



# Article Changes in the Microbiological Properties of Soils along the Gradient of the Altitude Zone of Mount Kivaka in Eastern Fennoscandia, Russia

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Abstract: This study was conducted on the territory of the national park Paanayarvi, located in the taiga zone of the European north. The altitude zone common in the territory of the national park is up to 350 m above sea level. The purpose of this work is to study the microbiological and biochemical properties of soils formed under conditions of a gradient of altitude zonation. This work was performed for the first time in this territory. Based on the fatty acid composition of the cell walls of microorganisms, the composition and structure of the microbial community were determined by chemato-mass spectrometry. The dominant microbocenosis of soils of undisturbed territories was revealed. Changes in prokaryotes and microscopic fungi in the gradient of the altitude zone occur in different directions, which is consistent with the work of other researchers. The results suggest that the formation of microbocenosis of soils located in different conditions of the phytocenotic environment depends on the location of the site relative to the height. The latter determines the flow of solar energy into the ecosystem and the hydrothermal regime of soils. The data obtained can be used in monitoring global climate changes, will become the basis for the formation of a general conceptual basis for the functioning of microbial communities of soils of low-mountain landscapes.

**Keywords:** Eastern Fennoscandia; mountain; soils; chemato-mass spectrometry; fatty acid composition; microbial communities

## 1. Introduction

The soils of high-altitude territories are of great importance in the general soil fund of the entire world, as they are widely distributed, have various properties, and form a soil continuum. Currently, due to global climate change, their properties may be violated, and consequently, they cannot fully perform their ecosystem functions or maintain the homeostasis of the biosphere. There are significant climatic differences along the elevation gradient; warmer conditions form at low altitudes, with increasing altitude conditions becoming colder and wetter [1]. It is interesting to note that the modeling of global circulations for the northern Rocky Mountains predicts the formation of warmer and less dry conditions over the next decades [2,3]. In this regard, the study of the current state of soils is important for understanding the soil-forming processes taking place in the future. Changes in soil properties in the gradient of the altitude zone will affect the microbiological properties. In the territory of Eastern Fennoscandia, low-mountain landscapes are common, the soils of which differ in a variety of properties, low buffer capacity, and anthropogenic impact [4]. Previous work performed in this area has indicated that when moving to the top of the mountain, vegetation changes, becomes more of the same type, and acquires the features of vegetation of the tundra zone [5]. Changes in soil properties occur in the direction of inhibition of the podzol-forming process, accumulation of litter, and changes



**Citation:** Medvedeva, M.V.; Bakhmet, O.N. Changes in the Microbiological Properties of Soils along the Gradient of the Altitude Zone of Mount Kivaka in Eastern Fennoscandia, Russia. *Forests* **2022**, *13*, 849. https:// doi.org/10.3390/f13060849

Academic Editors: Natalia Manucharova, Evgenia Blagodatskaya, Lev Pozdnyakov and Elena V. Demkina

Received: 7 May 2022 Accepted: 27 May 2022 Published: 29 May 2022

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**Copyright:** © 2022 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/). in the microelement composition of soils. Thus, colder environmental conditions have an adverse effect on the biotic component of forest ecosystems. However, the question remains open as to whether there are drastic changes in the microbial community in the soil formed under conditions of a low elevation difference, and whether microorganisms are indicators of environmental conditions at the highest sites. In a large volume of works devoted to the study of the relationship between the change in the state of the biota and the altitude zone, Zhao et al. changes in microbiological parameters in the gradient of the mountain landscape were reported [6]. According to his data, there is a large variability of microbiological indicators in hydromorphic soils. Another study reported in more detail that soil microorganisms formed at the foot of the mountain have more favorable conditions for their development [7]. As is known, in the summer, the upper organogenic horizons of forest soils (O) dry up. This can have an impact on the growth of plants, which are the "conductors" of the microbiological activity of soils. "Chronic water stress" can become one of the reasons for a decrease in microbiological activity [8], it will smooth out the overall picture of a sharp change in the gradient of temperature-humidity and altitude microbiological indicators of soils.

The rearrangement of the microbial community toward the dominance of microscopic fungi in areas located on high relief elements is associated with a change in the fall of plants entering the ecosystem. Xu et al. assumed that the spatio-temporal regularity of temperature and humidity changes is associated with altitude [9].

It is possible to somewhat expand the idea that height is a key component that regulates plant growth [10,11]. Height also regulates the development of microorganisms in the soil, while the physiological or ecological-trophic plasticity of microorganisms can be considered as a means by which the microbocenosis adapts to the heterogeneity of the edaphic conditions of low- and high-altitude landscapes [12]. However, it is not entirely clear how the deterioration of soil properties and changes in microbial communities affect the overall functional stability of the soil. Stability includes both stability, i.e., the ability to withstand disturbance or stress, and stability, i.e., the ability to recover to levels preceding the disturbance [13]. It has been suggested that the functional stability of the soil is primarily due to its inherent functional redundancy present in microbial diversity [2,13,14]. This hypothesis is referred to as the "starting hypothesis of biodiversity" [15,16] and was originally proposed for microorganisms [2,17].

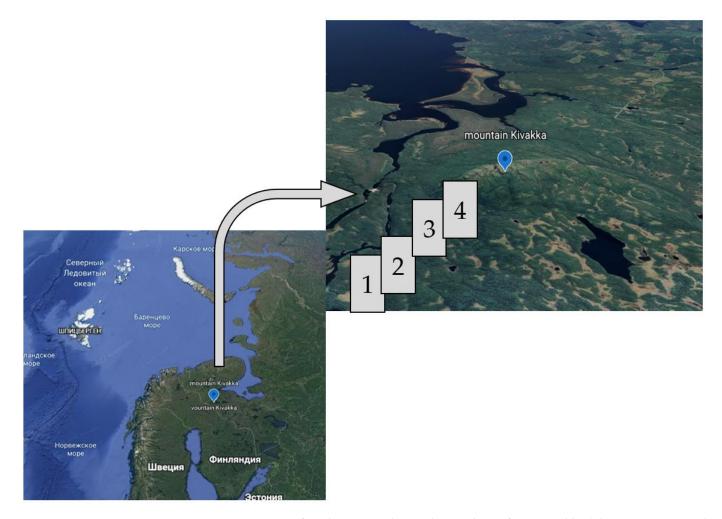
In mountainous conditions, psychrophilic microorganisms develop, whose reproductive survival strategy is aimed at forming adaptations to low temperatures, a short period of sunny days, and low partial pressure. The article deals with the issue of changing the composition of the microbial community of soils located in the gradient of the altitude zone. The analysis of the microbial community of soils was carried out based on the fatty acid composition of the cell walls of microorganisms, which are a fingerprint of their individuality and an indicator of taxonomic affiliation [8,18,19]. It is assumed that microscopic fungi will prevail in the microbial community of soils at the top of the mountain, the hydrolytic enzymatic complex of which is aimed at converting difficult-to-hydrolyze substrates and they are less dependent on climatic jumps. In order to test the hypothesis: (1) The ecological and trophic structure of the microbial community of soils formed in the conditions of the low-mountain landscape of Eastern Fennoscandia was established; (2) The composition of the microbial community of soils of the studied altitude gradient was determined; (3) Catalase activity was established in soils located along the gradient of the altitude zone. The obtained data can be used in monitoring global climate changes and they can become the basis for the formation of a general conceptual basis for the functioning of microbial communities of soils of low-mountain landscapes. The study was conducted for the first time. There is no doubt that the data obtained can be used to monitor the soils of not only Fennoscandia, but also the biosphere.

## 2. Materials and Methods

# 2.1. Study Area

The work was performed in the north of Karelia (Figure 1). The study was performed on one of the slopes of Mount Kivakka, which is located on the territory of the national park (NP) Paanayarvi. This site was chosen because of the presence of vertical zonality of vegetation, rather contrasting zones between zones, in addition to the formation of three different ecosystems. The latter are located close to each other, which allows for simultaneous research. Four ecosystems were identified along the elevation difference of 208–470 m a.s.l. were as follows:

- taiga forest ecosystem (TF),
- forest of mountain (FM),
- mixed forest (MF), boundary between taiga forest and forest mountain
- forest tundra, (FT), subgoltsy zone (Table 1).



**Figure 1.** Location of study sites on the southwest slope of Mt. Kivakka (The European Nowth, Russia: 1- Taiga forest, 2- Forest of mountain, 3- Mixed forest, 4- Forest tundra Photo taken from Google Earth.

Altitude m a.s.l.	Soil Type (WRB, 2015)	Dominant Vegetation	Ash, %	C/N	P %
208	Skeletic Albic Podzol	Taiga forest (TF) Picea abies, Vaccinium myrtillus, Avenella flexuosa (L.) Drej., Gymnocarpium dryopteris (L.) Newm., Linnaea borealis L., Luzula pilosa (L.) Willd., Maianthemum bifolium (L.) F. W. Schmidt, Melampyrum pratense L., Vaccinium vitis-idaea L., Pleurozium schreberi (Brid.) Mitt. (40%), Hylocomium splendens (Hedw.) Schimp.	8.2	35.8	0.09
213	Skeletic Histic Podzol	Forest of mountain (FM) Picea abies, Vaccinium myrtillus, Vacinium vitis-idaea, Pleurozium schreberi, Sphagnum	6.6	27.1	0.08
450	Hyperskeletic Entic Podzol	Mix forest (MF) Betula czerepanovii, Salix lapponum L., Sorbus aucuparia, Vaccinium myrtillus, Empetrum hermaphroditum Hagerup, Pleurozium schreberi, Hylocomium splendens, Dicranum	11.4	27.5	0.11
470	Hyperskeletic Albic Podzol	Forest tundra (FT) Picea obovata, Pinus sylvestris L., Betula czerepanovii, Betula nana L., Salix phylicifolia L., Empetrum hermaphroditum, Vaccinium myrtillus, Vaccinium uliginosum L., Arctous alpina (L.) Niedenzu, Pleurozium schreberi, Cladonia stellaris (Opiz) Pouzar & Vezda, Dicranum, Juncus trifidus L., Loiseleuria procumbens (L.) Desv.), Arctous alpina, Empetrum hermaphroditum, Lycopodium lagopus (Laest. ex Hartm.) Zinserl. ex Kuzen., Pinguicula villosa L. и др.)	4.2	29.5	0.12

**Table 1.** Characteristics of sites and soils of taiga forest (TF), forest of mountain (FM), mixed forest (MF), and forest tundra (FT) located along the southwest slope of Mt. Kivakka (208470 m a.s.l.).

It is important to emphasize that the studied sites are located on the territory of the Paanayarvi National Park, therefore they were not subject to anthropogenic influence.

The area of the NP Paanayarvi is characterized by the complicated geological structure, because bedrocks (crystalline basement) are represented by archaean gneisses, granitegneisses, amphibolites, and the deceased. Early Proterozoic metamorphic terrigenous and volcanic rocks, marble, and intrusive massifs of different compositions (including the massif of mafic and ultramafic rocks of Kivakka Mountain) [20,21]. The plants that dominate each site are presented in Table 1. The table is compiled based on data published in earlier works [5]. The climate of the area is extreme, as it is generally characterized by a short growing season (the frost-free period lasts 100 days), low air temperature (the number of days with an air temperature above 10 °C is 70–90 days), high humidity, with maximum precipitation occurring in summer. According to the conditions of soil heat supply, the area is moderately cold, and the average soil temperature in July is up to 15.5 °C.

As noted above, a detailed description of the natural and climatic features of the site, geology, and vegetation in addition to morphological, physical and chemical properties of soils were published in earlier works [4,5].

The soils were classified as Podsol, an important diagnostic criterion in the alphahumus process [22]. Detailed characteristics of soils are presented in a referenced study [4]. In this paper, the analysis of the state of the microbial component of soils formed under conditions of vertical zonation is performed.

#### 2.2. Soil Sampling and Microbiological Analysis

On each test area, plots were selected regardless of the location of the trees, so they were placed both under the crown and between the trees ("window"). At each site, 40 random soil cores were collected from 0 to 5 cm depth (horizon O) and pooled to form one composite sample. The soils were selected according to the recommendations of the International Co-operative Programme on Assessment and Monitoring of Air Pollution [23].

The selected soil samples were packed in sterile bags and transported to the laboratory as quickly as possible. In the laboratory, fresh soils were dried in air at 220 °C, then sifted and used for analyses [24].

In order to determine the qualitative composition of microbocenoses of the litter of the studied soils, the fatty acid composition of microorganisms was analyzed using chromatography-mass spectrometric analysis (GC-MS). It is based on the high-precision determination of fatty acid markers of cellular lipids of microorganisms, which are subsequently used for chemotaxonomic purposes [25,26]. The use of the computational method allows us to determine the composition of the microbial community not only qualitatively, but also quantitatively [26,27]. Studies of the fatty acid composition were performed on the HP-5985B chromatography-mass spectrometer (Hewlett-Packard, Palo Alto, CA, USA). The quadrupole mass spectrometer with a mass range of 2–1000 aem has a resolution of 0.5 aem in the entire operating range. Ionization occurred by electrons of 70 eV. The sensitivity of the device is 1 ng for methyl stearate in a continuous scanning mode and 10 pg in selective ion mode. For chromatographic separation of the sample, a capillary column of fused quartz with a length of 25 m and an internal diameter of 0.2 mm was used. The stationary phase was Ultra-1 "Hewlett-Packard" with a layer thickness of 0.32 microns. Chromatography was performed in the temperature programming mode from 50 to 320 °C at a speed of 5 degrees/min. The temperature of the injector and interface was 250 °C. Lipids were extracted from the sample using the Folch method with a mixture of chloroform–methanol–water. 5 mL of the mixture was added to the sediment suspension (3 g) and kept at room temperature for 1.5 h, twice initiating extraction on a Vortex vibrator. After extraction, the mixture was centrifuged at 3000 rpm. The supernatant was separated and water was added until a biphasic system was obtained. The lower chloroform phase containing the amount of lipids to kaolin, was separated with a micropipette and dried. The extraction of the fatty acid fraction was performed by acid methanolysis in 4.5N HC1 in dry methanol for 1.5 h at a temperature of 70 °C. After the reaction, the formed methyl esters of fatty acids were extracted with hexane, and the extract was dried and processed in 20 µL No. 0–6 is -(triethylsilyl)trifluoroacetamide to produce volatile derivatives of oxy acids.  $4 \mu L$  of the reaction mixture was injected into the chromatograph injector for analysis. The analysis was performed in two stages: in the mode of continuous full scanning of the sample substances eluted by the chromatograph, and in the mode of selective ions (mass fragmentography). The second stage was required to measure the concentration of minor components of the fatty acid composition of biomass and was performed according to a specially compiled program that allows recording the concentration of specific ions of marker substances of microorganisms at the right time, and bypassing the intense chromatographic peaks of the leading microorganisms of the community and the nonspecific biological background. All analyses were performed three times.

Catalase activity was determined by the gasometric method, which allows measurements of oxygen release during the decomposition of hydrogen peroxide by catalase, starting from the moment of the first mixing of reagents.

#### 2.3. Statistical Analysis

Statistical analysis was performed using the Statistica 10 software. Agglomerative hierarchical cluster analysis (ANS) and canonical correspondence analysis (CSA) were applied to obtain information on the dependence of environmental and microbiological indicators within the test sites under study.

### 3. Results

To analyze the changes in the number of microbocenosis of soils formed under conditions of a high-altitude gradient, it is necessary to consider the specifics of its formation in the whole studied biogeocenotic complex. During the study, bacterial communities of the upper horizons of soils formed in the conditions of a low-mountain landscape were reconstructed and described. The results indicated that the edifiers of the studied soils were the Acetobacter-Rhodobacter group, Caulobacter, Bacillus sp., Corynebacterium sp., Rhodococcus equi Rhodococcus terrae, Streptomyces-Nocardiopsis, Ruminococcus sp., Bradyrhizobium, Mezorhizobium Micrococcus/Arthrobacter sp., and Aspergillus sp. (Table 2). These microorganisms were present in the soils of all the studied sites and their numbers were high. Pseudomonas fluorescens, Sphingomonas capsulata, Xanthomonas sp., Acetobacterium sp., Butyrivibrio, Pseudonocardia sp., WolInella-Acholeplasma-Roseomonas-Burkholderia, and Nocardia carnea were also present at all sites, but their numbers were lower, and they were the co-dominant species of edifiers in the microbocenosis of the studied soils. A high number of microorganisms of individual biotypes was revealed for Caulobacter and *Riemirella*, of which the number was more than 150 cells/ $g \times 10^6$  in soils. A high number of *Rhodococcus equi* bacteria was noted, the number of which was higher than 50 cells/ $g \times 10^6$ in soils. Representatives of different biotypes of Acetobacter-Rhodobacter group, Bacillus sp., Corynebacterium sp., Nocardiopsis, Streptomyces-Nocardiopsis, Bradyrhizobium, and Mezorhi*zobium* were inferior to them in number, but they occupied not the lowest positions; their numbers varied within 10–20 cells/g  $\times$  10<sup>6</sup> in soils. For the remaining microorganisms, the number was below 10 cells/g  $\times$  10<sup>6</sup> in soils, while their variation in the soils of individual sites was noted. For example, the abundance of *Clostridium pasteureanum* varied from 0 to 9.50 and *Propionibacterium freudenreichii* varied from 0 to 6.60 cells/g  $\times$  10<sup>6</sup> in soils.

**Table 2.** The number of the most important microorganisms in the soils of the high-altitude gradient of Mount Kivakka of Eastern Fennoscandia (cells/g  $\times$  10<sup>6</sup>).

<b>Biotypes of Microorganisms</b>	TF	FM	MF	FT
Acetobacter-Rhodobacter group	6.05	8.52	11.49	9.36
Aeromonas hydrophila	0.00	39.50	14.94	8.61
Agrobacterium radiobacter	3.56	0.00	4.11	1.86
Caulobacter	30.66	173.12	52.74	0.72
Pseudomonas fluorescens	4.01	4.66	3.54	2.58
Pseudomonas putida	0.54	0.89	0.91	6.90
Pceudomonas vesicularis	0.54	0.72	0.61	0.00
Methylococcus/Clostridium sp.	9.50	0.00	0.00	8.71
Sphingobacterium spiritovorum	0.35	1.26	0.94	0.48
Sphingomonas adgesiva	0.81	1.98	1.05	0.84
Sphingomonas capsulata	0.83	2.09	2.25	1.93
Xanthomonas sp.	1.64	1.46	1.53	1.46
Specific iron-reduction bacteria	0.36	0.00	0.19	0.15
Acetobacterium sp.	2.02	2.05	1.04	0.37
Bacillus subtilis	2.60	2.70	4.78	3.07
Bacillus sp.	10.56	9.24	11.95	5.28
C.pasteureanum	9.50	0.00	0.00	8.71
Ċ.perfringens	0.10	0.04	0.04	0.05
Eubacterium lentum	1.39	0.97	1.00	0.82
Clostridium OPA *	1.82	0.00	0.33	2.46
Butyrivibrio 1-4-11	0.00	0.12	0.49	0.67
Butyrivibrio 7S-14-3	3.48	4.61	4.21	2.46
Bifidobacterium sp.	0.45	0.00	0.00	0.16
Corynebacterium sp.	6.47	32.97	9.18	1.08
Mycobacterium sp.	0.00	0.00	0.00	0.00
Микобактерии по 10Ме18	15.39	0.00	0.93	1.64
Nocardiopsis	10.83	20.49	2.34	0.00
Propionibacterium sp.	9.09	2.04	1.75	0.00
Propionibacterium freudenreichii	6.60	0.00	0.00	0.00
Pseudonocardia sp.	2.94	2.26	3.40	2.14
Rhodococcus equi	54.34	31.02	9.46	3.89
Rhodococcus terrae	8.55	4.72	6.01	6.41

Biotypes of Microorganisms	TF	FM	MF	FT
Streptomyces-Nocardiopsis	13.19	13.21	21.31	7.66
Bacteroides fragilis	0.26	0.00	0.00	0.00
Bacteroides hypermegas	0.05	0.05	0.06	0.06
Bacteroides ruminicola	0.36	0.46	0.54	0.42
<i>Cytophaga</i> sp.	0.41	0.73	1.33	1.33
Ruminococcus sp. + **	6.22	4.26	5.00	7.07
WolInella-Acholeplasma-Roseomonas-Burkholderia	1.62	3.75	4.41	2.40
Micromonospora sp.	2.74	1.75	0.99	1.17
Chlamydia sp.	0.00	0.00	0.00	0.00
Bradyrhizobium, Mezorhizobium	14.14	12.98	4.44	3.66
<i>Micrococcus/Arthrobacter</i> sp.	7.90	8.03	6.25	3.70
Eubacterium sp.	0.20	0.17	0.15	0.03
Nocardia carnea	3.89	5.79	7.33	5.46
Actinomadura roseola	1.02	1.00	4.20	3.20
Aspergillus sp.	4.01	20.81	7.37	10.43
Enterobacteriaceae (семейство)	2.08	0.00	0	0
Butyrivibrio 1-2-13	3.11	0.58	0.79	0.32
Enterococcus	0.49	1.24	0.85	0.56
Riemirella	0.00	10.10	7.79	6.2
Ochrobactrum	0.83	1.03	3.81	0.47
The amount	267.5	433.4	228	137
Fungy on 18:2, mkg/g	226	524	257	401
Yeasts on 10h16, cells/g $\times$ 10 <sup>6</sup>	0.06	0.02	0.02	0.01
Protozoa	0.00	21.00	8.75	6.98
Eucariotes	0.00	0.00	0.00	0.01
Planta	3.97	11.31	6.79	3.80

Table 2. Cont.

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Clostridium OPA \* (C. omelianskii, C. Pasterianum, C. acetobutyricum). Ruminococcus \*\*/Glomus/Scutellospora AMF/Acetobacterium/Specific iron-reduction bacteria from Lavly.

The most represented group was in the microbial community of Proteobacteria and Actinobacteria, while Bacteroidetes and Firmicutes were inferior in number in the microbial community (Table 3).

**Table 3.** Taxonomic structure of reconstructed microbial communities in soils along an elevation gradient in Mount Kivakka of North Karelia (%).

$\mathbf{N}^{\circ}$	Bacterial Genus	Research Sites, $N^{\circ}$			
	Dacterial Genus	TF	FM	MF	MF FT
	Pro	oteobacteria			
1	Acetobacter	3.14	2.50	6.75	10.38
2	Aeromonas	0.00	11.61	8.78	9.55
3	Agrobacterium	1.85	0.00	2.41	2.07
4	Caulobacter	15.91	50.90	30.98	0.80
5	Methylococcus	4.93	0.00	0.00	9.66
6	Pceudomonas	2.64	1.84	2.97	10.51
7	Sphingomonas	0.85	1.20	1.94	3.07
8	Xanthomonas sp.	0.85	0.43	0.90	1.62
9	Specific iron-reduction bacteria	0.19	0.00	0.11	0.16
	F	irmicutes			
10	Acetobacterium	1.05	0.60	0.61	0.41
11	Bacillus	6.83	3.51	9.83	9,26
12	Clostridium	5.93	0.01	0.22	12.44
13	Eubacterium	0.72	0.28	0.58	0.91

N°	Bacterial Genus	Research Sites, $N^{\circ}$			
1	Dacterial Genus	TF	TF FM MF		FT
	А	ctinobacteria			
14	Bifidobacterium	0.23	0.00	0.00	0.18
15	Butyrivibrio	1.80	1.39	2.76	3.47
16	Corynebacterium	3.36	9.69	5.39	1.20
17	Propionibacterium	8.14	0.60	1.03	0.00
18	Pseudonocardia	1.53	0.66	2.00	2.37
19	Rhodococcus	32.64	10.51	9.09	11.43
20	Streptomyces	6.85	3.89	12.52	8.50
	I	Bacteroidetes			
21	Bacteroides fragilis	0.14	0.00	0.00	0.00
22	Bacteroides hypermegas	0.02	0.02	0.04	0.07
23	Bacteroides ruminicola	0.19	0.14	0.32	0.47
24	<i>Cytophaga</i> sp.	0.22	0.21	0.78	1.47
Total ba	acterial cells number $\times 10^6$	192.68	340.11	170.24	90.17

Table 3. Cont.

Catalase activity in the studied soils was not high; it varied in the range of 2.5–4.5 mmlO2/5 min. (Figure 2).

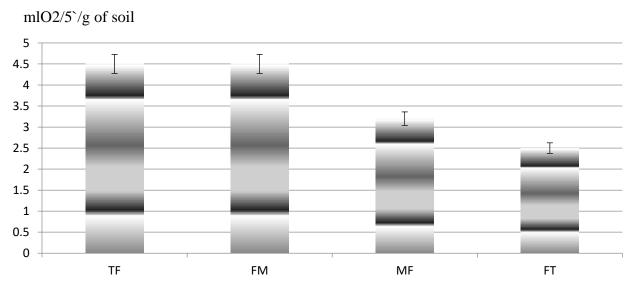


Figure 2. Change in catalase activity in soils gradient of the altitude zone of Mount Kivakka.

The change in the number of soil microorganisms located in the gradient of the altitude zone had certain multidirectional general trends. First, there was a decrease in the total bacterial population from 267 to 129 cells/g × 10<sup>6</sup> in soils (Table 2). At the same time, there was a rearrangement of the microbocenosis of prokaryotes. The increase of representatives of Butyrivibrio 1-4-11, Cytophaga sp., Nocardia carnea, and Riemirella in soils was revealed as they moved to the top of the mountain. On the contrary, against the background of an increase in these biotypes, a decrease in the number of Caulobacter, Bacillus sp., Corynebacterium sp., Nocardiopsis, Rhodococcus equi, Streptomyces-Nocardiopsis, Bradyrhizobium, and Mezorhizobium was noted in soils located in the gradient of altitude zone. It should be noted that microscopic fungi were observed to increase from 226 to 401 cells/g × 10<sup>6</sup> in soils as the altitude gradient increased. The number of yeasts in soils decreased from 0.06 to 0.01 cells/g × 10<sup>6</sup> in soils when moving to the top of the mountain.

An increase in the prokaryote complex of representatives of Proteobacteria, Firmicutes, and Bacteroidetes was noted in soils as they moved to the top of the mountain. Concurrently, a decrease in their number was detected for Actinobacteria (Table 2).

A decrease in catalase activity in the upper soil horizon was noted as we moved to the top of the mountain (Figure 2).

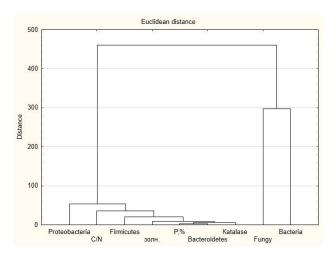
#### 4. Discussion

The reconstruction of fatty acid profiles of microorganisms in the studied soils allowed us to establish the features of the structure of the microbiocenosis and its functional activity. The study revealed a trend of monotonous changes in the biodiversity of soil microbocenosis and its functional activity in soils formed in various ecosystems along the gradient of the altitude zone of Mount Kivakka. There was no sharp jump in the changes in the studied indicators, which may be due to a small difference in heights in the observed space of environmental factors. It can also be assumed that this is the leveling effect of microorganisms when they arrive during the melting of snow, where they are in a state of anaerobiosis [28]. A humid climate and stagnant cooling during the period of precipitation may also have an effect [29]. Many researchers have seen a change in the diversity of the microbial community of soils located at high altitudes [7,9,11]. They explained this precisely by the existence of natural and climatic differences in mountain ecosystems. Our research and the work of other scientists once again emphasize the importance of the choice of ongoing research and the choice of sites for analysis. There is no doubt that the interval of placement of sites for research is also of great importance. Narrow-scale altitude gradients, which were present in this work, can provide an accurate description of changes in the structure of the microbial community, compared with a large height difference. The latter, as the works indicate, are quite informative and interesting precisely from the point of view of establishing changes in global biospheric processes and the impact of anthropogenic impacts on macroecosystems [30,31].

In the conducted study, a clear clustering of the studied microbiological and biochemical parameters and chemical properties of soils (C/N ratio, ash content, and P content) was established (Figure 3). The existence of a separate cluster of prokaryotes-fungi and all other indicators was revealed. This does not contradict the general concept of the formation of a microbial community of soils under conditions of insufficient heat (solar energy); those biotypes whose adaptive potential is high enough to develop in adverse environmental conditions survive [32–34]. Microscopic fungi, as is known, can be main environmental agents and edifiers of soil conditions. Unlike bacteria, they have a high set of enzymes that regulate the processes of transformation of organic matter. As a result of their activity, the necessary metabolites are formed for other participants in this soil-forming process [32,35]. The combination of chemical (ash content, P content) and microbial-biochemical parameters (catalase activity, the number of Bacteroites) into one cluster may be associated with their participation in synthetic processes when ash elements activate enzymes for the synthesis of glycerophospholipids [36]. The latter are structural analogues of sphingolipids, which comprise up to 20% of the cell wall of representatives of taxa of the Bacteroites type. We must not forget that there are complex interactions in the microbial community, when there is a fierce struggle for a substrate between prokaryotes and eukaryotes, those whose secondary metabolites are able to suppress competitors survive [37].

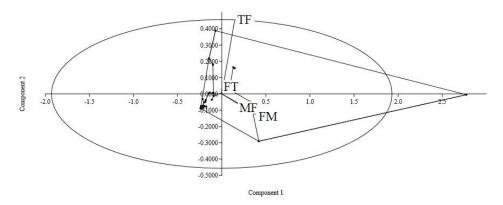
The microbiological properties of soils depend on various factors. One of the most important is the soil pH. The influence of soil pH on the composition and structure of the microbial community of soils was noted in [38–41]. In our studies, there was no sharp change in the acid-base properties of soils [4]. In this regard, it is impossible to speak unequivocally about the influence of this chemical indicator on the microbial community of the studied soils. As is known, the upper horizons of forest soils (areas in the TF and FM zone) undergo periodic drying in the spring-summer period, which can lead to a sharp decrease in the microbiological and biochemical parameters of soils. The appearance of Spagnum sp. in the plant community, which is a good accumulator, can somewhat neutralize the effect of the thermal factor and reduce the acid load on the microbiocenosis [42]. The accumulation of carbon occurs in hydromorphic soils and its mineralization is reduced [43]. The dependence of microbiological indicators on the carbon content was

noted in a previous study [44]. The authors emphasize the close association of microbial indicators from the content of organic carbon. The effect of temperature on the respiration of soils localized in the gradient of altitudinal zonality was also established, which indicates the rearrangement of soil microbocenosis and participants in gas formation [45]. The data obtained are consistent with the work of Shen et al., in which the variation of oligotrophic acidobacteria in soils was indicated depending on the altitude gradient [35]. Generally, the microbiological indicators of soils varied at different sites, reflecting rather heterogeneous conditions that are formed under conditions of a gradient of heights.



**Figure 3.** The data of cluster analysis of the studied microbiological and chemical indicators of soils in the gradient of the altitude zone of Mt. Kivakka.

The canonical analysis of the data obtained indicated a clear separation of the ecosystem of the taiga zone (TF), that is, a site that is located in "classical" taiga conditions (Figure 4). The tundra zone (FT) is also highlighted, which indicates the formation of specific conditions for the development of microorganisms. The sites located in the transition zone of the ecotone (MF, FT) may reflect an unstable environment for the development of the biotic component of soils, the influence of not only the altitude gradient, but also a complex of environmental factors [15]. The change of plants in different zones can also change the composition of the soil microbiocenosis [12]. Plants can act as "drivers" of directed changes in the microbiological activity of soils [46]. It should be noted that the "tail" of the presented graph forms the microbe-hydrophile Caulobacter. This is not accidental; in transitional ecotopic conditions, a more favorable edaphic environment develops for their development, while in the tundra zone, crystallization processes are possible, and consequently, the mobilization of water molecules in the soil.



**Figure 4.** Canonical correspondence analysis of the associations between different form of microorganisms and location of soils.

The influence of temperature on the decomposition of organic matter against a background of low temperatures can manifest itself directly and indirectly in the gradient of the altitude zone [47]. It is possible to reduce the diversity of microorganisms in the soils of the gradient of the altitude zone, which leads to inhibition of the processes of transformation of organic matter. This is confirmed by a decrease in catalase activity in soils. As is known, this enzyme regulates the decomposition of hydrogen peroxide, toxic to microorganisms, into water and oxygen. The genes encoding this enzyme are found in groups of microorganisms that are far away in the evolutionary series, whose ecological plasticity to environmental factors is different. It can be assumed that the rearrangement of the microbial community contributed to the elimination/reduction of the number of precisely those groups of microorganisms that are donors of this enzyme, for example, Pseudomonas sp., Specific iron-reduction bacteria, Baccilus sp., Corinebacterium sp., and others. It is also impossible to deny the influence of endogenous factors (nutrient regime of soils, changes in the composition of humic acids) on the formation of the enzymatic pool of soils [17]. This can also be argued about the possible participation of microorganisms adsorbed on solid rock particles [48].

Even though the data obtained are consistent with the data of other researchers [6,7,9] and, as noted above, general theoretical ideas about the formation of a microbial community in soils in an aggressive environment, there are some interesting, unexplained, and contradictory facts. Thus, an increase in the number of Cytophaga sp. was noted in the soils, as we moved to the top of the mountain. This microbe is known to destroy cellulose well, but it is limited in the utilization of amino acids [49]. At low temperatures, its cellulolytic abilities are not fully manifested and they do not work, but there is much of it in the soil. It can be assumed that it utilizes simple carbohydrates [50], which are abundantly saturated with the upper horizons of soils located in conditions of lack of heat, and thus retains a high abundance.

The obtained data gave a clear picture of the changes in the microbial community of soils in the conditions of a low-mountain landscape [51]. However, the answer to the question of what the root cause of the change in the microbiological activity of soils in the gradient of the altitude zone is has not yet been confirmed. One can agree with the works in which the influence of plants and microorganisms themselves on soil-chemical processes is noted [45,52,53]. The latter, in turn, determine the structure of the microbial community.

## 5. Conclusions

The altitude gradient in the mountains is a unique "open laboratory" for studying ecological hypotheses and analyzing the expected consequences of the global warming climate [46]. Our study indicates that the climatic factors (altitude zone in our case) have a greater influence on the structure of the microbial community of the soil than on the physical and chemical properties of the soil. Nevertheless, the change in the microbial community toward a decrease in prokaryotes in areas higher located was at the level of the trend. Eukaryotes were dominant at all sites, which can adapt to colder conditions and can be considered cosmopolitans. In addition to the specific features of the microbial community at each individual site, there were also common features that are characteristic of the soils of the taiga zone. We discovered an increase in representatives of Bacillus, which affect the pH of soils, but it would be beneficial to test this assumption already in model field experiments. The study did not find a sharp decrease in the number of microorganisms studied by large taxa. From a soil-chemical point of view, the different supply of solar energy to the ecosystem can have a versatile effect on the organic matter of soils, which serves as a substrate for the development of microorganisms. Therefore, it can be assumed that microbial transformation of organic matter in darker, humus soils will occur more intensively in comparison with soils of colder places of their formation. Although this was not the topic of the article, it is believed that it will be an interesting research question in future work. The mechanisms of microbial community formation in the gradient of the altitude zone have yet to be studied, it is not difficult to rock the

mountain "temperature swing" in conditions of anthropogenic impact, but it is difficult to stop, so it is too early to put a point in the study.

Author Contributions: Conceptualization, O.N.B., M.V.M.; methodology, M.V.M.; software, O.N.B.; validation, M.V.M. and O.N.B.; formal analysis, M.V.M.; investigation, M.V.M.; resources, O.N.B.; data curation, M.M; writing—original draft preparation, M.V.M.; writing—review and editing, M.V.M. and O.N.B.; visualization, M.V.M.; supervision, O.N.B.; project administration, O.N.B.; funding acquisition, O.N.B. All authors have read and agreed to the published version of the manuscript.

**Funding:** The work was carried out according to the state assignment of the Forest Institute of the Karelian Scientific Center of the Russian Academy of Sciences.

**Conflicts of Interest:** The authors declare no conflict of interest.

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