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Research Article

Microbiome composition of disturbed soils from sandy-gravel mining complexes with different reclamation approaches

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Abstract

Activities connected to mineral mining disrupt the soil layer and bring parent rock material to the surface. It leads to altering the environmental conditions and leaves behind vast areas of disturbed lands. Returning these lands to natural ecosystems is an important contemporary challenge, which can be acquired by reclamation practices. Soil microbiome composition reflects changes happening to disturbed lands; thus, its analysis is a powerful tool for evaluating the disturbance degree and estimating the effect of the implementation of reclamation techniques. Additionally, factors connected to the characteristics of a particular geographical region have a certain impact on the microbiome and should be taken into account. Thereby, studies of soil microbiomes of disturbed soils of different origins are essential in understanding the dynamics of soil restoration. Here, we focus on soil microbiomes from two sandy-gravel mining complexes in mountainous areas with a moderate continental climate of the Central Caucasus. These quarries share the same parent rock material, but differ in benchmark soil type and reclamation approach - one was

left for passive recovery and the other was technically reclaimed with overburden material. Comparative analysis of microbiome composition, based on sequencing of 16S rRNA gene libraries, showed that region and disturbance are the key factors explaining microbiome variation, which surpass the influence of local factors. However, the application of reclamation techniques greatly reduces the dissimilarity of soil microbiomes caused by disturbance. Linking of soil chemical parameters to microbiome composition showed that the disturbance factor correlates with a lack of organic carbon. Other chemical parameters, like pH, ammonium, nitrates and total carbon explain microbiome variability on a smaller scale between sampling sites. Thus, while regional and disturbance factors reflected differentiation of soil microbiomes, soil chemical parameters explained local variation of certain groups of microorganisms.

Keywords

16S rRNA, amplicon library sequencing, disturbance factor, open-pit mining, quarry, reclamation techniques, soil microbiome

Introduction

One of the global ecology and soil science problems is land degradation (Jie et al. 2002, Gregory et al. 2015, Prăvălie 2021). As the world's population grows, so does the demand for natural resources, such as minerals, raw materials and rock, leading to overexploitation of ecosystems by industry (Thakur et al. 2022). Minerals are extracted by mining, including surface and underground methods (Hartman and Mutmansky 2002). Open-pit (quarry) extraction is the cheapest method of surface mining and therefore prevails (Abakumov and Gagarina 2006). Open-pit mining causes the greatest damage to the landforms (Chen et al. 2015). For example, open-pit mining in forested areas is associated with cutting down trees, draining ponds and rivers and streams being diverted beyond the deposits. Negative changes occur, not only at the extraction sites, but also in adjacent territories. The areas affected by open-pit mining are much larger than the quarry area (Bekarevich et al. 1969, Melnikov 1977, Monjezi et al. 2008). Open-pit mining results in the formation of dumps which can serve as an example of a negative human impact on the ecosystem (Burlakovs et al. 2017, Puell Ortiz 2017). This negative impact can be eliminated by the implementation of mine reclamation techniques. These include diverse practices – restoration, rehabilitation or replacement - aimed at returning disturbed lands to the natural ecosystem by restoring or giving them new functions (Bradshaw 1984, Favas et al. 2018). The choice of reclamation approach depends on the available resources and tasks. In the case of open pit mining, the important task is to remove dumps and restore the surface level. It can be achieved by backfilling the quarry pit with dumps and overburden material (Jurek 2014, Legwaila et al. 2015). In cases when no techniques are applied to abandoned mines due to economical or other difficulties, they can undergo passive recovery with consequent spontaneous vegetation (Holl 2002, Prach et al. 2013).

The effect of degraded land transformations can be assessed by analysis of chemical and biological soil properties (Gavrilenko et al. 2011, Murugan et al. 2014, Gorobtsova et al. 2016, Kazeev et al. 2020). Studies of soil microbial biomass and microbe enzyme activity have shown that soil microbiota are the first to respond to changes in the soil (Józefowska et al. 2016). Nowadays, high-throughput sequencing of 16S rRNA gene libraries becomes a fast and effective tool for gathering huge amounts of genetic information, which becomes more effective in characterising changes in soil microbial communities. Although there are many studies connecting the effects of different types of agricultural practices on soil microbe communities (Coller et al. 2019, Chen et al. 2020, Liu et al. 2021), such studies of soils disturbed by mining are scarce (Epelde et al. 2014, Sun et al. 2019). Comparative analysis of soil microbiome composition can reveal relationships amongst its composition, soil disturbance and chemical parameters (Liddicoat et al. 2019). For example, it was shown that microbiomes of technically reclaimed coal mines differ by bacterial abundance and diversity from natural soil, but with time, their diversity evens out (Hou et al. 2018). Furthermore, some of the top bacterial taxa can be linked to chemical and functional changes, which appear in a disturbed land. Thus, there are a lot of factors, including the presence of disturbance and reclamation, soil type, vegetation, climate and chemical parameters, all of which, to a different extent, affect the microbiota of degraded soils. Here, we aimed to evaluate the degree of influence of these factors on the soil microbiome composition.

There are huge areas of degraded soil in the Central Caucasus regions. As specified in the government statement (Abramchenko et al. 2019), the degraded soil area in Stavropol Krai is 3400 ha and 1007 ha in the Kabardino-Balkarian Republic. The dominating activity that leads to land disturbance in the region is the extraction of common minerals, such as boulder-sand-gravel mixes, construction sand, building stone, clays etc. We found two boulder-sand-gravel mining complexes in both regions, in one of which quarry soils were technically reclaimed, in the other left for self-restoration. Thus, we aimed to compare microbiomes of benchmark and quarry soils from these complexes, which share disturbance type and climate, but differ in soil type and reclamation practices and to link microbiome composition with these factors.

Materials and Methods

Sampling sites were located in the foothills of the Central Caucasus in two regions – Urvan (Kabardino-Balkarian Republic, Russia) and Progress (Stavropol Krai, Russia) (Fig. 1a). The terrain of both study areas can be characterised as hilly plains. According to the classification (Sokolov and Tembotov 1989), they belong to the belt of meadow steppes (400-800 m above sea level) of the Elbrus variant of the zonation (Progress) and the steppe zone (200-400 m above sea level) of the Terek variant zonation (Urvan) of the Central Caucasus. In the studied territories, the climate is moderately continental, with a long frost-free period, hot summers and little snow, with frequent thaws in winter. In the zone of meadow steppes (Progress), the average annual precipitation is 579 mm/year, the average annual air temperature is 10.45°C and the total evaporation is 864 mm/year

(Razumov et al. 2003). In the steppe zone (Urvan), the average annual precipitation is 522 mm/year, the average annual air temperature is 11°C, the total evaporation is 818 mm/year (Ashabokov et al. 2005). Two regions have different soil types and water regimes: Phaeozems in Progress were formed under the influence of only atmospheric moisture, with a periodic leaching regime, while Umbric Gleyic soils in Urvan are characterised by increased surface watering and additional film-capillary moisture, the source of which is shallow (1.5-3 m) located groundwater. The bluish-grey inhomogeneous colouration of the lower horizons of meadow soils is a weakly pronounced sign of hydromorphism (Duchaufour 1982).

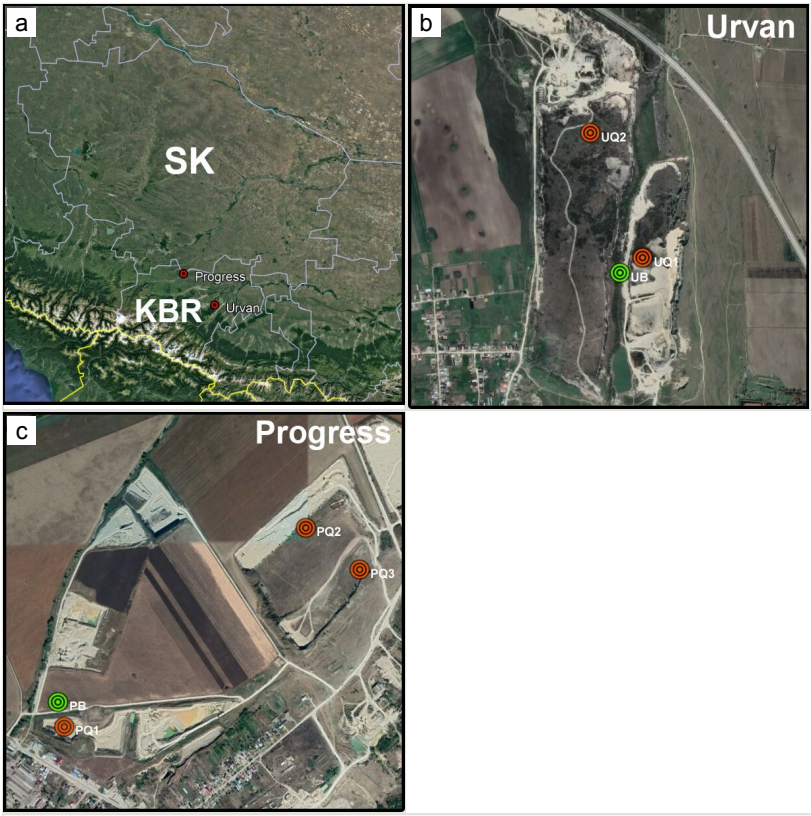

Figure 1.

Sampling sites. Maps based on Google Earth (Google, USA).

a: Relative position of Kabardino-Balkarian Republic (KBR) and Stavropol Krai (SK) regions.
b: Urvan in KBR: UB - benchmark site, UQ1 and UQ2 - quarry sites
c: Progress in SK: PB - benchmark site, PQ1, PQ2 and PQ3 - quarry sites

In each region, we found an abandoned territory of a quarry, located on a deposit of sand and gravel mixture. Both territories consist of multiple differently-aged pits and rock dumps. The first mining complex was found in the Urvan District of Kabardino-Balkaria near the terrace of the eponymous river, which flows between two quarry pits. The deposits in this area have been developed since 1958. The benchmark soil type for this area is Umbric

Gleyic, which remains undisturbed near the riverbanks. Abandoned quarry pits showed signs of passive recovery with spontaneous overgrowth by *Populus*, *Hippophae* and reed. The second mining complex was found in the Kirovsky District of Stavropol Krai near the Malka River. The field has been developed since the 2000s. The flat lands surrounding the quarry complex belong to the Phaeozem soil type and are completely converted for farming purposes. Thus, the nearest benchmark soil for this territory is Agrisol. Of course, Agrisol itself is a disturbed soil (Conacher 2009, Lupatini et al. 2017, Wipf et al. 2021), but in this case, we treat it as a benchmark soil, due to the lack of native soil nearby. Technical reclamation, consisting of backfilling the bottoms of the abandoned pits with a mixture of overburden Phaeozem, sand and gravel, was implemented in this area. Vegetation in the quarry pits varied from *Ambrosia* to *Acacia* thickets.

For the analysis we did not consider the time of the last extraction of minerals on the sites or the expansion of the extraction zone, just the fact of mining, which by itself had a negative impact on the soil, being a factor of disturbance. A similar assumption was applied to the reclamation factor; we considered reclamation practices as present in the Progress region and absent in the Urvan region. As disturbed soil no longer shares the same type as benchmark soil from the same region, we considered the regional factor instead of the soil type factor as determining the difference between Progress and Urvan soils. To estimate differences connected to local variation of vegetation and chemical parameters factors, we took biological replicates within one site from as diverse ecotopes as possible (e.g. different plant cover).

Profiles of weakly developed soils of quarries usually consist of two horizons: W - accumulated humic material and C - parent rock underneath, usually the overburden material (Abakumov 2008). In our previous studies, we compared microbiomes of these horizons within and between sampling sites and it turned out that the microbiome of parent material is a reflection of the topsoil horizon and that their microbiomes shift simultaneously between sites (Kimeklis et al. 2021). Taking this into consideration, in this study, we limited ourselves to the top horizon of each site.

Sampling was conducted in August 2020. In the Urvan region, we collected samples at the three sites: UQ1 and UQ2 - two neighbouring quarry pits: one fully abandoned at the time of collecting, the other partly functional and UB - benchmark soil near the river (Fig. 1b). In the Progress region, we collected samples at the four sites: PQ1 - newly excavated and freshly overgrown two-year mining pit, PQ2 and PQ3 - in the old overgrown quarry pit currently used for pasture and PB - Agrisol from the nearest field, where the crops (corn) have already been harvested (Fig. 1c). For each site, we made two to four soil cuts, depending on the variability of the ecological microniches. More detailed information is presented in Table S1 (Suppl. material 2). Temperature was measured in the top 2-5 cm layer using a digital thermometer. From the same top layer, soil samples were collected in 50 ml plastic tubes with same-day freezing at -20°C for subsequent molecular analysis and into plastic 1 litre bags with subsequent air drying for chemical analysis.

For all dried soil samples, chemical analysis was performed, including measuring of pH, organic carbon (OC), ammonium (NH_4^+), nitrate (NO_3-), mobile phosphorus (P_2O_5) and

potassium (K_2O), as previously described in Gladkov et al. 2019. Total carbon content (TC) was determined by direct combustion on the elemental analyser Euro-EA3028-HT (Evrovector, Italy) at the St. Petersburg University Research Park. To detect the effect of region and disturbance factors, ANOVA with Tukey HSD test, t-test group comparisons and correlation coefficients of the results were calculated in Statistica 13 (TIBCO Software Inc., USA).

From each sample of the frozen soil, total DNA was extracted in quadruplicate and consequently used for the construction and sequencing of the 16S rRNA amplicon libraries using Illumina MiSeq (Illumina, Inc., USA) as described in Gladkov et al. 2019 at the Centre for Genomic Technologies, Proteomics and Cell Biology (ARRIAM, Russia). Obtained data was processed and visualised as described in Kimeklis et al. 2021 in R (R Core Team 2021) and QIIME2 (Bolyen et al. 2019) software environments using the following tools: dada2 (Nearing et al. 2018), phyloseq (McMurdie and Holmes 2013), DESeq2 (Love et al. 2014), vegan 2.5-7 (Oksanen et al. 2020), ggpubr 0.4.0 (Kassambara 2019), picante (Kembel et al. 2010), ggforce 0.3.3 (Pedersen 2019), tidyverse (Wickham et al. 2019), ggtree (Yu et al. 2018), ampvis2 (Andersen et al. 2018) in RStudio (RStudio Team 2020) and SEPP package (Janssen et al. 2018). Taxonomy was assessed by RDP Classifier with 50% confidence threshold (Wang et al. 2007), using SILVA SSU database 138 (Quast et al. 2013). Alpha diversity was accessed by four indexes - Observed, Faith's phylogenetic diversity (PD) (Faith 1992), Shannon (Shannon and Weaver 1949) and inverted Simpson (Simpson 1949). Significance of mean differences between alpha-diversity indexes was calculated by the Mann-Whitney test (Mann and Whitney 1947). Beta diversity was calculated using Bray-Curtis distance matrix (Bray and Curtis 1957) and visualised by NMDS (Kruskal 1964). Differences of beta-diversity between sites were accessed by PERMANOVA (Anderson 2017) performed with adonis2 test (McArdle and Anderson 2001). Differences between biological replicates of beta-diversity within one site were accessed by analysis of multivariate homogeneity of group dispersions (Anderson 2005, Anderson et al. 2006). Canonical Correlation Analysis (CCA) (ter Braak 1986, Palmer 1993, McCune 1997) was used to link beta-diversity of microbiomes with soil chemical properties. Multicollinearity between soil parameters was checked by the Variance inflation factors (VIF) test (Fox and Monette 1992, Fox 1997). Analysis of compositional microbiota data (balances) was performed by PhILR transformation (Silverman et al. 2017). The code is available in the supplement (Suppl. material 3).

Results

Soil chemical parameters

Two mining complexes from Urvan and Progress were based on different soil types - Phaeozem and Umbric Gleyic, which determined variation in some soil chemical parameters, which we attribute to the region factor. Differences between disturbed and benchmark soils, which we classify as disturbance factor, are also reflected in some chemical parameters (Table 1). ANOVA with post-hoc Tukey HSD test showed that the region factor significantly affects soil temperature, pH, TC, potassium, ammonium and

nitrates. The disturbance factor (between the benchmark and disturbed soil samples) affected OC and pH. Soil pH in the Urvan region was alkaline (7.4-8) and did not show a significant difference between quarry (UQ1 and UQ2) and benchmark (UB) sites ($t = 1.09$, $p = 0.33$) (Suppl. material 2, Table S2). Soil pH in the Progress region was slightly alkaline, ranging between 6.9 and 7.6, with quarry sites (PQ1-PQ3) being more alkaline (7.2-7.6) than benchmark PB soil (6.9-7.1) ($t = 4.52$, $p < 0.01$). OC quantities ranged from low to very low and had significant differences between quarry (0.2-0.8%) and benchmark (1.8-2.7%) sites for both regions ($t = -14.60$, $p < 0.01$). Some factors had significant correlation between each other (Table S3): phosphorus and ammonium ($R^2 = 0.73$, $p < 0.05$), ammonium and nitrates ($R^2 = -0.53$, $p < 0.05$), pH and nitrates ($R^2 = -0.61$, $p < 0.05$), phosphorus and nitrates ($R^2 = -0.52$, $p < 0.05$) and phosphorus and potassium ($R^2 = 0.48$, $p < 0.05$). Phosphorus content variation could not be attributed to the region or disturbance factor. Ammonium content was higher than nitrates in all sites, except PB (benchmark Agrisol) and PQ1 (2-year self-growing quarry with fresh dumps of soil and rock mixture), which is very close to PB. Both PB and PQ1 samples stood out from the rest as they had the smallest amount of phosphorus, ammonium and the maximum of nitrates. Interestingly, PB soil samples taken before and after the rain did not differ significantly in any parameters, except nitrates, which increased twofold after the rain. Samples from sites PQ2 and PQ3 from the same quarry bottom had the highest potassium content amongst all samples. To conclude, while pH, TC, ammonium, nitrates and potassium values demonstrated region specificity, OC values were associated with the disturbance factor, being higher in benchmark soils compared to primary soils of quarries in both regions.

Table 1.

Sample description and soil chemical variables with post-hoc Tukey HSD for region and disturbance factors. Letters encryption: U - Urvan, P - Progress, B - benchmark, Q - quarry. P-values given in bold designate statistically significant influence of a certain factor: region - differences between Urvan and Progress samples, disturbance – between benchmark and primary soils in quarries.

Region	Site	Soil cut	Temp, C	pH	TC, %	OC, %	P_2O_5, mg/kg	K_2O, mg/kg	NH4, mg/kg	NO3, mg/kg
Urvan	Benchmark									
	UB	1	33	7.6	12	1.89	17.7	173.2	15.84	5.2
		2	30	7.5	11	2.71	40.1	389.6	37.34	0.01
		3	34.5	7.6	13	2.69	32.3	288.6	25.59	0.01
	Quarry									
	UQ1	1	32	7.7	15	0.29	34.4	259.7	44.96	0.01
		2	25.4	7.4	20	0.56	69.9	360.8	79.93	0.01
		3	35.7	7.4	17	0.34	43	274.2	54.46	0.01
		4	37.4	8	28	0.45	35.2	303	38.5	0.01
	UQ2	1	40	8	18	0.41	16.1	173.2	23.76	0.01
		2	38	7.9	17	0.36	30.9	303	36.55	0.01

Region	Site	Soil cut	Temp, C	pH	TC, %	OC, %	P_2O_5, mg/kg	K_2O, mg/kg	NH4, mg/kg	NO3, mg/kg
		3	28	7.7	18	0.41	44.1	346.3	38.14	0.01
Progress	Benchmark									
	PB	1	29	7.1	25	2.56	14	404	13.83	15.6
		2	25	6.9	23	2.21	14.5	389.6	12.37	33.32
	Quarry									
	PQ1	1	27	7.5	32	0.78	12.4	331.9	4.75	8.47
		2	25	7.5	21	0.63	15.1	404	6.46	7.8
		3	26	7.6	27	0.65	14	317.5	5.3	13.49
	PQ2	1	28	7.5	15	0.78	41.9	692.6	29.91	0.01
		2	26.5	7.5	16	0.79	42.8	678.2	32.04	0.01
		3	27	7.5	15	0.74	43	793.7	30.16	1.15
	PQ3	1	30	7.3	25	0.87	25.5	606.1	12.67	5.2
		2	31	7.4	24	0.81	80.9	894.7	29.18	0.56
		3	30.5	7.2	27	0.82	21.2	606.1	18.4	0.33
	p-value for Tukey HSD test									
	Region		**0.00293**	**0.00096**	**0.01465**	0.57106	0.40963	**0.00081**	**0.00235**	**0.00238**
	Disturbance		0.93055	**0.02319**	0.11788	**0.00015**	0.2228	0.10595	0.20609	**0.00245**

Sequencing data processing

A total of 84 libraries (four replicates for each of 21 soil cuts) of 16S rRNA gene were sequenced, resulting in 1768209 reads, which split into 10976 amplicon sequence variants (ASVs) or phylotypes. Minimum reads count per library was 7397, maximum 36229, mean - 21050. Reads not assigned on the phylum level (0.09% of the total count) were deleted from the dataset. From the remaining reads, 96.77% were attributed to class, 87.29% - to order, 70.03% - to family, 40.02% - to genus and 2.11% - to species. Microbiomes of different regions shared more than half (65.3%) of the total read count (Table 2). Microbiomes of benchmark and quarry sites in Progress had more common reads than those from Urvan (85.7% and 55.9%, respectively). The datasets generated and analysed for this study are available under accession numbers SAMN22858222-SAMN22858271 with links to BioProject accession number PRJNA777426 in the NCBI BioProject database (https://www.ncbi.nlm.nih.gov/bioproject/).

Alpha and beta diversity analysis

Alpha diversity indexes, calculated for individual sites, had little variation, but some significant differences were observed. For both regions, we detected significant differences between benchmark and disturbed samples for the inverted Simpson index, which

represents the probability that two randomly-selected sequences belong to different phylotypes (Fig. 2). In both cases, it was higher for quarry sites than for the benchmark. In Urvan, all indexes for separate samples from all sites differed significantly between each other with no relation to disturbance factor, with UQ2 site being the most diverse and UQ1 – the least (Suppl. material 1, Fig. S3). Apart from that, the dispersion of most alpha indexes of samples from Urvan was higher than in Progress. Indexes of alpha diversity allow us to estimate microbiome variation within samples and, in our case, we can assume that microbiome variation from Progress is more consistent across different sites and biological replicates, while from Urvan, it is more diversified.

Table 2.

Distribution of phylotypes (expressed in number of ASVs) between soil samples.

	Total			Urvan			Progress		
	Urvan	Common	Progress	Benchmark	Common	Quarry	Benchmark	Common	Quarry
ASV Count	6113	1625	3238	1917	711	5110	534	1064	3265
% of total reads	20.7	65.3	14	17.4	55.9	26.7	2.9	85.7	11.3

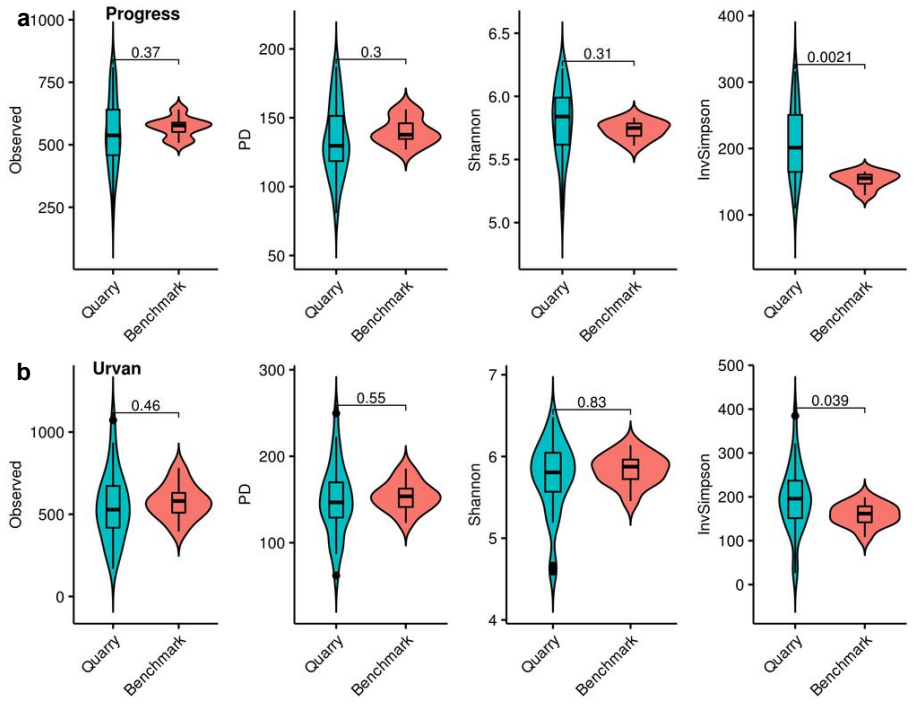

Figure 2.

Alpha diversity in four indexes – Observed, Faith (PD), Shannon, Inverted Simpson for quarry/benchmark sites in different regions.

a: Progress region
b: Urvan region

Unlike alpha-diversity, beta-diversity revealed differences between samples in a more defined manner. PERMANOVA showed that microbiomes of quarry and benchmark samples differ significantly for both regions - with R^2 = 0.26 (p-value = 0.001) for Urvan and R^2 = 0.11 (p-value = 0.002) for Progress. Its values also show that disturbance is a greater factor of explained variability in microbiomes for the soils in Urvan than in Progress. Data visualised by NMDS matches with PERMANOVA, as we can see three distinct groups:

1. Urvan quarry samples UQ1 and UQ2,
2. Urvan benchmark UB and
3. All Progress samples PB, PQ1-PQ3 (Fig. 3).

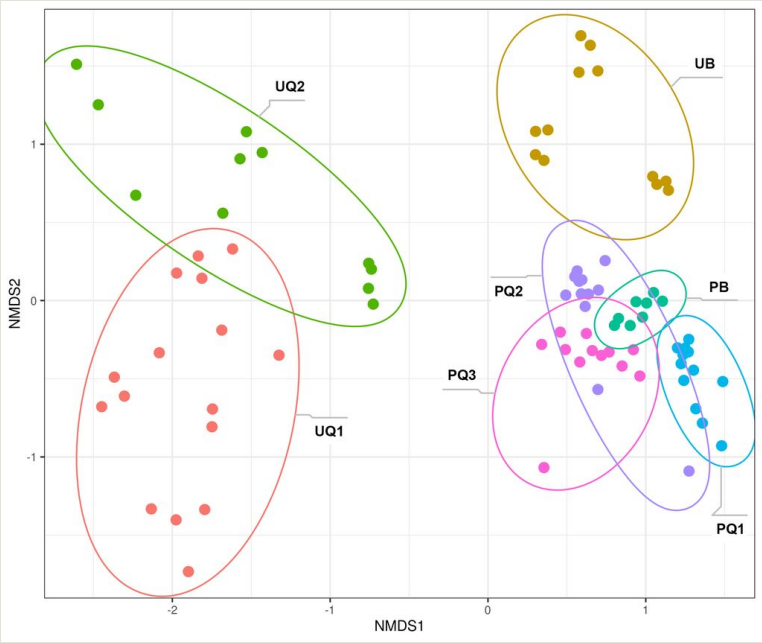

Figure 3.

Beta-diversity of soil sites. Biological and technical replicates of each site are surrounded by ellipses. Urvan: UQ1 and UQ2 – Quarry, UB – Benchmark. Progress: PQ1, PQ2 and PQ3 – Quarry, PB – Benchmark.

For the Urvan region, samples from both quarry pits group closer together, while benchmark samples are separated from them. On the other hand, for the Progress region, separation of microbiomes of benchmark and disturbed soils is less apparent.

Apart from differences between sites, we also investigated differences between biological replicates within one site. Analysis of multivariate homogeneity of group dispersions showed significantly higher distance to centroids values between replicates at Urvan sites (ANOVA p-value < 0.001) than for Progress sites (Suppl. material 1, Fig. S4). Thus, despite similar levels of differences in ecological microniches (variance in vegetation, climate and insolation), dispersion between biological replicates in Urvan was higher than in Progress.

Phylogeny composition

The most abundant phyla across all samples were typical of soil microbiomes - Actinobacteriota, Acidobacteriota, Alpha- and Gamma- proteobacteria, Bacteroidota, Crenarchaeota, Firmicutes, Verrucomicrobiota, Planctomycetota, Chloroflexi, Myxococcota and Gemmatimonadota (Fig. 4). According to the heatmap, the relative abundance of phyla reflects differences between samples like beta-diversity: benchmark (UB) and quarry (UQ1, UQ2) samples from Urvan site demonstrate the difference in quantities of the phyla Bacteroidota, Crenarchaeota, Firmicutes, RCP2-54, Patescibacteria and Entotheonellaeota, while for Progress samples, there is no evident difference in major phyla composition between benchmark (PB) and quarry samples (PQ1-PQ3). As for location-specific phyla, Acidobacteriota, Planctomycetota and Chloroflexi show higher relative abundance in Urvan, while Verrucomicrobiota - in Progress.

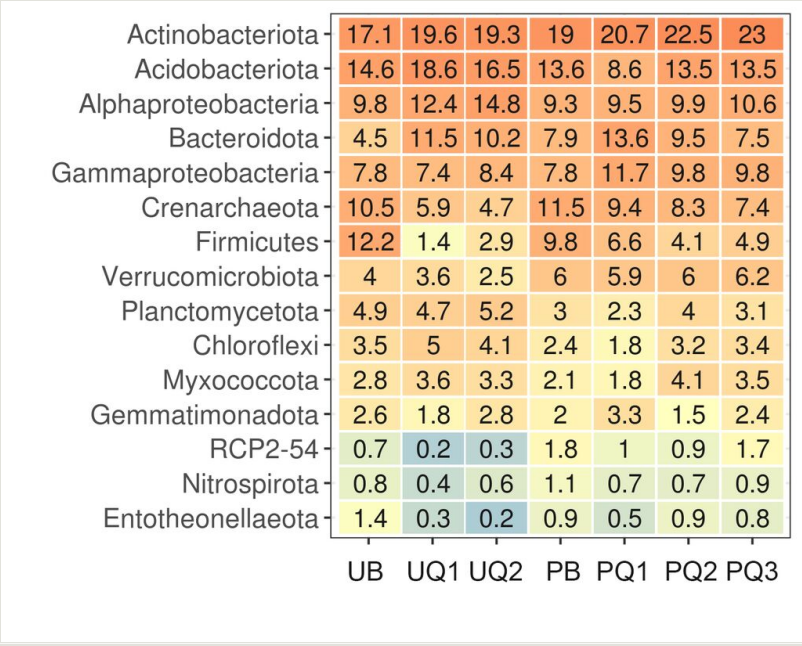

Figure 4.

Heat map of the phyla relative abundance across soil sites. Orange stands for the highest and blue - for the lowest values. Urvan: UQ1, UQ2 – Quarry, UB – Benchmark. Progress: PQ1-PQ3 – Quarry, PB – Benchmark.

On the family level, we still see that major groups are present in all samples, but their abundance differs between samples (Suppl. material 1, Fig. S5). Top taxa are Nitrososphaeraceae and Planococcaceae (higher values at benchmark sites), Chitinophagaceae (higher values at quarry sites), Pyrinomonadaceae, Sphingomonadaceae and Chthoniobacteraceae. Apart from these, Urvan sites have variation in the content of the following families between benchmark and quarry samples: Pseudonocardiaceae, Micromonosporaceae, Beijerinckiaceae, Bryobacteraceae and

Comamonadaceae are more prevalent in the quarries UQ1 and UQ2, while Propionibacteriaceae - in the benchmark UB. For Progress, distribution of families does not seem to be linked to quarry/benchmark distinction, but rather to different quarry sites.

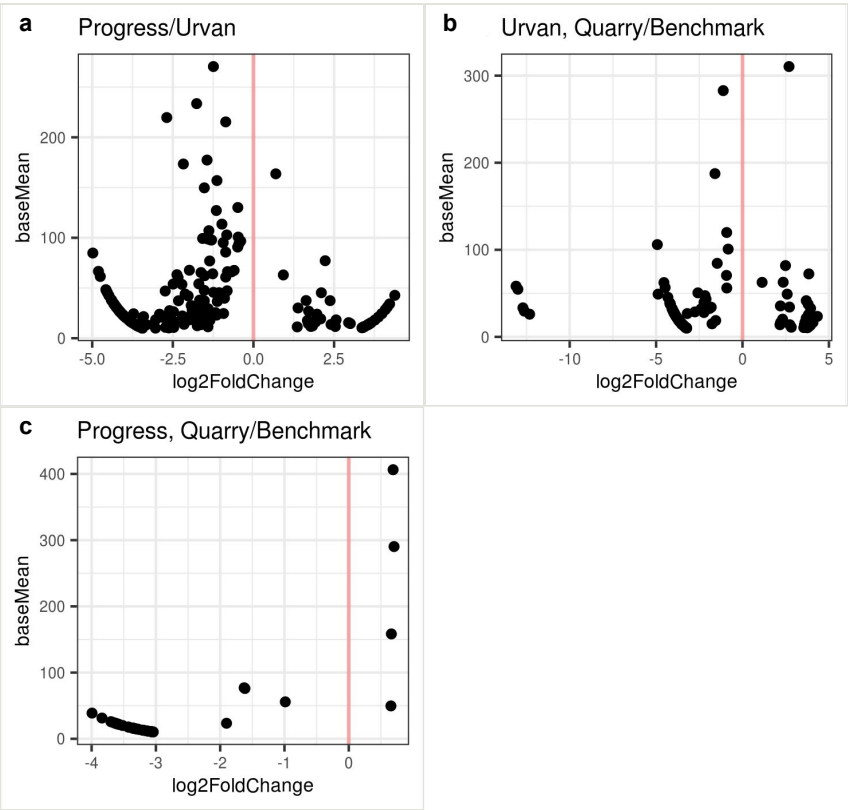

Figure 5.

Plots for DESeq analysis results. Dots represent phylotypes (ASVs), on the Y-axis is their baseMean and, on the X-axis, log2FoldChange value. The further the dot is from zero, the stronger the shift between compared groups, with negative values meaning more of the certain ASV in one group and positive - in the other.

a: Log2FoldChange values between sites from different regions, Progress on the left and Urvan on the right.
b: Log2FoldChange values between quarry and benchmark sites in Urvan, quarry on the left and benchmark on the right.
c: Log2FoldChange values between quarry and benchmark sites in Progress, quarry on the left and benchmark on the right.

Shifts in abundance of phylotypes

Statistically significant differences at the genus level between microbiomes from different sites were assessed by DESeq2 analysis, which estimates dependence between the mean read count (baseMean) and the variance of a phylotype between a set of samples. The

outcome is expressed in a log2FoldChange value, which indicates how much the phylotype abundance has shifted between the compared samples. The higher the modulo value of log2FoldChange, the higher is the shift. Positive or negative values of log2FoldChange indicate the direction in which the shift occurs. We applied DESeq2 to detect shifts between regions (Fig. 5a), quarry and benchmark in Urvan (Fig. 5b), quarry and benchmark in Progress (Fig. 5c).

Only phylotypes with baseMean equal to 10 reads or more were left in the analysis, with log2FoldChange adjusted p-value < 0.05. With this cutoff region, comparisons revealed that there are 45 phylotypes, which are more abundant in Urvan and 164 - in Progress (Fig. 5a, Suppl. material 2, Table S4). The highest modulo values of log2FoldChange are detected for the phylotypes with baseMean < 100 reads, meaning that the highest differences are detected in minor phylotypes. On the contrary, phylotypes with baseMean values exceeding 100 reads have lower log2FoldChange values, meaning they are present in both regions, but most of them are prevalent in Progress. No apparent phylum tends to be more characteristic of any region. Both regions have different prevalent phylotypes from Acidobacteriota, Actinobacteriota, Bacteroidota, Crenarchaeota, Gemmatimonadota, Proteobacteria and others.

Comparisons between benchmark/quarry samples show different phylotype distributions in the two regions. In Urvan, there are 37 phylotypes which are more prevalent in the benchmark samples and 106 - in the quarry (Fig. 5b, Suppl. material 2, Table S5). The most abundant phylotypes in the Urvan benchmark site belong to Acidobacteriota (5), Actinobacteriota (6), Firmicutes (11) and Crenarchaeota (7). Phylotypes from quarry belonged to Acidobacteriota (24), Actinobacteriota (31), Bacteroidota (13), Proteobacteria (19) and Crenarchaeota (6). In Progress, four phylotypes were more abundant in benchmark soil microbiomes, all of which belong to Crenarchaeota; while 33 phylotypes were detected as more abundant in the quarry microbiomes, most of them belonging to Acidobacteriota (3), Actinobacteriota (10), Bacteroidota (8) and Proteobacteria (7) (Fig. 5c, Suppl. material 2, Table S6).

Several trends could be highlighted from the DESeq2 analysis data. Shifts of phylotypes quantities are the most contrasting between regions. Within regions, contrast between quarry and benchmark is more pronounced in Urvan than in Progress. Quarry microbiomes of both Urvan and Progress regions have a larger proportion of minor phylotypes in comparison to benchmark microbiomes. In all comparisons, phylotypes with higher baseMean values had lower modulo values of log2FoldChange, while phylotypes with low baseMeans have higher modulo values of log2FoldChange.

Links between taxonomic composition and soil chemical properties

Canonical Correlation Analysis (CCA) was used to link beta-diversity of microbiomes from all sites with soil chemical properties. Biological replicates of microbiomes from different sites allowed us to build a significant model (ANOVA p-value = 0.002). For this analysis, temperature data were scaled to the deviation from the day's mean to level the differences between sampling days. The most significant factors were pH (p-value = 0.003), OC (p-

value = 0.009), ammonium (p-value = 0.006) and scaled temperature (p-value = 0.032) (Table S7). According to the VIF test, these factors were not multicollinear, meaning their values cannot be linearly predicted from each other and their effect on sample microbiomes in this model was independent (Suppl. material 2, Table S7). Data were visualised on the CCA plot, where arrows point the direction of the factors' influence and dots represent microbiomes or individual phylotypes (Fig. 6). The further the dot is relative to the direction of the arrow, the more the factor explains the variation. If the dot is in the direction opposite to the arrow, then the value of the factor correlates negatively with the composition of the microbiome or the presence of the phylotype. In Urvan, microbiomes of quarry sites UQ1 and UQ2 are mostly affected by pH and ammonium, while those of benchmark UB site are mostly affected by OC. All microbiomes from the Progress site are influenced by nitrates and TC quantities. Progress samples show less dependence on chemical factors than Urvan because they are grouped closer to each other and are closer to the 0.0 point. On the other hand, Urvan samples are quite dispersed far from 0.0. In accordance with the beta-diversity, microbiomes from benchmark and quarry samples from Urvan (UQ1 and UQ2) exhibit more pronounced differences between each other, which can be linked to the influence of chemical parameters, than samples from Progress (PQ1-PQ3), which group closer to each other (Fig. 6a).

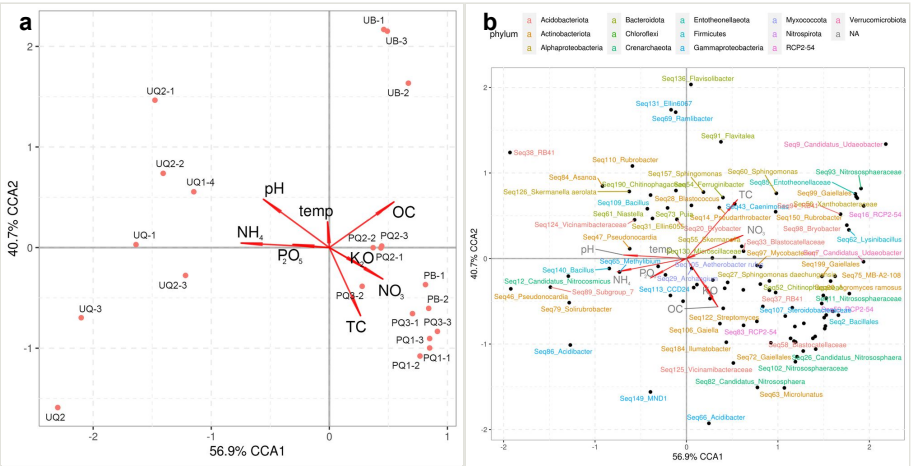

Figure 6.

Plots for CCA analysis, the further the dot is from the arrow, the more it is influenced by the factor. Dot - a microbiome of a single soil cut or a single phylotype. TC – total carbon, OC – organic carbon, temp – temperature scaled to day's mean.

a: Relationship of the microbiome composition of individual sites to soil chemical parameters.
b: Relationship of the top 100 abundant phylotypes (expressed in ASVs) to soil chemical parameters.

The CCA plot on Fig. 6b shows how singular phylotypes in this dataset are affected by chemical factors. The majority of the top 100 abundant phylotypes are dispersed in the direction of OC and nitrates. These include phylotypes from different phyla, the most reactive ones belong to *Bacillus*, Nitrososphaeraceae, *Microlunatus*, *Acidibacter*,

Xiphinematobacter, *Nitrospira* and Gaiellales. Some of these phylotypes match those which are statistically more prevalent in benchmark sites (Suppl. material 2, Table S5 and S6). In the opposite direction of OC, there are phylotypes, associated with the lack of OC. These are RB41, *Ramlibacter*, *Flavisolibacter*, *Asanoa*, *Puia*, *Niastella* and *Briobacter*. Some of these phylotypes are also detected as characteristic of quarry microbiomes by Log2FoldChange analysis. Other factors influence microbiome composition, which could be linked to some other differences between samples, not linked to disturbance or region factors. Such factors include ammonium and nitrates: they influence the microbiome composition in opposite directions, so that phylotypes reacting to the presence on ammonium (*Pseudonocardia*, *Solirubrobacter*, *Acidibacter*) and nitrates (*Udaeobacter*, Nitrososphaeraceae, Gaiellales) could be distinguished.

We also used CCA to show the connection between microscale (chemical parameters) and macroscale (region, disturbance) factors and their influence on microbiome composition. If we put on the CCA plot only phylotypes, significantly changing between regions (detected by DESeq, Suppl. material 2, Table S4), we see that phylotypes split into two groups: the ones from Urvan are on the side of ammonium and pH influence, while on the opposite side, there are phylotypes from the Progress region, which are more influenced by TC and nitrates. Both regions have characteristic phylotypes from Acidobacteriota, Actinobacteriota, Proteobacteria, Crenarchaeota and other phyla.

Fig. S6b (Suppl. material 1) demonstrates the CCA plot with phylotypes that were revealed as statistically different between quarry and benchmark samples for each region by DESeq analysis. Here, phylotypes are located on opposite sides of OC, which is consistent with the fact of correlation between OC quantities and soil disturbance. These phylotypes are mostly from Acidobacteriota, Proteobacteria and Actinobacteriota. Groups corresponding to the presence of OC (Crenarchaeota, Firmicutes) are divided into two: one between OC and ammonium, corresponding to phylotypes from the Urvan benchmark and the other between OC and nitrates, corresponding to the Progress benchmark. Notable, phylotypes with the same taxonomy (Nitrososphaeraceae, Vicinamibacteraceae, Gemmatimonadaceae) can be seen in the groups correlating with both the presence and the absence of OC.

Phylogenic compositional analysis

Analysis of 16S rRNA gene libraries is often based on the negative binomial distribution, which has some limitations. These methods make a Type I error in assessing changes in the microbial community at high taxonomic levels (Lin and Peddada 2020, Nearing et al. 2022). The PhILR transformation offers an approach to overcome statistical artifacts of relative abundance of microbiota and analyse compositional data. It reveals “balances” which allows further investigation into the relating of phylogenetically close microorganisms to different factors. We applied this approach to detect changes in microbiota associated with the disturbance factor from each region. Nine significant balances for Urvan and seven significant balances for Progress were identified. It was shown that, for Progress, significant differences between benchmark and disturbed soils appear at low taxonomic

levels (differences in individual phylotypes within genus or family) (Suppl. material 1, Fig. S7A). In contrast, for Urvan, several balances (n210, n733, n788) show differences at the phylum-class levels (Suppl. material 2, Fig. S7B). The response is especially diverse at different taxonomic levels within the Acidobacteriota phylum. Differences in the phylotype content within the phyla Firmicutes, Chloroflexi, and Verrucomicrobiota is also shown in the quarry sites. These results support previous observations: microbiomes of disturbed, but reclaimed quarry soils in Progress are much more similar to benchmark soil than microbiomes of unreclaimed quarry soils in Urvan.

Discussion

Linking to previous studies

This work is a continuation of the research on the microbiomes of soils from different climate zones, recovering from anthropological damage, primarily mining of parent rock material (Gladkov et al. 2019, Ivanova et al. 2020, Pershina et al. 2020, Zverev et al. 2020, Abakumov et al. 2021, Kimeklis et al. 2021). Here, we explore the area with a moderate continental climate, located in the northern foothills of the Caucasus mountains. The specificity of this study is that we collected samples from the same type of sandy-gravel quarries in close regions (approximately 50 km) with different benchmark soil types. The key difference between sampling sites was that quarry pits at one region (Progress) were reclaimed by backfilling using soil heaps from the overburden Agrisol, while the others (Urvan) were left to passively recover with spontaneous vegetation overgrowth on parent rock material. Thus, we were able to analyse different patterns of microbiome restoration on similar parent rock material in one climatic zone, but with different benchmark soil types and applied reclamation practices.

In our previous studies from the quarries of northern regions, we observed that primary soils of quarries are colonised by photosynthetic bacteria – Cyanobacteria and Chloroflexi (Gladkov et al. 2019, Kimeklis et al. 2021). These microorganisms form biofilms or soil crusts and can successfully colonise substrates deprived of organic carbon resources (Malard and Pearce 2018), but in this work, presence of these groups of microorganisms was minuscule. Perhaps, it can be explained by the overall lower humidity of the southern region and warm arid conditions during the period of sample collecting.

Factors influencing microbiome composition

Factors that influence microbiome composition can be put into hierarchical categories, based on their complexity and scale of effect (Deakin et al. 2018). Large-scale differences, like regions, distance or type of agricultural practice, usually are considered the main factors of microbiome variation (O'Brien et al. 2016, Deakin et al. 2018, Shi et al. 2018). On the other hand, local overgrown vegetation, which is one of the bases of humic layer accumulation (Abakumov et al. 2020), usually creates spatial variations, which translate into microscale differences in microbiomes (Schreiter et al. 2014, Mitter et al. 2017). The same goes for comparisons between seasons and distance - while seasons create

variation due to fast-changing factors, geographical differences explain more of microbial variation (Zhang et al. 2020, Wang et al. 2021). In our study, we detected differences between biological replications caused by microscale factors, like vegetation, insolation or water regime, but they did not overcome diversity created by large-scale factors - region and disturbance. There is evidence that the application of soil reclamation techniques shortens the recovery period and stabilises the microbial community (Hou et al. 2018). Here, we detected the same effect: application of backfilling in the quarries of the Progress region led to a significant reduction in microbiome dispersion and the difference between disturbed and benchmark sites. On the other hand, quarry microbiomes of the Urvan region demonstrated higher distinction from benchmark samples and higher dispersion of biological replicates. This effect can be explained by the fact that, in poor unreclaimed gravel heaps, microbiota has higher sensitivity to microscale spatial variation of nutrients introduced by plants than in primary soils mixed with Agrisol (Naylor et al. 2020, Ayangbenro and Babalola 2021).

Another effect that happens with soil disturbance is the adaptation of microorganisms to the new conditions. It was shown that, in treated soils, relevance of abundant microorganisms (bacteria and fungi) is reduced and the relevance of low-abundance microorganisms is increased (Bossolani et al. 2021), which can happen since conditions have become less favourable for major microbiota and more favourable for the growth of minor microbiota. We observed this effect in both regions: in comparison to benchmark soils, in disturbed soils, major phylotypes decrease their abundance, while higher quantities of minor phylotypes emerge. In Progress, microbiomes of disturbed soils still carried the same major phylotypes from Firmicutes and Crenarchaeota as in benchmark Agrisol, but their quantities were relatively lower. At the same time, disturbed soils carried many minor phylotypes, some of which from cellulose decomposing Chitinophagaceae and Cellulomonas. The presence of these taxa can be linked to the increased content of plant residues, which accumulate in quarry soils due to lack of crop harvesting (Kolton et al. 2013).

Soil chemical parameters and the microbiome

The content of the most measured chemical parameters, including OC, phosphorus and nitrates was low across all sampling sites, which is typical for the local soils (Gorobtsova et al. 2017, Gorobtsova et al. 2021). The acidity of the benchmark and quarry soils corresponds to their genetic features, which is explained by the chemical composition of the mineral waste (Gorobtsova et al. 2016, Gorobtsova et al. 2017, Gorobtsova et al. 2021). In Urvan region, the main difference between benchmark and quarry soils was reflected in carbon content: benchmark soil retained higher percentages of organic carbon, while primary soils of quarries showed high quantities of total carbon, enhanced by parent rock material. Soil cover in Progress reacts differently to the introduction of parent materials: initial Agrisol already has high quantities of carbon, it rises in the freshly reclaimed quarry bottom, but is reduced in older quarry bottoms. Organic matter content reduction in disturbed lands with reclamation was reported earlier (Liu et al. 2017).

Benchmark soil in Progress - Agrisol - was the only soil showing the prevalence of nitrates over ammonium, which is typical for agricultural soils (Cui and Song 2007). This feature is preserved in the mining pit neighbouring the field, which showed signs of recent reclamation with the mixture of rock dumps and soil heaps. In the soil of the older quarry, the balance of nitrates and ammonium shifts back to ammonium prevalence. It could be linked to soil acidic status, nitrate leaching or an introduction of plant residues since crops were no longer being harvested (Dejoux et al. 2000, Miller and Cramer 2005).

Using several biological replicates with varying chemical parameters allowed us to create a reliable model of factors influencing the microbial community. The key factor defining soil disturbance in both regions was OC, which revealed the same phylotypes from the two regions reacting to its content - Nitrososphaeraceae in benchmark soil and Nitrososphaeraceae, Azospirillaceae, Cellulomonadaceae, Vicinamibacteraceae, Nocardioidaceae and Chitinophagaceae in quarries. Members of Azospirillaceae were reported to be associated with plants and to be involved in carbon and nitrogen cycles (Sun et al. 2020). Vicinamibacteraceae from Acidobacteriota were reported to be flexible in their preferred carbon source (Navarrete et al. 2015). Cellulomonadaceae can degrade not only plant residues, but other carbon sources, like DNA and chitin (Stackebrandt and Schumann 2014). Nocardioidaceae are considered mostly chemoorganotrophs (Tóth and Borsodi 2014). Thus, with the lack of easy organic carbon in disturbed soil, microbiomes are becoming enriched by microbiota, flexible to available energy resources.

Traditionally, microorganisms are divided by their life-history strategy into fast-growing copiotrophs (or r-strategs) and slow-growing oligotrophs (K-strategs) (de Vries and Shade 2013). Based on their growth rates, usually gram-minus soil bacteria, like Proteobacteria, Bacteroidota and Gemmatimonadota are treated as copiotrophs, while gram-plus bacteria (Firmicutes, Actinobacteriota) as oligotrophs (Fierer et al. 2007, Zhang et al. 2020). However, this division is quite arbitrary and does not always follow taxonomic division (Ernebjerg and Kishony 2012, Ho et al. 2017, Song et al. 2017). For example, archaea from *Nitrososphaera* are reported to correlate with nitrate composition in soil (Zhalnina et al. 2014), but in our dataset, we found different *Nitrososphaera* phylotypes correlating with contents of nitrates, ammonia and organic carbon. Moreover, *Ramlibacter* representatives were described from poor nutrient desert environments (Heulin et al. 2003) and alongside this fact, we found phylotypes from Gammaproteobacteria - *Ramlibacter* and Ellin6067 - associated with the lack of OC. However, there were also other phylotypes attributed to *Ramlibacter* and *Acidibacter*, associated with the presence of OC. The same trend was detected in Acidobacteriota - phylotypes from Vicinamibacteraceae and Blastocatellaceae were detected in OC-rich soil samples and Vicinamibacteraceae, *Bryobacter* and RB41 in OC-deprived soils. Thus, while the prevalence of a certain phylum in the dataset can be linked to some microbiome-forming factors, our analysis showed once again that phyla are formed by phenotypically paradox lower taxons.

Conclusions

Here, we described factors influencing the microbiome composition of disturbed soils. The disturbance factor acts on the macroscale level and shapes the microbiome of unreclaimed soil in almost the same way as the soil type factor. Vegetation brings diversity on the microscale level and has a higher impact on the unreclaimed soils. Applying reclamation techniques reduces the effect of disturbance and vegetation on the microbiome, but does not eliminate it. Soil chemical parameters help to explain variation for some groups of microorganisms, regardless of macroscale factors. In the Central Caucasus region, soil disturbance can be linked to the loss of organic carbon, which reduces the presence of major representatives of Firmicutes and facilitates the growth of minor representatives from Acidobacteriota, Actinobacteriota, Bacteroidota and Proteobacteria.

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Author contributions

A.K.K. - sampling, DNA isolation, soil chemical data analysis, manuscript preparation, G.V.G. - sampling, microbiome sequencing data analysis, manuscript preparation, R.H.T. – choice of study objects, sampling, A.A.K. - construction and sequencing of the 16S rRNA amplicon libraries, A.G.P. - construction and sequencing of the 16S rRNA amplicon libraries, S.L.H. – manuscript proofreading, E.E.A. – project conceptualisation, manuscript proofreading, E.V.A. – project conceptualisation, manuscript proofreading, funding acquisition. All authors have read and agreed to the published version of the manuscript.

Conflicts of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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