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Soil Functional Responses to Natural Ecosystem Restoration of a Pine Forest *Peucedano-Pinetum* after a Fire

Edyta Hewelke ^{1,*} , Ewa Beata Górka ², Dariusz Gozdowski ³ , Marian Korc ⁴, Izabella Olejniczak ⁵ and Anna Prędecka ⁶

¹ Water Centre WULS, Institute of Environmental Engineering, Warsaw University of Life Sciences-SGGW, Nowoursynowska 166, 02-787 Warsaw, Poland

² Department of Biochemistry and Microbiology, Institute of Biology, Warsaw University of Life Sciences - SGGW, Nowoursynowska 166, 02-787 Warsaw, Poland; ewa_gorska@sggw.pl

³ Department of Biometry, Institute of Agriculture, Warsaw University of Life Science, Nowoursynowska 159, 02-776 Warszawa, Poland; dariusz_gozdowski@sggw.pl

⁴ Department of Agricultural Chemistry, Warsaw University of Life Sciences-SGGW, Nowoursynowska 166, 02-787 Warsaw, Poland; marian_korc@sggw.pl

⁵ Institute of Biological Sciences, Cardinal Stefan Wyszyński University in Warsaw, Wóycickiego 1/3, 01-938 Warsaw, Poland; i.olejniczak@uksw.edu.pl

⁶ Faculty of Safety Engineering and Civil Protection, The Main School of Fire Service, Słowackiego 52/54, 01-629 Warsaw, Poland; apredecka@sgsp.edu.pl

* Correspondence: edyta_hewelke@sggw.pl

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Abstract: Progressing climate change increases the frequency of droughts and the risk of the occurrence of forest fires with an increasing range and a dramatic course. The availability of water and its movement within an ecosystem is a fundamental control of biological activity and physical properties, influencing many climatic processes, whereas soil water repellency (SWR) is a key phenomenon affecting water infiltration into the soil system. Focusing on wide-spectrum effects of fire on the soil system, the research was conducted on a pine stand (*Peucedano-Pinetum* W. Mat. (1962) 1973) in Kampinos National Park located in central Poland, affected by severe and weak fires, as well as control plots. The main aim of the study was to examine the regeneration of the ecosystem 28 months after the occurrence of a fire. The effect of SWR and soil moisture content, total organic carbon, nitrogen and pH, and gain an understanding of the environmental conditions and processes that shaped the evolution of the species structure of soil microorganism communities (fungal vs. bacterial) have been examined. The Water Drop Penetration Time (WDPT) test was used to assess spatial variability of SWR in 28 plots. Soil bacterial and fungal communities were analysed by Illumina MISEq using 16S rRNA and Internal Transcribed Spacers 1 (ITS1) regions in six selected plots. After a relatively wet summer, elevated hydrophobicity occurred in areas affected by a weak fire as much as 20 cm into the soil depth. The severe fire and subsequent increase in the richness of the succession of non-forest species contributed to the elimination of hydrophobicity. SWR was more closely linked to the structure and diversity of soil microbial communities than soil physicochemical properties that took place in response to the fire. A statistically significant relationship between the relative occurrence of microorganisms ($\geq 1.0\%$ in at least one of the samples) and SWR was established for the following fungi and bacteria species: *Archaeorhizomyces* sp., *Leotiomyces* sp., *Byssonectria fusispora*, *Russula vesca*, *Geminibasidium* sp., family *Isosphaeraceae* and *Cyanobacteria* (class 4C0d-2, order MLE1-12). Insight into the functional roles of the individual identified microbial taxa that may be responsible for the occurrence of hydrophobicity was also presented.

Keywords: soil water repellency; soil water content; soil microorganisms; fire severity; ecosystem services; climate change

1. Introduction

Progressing climate change is exerting increased pressure on the natural environment. It is expected that an increase in the frequency and intensity of droughts will significantly influence the carbon and water cycles in the Earth's biosphere [1]. We can, therefore, expect significant changes in the functions and services provided by ecosystems particularly abundant in carbon and water.

Accounting for the fact that the most stable sources of fresh water, which are furthermore characterized by the highest quality, are created in forest ecosystems [2], better adaptation to climate change in forest ecosystems deserves special attention. The Global Climate Observing System (GCOS) initiative has defined soil moisture as a fundamental climate variable [3]. In particular, negative processes connected with the drying out of organic substances leads to their mineralization and emission of significant amounts of CO₂ into the environment. At the same time, decreased moisture content along with high temperatures can lead to the phenomenon of soil water repellency SWR [4]. More severe droughts induce a hydrophobic state of the ecosystem, with podzolic soils under forests being particularly prone to drying out and not rewetting [5].

In the context of increasingly frequently occurring hydrological and soil droughts, we can expect to face a growing problem of maintaining the permanence of forest ecosystems. The frequency and scale of fires are continuously increasing and, territorially speaking, also becoming a threat to Northern European countries [6].

The impact of a fire is manifold, being dependent on, among others: its intensity, the time of the year that it occurs, and the incidence rate/frequency [7,8]. The fire itself is controlled by many factors, such as the type and moisture content of the fuel, the temperature and humidity of the air, wind speed and the topography of the terrain [9]. Similarly to the effects of a fire, the restoration of ecosystems after a fire is also influenced by the intensity and frequency of fires, metrological conditions, vegetation type and the physicochemical and biological properties of the soil [10,11].

The effects of fires on the soil are changes in the physical, chemical and biological properties of the soil [9,12]. It is a well-known fact that fires affect the abundance, biomass, activity and diversity of microorganisms [13]. The enzymatic activity of soil decreases due to changes in the quality of organic matter. However, increased pH (due to ash deposition) has been argued as the cause of the greater post-fire increase in the number of bacteria as compared to fungi.

Changes in the soil moisture regime after a fire are difficult to predict due to changes in hydrological and geomorphological processes [14–16] and the occurrence of SWR [17–19]. This is a phenomenon presenting the degree of affinity of the analysed surface to absorbing water. SWR can persist from a few seconds up to a few hours, or even for a longer period of time [20].

Forest fires are an example of an external factor causing SWR and, depending on the temperature, can strengthen SWR, though sometimes reducing it [21–24]. The natural SWR of some forest soils, on the other hand, can lead to a divergent course of fires, especially so-called low fires, and impede firefighting action. Many researchers point to the relationship between pine tree stands releasing significant amounts of waxes and the phenomenon of SWR [25–27]. Microbial activity, especially in the rhizosphere, which impacts hydrophobicity [28], alters hydraulic soil functions. Microorganisms play a crucial role in numerous functional roles in forest ecosystems, including serving as sources and sinks of key nutrients and catalysts of nutrient transformations, acting as the engineers and maintainers of soil structure, and forming mutualistic relationships with roots that improve plant fitness [15]. Sandy soils provide a better habitat for fungi than bacteria because the small particle surface area and pore size distribution make for a poor bacterial habitat [29]. The rhizosphere has also been shown to have higher levels of SWR than bulk soil [30]. According to a study by [31], specific compounds produced by

plant roots have been shown to induce SWR, with the effects also possibly stemming from secondary microbial metabolites which are a product of root exudate decomposition.

SWR generally changes the way water infiltrates and moves through the soil. Decreasing the infiltration of water has a detrimental impact on the retention, habitat and production functions of the soil. Typically, increased surface runoff and erosion [17,32–34] make it impossible to fully take advantage of the retention abilities of the soil, thus increasing its susceptibility to droughts. An irregular wetting front and preferential flow in the soil profile [35–37], due to the faster infiltration of water through privileged flow paths, can lead to the contamination of groundwater. Speedy redistribution of rainwater to deeper layers of the soil also limits its take-up by plants [38,39]. The water repellent areas of soil make their rehydration more complicated and have an indirect influence on deepening the effects of a drought. The ecological role of repellency in promoting the resilience of plant communities and soil carbon stock to wildfire or drought stress in various ecosystems were presented in multiple studies [40–44]. The SWR phenomenon of forest soils can be a significant factor intensifying droughts, especially in the case of light and very light soils.

The above-presented findings indicate that the further development of studies on counteracting droughts and their effects is a condition that must be met if the stability and permanence of forest ecosystems are to be maintained.

Understanding the bio-physical feedbacks on soil as well as the subsequent soil moisture state behaviour and influence on environmental processes together represent a significant challenge [5] for modelling soil functions under impending environmental changes.

Considering the above, the impact of external forces, i.e., the change of forests into areas affected by forest fires can alter the boundary conditions of the system and change the system itself [45]; hence, the identification of the main parameters driving system dynamics is essential for setting up measuring schemes and building comprehensive models that comprise the entire dynamics of a system. According to Robinne et al. [46], the understanding of how ecosystems respond to a fire is essential to managing landscapes where fires are prevalent. The combined risks of changes in fire regimes and the climate have great potential to alter the characteristics of vegetation and dynamics of the ecosystem by altering the balance of species and reducing post-fire regeneration. In order to better adapt to climate change, it is necessary to gain a better understanding of the soil regeneration processes and climate variability on regional as well local scales.

The main aim of the study was to examine the ecosystem regeneration effect on SWR and soil moisture content 28 months after a fire, and better understand the environmental conditions and processes that have shaped the development of the structure and diversity of soil microorganism communities (fungal vs. bacterial). An attempt was made to identify which taxa of fungi and bacteria and their features contributed to the increased phenomena of soil hydrophobicity.

2. Materials and Methods

2.1. Study Area

The research was conducted in the area of Kampinos National Park (KNP), which is located in the Middle Mazovian Lowland in the pre-valley of the Vistula River in central Poland, on which the proximity of the Warsaw metropolitan areas have exerted intense anthropogenic pressure [47]. In the 19th century, massive deforestation occurred here for the needs of settlement and agriculture. The construction of flood banks along the nearest rivers significantly changed the hydrological conditions, eliminating flood plains. The system of drainage ditches, built in the first half of the 20th century, was to fulfil agricultural requirements and did not account for environmental conditions. Intensive drainage, including the drying out of swampy areas, resulted in the permanent lowering of the level of ground waters and impoverishment of ecosystems dependant on water, leading to the partial disappearance of marshy areas and swamps; contributing to even further lowering of the groundwater table are numerous groundwater intakes connected with the urbanization of areas

adjacent to KNP. For a few years now, actions have been taken to increase water retention, which will protect the Kampinos swamps against summer droughts [48]. An unfavourable change in the hydrological conditions in the area of KNP and the effects of global warming have caused an increase in the risk of the occurrence of soil droughts. Additionally, the dominance of pines (*Pinus sylvestris* L.) in the forest areas in KNP stands, i.e., about 69% acc. Szczygielski [49], signifies a particular increase in fire risk.

KNP is considered to be in the highest category of forest fire risk, and fires occurring there make for 50% of all fires in Polish national parks. In 2015, soil drought occurred in nearly all forests throughout Poland [50] and, as a result of the existing weather conditions, the number of noted forest fires came close to the record for the 21st century [51].

The study area was located in the north-eastern part of the KNP (N 52°20′36.67″–N 52°20′25.53″ and E 20°45′49.10″–E 20°46′13.87″). The surface was covered by a plant group of *Peucedano-pinetum*, which varied in age from 60–90 (in the area of active protection), namely young pine stand to 17–200 years (in the area of strict protection), i.e., old pine stand. The late spring fire which occurred in 2015 covered a total area of approximately 11 ha.

2.2. Meteorological Conditions

According to daily meteorological data from the nearest measurement point of the KNP station in Granica (N 52°17′10″ E 20°27′16″ 52°17′10″ N, 73 m a.s.l.), 2017 was characterized by the highest precipitation in the history of the station (1994–2017) [52].

The sum of atmospheric precipitation in the 2017 hydrological year was 742.2 mm, which is 131% of the average annual rainfall of 575.4 mm for the many-year period. The average rainfall for September, the rainiest month in 2017, was 93.5 mm, with a many-year average of 62.4 mm.

For the observation years, the average annual air temperature shows a slight upward trend. In 2017, the thermal conditions of the Kampinos catchment area under study were 0.1 °C below the multi-year average of 8.6 °C.

Starting from the 1994 hydrological year, groundwater levels were measured by piezometers of the KNP network. In 2017, an increase in the characteristic values of groundwater levels was observed. After a series of dry years, i.e., 2002–2006, there were relatively more wet years, i.e., 2007–2014, during which there was a tendency to rebuild groundwater resources. However, this streak was broken by the years 2015 and 2016, both of which were characterized by mild and snowless winters and a relatively unfavourable distribution of rainfall times. Additional details of the meteorological conditions in 2015/2016 and the study area had been published in an earlier work [53]. These two years did not reverse the general tendency, but the levels of groundwater in 2015/2016 were the lowest in the history of measurements after 2003. In the hydrological year of 2017, the average monthly levels of the groundwater table were in the medium and high state zones.

2.3. Soil Description and Soil Sampling

According to the IUSS Working Group WRB [54], the analysed soil was classified as Brunic Arenosol, and soil humus as a moder-mor type. According to Keeley's [55] suggestion, the degree of burnout of the organic layer was adopted as the criterion of fire severity. Almost the entire organic layer was burnt in the central areas affected by the severe fire (CF), whereas in the peripheral areas of the fire (PF), the low severity fire only partially damaged the organic layer [56]. The control plots (C) in the unburnt areas were located 20 m and 40 m away from the border of the fire.

In September 2017, 28 months after the fire, on three sites of varying fire severity in two ecosystems of differing ages of the pine stand, six study sites, with a surface area of 100 m² each, were selected. The topsoil (0–20 cm) was sampled from six randomly selected points for each site, and a pooled sample was prepared. Total organic carbon was measured using a Shimadzu TOC-V analyser with a solid-sample module (Shimadzu TOC 5000 A, Kyoto, Japan) by a non-dispersive infrared method.

Nitrogen levels were determined using the Kjeldahl method (analyser Kjelttec-Tecator). The soil pH in H₂O and 1 m KCl was measured potentiometrically.

The properties of the burned soils and the adjacent unburnt (control) areas are given in Table 1. Based on the Tuckey test analysis of soil properties, it can be observed that the fire severity led to decreased proportions of total organic carbon only in the soil under a young pine stand affected by the severe fire. Other soil properties revealed no differences.

Table 1. Selected chemical properties of soil two years after a fire under young and old pine stands taken from control, peripheral and central fire sites; mean values ($n = 3$) with standard deviation (SD) in brackets. TOC—total organic carbon, N—nitrogen, pH—acidity.

Ecosystem	Site	TOC (%)	N (%)	C/N	pH H ₂ O	pH KCl
Old pine stand	Control	1.31 a (0.34)	0.061 a (0.026)	22.98 a (5.38)	2.87 a (0.14)	3.43 a (0.09)
	Peripheral Fire	1.26 a (0.20)	0.057 a (0.002)	22.17 a (3.34)	2.76 a (0.06)	3.43 a (0.07)
	Central Fire	1.10 a (0.22)	0.058 a (0.003)	18.94 a (2.73)	2.85 a (0.01)	3.48 a (0.16)
Young pine stand	Control	1.13 b (0.13)	0.056 a (0.015)	21.84 a (8.80)	2.94 a (0.01)	3.62 a (0.21)
	Peripheral Fire	1.11 ab (0.12)	0.059 a (0.013)	19.16 a (1.10)	2.97 a (0.10)	3.44 a (0.07)
	Central Fire	0.77a (0.05)	0.050 a (0.005)	15.50 a (2.64)	2.78 a (0.23)	3.20 a (0.15)

Note: different letters refer to statistically significant differences (by Tukey test) between the respective values of soil properties affected by different intensities of fire.

2.4. SWR and SMC Measurements

Previously presented SWR phenomena results during dry summers 2015/2016 [53] were characterized by significant spatial and temporary variability. Keeping the variability of the SWR phenomenon in mind, the assessment of SWR was carried out on 28 sites, 14 plots in burned areas: 6 CF, 8 PF and 14 sites in unburned—control C areas of 100 m². The persistence of SWR in the soil samples was determined for each of the three mineral layers, i.e., 0–5 cm, 5–10 cm and 10–20 cm. The water drop penetration time (WDPT) test was used, which is the most suitable and most widespread method [26,38,57]. This test involves dropping distilled water over the soil sample and measuring the time it takes to penetrate it. The median values of 8 measurements for each of the 84 soil samples were evaluated. SWR was measured at field moisture conditions (actual SWR) in all instances, and the measurements were supplemented with gravimetric soil moisture content (SMC).

Values of the WDPT test were used for statistical analysis, with the results making it possible to establish SWR classes according to the classification proposed by [58], namely: class 0—wetable or non-water repellent, WDPT < 5 s; Class 1—slightly repellent, 5 s < WDPT ≤ 60 s; Class 2—strongly repellent, 60 s < WDPT ≤ 600 s; Class 3—severely repellent, 600 s < WDPT ≤ 3600 s; and Class 4—extremely repellent, WDPT > 3600 s.

2.5. Estimation of the Diversity of Microorganism Communities in the Soil

According to previous research by Olejniczak et al. [59,60] and Górska et al. [61] regarding reproduction in the population of microorganisms after a fire, soil samples from six selected areas were prepared for DNA extraction sequencing. Genomic DNA from 1 g of fresh soil samples was extracted using the Sherlock AX kit (A&A Biotechnology, Gdynia, Poland) with an additional enzymatic lysis step and mechanical lysis with zirconia beads using a FastPrep-24 instrument step. The V3-V4 hypervariable region of the 16S rRNA gene was amplified using a Q5 Hot Start High-Fidelity 2X Master Mix (New England Biolabs, Ipswich, MA, USA) and specific primers 341F and 785R extended with the adaptor sequence, which enabled indexing in the second PCR reaction using Nextera XT Index primers (Illumina Inc., San Diego, CA, USA). The ITS1 hypervariable region for fungi metabarcoding was amplified using a Q5 Hot Start High-Fidelity 2X Master Mix (New England Biolabs, Ipswich, MA, USA) and specific primers ITS1F12 and 5.8S extended with the adaptor sequence, which enabled indexing in the second PCR reaction as mentioned for the V3-V4 region. The sequencing was performed using the v2 sequencing kit on MiSeq sequencer (Illumina Inc., San Diego, CA, USA) with 2 × 250 paired-end reads in the Genomed SA company, Warsaw. Secondary analysis, including automatic demultiplexing

and FASTQ generation, was performed using MiSeq Reporter Software v2.6 (Illumina Inc., San Diego, CA, USA). The adaptor and primer sequences were trimmed using cutadapt version 1.9 [62] and joined using a fastq-join algorithm [63]. Further analysis was performed using the QIIME software package [64]. UCLUST-ref [65] was used for open-reference operational taxonomic units (OTUs) picking based on the GreenGenes v13_8 database [66] for 16S analysis and the UNITE version of the 2-03-2015 database [67] for ITS1 analysis. Chimera detection was performed using ChimeraSlayer [68] and usearch61 [64] for 16S analysis and ITS1 analysis, respectively. Singletons and OTUs with less than ten sequences were filtered out.

2.6. Statistical Analysis

SWR expressed as the results of the WDPT test for the control, peripheral fire and central fire areas were evaluated by statistical tests. Non-parametric statistical analysis—the Kruskal–Wallis test was used for comparisons between the experimental objects because the WDPT test values do not follow a normal distribution. Statistical tests were conducted on the sub-datasets for each soil layer (0–5, 5–10 and 10–20 cm of depth), and the two age groups of pine stands (i.e., young and old).

The mean values of soil moisture content were compared between the experimental objects by three-way analysis of variance; homogeneous groups were distinguished by the Tukey test for $\alpha = 0.05$ using the Statgraphics Centurion version XVI program, (StatPointTechnologies, Inc., 2009, Warrenton, VA, USA).

Spearman's rank correlation coefficient was used to provide information about the soil moisture content and median WDPT relationships. Statistical analyses were carried out using the Statistica 13 statistical software-package (StatSoft, Ltd., Kraków, Poland).

Principal component analysis (PCA) was used to investigate the relationships between the examined variables (i.e., SWR, significant microorganism species, SMC, C, N and pH) and multivariate differences between the studied objects. PCA was performed in Statistica 13 statistical program.

3. Results and Discussion

3.1. Actual Soil Water Repellency

Figure 1a shows significant differences in WDPT test median values (Kruskal–Wallis test, and upper and lower quartiles) in the 0–5 cm, 5–10 cm and 10–20 cm layers in the three studied soil areas during the wet period, 28 months after the fire. It can be observed that WDPT values vary markedly depending on the strength/force of the fire. In the 0–5 cm and 5–10 cm layers the values in the area of unburned soil (control) and in the area of the peripheral fire did not differ significantly, and were classified as Class 2—strongly repellent. On the other hand, the median WDPT test value in the central fire area was identified as fundamentally different in 0–5 cm and classified in the 1st class, i.e., slightly repellent. Results in the 10–20 cm layer did not show significant differences in all studied areas, and control and peripheral fires areas were in the 1st class. Central fire areas were classified in Class 0 i.e., wettable. Noteworthy are the changes in SWR classes in the control areas; the occurrence of SWR decreased along with an increase in soil depth.

The obtained WDPT test results were analysed by the Kruskal–Wallis test in relation to the age of pine ecosystems (Figure 1b,c). Greater significant statistical variability was noted in areas beneath young pine stands. For young pine stand ecosystems, the soil in peripheral fire areas had the highest SWR classes, i.e., Class 3—severely repellent class in the 0–5 cm and 5–10 cm layers, and Class 1 in 10–20 cm layer. The lowest wettability class 0 was obtained in central fire areas for all studied layers. For the old pine stand ecosystem, the 3rd class of SWR was identified only in the 0–5 cm layer in control areas. The lowest WDPT median value occurred in central fire areas. Changes in the SWR classes in control areas were observed in both the young and old pine stand ecosystems.

Two restoration processes of vegetation disturbed by a fire were highlighted by Zaniewski and Otręba [56], with the first of these processes—classified as regeneration with an increase in the richness

of forest species—occurring in the peripheral fire areas. The second process was defined as similar to secondary succession, where non-forest species occurred in the highest burnout in central fire areas. As noted above, significant burning of litter, i.e., the waxy, hydrophobic materials in the mineral layer, and the secondary plant succession in the area of the central fire caused the soil to be characterized by hydrophilicity.

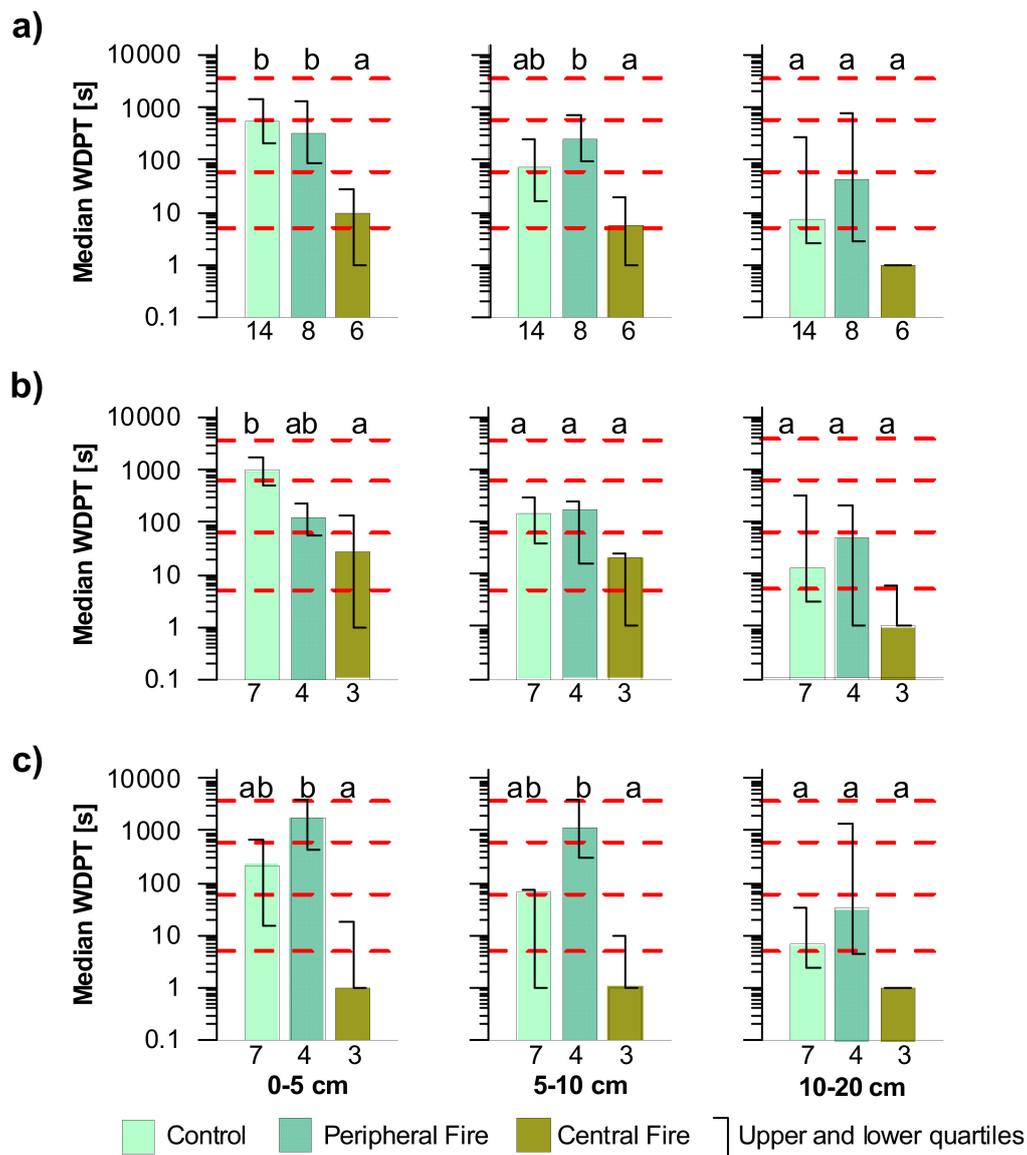


Figure 1. Median value of Water Drop Penetration Time (WDPT) test with upper and lower quartiles for (a) all soil samples, under (b) old and (c) young pine stand on the control site, and in the areas of a peripheral fire and central fire for three soil depths: 0–5 cm, 5–10 cm and 10–20 cm. Note: different letters above columns denote significant differences in each depth, as determined with the Kruskal–Wallis test ($\alpha < 0.05$). Different numbers below columns denote n, the number of replications. Red dashed lines denote the soil water repellency (SWR) classes: 0—wettable or non-water repellent, $WDPT \leq 5$ s; 1—slightly repellent, $5 \text{ s} < WDPT \leq 60$ s; 2—strongly repellent, $60 \text{ s} < WDPT \leq 600$ s; 3—severely repellent, $600 \text{ s} < WDPT \leq 3600$ s; and 4—extremely repellent, $WDPT > 3600$ s.

3.2. Soil Moisture Content

The analysis of soil moisture content (SMC) values has been presented in Figure 2. The highest SMC values were noted in the 0–5 cm layer, decreasing along with depth. In the control areas (Figure 2a),

significant differences were noted between each layer, and in areas of the peripheral and central fire, the 0–5 cm layer differs significantly from the 5–10 cm and 10–20 cm layers. The highest SMCs were found in central fire areas, in all studied layers. However, a significant statistical difference was obtained only for the 10–20 cm layer. There were no statistically significant differences in soil moisture distribution connected with the age of the pine stand ecosystem (Figure 2b), though differences between layers were noted in the two stands.

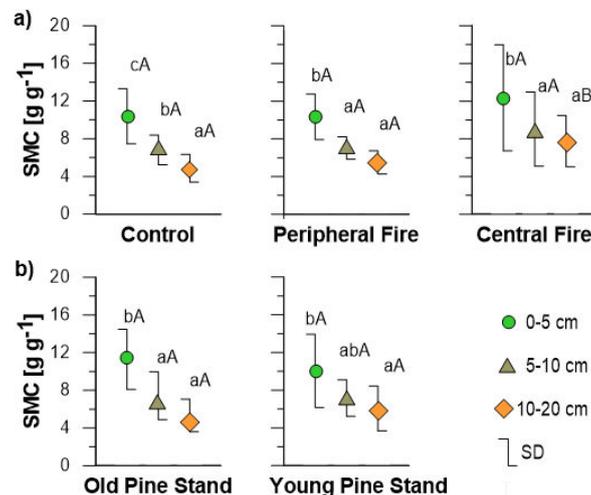


Figure 2. The average value of SMC—soil moisture content and SD—standard deviation for three soil depths: 0–5 cm, 5–10 cm and 10–20 cm, (a) on sites with different strengths of fire (i.e., control, peripheral fire and central fire); (b) for soil under an old and young pine stand. Note: different small letters denote significant differences in soil depth, different capital letters denote significant differences (a) between sites with different strengths of a fire; (b) between the age of a pine stand based on three-way analysis of variance by Tukey’s procedure ($\alpha < 0.05$).

It ought to be highlighted that the obtained higher SMC results for the area of the central fire may be dependent on layer of organic (litter) severely damaged by the fire, which definitely facilitated the penetration of rainwater into the soil surfaces. Characteristics of the water-binding potential in the soil reveal a significant difference in the possibility of water retention in the surface layers at field water capacity. The obtained total water capacity for the organic layer was equal to 69.33% vol. (bulk density 0.486), meaning that rainwater was partially retained in the organic layer in control areas and in peripheral areas.

Results of three-way analysis of variance (Table 2) for SMC demonstrate the strong significant relation of soil layer depth; the strength of the fire was found to be less though also significant. The age of the pine stand was determined as not being statistically significant.

Table 2. Results of three-way analysis of variance for soil moisture content. Note: *F* test, *p*—significance level; statistically significant values are marked in bold.

Characteristic	<i>F</i>	<i>p</i>
Site	5.85	0.005
Depth	21.64	<0.001
Age of pine stand	0.11	0.742

3.3. SWR and SMC Relation

An essential factor in varying SWR is soil moisture. A negative relationship between SWC and SWR has been reported, and hydrophobicity is generally considered to be the most severe in air-dry soil (e.g., [38,39,69]).

Many authors have reported that, with increasing rainfall, the wetting resistance of the soil is reduced when SMC reaches a threshold value, referred to as the “critical soil moisture content”, above which soil becomes hydrophilic. The values can range from 2% by volume for dune sand [70], 14%–27% in loamy sand [68], to as much as 64%–69% and 83%–86% for alder and reed peat, respectively [38].

Table 3 presents the results of the statistical relation of SWR and SMC. Statistically significant dependencies were found in regards to the studied changes of moisture content in the individual layers, i.e., for the 10–20 cm layer in the control areas, 0–5 cm in areas of the peripheral fire and 5–10 cm in those of the central fire. Additionally, significant relationships were found for the 10–20 cm layer in the old pine stand and the 5–10 and 10–20 cm layers of soil covered by a young pine stand.

Table 3. Spearman’s rank correlation coefficients between SWR (median WDPT test value) and the soil moisture content divided into the level of factors (depths and sampling sites and divided into depths and ages of the pine stand). Statistically significant values are in bold.

Site	Depth (cm)	Correlation Coefficient
Control	0–5	0.029
	5–10	−0.229
	10–20	−0.741
Peripheral Fire	0–5	−0.714
	5–10	−0.500
	10–20	−0.683
Central Fire	0–5	−0.759
	5–10	−0.880
	10–20	−0.655
Old pine stand	0–5	−0.140
	5–10	−0.339
	10–20	−0.694
Young pine stand	0–5	−0.550
	5–10	−0.673
	10–20	−0.781

As can be seen, all statistically significant correlations are negative, i.e., SWR decreases with increasing soil moisture. Although SWR generally disappears when soils become wet, the SMC and SWR relationship seems to be more complex in the presented studies.

3.4. Dominant Eukaryotic and Prokaryotic Species in the Control and Recovery Soil Sites

Mycorrhizal fungi and undefined fungi (their sequences were not found in the Blast database) dominated among mushrooms, whose occurrence in the soil is equal to 1% or more (Figure 3). The highest occurrence of the undefined groups of fungi was noted in soil under the old pine stand (ca. 19%) and the young pine stand (ca. 36%) in central fire areas. However, regardless of the age of the trees, a similar occurrence of these fungal groups was estimated in the control soils and peripheral fire sites. In sites where the severe fire blazed (CF), the fungi population present in soil significantly decreased under young trees as compared to old trees. The percentage of fungi of the *Archaeorhizomyces* genus, which colonize the host root surface, was comparable in each researched soil site. The relative occurrence of *Archaeorhizomyces* spp. under young trees in the soil decreased as a result of a peripheral fire and amounted to about 2.74% compared to the control soil (8.58%) and central fire sites (9.71%) (Figure 3). However, two years after the fire, recolonization of the soil by *Archaeorhizomyces* spp. did not depend on the fire severity and was significantly lower when compared to the control soil (ca. 11%).

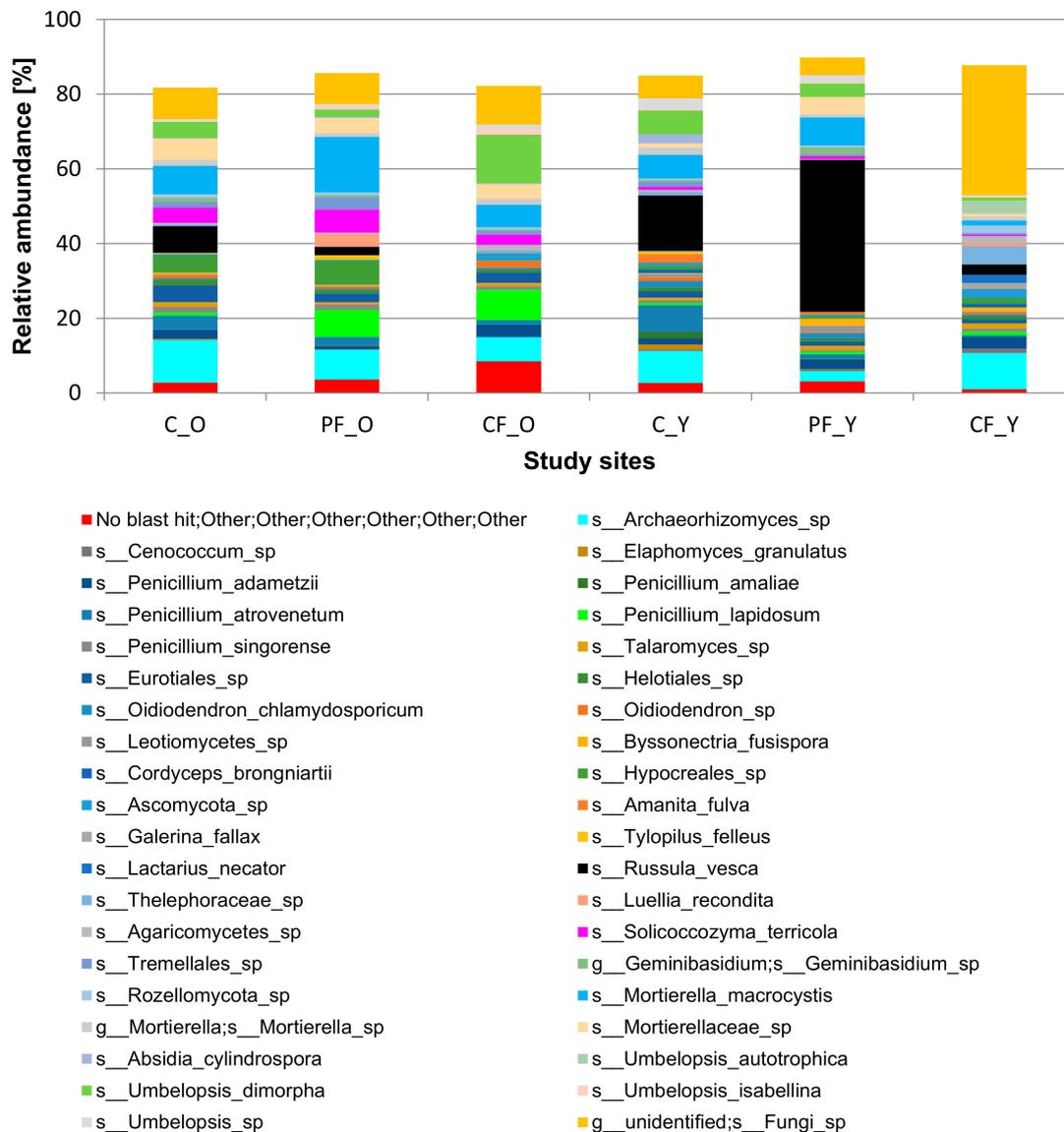


Figure 3. The relative distribution of dominant eukaryote (fungal) species in soil collected from the C—control; PF—peripheral fire; CF—central fire areas; Y—young pine stand; O—old pine stand. Note: little letter estimate: g—genus, s—species. The data represent the mean abundances from six study areas ($n = 3$). OTUs are defined at 97% sequence identity threshold. Major taxa (species level) and candidate taxonomic groups detected with a relative sequence abundance $\geq 1.0\%$ in at least one of the samples.

The relative occurrence of *Russula vesca* in the soil varies from 0.03% for severe-fire recovery soil under old trees, up to approximately 41% for peripheral soil sites covered by a young pine forest. The recolonisation of *R. vesca* in the soil after the fire is expressed by relative occurrence (%) and depends not only on the fire intensity but also on the age of the pine forest. *Russula vesca* proved to better colonize the control soil and areas of soil after a fire in young tree stands as compared to the same research sites with an old pine stand. The fire, regardless of its severity, drastically lowered the recolonization of *R. vesca* in soil, i.e., to 2.28% (PF_O) and 0.03% (CF_O), respectively, compared to the control soil (7.10%) under an old forest. Peripheral fire stimulates soil recolonization by *R. vesca* under young trees, which is shown by an increase in the relative abundance of this genus of fungi in soil ranging from 14.8% (C_Y) to about 41% (PF_Y), whereas a severe fire (CF_Y) significantly reduces its occurrence to 2.74%. This can be explained by the litter covering the soil surface underneath

old trees being richer in lignins and aromatic compounds as well as dying old pine roots than litter that is characteristic of a young forest [71]. *Basidiomycota* and *Ascomycota*, due to the synthesizing of phenoloxydases, are the key biological factors responsible for the degradation of organic matter in soil, including lignins, resins, waxes and other compounds which might affect soil hydrophobicity. *R. vesca* does not synthesize phenoloxidase, which in turn leads this species winning the competition with other mushrooms regarding simple chemical compounds present in the forest floor of young trees, which is deficient in aromatic compounds, though it has been noticed that the percentage share of *R. vesca* is highest in PF_Y sites. This could be the result of the antagonistic relation of this fungi genus with other mushrooms, including ectomycorrhizal fungi, which is in line with the results obtained by Koide et al. [72]. Despite the high resistance of ectomycorrhizal fungi to a fire, which is due to the formation of fungal propagules (spores, sclerotia) in the soil, the strong fire negatively affected the recolonization of *R. vesca*, while the peripheral fire stimulated their growth in the soil. Mats of fungi can survive a fire, especially a peripheral fire, because the soil does not burn evenly. When soil is burning, the temperature is the highest and most damaging for living organisms at the highest level of the soil profile and gradually decreases. Therefore, ectomycorrhizal fungi can be resistant to the moderate temperatures present in the deeper layers of the soil, and hence survive a fire. Sometimes, rising temperatures stimulate fungal growth and their recolonization. The fungal mats can also die due to the inhibited transport of assimilates from the dying host roots to hyphae [73]. Microfungi can positively or negatively affect the growth and development of ectomycorrhizal fungi [74]. These include, among others, *Penicillium* spp., *Mortierella* spp., *Umbelopsis* spp. and others [75]. The results of our research confirm the occurrence of *Penicillium adametzii*, *P. atrovenetum* and *P. lapidosum* in the soil of a pine forest. However, regardless of the age of the trees, the percentage share of *P. adametzii* and *P. lapidosum* in soil after a central fire increased, compared to the control areas. On the other hand, *P. atrovenetum* colonized CF sites to a lesser extent when compared to soil from PF and C sites.

Bacterial species belonging to *Acidobacteria* phylum and the orders of *Acidobacteriales* (families: *Koribacteriaceae* and *Acidobacteriaceae*) as well as Ellin6513 dominated in the studied soils regardless of the study site (Figure 4). However, the relative occurrence of species from the *Acidobacteriaceae* family was greater in the central fire soil site as compared to the other sites. The occurrence of *Acidobacteria* is dependent on the pH of the soil, with these bacteria dominating in acidic soils, including forest and peat soils. Actinomycetes of the order Actinomycetales were also abundant in these soils, mainly in central fire zones, regardless of the age of the trees. In contrast, the occurrence of Actinomycetes from the species *Mycobacterium celatum* increased only in the soil of a young pine stand ecosystem which had undergone a severe fire. This is connected with the hydrophobicity of the cell wall of *Mycobacterium* species, which consists of waxes and mycolic acids. In terms of the Proteobacteria phylum, bacterial species in the Rhodospirillaceae and Sinobacteriaceae families predominated in the studied soils. However, in the areas of the central fire, the occurrence of representatives of the Rhodospirillaceae family increased in soil under young trees, while the amount of Sinobacteriaceae in soil decreased regardless of the age of the trees.

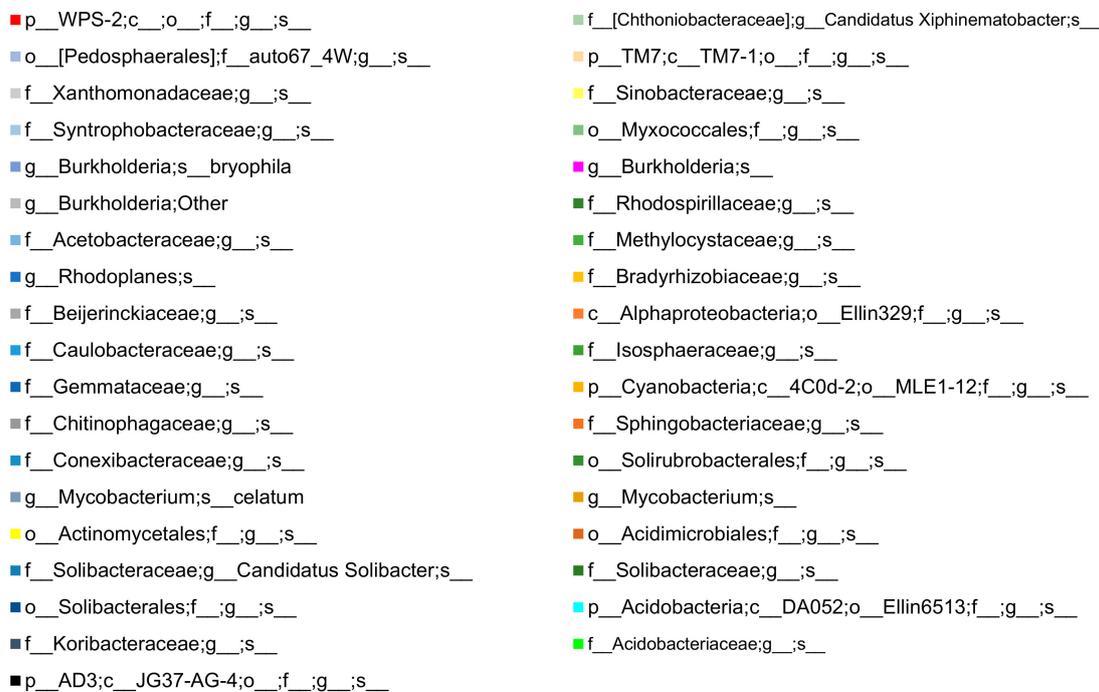
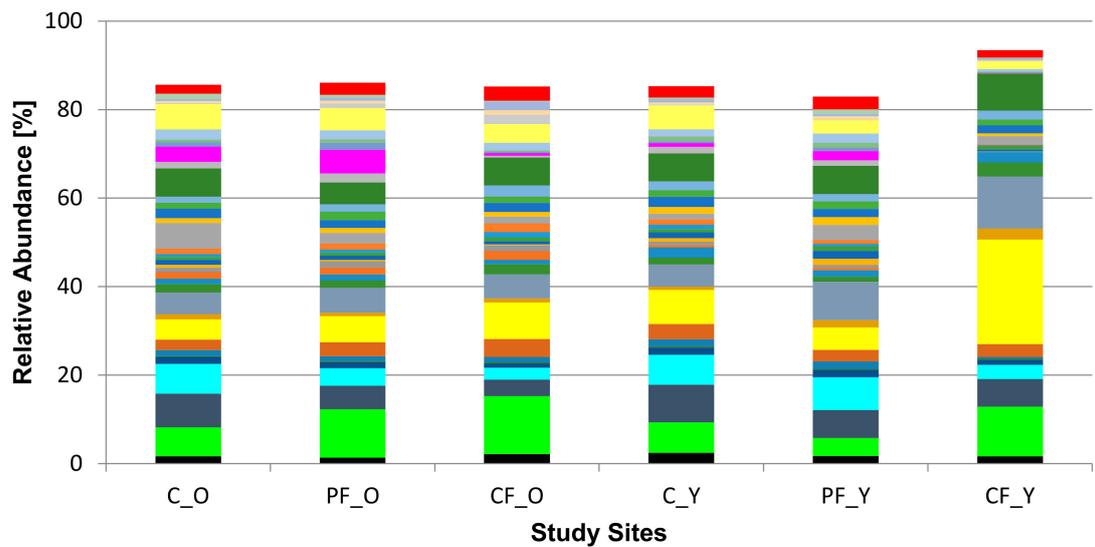


Figure 4. The relative distribution of dominant prokaryote species in soil collected from the C—control; PF—peripheral fire; CF—central fire areas; Y—young pine stand; O—old pine stand. Note: little letter estimate: p—phylum, c—class, o—order, f—family, g—genus, s—species. The data represent the mean abundances from six study areas ($n = 3$). OTUs are defined at 97% sequence identity threshold. Major taxa (species level) and candidate taxonomic groups were detected with a relative sequence abundance of $\geq 1.0\%$ in at least one of the samples.

3.5. Fungal and Prokaryote Species and the SWR Relation

Fungi of the *Russula* species, commonly found in forest soils, form mutualistic associations (ectomycorrhizal) with various plants, including pine roots (*Pinus sylvestris*) [76]. The occurrence of *R. vesca* is largely positively correlated with the SWR (Figure 5).

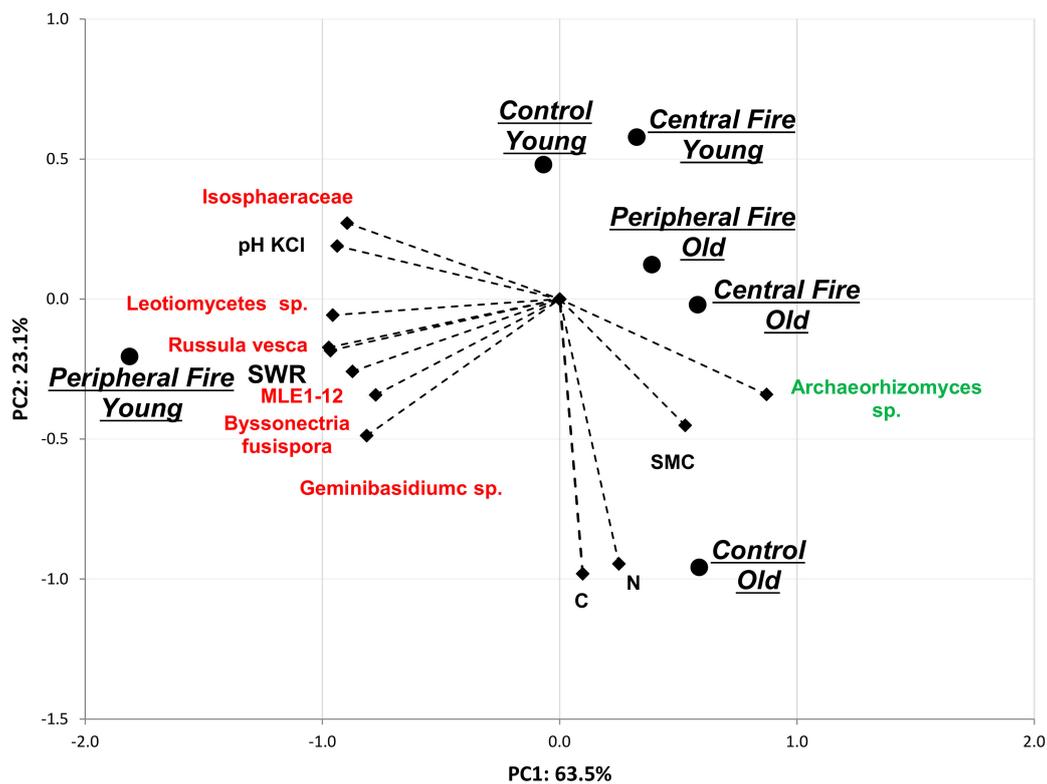


Figure 5. Results of principal component analysis (PCA) of relative abundances of fungal and prokaryote species and the statistically significant relation with soil water repellency (SWR) from the Control Site, Peripheral Fire Site, Central Fire site; Young—young pine stand, Old—old pine stand sites and environmental variables. All genera with > 0.01% abundance and a statistically significant relationship with SWR based on correlation coefficients were considered. Note: SMC—soil moisture content; N—nitrogen; C—carbon; pH KCl. PCA was calculated using means, which were calculated using 3 replications.

R. vesca is mainly known as an ectomycorrhizal organism, which rarely grows in soil [77]. Therefore, *R. vesca* cannot degrade aromatic compounds that affect soil hydrophobicity because it does not generate phenolic oxidases. Furthermore, *R. vesca* hyphae are rich in fat (about 3.07 g/100 g d.w.), which can result in soil hydrophobicity when this mycelium ages and dies [78]. *Russula* spp. can survive in unfavourable environmental conditions (e.g., drought, high temperatures and others) due to rhizomorphs that are formed as a result of the coordinated growth of millions of aggregated hyphae which are joined together by mucous substances [79]. This can also affect soil hydrophobicity. The results of our research (Figure 5) showed a positive correlation between soil hydrophobicity and other ectomycorrhizal fungi, including *Byssonectria fusispora* and *Geminibasidium* sp. According to Fujimura et al. [80] and Nguyen et al. [81], these fungi are xerotolerant, and can therefore be resistant to heat which is always present after a fire in forest soils. A positive correlation was also found between the SWR and the occurrence of *Leotiomycetes* sp. These fungi may be endophytes (e.g., of *Pinus ponderosa*), symbionts, as well as saprophytes. If they are endophytes, they make use of plants assimilates similarly to mycorrhizal fungi because they inhabit their tissues [82].

The occurrence of non-cultured in vitro *Cyanobacteria* of the order MLE1-12 classified as *Melainobacteria*—the new sister phylum of *Cyanobacteria*—is also positively correlated with soil hydrophobicity. These gram-minus bacteria do not carry out photosynthesis but instead gain energy during certain fermentation processes as well as by aerobic respiration. The MLE1-12 genome has genes encoding hydrolases that degrade simple sugars and polysaccharides, e.g., starch and cellulose. *Melainobacteria* inhabit various environments, including soil, water reservoirs and aquifers [83].

Metagenomic analyses of soils from various habitats of all continents have shown that *Archaeorhizomycetes* is one of the main components of soil fungal communities, including 250 alleged species from the genera *Archaeorhizomyces*. Some of them are characterized by the specificity of their relationships with tree-grown habitats, including *Pinus* sp. [84,85]. Presumably, *Archaeorhizobacter* species, revealing the specifics of a given habitat, are more strongly associated with plant roots, mainly colonizing their surface, although they can also form mycorrhizal relationships. However, no pathogens have been identified among them [86]. *Archaeorhizomycete* fungi also occur on living and dead roots in the soil, as well as on rotting wood [84]. Due to the degradation of lignins and aromatic compounds that affect soil hydrophobicity, these mushrooms could be one of the reasons for the strong negative correlation between hydrophobicity and *Archaeorhizomyces* sp. in the studied forest soils. Menkis et al. [87] and Rosling et al. [84] claim that *Archaeorhizomycetes* grow poorly on cellulose and glucose, which may explain why their occurrence does not depend on the exudation of plant roots in the soil, as well as the exfoliation of the cap of a root and the root skin. If *Archaeorhizomycetes* fungi do not use these compounds and yet, in spite of this, colonize the surface of a root, they probably synthesize oxidative enzymes that can transform and degrade lignins and some aromatic compounds. This has been confirmed by studies of fungal genomes classified as *Taphrinomycotina* clade, belonging to *Ascomycota*, which also includes *Archaeorhizomyces* spp. [85]. It was moreover discovered that there are genes that encode some peroxidases in the *Taphrinomycotina* genome [88]. Peroxidases are not specific enzymes, so they can degrade not only lignins, but also various complex and aromatic compounds; this, in turn, means that they may cause a negative correlation between SWR and the occurrence of *Archaeorhizomyces* spp. Scots pine (*Pinus sylvestris*) creates various hydrophobic compounds (essential oils, waxes, resins, dyes, rubbers, tannins, latexes) that are found in the above-ground and underground tree parts. Thus, when needles, cones, branches, bark and rotting roots of older pine trees are present on the forest floor, hydrophobic compounds find their way into the soil and induce soil hydrophobicity [89]. However, the presence of *Archaeorhizomyces* spp. may cause increased soil wettability, due to the degradation of various hydrophobic compounds through the synthesis of peroxidases in soil. Some ectomycorrhizal fungi may gain access to water from deeper soil layers due to the transport of water through the host roots of the plant or the hyphae of the fungi, which also applies to *Archaeorhizomyces*.

Statistical analysis did not point to a significant correlation between repellency and the presence of high numbers of bacterial taxons. Presented investigations have demonstrated that repellency of forest soil was connected mainly with fungi, but not bacteria.

These water transport mechanisms may result in the survival of the mentioned fungi and their reproduction, as well as their symbiotic relationship during dry periods [90]. This feature is significant from the point of view of progressive climate change and the higher prevalence of soil drought.

4. Conclusions

The occurrence of the SWR phenomena differs on a spatial scale based on the severity of the fire in the second, wet year of ecosystem regeneration. The soil in areas affected by severe fires was characterized by hydrophilicity. The highest SWR classes were observed for soils in young pine stand ecosystem (60–90 years) in areas of peripheral fires.

A strong significant relationship between soil moisture of soil layer depth was noted, with the strength of the fire found to be less though also significant, whereas the age of the pine stand was recognized as not statistically significant.

Statistically significant negative correlations between SWR and SWC were found only in some individual layers, which may indicate new research areas for environmental microbiology.

Natural regeneration involves many processes connected with soil microbiotic activities in the restoration of soil systems. Since fungi are considered the main decomposers of complex organic matter in terrestrial ecosystems, a stronger response of fungal communities may have implications for organic matter transformation in forest soils under the impact of environmental stressors. Based on the obtained results, the water repellency of forest soil is connected mainly with fungi, not bacteria. The

indication of significant positive relationships between SWR and *Leotiomycetes* sp., *Byssonectria fusispora*, *Russula vesca*, *Geminibasidium* sp., bacteria *Isosphaeraceae* and *Cyanobacteria* (class 4C0d-2, order MLE1-12) and a negative relationship with *Archaeorhizomyces* sp., are of high cognitive value. Furthermore, insight into the functional roles of individual microbial taxa allows for a better understanding of complex processes in the soil environment.

We are aware of the limitations of the narrow scope of research, hence interdisciplinary research is required to gain a better understanding of the effects of how an ecosystem will respond following the occurrence of a fire, and ultimately develop a climate-adaptation plan to enhance forest resilience to long-term climate change. The essence of future research is to indicate and confirm which species of microorganism communities could be a bioindicator of the occurrence of SWR.

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