. Methane emissions from sources like peatlands in the Leningrad region can trigger feedback loops that further exacerbate climate change. It is important to understand that the taxonomic composition of soil microbiota can change depending on various environmental and indoor factors such as pH, moisture, groundwater salinity, changes in soil and atmospheric temperature regimes, and soil density [56,65]. Therefore, additional seasonal studies of microbial diversity at key sites are needed to understand the functioning of microbial interactions on soil carbon cycling.

4. Conclusions

A retrospective analysis of soil and vegetation development in the southern part of the Karelian Isthmus (Koltushskaya Upland) on the territory of "Ladoga" carbon polygon as the most representative object of central Fennoscandia has been carried out. It has been established that modern soil formation on the Koltushskaya Upland is largely related to long-term agrogenic development and intensive recreation, which led to changes in natural processes of ecogenesis in most of the Karelian Isthmus and on the territory of the Koltushskaya Upland in particular. Transformations in vegetation cover occur everywhere on the territory of the Koltushskaya Upland, and there is a tendency to restore native southern taiga pine forests, enriched with nemoral elements of flora, both among herbaceous plants and broad-leaved species of trees and shrubs (oak, maple, and hazel). However, even despite the protected status of the territory, the communities experience significant recreational pressure. For this reason, succession to the climax state seems unlikely. The ubiquitous presence of synanthropic species in the communities was noted, which along with significant heterogeneity of the vegetation itself and fragmentation of forest areas is a consequence of the constantly growing anthropogenic load on the territory. At present, stable phytocenoses have been formed on the territory, which is generally characteristic of the existing soil and climatic factors, as well as the range and intensity of anthropogenic impact. The soil cover of the carbon polygon is agrogenically transformed, and there are very few soils of natural composition (or they have managed to acquire a profile similar to the natural one). Agrogenically transformed soils are easily diagnosed morphologically by a thick gray humus post-agricultural horizon with a flat boundary. A large area of the key site is occupied by peat soils, which are artificially drained in some places. Postagrogenic and natural soils are acidic, and pH values are mostly below 5.5-6; in soils of hydromorphic and semi-hydromorphic landscapes, the values are mostly below 5. Agrozems on the territory of the "Ladoga" carbon polygon do not statistically differ in SOC stocks in the 0–10 and 0–100 cm layers. For the 0–10 cm layer carbon stocks, sodpodbur -2.7 ± 0.7 kg × m⁻²; postagrogenic agrozems -2.5 ± 1.1 kg × m⁻². For the 0–100 cm layer carbon stocks, sod-podur -8.3 ± 1.3 kg × m⁻²; postagrogenic agrozems -12.8 ± 2.9 kg \times m⁻². Swamp peat soils have significantly higher SOC stock: 0–10 cm – 5.7 ± 1.6 kg×m⁻²; $0-100 \text{ cm}-60.0 \pm 19.8 \text{ kg} \times \text{m}^{-2}$. Soils of wetlands are also characterized by a large stock and content of potentially mineralizable (C_{pm}) organic carbon (3394.7 ± 380.3 mg × 100 g⁻¹ $(8.8 \pm 0.9\% \text{ of SOC})$ in comparison with sod-podbur (502.5 ± 104.6 mg × 100 g⁻¹ (15.1 ± 3.1% of SOC)). The mineralization intensity of peat soils is higher than that of sod-podbur $(9.2 \pm 0.1 \text{ vs}, 2.5 \pm 0.2 \text{ mg} \times 100 \text{ g}^{-1} \times \text{day}^{-1})$ and is more stable, but the mineralization intensity of peat soils can change significantly depending on temperature regime and humidity. The dominant phyla in the microbiome community of anthropogenically disturbed soils are Actinobacteria, Bacteroidetes, and Proteobacteria. Differentiation of abundance by soil profile was revealed for individual phyla. In peat soils, the presence of methane-producing archaea—*Euryarchaeota*—in organogenic parent material was detected. To obtain a complete overview of the functioning of microbiome communities, it is necessary to conduct seasonal monitoring studies taking into account the functional groups of microorganisms of the carbon cycle. Thus, the alfehumus soils of the region have been studied for the first time after a break of many years with the help of modern instrumental, chemical, and bioinformatic methods. The nature of the soil-forming process of the alfehumus type in the models of dynamic soil evolution in the late Anthropocene has been largely clarified.

Author Contributions: E.A. (Evgeny Abakumov)—Conceptualization; Resources; Funding acquisition; Writing—review and editing. T.N.—Investigation; Methodology; Formal Analysis; Visualization; Writing—original draft. D.Z.—Investigation; Software; Visualization; Formal Analysis; Writing—review and editing. A.S.—Investigation; Data curation; Software. E.S.—Project administration; Supervision; Funding acquisition. E.K.—Investigation; Validation; Writing—review and editing. A.K.—Investigation; Data curation; Software. V.P.—Investigation; Validation; Methodology. E.N.— Investigation; Formal Analysis; Writing—review and editing. G.G.—Investigation; Software; Methodology. E.A. (Evgeny Andronov)—Conceptualization; Resources; Data curation. All authors have read and agreed to the published version of the manuscript.

Funding: The authors acknowledge Saint Petersburg State University for a research project 123042000071-8

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data can be obtained upon request from the corresponding author. The data are not publicly available due to privacy

Acknowledgments: The article is dedicated to the memory of M.G. Noskova and D.N. Kovalev, employees of the Department of Applied Ecology of St. Petersburg State University, founders of the "Koltushkie Vysoty" nature reserve, who tragically passed away in Vsevolozhsk in 2017.

Conflicts of Interest: The authors declare no conflicts of interest.

References

- 1. Abakumov, E.V.; Polyakov, V.I.; Chukov, S.N. Approaches and Methods for Studying Soil Organic Matter in the Carbon Polygons of Russia (Review). *Eurasian Soil Sci.* 2022, *55*, 849–860. https://doi.org/10.1134/S106422932207002X.
- 2. Carbon Supersites. Russian Federation. Available online: https://carbon-polygons.ru/en/ (accessed on 10 January 2024).
- Bossio, D.A.; Cook-Patton, S.C.; Ellis, P.W.; Fargione, J.; Sanderman, J.; Smith, P.; Wood, S.; Zomer, R.J.; von Unger, M.; Emmer, I.M.; et al. The role of soil carbon in natural climate solutions. *Nat. Sustain.* 2020, *3*, 391–398. https://doi.org/10.1038/s41893-020-0491-z.
- Polyakov, V.; Abakumov, E.; Nizamutdinov, T.; Shevchenko, E.; Makarova, M. Estimation of Carbon Stocks and Stabilization Rates of Organic Matter in Soils of the «Ladoga» Carbon Monitoring Site. *Agronomy* 2023, *13*, 807. https://doi.org/10.3390/agronomy13030807.
- Makarova, M.V.; Abakumov, E.V.; Shevchenko, E.V.; Paramonova, N.N.; Pakhomova, N.V.; Lvova, N.A.; Vetrova, M.A.; Foka, S.C.; Guzov, Y.N.; Ivakhov, V.M.; et al. From carbon polygon to carbon farm: The potential and ways of developing the sequestration carbon industry in the Leningrad Region and St. Petersburg. *Earth Sci.* 2023, 68, 82–102. https://doi.org/10.21638/spbu07.2023.105.
- Suleymanov, A.; Abakumov, E.; Nizamutdinov, T.; Polyakov, V.; Shevchenko, E.; Makarova, M. Soil organic carbon stock retrieval from Sentinel-2A using a hybrid approach. *Environ. Monit. Assess.* 2024, 196, 23. https://doi.org/10.1007/s10661-023-12172v.
- 7. Batjes, N.H. Total carbon and nitrogen in the soils of the world. *Eur. J. Soil Sci.* **1996**, 47, 151–163. https://doi.org/10.1111/j.1365-2389.1996.tb01386.x.
- 8. Rehman, Z.U.; Junaid, M.F.; Ijaz, N.; Khalid, U.; Ijaz, Z. Remediation methods of heavy metal contaminated soils from environmental and geotechnical standpoints. *Sci. Total Environ.* **2023**, *867*, 161468. https://doi.org/10.1016/j.scitotenv.2023.161468.
- 9. Zomer, R.J.; Bossio, D.A.; Sommer, R.; Verchot, L.V. Global Sequestration Potential of Increased Organic Carbon in Cropland Soils. *Sci. Rep.* 2017, *7*, 15554. https://doi.org/10.1038/s41598-017-15794-8.
- 10. Kudeyarov, V.N. Current state of the carbon budget and the capacity of Russian soils for carbon sequestration. *Eurasian Soil Sci.* **2015**, *48*, 923–933. https://doi.org/10.1134/S1064229315090070.
- Kurganova, I.N.; de Gerenyu, V.O.L.; Ipp, S.L.; Kaganov, V.V.; Khoroshaev, D.A.; Rukhovich, D.I.; Sumin, Y.V.; Durmanov, N.D.; Kuzyakov, Y.V. Pilot carbon polygon in Russia: Analysis of carbon stocks in soils and vegetation. *J. Soils Environ.* 2022, *5*, e169. https://doi.org/10.31251/pos.v5i2.169. (In Russian with English Abstract)
- 12. Chernova, O.V.; Golozubov, O.M.; Alyabina, I.O.; Schepaschenko, D.G. Integrated Approach to Spatial Assessment of Soil Organic Carbon in the Russian Federation. *Eurasian Soil Sci.* 2021, *54*, 325–336. https://doi.org/10.1134/S1064229321030042.
- 13. Zhao, F.; Wu, Y.; Hui, J.; Sivakumar, B.; Meng, X.; Liu, S. Projected soil organic carbon loss in response to climate warming and soil water content in a loess watershed. *Carbon Balance Manag.* **2021**, *16*, 24. https://doi.org/10.1186/s13021-021-00187-2.
- 14. Beillouin, D.; Corbeels, M.; Demenois, J.; Berre, D.; Boyer, A.; Fallot, A.; Feder, F.; Cardinael, R. A global meta-analysis of soil organic carbon in the Anthropocene. *Nat. Commun.* **2023**, *14*, 3700. https://doi.org/10.1038/s41467-023-39338-z.
- 15. Winkler, K.; Fuchs, R.; Rounsevell, M.; Herold, M. Global land use changes are four times greater than previously estimated. *Nat. Commun.* **2021**, *12*, 2501. https://doi.org/10.1038/s41467-021-22702-2.
- Bullock, E.L.; Woodcock, C.E. Carbon loss and removal due to forest disturbance and regeneration in the Amazon. *Sci. Total Environ.* 2021, 764, 142839. https://doi.org/10.1016/j.scitotenv.2020.142839.
- 17. Fokich, Y.V. (Ed.) *Red Data Book of Nature of the Leningrad Region. Volume 1: Protected Areas;* Biological Research Institute of the St. Petersburg State University: St. Petersburg, Russia, 1999; 352p.
- 18. Glushkovskaya, N.B.; Semenova, I.S. Major periods in the Koltushi heights background, their current state and outlooks for development. *Proc. Russ. State Hydrometeorol. Univ.* **2009**, *11*, 123–131.
- 19. Malakhovsky, D.B.; Markov, K.K. (Ed.) *Geomorphology and Quaternary Deposits of the North-West of the European Part of the USSR*; Nauka: Leningrad, Russia, 1969; 256p
- 20. Gagarina, E.I.; Matinyan, N.N.; Schastnaya, L.S.; Kasatkina, G.A. *Soils and Soil Cover in Northwest Russia*; Saint-Petersburg State University: Saint-Petersburg, Russia, 1995; 236p.
- 21. Gagarina, E.I. *Lithological Factor of Soil Formation (on Example of North-West of Russian Plain)*; Saint-Petersburg State University: Saint-Petersburg, Russia, 2004; 260p.
- 22. IUSS Working Group WRB. World Reference Base for Soil Resources. In *International Soil Classification System for Naming Soils and Creating Legends for Soil Maps*, 4th ed.; International Union of Soil Sciences (IUSS): Vienna, Austria, 2022.
- 23. V.V. Dokuchaep Soil Institute (VASKhNIL). *Classification and Diagnostics of Soils in Russia*; Oykumena: Smolensk, Russia, 2004; 342p.
- 24. Khitrov, N.B.; Gerasimova, M.I. Diagnostic Properties and Soil Forming Materials in the Classification System of Russian Soils: Version of 2021. *Eurasian Soil Sci.* 2022, 55, 1–10. https://doi.org/10.1134/S1064229322010082.
- 25. Khitrov, N.B.; Gerasimova, M.I. Diagnostic Horizons in the Classification System of Russian Soils: Version 2021. *Eurasian Soil Sci.* 2021, *54*, 1131–1140. https://doi.org/10.1134/S1064229321080093.
- 26. Ipatov, V.S.; Mirin, D.M. Description of Phytocenosis. Methodical Recommendations. Educational and Methodical Manual; Saint Petersburg State University: Saint Petersburg, Russia, 2008; 71p.
- 27. Vorobyeva, L.N. (Ed.) Theory and Practice of Chemical Analysis of Soils; GEOS: Moscow, Russia, 2006; 400p.

- 28. Shein, E.V. (Ed.) *Field and Laboratory Methods of Research of Physical Properties and Soil Regimes;* Moscow State University: Moscow, Russia, 2001; 200p.
- Semenov, V.M.; Lebedeva, T.N.; de Gerenyu, V.O.L.; Ovsepyan, L.A.; Semenov, M.V.; Kurganova, I.N. Pools and fractions of organic carbon in soil: Structure, functions and methods of determination. *J. Soils Environ.* 2023, 6, e199. https://doi.org/10.31251/pos.v6i1.199.
- Semenov, V.M.; Ivannikova, L.A.; Kuznetsova, T.V.; Semenova, N.A.; Tulina, A.S. Mineralization of organic matter and the carbon sequestration capacity of zonal soils. *Eurasian Soil Sci.* 2008, 41, 717–730. https://doi.org/10.1134/s1064229308070065.
- Pinaev, A.G.; Kichko, A.A.; Aksenova, T.S.; Safronova, V.I.; Kozhenkova, E.V.; Andronov, E.E. RIAM: A Universal Accessible Protocol for the Isolation of High Purity DNA from Various Soils and Other Humic Substances. *Methods Protoc.* 2022, 5, 99. https://doi.org/10.3390/mps5060099.
- 32. R Core Team. R: A Language and Environment for Statistical Computing; R Foundation for Statistical Computing: Vienna, Austria, 2021.
- Callahan, B.; Mcmurdie, P.; Rosen, M.; Han, A.; Johnson, A.J.; Holmes, S. DADA2: High-Resolution Sample Inference from Illumina Amplicon Data. *Nat. Methods* 2016, 13, 581–583.
- 34. Mcmurdie, P.; Holmes, S. Phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data. *PLoS ONE* **2013**, *8*, e61217.
- Quast, C.; Pruesse, E.; Yilmaz, P.; Gerken, J.; Schweer, T.; Yarza, P.; Peplies, J.; Glöckner, F. The SILVA Ribosomal RNA Gene Database Project: Improved Data Processing and Web-Based Tools. *Nucleic Acids Res.* 2013, 41, D590–D596.
- Parte, A.C.; Carbasse, J.S.; Meier-Kolthoff, J.P.; Reimer, L.C.; Göker, M. List of Prokaryotic Names with Standing in Nomenclature (LPSN) Moves to the DSMZ. Int. J. Syst. Evol. Microbiol. 2020, 70, 5607–5612.
- Isachenko, A.G.; Dashkevich, Z.V.; Karnaukhova, E.V. Physical-Geographical Zoning of the North-West of Russia; Nauka: Leningrad, Russia, 1965.
- 38. Lukina, E.V.; Noskov, G.A. To the avifauna of Koltushsky heights (Leningrad region). Russ. Ornithol. J. 2015, 24, 3476–3477.
- Sukhacheva, E.U.; Aparin, B.F. Soil Cover Patterns in Anthropogenically Transformed Landscapes of Leningrad Oblast. *Eurasian* Soil Sci. 2019, 52, 1146–1158. https://doi.org/10.1134/S1064229319070123.
- Zakharova, M.K.; Morgach, Y.R. Specific Features of the Soil Cover of Recreation Areas in Leningrad Oblast. *Eurasian Soil Sci.* 2023, 56 (Suppl. S2), S202–S213. https://doi.org/10.1134/S1064229323601506.
- Subetto, D.A. (Ed.) The Atlas of the Leningrad Region; Publishing House A. I. Herzen Russian State Pedagogical University: Saint Petersburg, Russia, 2022; 112p.
- 42. Gorbatenko, S. World Heritage—The Historical Landscape of the Saint Petersburg Agglomeration; Documentation; ICOMOS St. Petersburg Regional Branch: Saint Petersburg, Russia, 2011; 115p.
- 43. Isachenko, G.A. "Window to Europe": History and Landscapes; Saint Petersburg State University: St. Petersburg, Russia, 1998; 476p.
- 44. Pestryakov, V.K. (Ed.) Soils of Leningrad Oblast; Leningraddat: Leningrad, Russia, 1973; 344p.
- 45. Zmitrovich, I.V. Middle taiga of Karelian isthmus: Zonal, intrazonal and extrazonal phenomena. Vestn. Ekol. Lesoved. Land-shaftoved. 2011, 12, 54–76.
- Kovalev, D.N.; Noskov, G.A.; Noskova, M.G.; Popov, I.Y.; Rymkevich, T.A. A developmental concept for regional networks of protected areas as applied to Saint Petersburg and Leningrad oblast. Part I: Ecological aspects. *Biosfera* 2012, *4*, 427–462.
- 47. Chertov, O.G. Ecology of Forest Lands; Botanical Institute Named after V.L. Komarov: Leningrad, Russia, 1981; 192p.
- 48. Aparin, B.F.; Kasatkina, G.A.; Matinan, N.N.; Sukhacheva, E.Y. Red Soil Data Book of Leningrad Region; Aeroplan: Saint-Petersburg, Russia, 2007; 320p.
- Rehman, Z.U.; Khalid, U.; Ijaz, N.; Mujtaba, H.; Haider, A.; Farooq, K.; Ijaz, Z. Machine learning-based intelligent modeling of hydraulic conductivity of sandy soils considering a wide range of grain sizes. *Eng. Geol.* 2022, 311, 106899.
- Kuznetsova, A.I.; Geraskina, A.P.; Lukina, N.V.; Smirnov, V.E.; Tikhonova, E.V.; Shevchenko, N.E.; Gornov, A.V.; Ruchinskaya, E.V.; Tebenkova, D.N. Linking Vegetation, Soil Carbon Stocks, and Earthworms in Upland Coniferous–Broadleaf Forests. *Forests* 2021, 12, 1179. https://doi.org/10.3390/f12091179.
- 51. Lukina, N.V. (Ed.) Carbon Accumulation in Forest Soils and Successional Status of Forests; Partnership of Scientific Publications KMK: Moscow, Russia, 2018; 232p.
- 52. Kurganova, I.N.; Semenov, V.M.; Kudeyarov, V.N. Climate and land use as key factors of the stability of organic matter in soils. *Dokl. Biol. Sci.* **2019**, *489*, 189–192.
- 53. Semenov, V.M.; Kogut, B.M.; Zinyakova, N.B.; Masyutenko, N.P.; Malyukova, L.S.; Lebedeva, T.N.; Tulina, A.S. Biologically Active Organic Matter in Soils of European Russia. Eurasian Soil Sci. 2018, 51, 434-447. https://doi.org/10.1134/S1064229318040117.
- 54. Semenov, V.M.; Tulina, A.S. Comparative characteristics of mineralizable organic matter pool in soils of natural and agricultural ecosystems. *Agrochimia* **2011**, *12*, 53–63.
- Mau, R.L.; Liu, C.M.; Aziz, M.; Schwartz, E.; Dijkstra, P.; Marks, J.C.; Price, L.B.; Keim, P.; Hungate, B.A. Linking soil bacterial biodiversity and soil carbon stability. *ISME J.* 2014, *9*, 1477–1480. https://doi.org/10.1038/ismej.2014.205.
- 56. Wu, H.; Cui, H.; Fu, C.; Li, R.; Qi, F.; Liu, Z.; Yang, G.; Xiao, K.; Qiao, M. Unveiling the crucial role of soil microorganisms in carbon cycling: A review. *Sci. Total Environ.* **2024**, *909*, 168627. https://doi.org/10.1016/j.scitotenv.2023.168627.
- 57. Xue, P.; Minasny, B.; McBratney, A.; Pino, V.; Fajardo, M.; Luo, Y. Distribution of soil bacteria involved in C cycling across extensive environmental and pedogenic gradients. *Eur. J. Soil Sci.* **2023**, *74*, e13337. https://doi.org/10.1111/ejss.13337.

- Trifonova, T.; Kosmacheva, A.; Sprygin, A.; Chesnokova, S.; Byadovskaya, O. Enzymatic Activity and Microbial Diversity of Sod-Podzolic Soil Microbiota Using 16S rRNA Amplicon Sequencing following Antibiotic Exposure. *Antibiotics* 2021, 10, 970. https://doi.org/10.3390/antibiotics10080970.
- Manucharova, N.A.; Pozdnyakov, L.A.; Vlasova, A.P.; Yanovich, A.S.; Ksenofontova, N.A.; Kovalenko, M.A.; Stepanov, P.Y.; Gennadiev, A.N.; Golovchenko, A.V.; Stepanov, A.L. Metabolically Active Prokaryotic Complex in Grassland and Forests' Sod-Podzol under Polycyclic Aromatic Hydrocarbon Influence. *Forests* 2021, *12*, 1103. https://doi.org/10.3390/f12081103.
- Evdokimova, E.V.; Gladkov, G.V.; Kuzina, N.I.; Ivanova, E.A.; Kimeklis, A.K.; Zverev, A.O.; Kichko, A.A.; Aksenova, T.S.; Pinaev, A.G.; Andronov, E.E. The difference between cellulolytic 'culturomes' and microbiomes inhabiting two contrasting soil types *PLoS ONE* 2020, 15, e0242060. https://doi.org/10.1371/journal.pone.0242060.
- 61. Bünger, W.; Jiang, X.; Müller, J.; Hurek, T.; Reinhold-Hurek, B. Novel cultivated endophytic Verrucomicrobia reveal deep-rooting traits of bacteria to associate with plants. *Sci. Rep.* 2020, *10*, 8692. https://doi.org/10.1038/s41598-020-65277-6.
- 62. Tsitko, I.; Lusa, M.; Lehto, J.; Parviainen, L.; Ikonen, A.T.K.; Lahdenperä, A.-M.; Bomberg, M. The Variation of Microbial Communities in a Depth Profile of an Acidic, Nutrient-Poor Boreal Bog in Southwestern Finland. *Open J. Ecol.* **2014**, *4*, 832–859. https://doi.org/10.4236/oje.2014.413071.
- 63. Christiansen, N.A.; Green, T.J.; Fryirs, K.A.; Hose, G.C. Bacterial communities in peat swamps reflect changes associated with catchment urbanisation. *Urban Ecosyst.* 2022, *25*, 1455–1468. https://doi.org/10.1007/s11252-022-01238-3.
- 64. Rakitin, A.L.; Begmatov, S.; Beletsky, A.V.; Philippov, D.A.; Kadnikov, V.V.; Mardanov, A.V.; Dedysh, S.N.; Ravin, N.V. Highly Distinct Microbial Communities in Elevated Strings and Submerged Flarks in the Boreal Aapa-Type Mire. *Microorganisms* **2022**, *10*, 170. https://doi.org/10.3390/microorganisms10010170.
- Aksenov, A.S.; Shirokova, L.S.; Kisil, O.Y.; Kolesova, S.N.; Lim, A.G.; Kuzmina, D.; Pouillé, S.; Alexis, M.A.; Castrec-Rouelle, M.; Loiko, S.V.; et al. Bacterial Number and Genetic Diversity in a Permafrost Peatland (Western Siberia): Testing a Link with Organic Matter Quality and Elementary Composition of a Peat Soil Profile. *Diversity* 2021, 13, 328. https://doi.org/10.3390/d13070328.
- 66. Serkebaeva, Y.M.; Kim, Y.; Liesack, W.; Dedysh, S.N. Pyrosequencing-based assessment of the bacteria diversity in surface and subsurface peat layers of a northern wetland, with focus on poorly studied phyla and candidate divisions. *PLoS ONE* 2013, *8*, e63994. https://doi.org/10.1371/journal.pone.0063994.
- 67. Kulichevskaya, I.S.; Pankratov, T.A.; Dedysh, S.N. Detection of representatives of the Planctomycetes in Sphagnum peat bogs by molecular and cultivation approaches. *Microbiology* **2006**, *75*, 329–335. https://doi.org/10.1134/S0026261706030155.
- Feng, H.; Guo, J.; Peng, C.; Ma, X.; Kneeshaw, D.; Chen, H.; Liu, Q.; Liu, M.; Hu, C.; Wang, W. Global estimates of forest soil methane flux identify a temperate and tropical forest methane sink. *Geoderma* 2023, 429, 116239 https://doi.org/10.1016/j.geoderma.2022.116239.
- 69. Bräuer, S.L.; Basiliko, N.; Siljanen, H.M.P.; Zinder, S.H. Methanogenic archaea in peatlands. *FEMS Microbiol. Lett.* 2020, 367, fnaa172. https://doi.org/10.1093/femsle/fnaa172.
- 70. Shcherbakova, V.; Yoshimura, Y.; Ryzhmanova, Y.; Taguchi, Y.; Segawa, T.; Oshurkova, V.; Rivkina, E. Archaeal communities of Arctic methane-containing permafrost. *FEMS Microbiol. Ecol.* **2016**, *92*, fiw135. https://doi.org/10.1093/femsec/fiw135.
- 71. Juottonen, H. Archaea, Bacteria and Methane Production along Environmental Gradients in Fens and Bogs. Ph.D. Thesis, University of Helsinki, *Helsinki*, Finland, 2008.
- 72. Korzhenkov, A.A.; Toshchakov, S.V.; Bargiela, R.; Gibbard, H.; Ferrer, M.; Teplyuk, A.V.; Jones, D.L.; Kublanov, I.V.; Golyshin, P.N.; Golyshina, O.V. Archaea dominate the microbial community in an ecosystem with low-to-moderate temperature and extreme acidity. *Microbiome* **2019**, *7*, 11.

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.