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Wildfire-associated changes in bacterial profiles of annual and perennial plants in the Amankaragai pine forest

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Introduction: Wildfires impact the soil- and plant-associated bacterial communities both directly through temperature shifts and indirectly by altering the physical, chemical, and biological properties. However, knowledge of post-fire soil- and plant-associated bacterial communities in Kazakhstan's strongly continental climate, with pronounced seasonal variability, remains limited. The aim of this study is to investigate how wildfire shapes the diversity of plant-associated bacterial communities and their role in post-fire ecosystem resilience and recovery.

Methods: The study was conducted in the Amankaragai pine forest (Kostanay region, Kazakhstan) 2 years after wildfire. This study provides the first comprehensive analysis of the bulk soil, the rhizosphere, and the root bacterial microbiomes of *Carex supina* Willd. ex Wahlenb., *Calamagrostis epigeios* (L.) Roth, *Conyza canadensis* (L.) Cronquist, *Chenopodium album* L., and *Lactuca serriola* L., comparing control and burn sites.

Results: The wildfire significantly altered the composition of bacterial profiles across all plant-associated microbiomes. Beta diversity was affected across all plant species, while alpha diversity decreased in annual species but remained stable in perennials. Moreover, annual species showed a stronger disturbance response, with more differentially abundant taxa between control and burn sites, than perennial species. Burned sites were enriched with fire-associated bacterial taxa, including *Arthrobacter*, *Pseudarthrobacter*, and *Massilia*.

Discussion: Overall, the results reveal how wildfire alters the taxonomic diversity of soil bacterial communities, highlight differences in the bacterial microbiomes of annual and perennial plants, and provide a basis for assessing post-fire forest soil recovery.

KEYWORDS

16S rRNA gene amplicons, metataxonomics, microbiome, plants, V1–V2 region, wildfire

1 Introduction

Wildfires are a widespread disturbance in terrestrial ecosystems. Soils are particularly affected as their physical, chemical, and biological properties are strongly altered after fires (Köster et al., 2021). These changes include, among others, reductions in pH, soil fertility, and nutrient availability (Bárcenas-Moreno et al., 2011). In turn, they affect biodiversity, leading to either a decrease or an increase in species richness (Li et al., 2024).

In Kazakhstan, forests occupy only approximately 5% of the country's territory (Zhanbossinova et al., 2024). Over the past decade, fires have destroyed approximately 438,000 ha of forest (6,265 cases) (Bureau of National Statistics, 2025). In September 2022, a massive wildfire devastated a large portion of the Amankaragay pine forest in the Kostanay region (Ozgeldinova et al., 2025). According to official statistics, wildfires occur regularly in the Amankaragay pine forest (Forestry and Wildlife Committee Ministry of Ecology, 2026). Therefore, investigating the consequences of wildfires is among the most urgent environmental challenges facing Kazakhstan.

The natural recovery of forest ecosystems is a complex, long-term process (Aerts and Honnay, 2011; Zhanguzhina et al., 2025). It depends not only on fire characteristics but also on the condition of the soil microbiome (Certini, 2005; Rodríguez et al., 2018; Köster et al., 2021), which is a key component of ecosystem resilience. Unlike soil's physical and chemical properties, bacterial communities respond rapidly to disturbances by altering biomass, metabolic activity, and community structure. Wildfires influence the soil microbiome through two primary pathways: directly through heat stress and indirectly via changes in soil physicochemical properties (Rodríguez et al., 2018; Köster et al., 2021). Taken together, these factors lead to reduced abundance and restructuring of microbial communities (including bacteria) with the most pronounced shifts occurring in the upper soil layers directly exposed to heating (Gladkov et al., 2020).

Changes in soil quality caused by wildfires not only severely impact the local plant community but also significantly influence its recovery over time (Ozgeldinova et al., 2025). Two years after the wildfire in the Amankaragay pine forest, a herbaceous community has formed on the burn sites, including *Carex supina* Willd. ex Wahlenb (weak arctic sedge), *Calamagrostis epigeios* (L.) Roth (wood small-reed or bushgrass), *Conyza canadensis* (L.) Cronquist (Canadian horseweed), *Chenopodium album* L. (lamb's quarters), and *Lactuca serriola* L. (wild lettuce), thereafter referred to as *C. supina*, *C. epigeios*, *C. canadensis*, *C. album*, and *L. serriola*, respectively (Sultangazina et al., 2025). These species are common herbaceous (non-woody) plants with both annual (*C. album*, *C. canadensis*, and *L. serriola*) and perennial (*C. epigeios* and *C. supina*) life cycles and with different root structures—taproot for annuals and rhizomatous for perennials (Grefing et al., 1803; Antos and Halpern, 1997; Rebele and Lehmann, 2001; Chadha and Florentine, 2021; Shams et al., 2023). For this study, the aforementioned species were selected to represent both annual and perennial plants as they were consistently present at both control and burn sites in the Kalininsky (KLN) and Novonezhinsky (NVN) forestry units. Plant populations mainly survive repeated disturbances through two key

methods: resprouting from existing tissues and recruiting new seedlings (Pausas and Keeley, 2014). Perennial rhizomatous species (*C. supina* and *C. epigeios*) possess deep-seated renewal buds (Matus et al., 2003; Veselkin et al., 2015; Sultangazina et al., 2025) that maintain the viability of the rhizosphere microbiome even after moderate heat exposure. In annual plants, microbial associations are concentrated in the upper soil horizons (Loster et al., 2011; Sultangazina et al., 2025) and are exposed to more intense heating, which reduces microbial biomass and promotes the formation of new pioneer communities on degraded substrates. Therefore, variations in the depth of renewal organs and the type of plant reproduction can significantly influence the rate and direction of soil microbiome recovery during the post-fire period.

Since soil microbial communities play a key role in post-fire ecosystem functioning (Pérez-Valera et al., 2020), investigating how wildfire alters bacterial communities across soil-plant systems is important. This is particularly relevant in the Amankaragai pine forest, where forest and steppe fires frequently occur due to the climate. The aim of this study is to investigate how wildfire shapes the diversity of plant-associated bacterial communities and contributes to post-fire ecosystem resilience and recovery. For these purposes, bulk soil (BS), rhizosphere (RhS), and root (Rt) samples of *C. supina*, *C. epigeios*, *C. canadensis*, *C. album*, and *L. serriola* were collected 2 years after the wildfire, from both control and burn sites in the Amankaragai pine forest.

2 Materials and methods

2.1 Description of the study area

The Amankaragai pine forest is classified as part of the Ural-Kazakhstan formations, which include steppe-modified and desertified pine and birch forests. It is characterized by herbaceous and shrub-herbaceous vegetation and is geographically associated with the ancient runoff channel of the Abugo--Tobol hydrographic system (Koblanova et al., 2024). The study area has a strongly continental climate with pronounced seasonal variability, long cold winters and short dry summers. The mean annual air temperature is 3.9 °C, and the annual precipitation is 284 mm. Relative humidity is 30%–45%. The soil freezing depth is 40–50 cm. Winters are severe, with frequent snowstorms and stable snow cover. Temperatures can decrease to −47 °C. Summers are hot and dry, with mean daily air temperatures above +20 °C, and temperatures can reach 40 °C–45 °C during extreme heat events. Dry winds and dust storms are common in summer. Spring is short and dry, with rapidly increasing temperatures and strong, dry winds. Autumn is cooler and more humid, with more frequent cloud cover and rainfall (Simanchuk and Sultangazina, 2023). The herbaceous layer is dominated by perennial grasses and sedges, particularly *C. epigeios*, *C. supina*, and *Festuca valesiaca*. It also includes ruderal forbs such as *Artemisia austriaca*, *Elytrigia repens*, and *Chamerion angustifolium*, which are typical of herbaceous pine forest understories (Sultangazina et al., 2025). The area is prone to fires. The fire season lasts approximately 208 days, from April to the end of October. During the warm period, dry, hot weather is

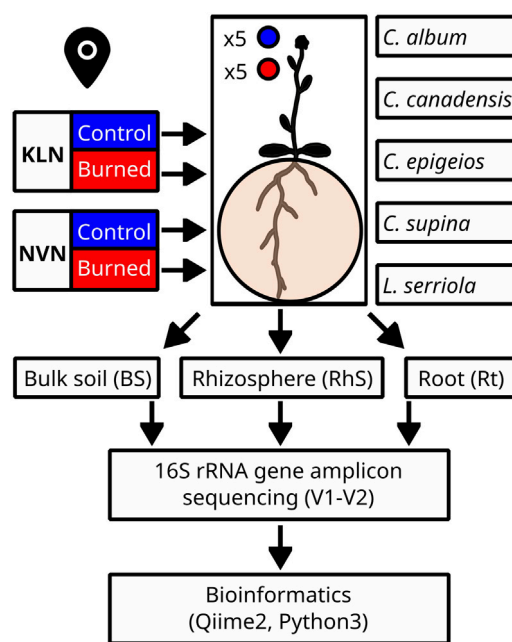


FIGURE 1

Graphical representation of the experimental setup. Soil and roots were collected together from five plant species (*C. supina*, *C. epigeios*, *C. canadensis*, *C. album*, and *L. serriola*), at both burn and control sites. Each plant species was represented by five biological replicates ($n = 5$) for each unit/site combination, resulting in 100 field samples. These were later separated by sample type (roots, rhizosphere, and bulk soil), yielding a total of 300 laboratory samples.

typical, and forest and steppe fires occur more frequently (Zhanguzhina et al., 2025).

2.2 Sample collection

The study was conducted in KLN and NVN forestry units, located within the Amankaragai pine forest under the Semiozornoe Forestry Enterprise. Sampling was conducted on 25 June 2024 in areas affected by a large wildfire that occurred between 2 September 2022 and 10 September 2022. The wildfire burned a total of 29,392.4 ha, including 26,804.5 ha of forest land (24,919.8 ha forested and 2,587.9 ha non-forested). However, the present study was conducted at a local scale within these two selected forestry units rather than across the entire burn, with sampling restricted to localized plots. Both forestry units include control (52°24′36.93″N, 64°12′19.80″E for KLN and 52°30′19.55″N, 64°04′15.49″E for NVN) and burn (52°24′29.41″N, 64°12′20.02″E for KLN and 52°28′18.26″N, 64°05′46.61″E for NVN) sites. According to data from the Semiozornoe forestry enterprise, the two forestry units were affected by both crown and ground intense fires.

Sampling was conducted within 2–10 m² frames at both control and burn (affected by both crown and ground intense fires) sites in each forestry unit. All samples were collected using a sterilized stainless steel spade. Field sampling was performed using sterile gloves, and all instruments were sterilized prior to sampling to minimize contamination. Soil and root materials were collected together from the 10–15-cm soil layer by excavating the root zone of each selected plant. Each field sample consisted of approximately

20 g of material (soil and associated root system) collected from an individual plant (Figure 1). Each individual plant yielded a single field sample. Visible plant debris was removed prior to processing. Five plant species (*C. supina*, *C. epigeios*, *C. canadensis*, *C. album*, and *L. serriola*) were selected based on their high abundance and consistent presence at both burn and control sites. For each of the collected plant species, one representative was included into the herbarium collection “TOBYLKZ” (Supplementary Figure S1). Each plant species was represented by five biological replicates ($n = 5$), with each replicate corresponding to a single individual plant. Individuals were sampled opportunistically within the plots, and no fixed inter-plant distance or systematic spatial design was applied. In total, 100 field samples (each field sample contained three sample types: roots, rhizosphere, and bulk soil) were collected across two forestry units, two site types (burn and control), five plant species, and five replicates per species. Samples were transported in an insulated cooler bag with cold packs and spent outside the freezer up to 48 h due to issues associated with the sampling location and logistics. Thereafter, they were preserved at -80°C until DNA extraction.

Soil samples for the assessment of physicochemical properties were collected and processed as described in the Supplementary Material, directions “1. Measurements of Soil Physicochemical Properties” and “2. Soil Physicochemical Properties.”

2.3 DNA extraction

For DNA extraction, samples were thawed on ice and divided into three sample types: BS (bulk soil, loosely attached to roots), RhS

(rhizosphere soil, tightly adhering to the root surface), and Rt (fine roots) (Figure 1B). RhS was obtained by gently shaking the roots to remove loosely attached soil, while the detached soil was collected as BS. Prior to DNA extraction, Rt samples were washed with 200 μ L of Milli-Q water and cut into small fragments (~0.2–0.5 mm in length). Each field sample was processed individually. After separation by the sample type, 100 field samples yielded a total of 300 laboratory samples. Total DNA was extracted using the FastDNA SPIN Kit for Soil (MP Biomedicals, Eschwege, Germany). Before extraction, the Rt samples were washed with 200 mL of Milli-Q water and cut into small fragments (0.2–0.5 mm in length). The suspension was vortexed, transferred into Lysing Matrix E tubes provided in the FastDNA SPIN Kit, and subjected to the standard extraction protocol. For each fraction, 500 mg of material was mixed with 978 μ L of sodium phosphate buffer (provided with the kit) and 122 μ L of MT buffer in Lysing Matrix E tubes. The mixture was homogenized using a FastPrep® instrument for 40 s at a speed setting of 6.0. This homogenization step was performed twice with a 3-min cooling interval on ice between runs. All subsequent steps involving proprietary reagents and spin filters were performed according to the manufacturer's instructions. DNA was eluted in 60 μ L of DES solution (provided in the kit) and stored at -20°C .

The concentration (A260) and purity (A260/230 and A260/280 ratios) of the extracted DNA were determined spectrophotometrically using a NanoDrop spectrophotometer (Thermo Fisher Scientific, Waltham, MA, United States).

2.4 Illumina amplicon sequencing

Library preparation, including PCR amplification, purification, and equimolar pooling of samples for amplicon sequencing of the V1–V2 region of the 16S rRNA gene, was performed as previously described (Camarinha-Silva et al., 2014). The V1–V2 region was amplified using primers 27F (AGA GTT TGA TYM TGG CTC AG) and 338R (GCT GCC TCC CGT AGG AGT). The first PCR was performed in 20 μ L reactions containing 4 μ L of 5 $\times$ PrimeStar buffer (TaKaRa Bio Inc., Kusatsu, Japan), 1.6 μ L of dNTP mix, 0.5 μ L of each primer (1:10 diluted), 0.2 μ L of PrimeSTAR HS DNA Polymerase (250 U, TaKaRa Bio Inc.), 1 μ L of PCR enhancer (BioStab PCR Optimiser (II), Sigma-Aldrich®, Merck KGaA, Darmstadt, Germany; used only in the first PCR), and 1 μ L of template DNA. Thermocycling conditions consisted of an initial denaturation at 95°C for 3 min, followed by 10 cycles of denaturation at 98°C for 10 s, annealing at 59°C for 10 s, and extension at 72°C for 45 s, with a final extension at 72°C for 2 min. One microliter of the first PCR product was used as a template in the second PCR (15 cycles), which was performed under the same cycling conditions. In this step, the forward primer contained a six-nucleotide barcode (Hamady et al., 2008) and a two-nucleotide GT linker (Meyer and Kircher, 2010). The third PCR (20 cycles) was performed in a 50 μ L reaction under identical conditions, using primers incorporating Illumina multiplex sequencing adapters and index primers (Camarinha-Silva et al., 2014). Amplicons were checked by 1.5% agarose gel electrophoresis, normalized using the SequalPrep™ Normalization Kit (Applied Biosystems), and purified using the MinElute PCR Purification Kit (Qiagen).

Sequencing was performed by Novogene Company Ltd. (Cambridge, UK), on an Illumina MiSeq platform using 250 bp paired-end chemistry.

2.5 Statistical analysis and bioinformatics

Raw 16S rRNA gene amplicons were demultiplexed using Sabre (<https://github.com/najoshi/sabre>) and further analyzed in Qiime2 (Bolyen et al., 2019). Primers were trimmed using the q2-cutadapt plugin (Martin, 2011). Denoising, quality filtering, merging of paired reads, and removal of chimeras were performed using q2-dada2 (Callahan et al., 2016), which produced amplicon sequence variant (ASV) counts and representative sequences. Taxonomic assignment of representative sequences was performed using VSEARCH-based consensus (Rognes et al., 2016) and pre-fitted sklearn-based (Pedregosa et al., 2011) classifiers with the SILVA database (version 138.2, 99% identity) (Quast et al., 2013). ASVs detected in only one sample or with a total frequency across all samples less than 10 were removed, along with ASVs taxonomically assigned to organelles (mitochondria and chloroplasts). Reference reads and taxonomies were accessed and preprocessed using RESCRIPt (Robeson et al., 2021), which included obtaining reference sequences and taxonomy, along with their dereplication and “cooling” (filtering based on the number of allowed IUPAC-compliant degenerate bases, with a default value of 5). Alpha diversity was assessed using Shannon's entropy (Shannon, 2001) and Faith's phylogenetic diversity (further Faith's PD) (Faith, 1992) indices, and beta diversity was evaluated using robust Aitchison distances (Martino et al., 2019) with the Gemelli q2-plugin. Alpha diversity metrics were compared using the Kruskal–Wallis test (Kruskal and Wallis, 1952), and beta diversity distances were assessed using the Adonis test (999 permutations) (Anderson, 2001). All P-values obtained from multiple comparisons were adjusted using the Benjamini–Hochberg procedure (Benjamini and Hochberg, 1995) and referred to as “P-adj.” Differentially abundant genera [only for counts of genera with relative abundance $\geq 1\%$ and prevalence $\geq 10\%$; P-adj < 0.05 , LFCs (log fold changes, or estimated differences in the natural log) ≥ 2] were detected using ANCOM-BC2 (Lin and Peddada, 2024).

3 Results

3.1 ASV denoising and filtering

After primer removal and denoising, all samples retained a relatively high number of reads, with a minimum of 7,783 and a median of 24,896, along with 81,824 unique ASVs with a total frequency of 7,975,990 across the whole dataset (300 samples). After additional filtering based on the ASV frequency and prevalence (ASVs with frequency < 10 and those detected only in one sample were discarded), along with the removal of ASVs assigned to organelles (mitochondria and chloroplasts), a total of 30,546 unique ASVs were retained for downstream analyses, with a frequency of 7,447,966 across all the samples. The minimum frequency among all the samples was 7,016, which was chosen as the

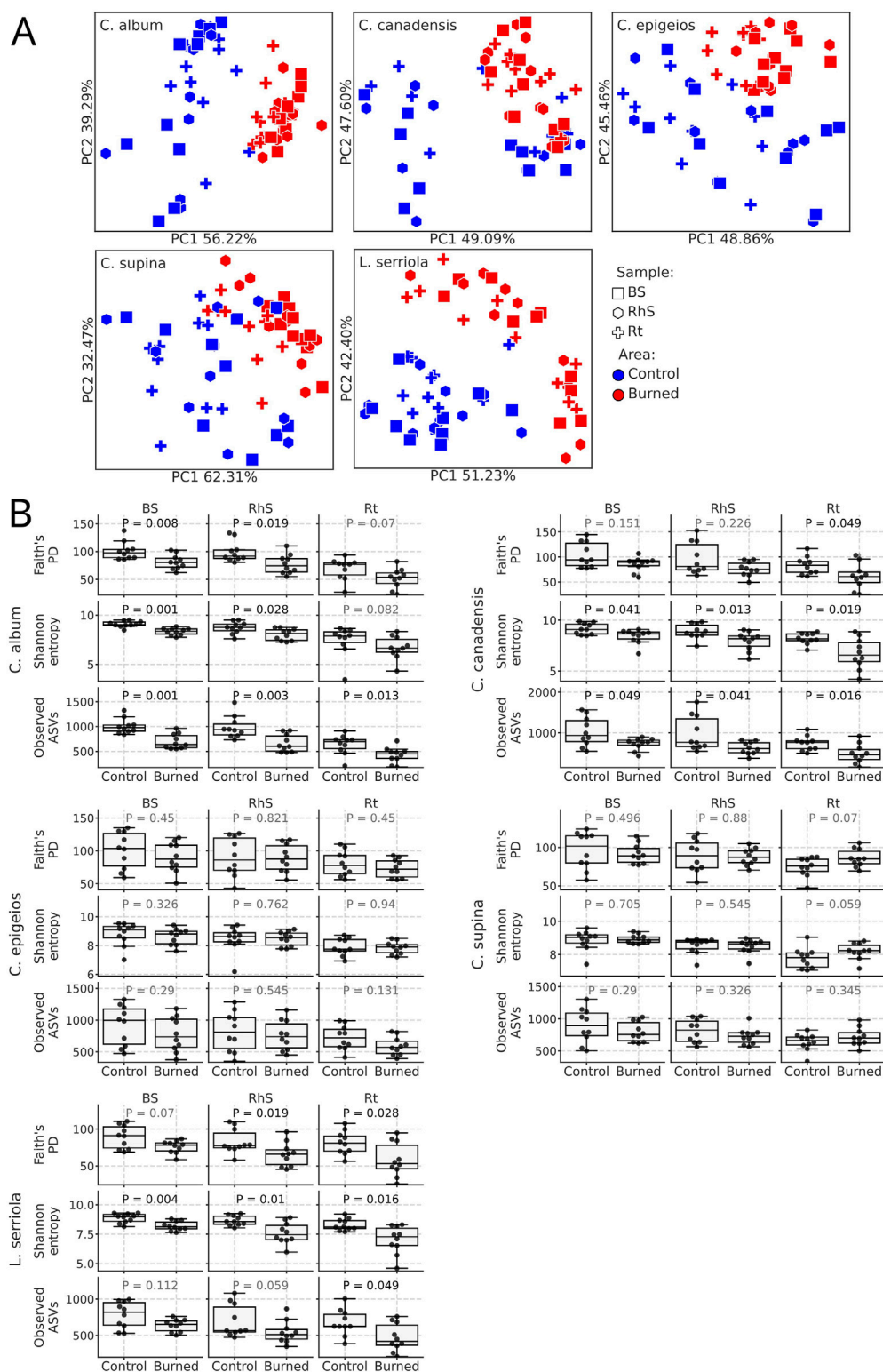


FIGURE 2

Composition and diversity of collected samples by plant species. (A) PCoA plots based on robust Aitchison distances. (B) Boxplots and dotplots representing alpha-diversity metrics (Shannon's entropy, Faith's phylogenetic diversity, and observed ASVs). P-values of the Kruskal–Wallis test are plotted at the upper part of the subplots.

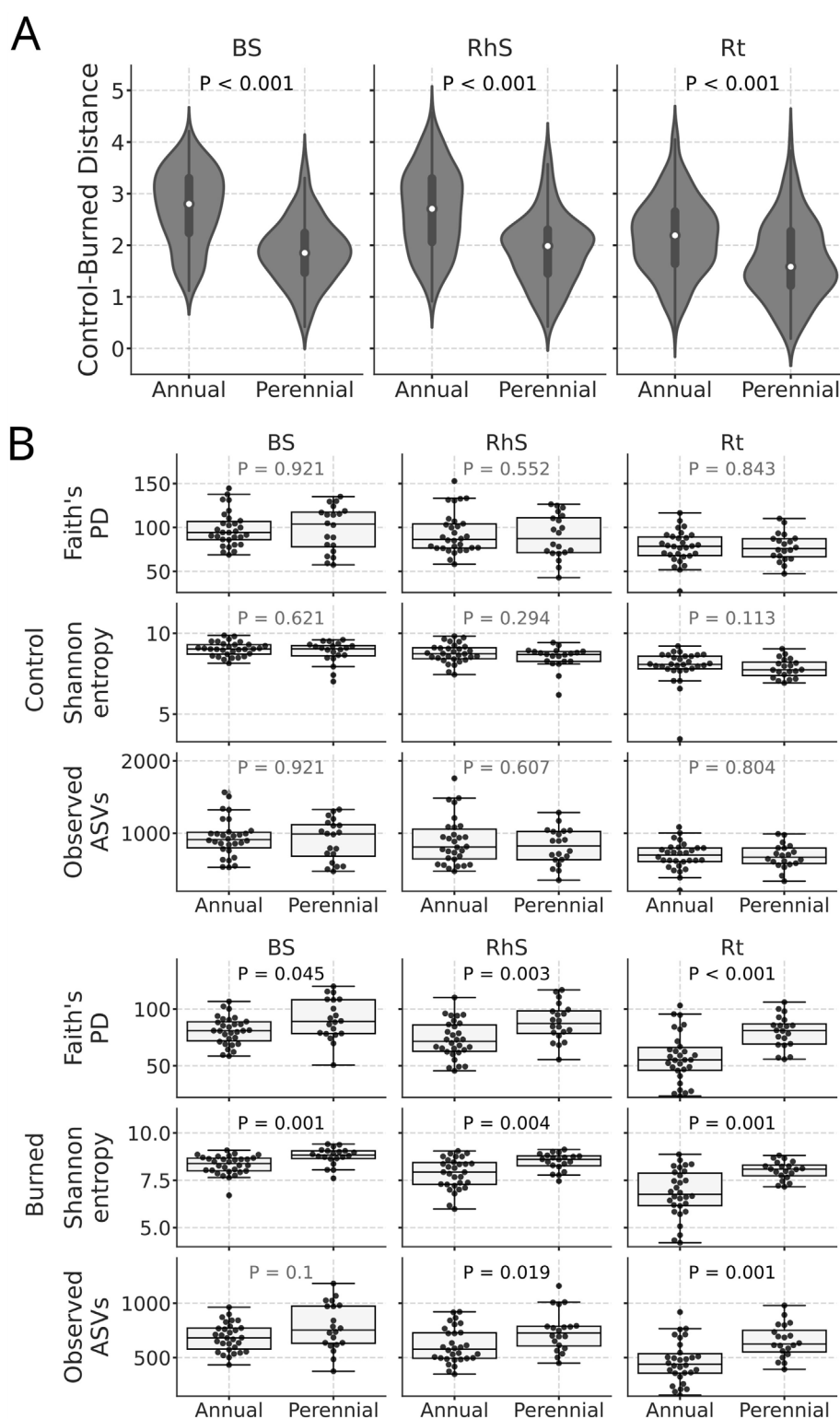


FIGURE 3

Control-to-burn distances and alpha diversity of annual and perennial plants. (A) Control-to-burn distances based on robust Aitchison distances. (B) Boxplots and dotplots representing alpha-diversity metrics (Shannon's entropy, Faith's phylogenetic diversity, and observed ASVs). P-values of the Kruskal–Wallis test are plotted at the upper part of the subplots.

sampling depth for diversity estimation. Alpha rarefaction curves demonstrated that the chosen sampling depth was sufficient for analyses (Supplementary Figure S2).

3.2 Wildfire shaped bacterial community

To investigate the effect of the wildfire on the bacterial composition of collected samples, an Adonis test was performed on robust Aitchison distances. It revealed that plant species and burn status were the factors affecting bacterial composition (all $P \leq 0.001$), whereas sample type was not ($P = 0.13$). Pairwise comparisons between plant species (with “Burn status” as covariate) revealed that bacterial composition of *C. supina* and *C. epigeios* was distinct from that of other plant species (all $P\text{-adj} \leq 0.002$). All other plant species comparisons, including *C. supina* vs. *C. epigeios*, yielded insignificant differences (all $P\text{-adj} > 0.1$).

Further analyses were performed separately for each plant species (Figure 2A). Across species, burn status shaped bacterial composition (all $P \leq 0.001$, $R^2 \geq 0.226$). In addition, when separated by plant species, the sample type was a significant driver of bacterial community composition in all species (all $P \leq 0.017$, $R^2 < 0.1$), except for *C. album* ($P = 0.101$, $R^2 = 0.011$). However, pairwise comparisons detected differences only between the Rt and BS samples of *C. supina* ($P\text{-adj} = 0.012$) and *C. epigeios* ($P\text{-adj} = 0.03$).

Alpha diversity was assessed using Shannon entropy, Faith's PD, and observed ASVs and compared based on the burn status by plant species and sample types using the Kruskal–Wallis test (Figure 2B). In all the sample types from *C. supina* and *C. epigeios*, no differences between control and burn sites were detected for all three metrics (all $P\text{-adj} > 0.05$). Among the *C. album* samples, both Shannon entropy and Faith's PD were higher at the control site than at the burn site among BS and RhS samples (all $P\text{-adj} \leq 0.028$), with no statistical differences in Rt samples (all $P\text{-adj} \geq 0.07$). At the same time, the number of observed ASVs was consistently higher in the control in all sample types (all $P\text{-adj} \leq 0.013$). Independent of the sample type, Shannon entropy of *C. canadensis* and *L. serriola* was higher in the control than at the burn site (all $P\text{-adj} \leq 0.041$). Faith's PD was also higher in the control samples than in the samples from the burn for *C. canadensis* ($P\text{-adj} = 0.049$) and *L. serriola* ($P\text{-adj} = 0.028$) Rt samples and *L. serriola* RhS samples ($P\text{-adj} = 0.019$). Similar to *C. album*, the number of observed ASVs in *C. canadensis* samples was higher in the control, regardless of sample type (all $P\text{-adj} \leq 0.049$), while in *L. serriola* samples, such a difference was found only in the Rt ($P\text{-adj} = 0.049$).

Additional analyses were conducted to determine whether the plant life cycle (*C. album*, *C. canadensis*, and *L. serriola* as annual and *C. epigeios* and *C. supina* as perennial) affects the bacterial microbiome differently at the burn and control sites. For each plant species and sample type, control-to-burn robust Aitchison distances were calculated and compared between annual and perennial plants, with perennial plants yielding shorter distances regardless of the sample type (all $P\text{-adj} < 0.001$; Figure 3A). Moreover, when separated based on burn status and evaluated by the sample type, all tested alpha diversity metrics (Shannon entropy, Faith's PD, and observed ASVs) revealed no differences based on the life cycle in the control (Figure 3B). In contrast, in the burns, the same metrics were higher within each sample type in perennial

plants than in annual plants (all $P\text{-adj} \leq 0.045$), with the exception of observed ASVs in BS ($P = 0.1$).

3.3 Burn status affected dominant bacteria

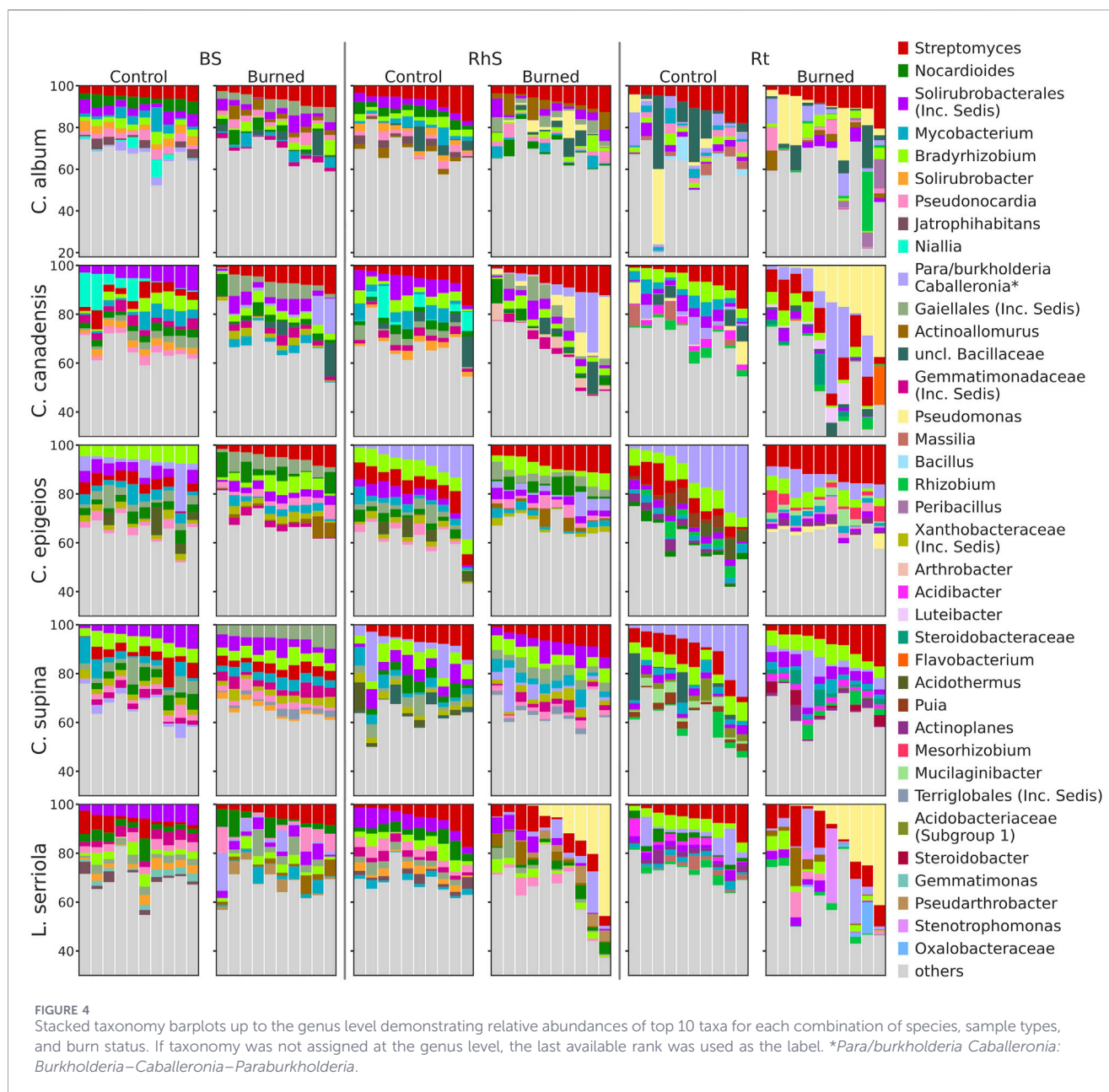
To investigate the effect of wildfire on bacterial profiles, we plotted the relative abundances of the top 10 taxa for each combination of plant species, sample type, and burn status.

As shown in the taxonomy barplots (Figure 4), there were some shifts in the relative abundances of dominant bacterial taxa between the control and burn sites. For example, among *C. album* samples, *Streptomyces* was the dominant genus, regardless of the sample type and burn status. In *C. canadensis* BS samples, the first and third genera by dominance from the control site—*Solirubrobacterales* (Inc. Sedis) and *Streptomyces*—reversed their positions at the burn site, with *Streptomyces* accounting for most of the reads and *Solirubrobacterales* (Inc. Sedis) being reported as third based on the relative abundances. In the RhS samples, as in *C. album*, *Streptomyces* was the dominant genus independent of burn status. In the Rt samples of the same plant, the dominant position of *Streptomyces* in the control was replaced by *Pseudomonas* in the burn. In the *C. epigeios* samples, the *Streptomyces* genus was dominant, regardless of sample type from the burn. In contrast, in the control BS samples, *Bradyrhizobium* was dominant, while *Burkholderia*–*Caballeronia*–*Paraburkholderia* dominated in Rt and RhS samples. Similarly to *C. epigeios*, in *C. supina* RhS samples, *Burkholderia*–*Caballeronia*–*Paraburkholderia* dominated in the control but was replaced by *Streptomyces* in the samples from the burn site, which was also dominant in the Rt samples of the same plant species, regardless of burn status. In the *C. supina*-related BS samples, *Solirubrobacterales* (Inc. Sedis) was most abundant in the control, and *Gaiellales* (Inc. Sedis) in the burn site. The *Streptomyces* genus, which most frequently dominated the bacterial communities of other plant species, was also the most abundant in *L. serriola*-related samples in BS samples from the burn, along with Rt and RhS samples from the control. *Solirubrobacterales* (Inc. Sedis) dominated in BS samples related to the same species in the control, along with *Pseudomonas* in Rt and RhS samples taken from the burn site.

3.4 Differentially abundant genera by burn status

Species *L. serriola* exhibited the highest total number of unique differentially abundant bacterial taxa (26) when burn status was compared within each sample type (Figure 5A). Other plant species exhibited fewer taxa that were differentially abundant by burn status (*C. album*—18, *C. canadensis*—12, *C. epigeios*—11, and *C. supina*—1).

All differentially abundant taxa, regardless of the plant species and sample type, were divided into two groups: those more abundant in the burns and those more abundant in the control (Figure 5B). *Pseudarthrobacter*, *Pseudomonas*, and *Arthrobacter* were three genera that reacted the most to the wildfire and were more abundant in samples from the burn site than those from the control. *Pseudarthrobacter*, whose LFC ranged from 3.3 to 5.2, was



more abundant in samples from *C. epigeios* and *L. serriola*, regardless of the sample type. *Pseudomonas* (LFC = 2.6–4.8) was detected as differentially abundant in *C. canadensis* (RhS samples), *C. epigeios* (RhS and Rt), and *L. serriola* (BS and RhS). Finally, *Arthrobacter* (LFC = 3.5–4.1) was differentially abundant in *C. album* (BS) and *L. serriola* (BS, RhS, and Rt). Among other bacterial taxa that increased their abundances in burn samples compared to the control and independent from the plant species were unclassified *Streptosporangiaceae*, *Leifsonia*, *Paenarthrobacter*, unclassified *Pyrinomonadaceae*, *Rhodococcus*, unclassified *Micrococcaceae*, *Methylothermus*, *Massilia*, *Fictibacillus*, *Plantibacter*, *Neobacillus*, *Fibrobacteraceae* (genus 04), *Acidobacteriaceae* (Inc. Sedis), *Pantoea*, *Gaiella*, unclassified *Xanthobacteraceae*, *Shimazuella*, *Myxococcota* (Inc. Sedis), *Paenibacillus*, unclassified *Hyphomicrobiales*, *Mucilaginibacter*, *Saccharimonadales* (Inc. Sedis), *Cohnella*, and

Burkholderia–Caballeronia–Paraburkholderia. The exact LFC values, along with the tested sample type and plant species, are indicated in Figure 5.

Among all the taxa that were more abundant in the samples from the control, three taxa with the greatest change were *Parafilimonas* (*C. album* BS and RhS, LFC = 4.3–4.4), *Amycolatopsis* (all sample types of *C. album*, LFC = 4–4.2), and *Actinomyces* (all sample types of *C. album* and RhS of *L. serriola*, LFC = 3.1–4.5). Other taxa that were more abundant in any of the sample types from the control site than those from the burn site include *Chitinophaga*, *Sporosarcina*, *Roseiflexaceae* (Inc. Sedis), *Niallia*, *Crossiella*, *Niastella*, *Rubrobacter*, *Rhizobacter*, *Acetobacteraceae* (Inc. Sedis), *Edaphobacter*, *Aggregatilineales* (Inc. Sedis), *Lysinibacillus*, *Thermoanaerobaculaceae* (S10), *Rhodanobacter*, *Polyangiales* (Inc. Sedis), *Kineosporia*, *Microtholus*,

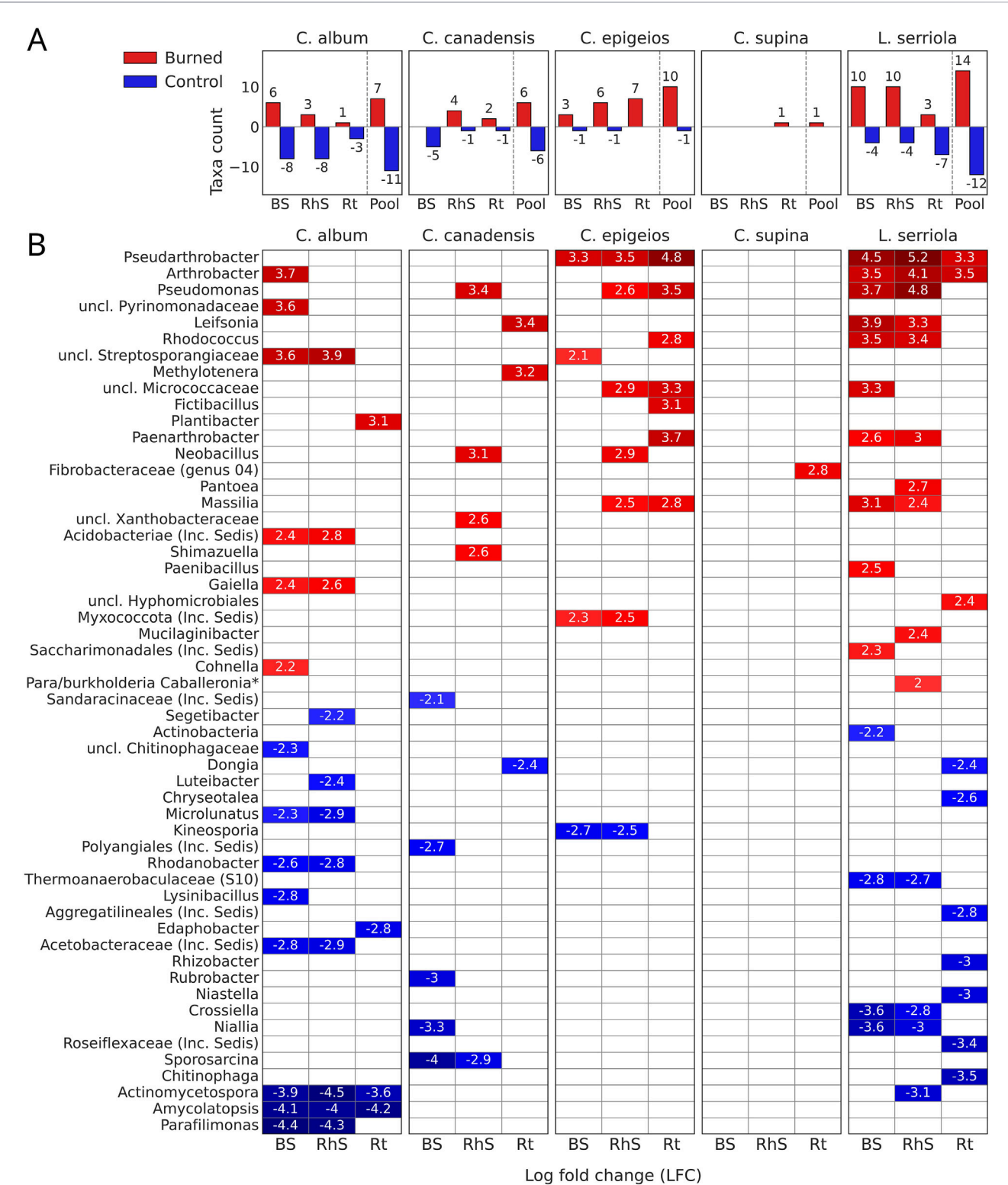


FIGURE 5 Differentially abundant taxa up to the genus level (ANCOM-BC2). **(A)** Counts of differentially abundant taxa by sample type and species. “Pool” represents the number of unique differentially abundant taxa for each plant species, regardless of the sample type. **(B)** Log fold changes (LFCs) of differentially abundant genera ($P\text{-adj} < 0.05$, $LFC \geq 2$). Only taxa with relative abundance $\geq 1\%$ and prevalence $\geq 10\%$ were used for comparisons. Negative (blue background) values represent LFC values of features, more abundant in the control, while positive LFC (red background) are more abundant in the burn sites. If taxonomy was not assigned at the genus level, the last available rank was used as the label. **Para/burkholderia Caballeronia*: *Burkholderia*–*Caballeronia*–*Paraburkholderia*.

Chryseotalea, *Luteibacter*, *Dongia*, unclassified *Chitinophagaceae*, *Actinobacteria*, *Segetibacter*, and *Sandaracinaceae* (Inc. Sedis).

4 Discussion

4.1 Bacterial diversity in perennial plants is more fire-resistant than in annuals

Two years after wildfire, bacterial diversity differed between annual and perennial plants, indicating contrasting responses of plant-associated microbial communities to fire disturbance. These differences were reflected in alpha-diversity metrics, with perennial plants exhibiting greater bacterial community stability than annual plants.

Among annual species (*C. canadensis*, *C. album*, and *L. serriola*), differences in at least one of the tested alpha-diversity metrics between the burn and control sites were detected across all sample types, with samples from the burn site showing lower diversity. These observations are consistent with those from other studies reporting a decrease in alpha-diversity metrics at burn sites (Nelson et al., 2022; Macias et al., 2025).

In contrast, no such differences by burn status were observed among perennial species (*C. epigeios* and *C. supina*). Moreover, when samples were separated by burn status, no differences in alpha diversity were detected between annual and perennial plants at the control site, regardless of the sample type. At the same time, in samples from the burn site, alpha-diversity metrics were higher in all sample types of perennial plants than those of annual plants.

In addition to alpha diversity, control-to-burn robust Aitchison distances were greater for annual plants than for perennials, indicating stronger differences in bacterial composition. Taken together, these findings suggest that the bacterial diversity of perennial species is more resilient to fires than that of annual plants.

4.2 Perennials preserved bacterial taxa and their abundances through the fire

Differences in the responses of annual and perennial plant microbiomes were also confirmed using a differential abundance test. When comparing control and burn sites, perennial plants exhibited fewer differentially abundant taxa than annuals. Only one bacterial taxon showed a difference in abundance when comparing *C. supina* samples: unclassified *Fibrobacteraceae* (genus 04) was more abundant in root samples from the burn site. The same test identified 11 differentially abundant taxa in *C. epigeios* samples, with only one taxon, *Kineosporia*, being more abundant in samples from the control site. This indicates that although some bacterial taxa in burn site samples were absent or underrepresented in the control site, most bacteria in the control site samples retained their abundances in the burn site plants. Annual species showed higher numbers of differentially abundant taxa by burn status, including those that were more abundant in the control site (from 6 to 12).

The lower number of between-sites differentially abundant taxa in perennial species, together with the absence of differences in alpha-diversity metrics associated with burn status, indicates that bacterial communities in perennial species were preserved through the fire. We

assume that deep renewal buds of perennial plants served as a microbiota reservoir and therefore contributed to faster recovery not only of the root and rhizosphere bacterial profiles but also of the bulk soil due to the “microhabitat effect.” However, this assumption should be confirmed by further studies. In contrast, the bacterial microbiomes of annual species were more affected by fire-related changes as they utilize soil as a seed bank to shape the rhizosphere and, consequently, their root microbiomes (Ling et al., 2022).

4.3 Differentially abundant taxa by burn status

Among the taxa that were more abundant in the burn site than in the control, the greatest changes were exhibited by *Pseudarthrobacter* (in *C. epigeios* and *L. serriola*) and *Arthrobacter* (*L. serriola* and *C. album*). Both genera are known as “fire-favored” bacteria (Fernández-González et al., 2017; Fernández-González et al., 2024). Additionally, *Arthrobacter* and *Massilia*, which were also more abundant in burn sites, have been identified as long-term biomarkers of fire-induced dysbiosis (Whitman et al., 2022; Fernández-González et al., 2023). It is known that wildfires may lead to the accumulation of heavy metals in the soil (Ozgeldinova et al., 2025), including hexavalent chromium (Lopez et al., 2023), along with organic compounds such as levoglucosan, which is produced by burning biomass (Bhattarai et al., 2019). Among other taxa that were more abundant in samples from the burn site are *Leifsonia*, *Paenarthrobacter*, *Rhodococcus*, *Methylobacter*, *Fictibacillus*, *Neobacillus*, *Pantoea*, *Paenibacillus*, *Mucilaginibacter*, and *Cohnella*. Three of them, *Paenarthrobacter* (Kaur et al., 2023), *Paenibacillus* (Arya et al., 2022), and *Rhodococcus* (Xiong et al., 2016), have been shown to degrade levoglucosan, aiding in post-fire soil recovery. Other bacterial genera, such as *Pseudomonas* (Bhattacharya et al., 2015) and *Pantoea* (Ozdemir et al., 2004), are reported to remove hexavalent chromium or have been detected in areas with high levels of it, including *Methylobacter* (Zhu et al., 2023). *Leifsonia* (Kang et al., 2017), *Neobacillus* (Bakkali Bouarrakia et al., 2023), and *Mucilaginibacter* (Li et al., 2022) are known for their ability to tolerate high contents of heavy metals. Finally, *Paenarthrobacter* (Niza Costa et al., 2023), *Pseudomonas* (Niza Costa et al., 2023), *Fictibacillus* (Enright et al., 2022), *Mucilaginibacter* (Brown et al., 2019), and *Cohnella* (Villadas et al., 2019) were found to be more abundant in the burn site.

As shown in the literature, most bacterial taxa that were more abundant in our control-site samples were already known to favor fire-affected territories. Those taxa were detected in both perennial and annual plants, suggesting that the bacterial microbiomes of both plant groups were affected by fires. However, only one bacterial genus, *Kineosporia*, was reported to be more abundant in the control site among perennial plant bacterial profiles. A greater number of such genera observed in annual plants (27 in total) highlights differences between perennial and annual plants in their responses to fire.

4.4 Study limitations

In this study, metataxonomic analyses were performed targeting the 16S rRNA gene, and no ITS amplicons were sequenced. As a

result, this study is limited to the bacterial microbiome and does not provide insights into changes in fungal or archaeal communities. Moreover, samples were collected at a single time point, without assessing the temporal dynamics of bacterial communities. Although most studies in the field targeted the V3–V4 region of the 16S rRNA gene, we selected the V1–V2 region to avoid potential “off-target” amplification (Deissová et al., 2023). Moreover, based on the author’s experience, the V3–V4 forward and reverse reads often exhibit a rapid decrease in quality toward their ends, leading to various issues during filtering and merging.

As a metataxonomic approach was used in this study, no insights into functional profiles were provided. In addition, no statistical analyses were performed on the soil physicochemical properties due to insufficient replicates.

Another limitation of this study is that the collected samples were stored and transported in an insulated cooler bag with cold packs for up to 48 h, potentially introducing biases into the reported bacterial communities. However, the main results and conclusions of our study are based on differences observed among samples collected from sites with different burn statuses, and all samples were treated under the same conditions. Previous studies have shown that although storage can influence soil microorganisms, relative comparisons among samples remain robust when identical storage conditions are used (Fromin, 2025). Moreover, it was reported that storing soil samples with cooler packs, followed by freezing, is an adequate approach for metabarcoding studies (Delavaux et al., 2020).

5 Conclusion

Two years after the wildfire in the Amankaragai pine forest, the composition and taxonomic profiles of the bulk soil, root, and rhizosphere bacterial microbiota still differed between control and burn sites, with burn status explaining a significant proportion of the variance in bacterial composition ($R^2 \geq 0.226$, all $P \leq 0.001$). Perennial plants (*C. epigeios* and *C. supina*) showed greater bacterial community resilience than annual plants (*C. canadensis*, *C. album*, and *L. serriola*). Alpha-diversity metrics (Shannon entropy, Faith’s PD, and observed ASVs) were stable between control and burn sites in perennial plants (all $P\text{-adj} > 0.05$), whereas annual plants showed significantly lower diversity at burn sites (all $P\text{-adj} \leq 0.049$). Control-to-burn robust Aitchison distances were greater in annual plants than in perennials, regardless of sample types (all $P\text{-adj} < 0.001$), further supporting stronger fire-associated community shifts in annuals. This pattern was consistent across all three microbiome compartments (bulk soil, rhizosphere, and root), suggesting that soil recovery after fire is linked to the plant life cycle. Among perennial plant microbiota, only one genus (*Kineosporia*) was more abundant at control sites, whereas annual plants showed 6–12 genera with higher abundance at control sites, highlighting more extensive compositional change in annuals. Burned sites across all plant species were enriched for fire-associated bacterial taxa, including *Pseudarthrobacter* (LFC 3.3–5.2), *Arthrobacter* (LFC 3.5–4.1), and *Massilia*, which have previously been identified as long-term biomarkers of fire-induced dysbiosis. These findings

provide a basis for assessing post-fire forest soil recovery and highlight the role of the plant life cycle in shaping bacterial community resilience.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: <https://www.ebi.ac.uk/ena>, PRJEB103077.

Author contributions

DI: Conceptualization, Data curation, Formal Analysis, Investigation, Methodology, Validation, Writing – original draft, Writing – review and editing. TY: Conceptualization, Data curation, Formal Analysis, Investigation, Visualization, Writing – original draft, Writing – review and editing. Y-HC: Data curation, Formal Analysis, Writing – original draft, Writing – review and editing. AK: Conceptualization, Data curation, Validation, Writing – original draft, Writing – review and editing. AC-S: Conceptualization, Data curation, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Writing – original draft, Writing – review and editing. GS: Conceptualization, Data curation, Methodology, Project administration, Supervision, Validation, Writing – original draft, Writing – review and editing.

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Conflict of interest

The author(s) declared that this work 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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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fenvs.2026.1804771/full#supplementary-material>

References

- Aerts, R., and Honnay, O. (2011). Forest restoration, biodiversity and ecosystem functioning. *BMC Ecol.* 11, 29. doi:10.1186/1472-6785-11-29
- Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26 (x), 32–46. doi:10.1111/j.1442-9993.2001.01070
- Antos, J. A., and Halpern, C. B. (1997). Root system differences among species: implications for early successional changes in forest of Western Oregon. *Am. Midl. Nat.* 138, 97–108. doi:10.2307/2426658
- Arya, A. S., Hang, M. T. H., and Eiteman, M. A. (2022). Isolation and characterization of levoglucosan-metabolizing bacteria. *Appl. Environ. Microbiol.* 88, e01868-21. doi:10.1128/aem.01868-21
- Bakkali Bouarrakia, M., Elyemlahi, A., El Galoui, O., Hassani Zerrouk, M., Laglaoui, A., Bakkali, M., et al. (2023). Single and dual inoculation with rhizobacteria on alfalfa (*Medicago sativa* L.) growth under lead stress conditions. *Int. J. Environ. Sci. Technol.* 20, 9767–9778. doi:10.1007/s13762-022-04669-9
- Bárcenas-Moreno, G., García-Orenes, F., Mataix-Solera, J., Mataix-Beneyto, J., and Bååth, E. (2011). Soil microbial recolonisation after a fire in a mediterranean forest. *Biol. Fertil. Soils* 47, 261–272. doi:10.1007/s00374-010-0532-2
- Benjamini, Y., and Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J. R. Stat. Soc. Ser. B Methodol.* 57, 289–300. doi:10.1111/j.2517-6161.1995.tb02031.x
- Bhattacharya, P., Barnebey, A., Zemla, M., Goodwin, L., Auer, M., and Yannone, S. M. (2015). Complete genome sequence of the chromate-reducing bacterium *Thermoanaerobacter thermohydrosulfuricus* strain BSB-33. *Stand. Genomic Sci.* 10, 74. doi:10.1186/s40793-015-0028-7
- Bhattarai, H., Saikawa, E., Wan, X., Zhu, H., Ram, K., Gao, S., et al. (2019). Levoglucosan as a tracer of biomass burning: recent progress and perspectives. *Atmos. Res.* 220, 20–33. doi:10.1016/j.atmosres.2019.01.004
- Bolyen, E., Rideout, J. R., Dillon, M. R., Bokulich, N. A., Abnet, C. C., Al-Ghalith, G. A., et al. (2019). Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. *Nat. Biotechnol.* 37, 852–857. doi:10.1038/s41587-019-0209-9
- Brown, S. P., Veach, A. M., Horton, J. L., Ford, E., Jumpponen, A., and Baird, R. (2019). Context dependent fungal and bacterial soil community shifts in response to recent wildfires in the southern appalachian Mountains. *For. Ecol. Manag.* 451, 117520. doi:10.1016/j.foreco.2019.117520
- Bureau of National Statistics (2025). Agency for strategic planning and reforms of the Republic of Kazakhstan bureau of national statistics. Available online at: <https://stat.gov.kz/en/> (Accessed October 7, 2025).
- Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J. A., and Holmes, S. P. (2016). DADA2: high-resolution sample inference from illumina amplicon data. *Nat. Methods* 13, 581–583. doi:10.1038/nmeth.3869
- Camarinha-Silva, A., Jáuregui, R., Chaves-Moreno, D., Oxley, A. P. A., Schaumburg, F., Becker, K., et al. (2014). Comparing the anterior nare bacterial community of two discrete human populations using illumina amplicon sequencing. *Environ. Microbiol.* 16, 2939–2952. doi:10.1111/1462-2920.12362
- Certini, G. (2005). Effects of fire on properties of forest soils: a review. *Oecologia* 143, 1–10. doi:10.1007/s00442-004-1788-8
- Chadha, A., and Florentine, S. (2021). Biology, ecology, distribution and control of the invasive weed. *Lact. Serriola L. (Wild Lettuce)* *A Glob. Rev. Plants* 10, 2157. doi:10.3390/plants10102157
- Deissová, T., Zapletalová, M., Kunovský, L., Kroupa, R., Grolich, T., Kala, Z., et al. (2023). 16S rRNA gene primer choice impacts off-target amplification in human gastrointestinal tract biopsies and microbiome profiling. *Sci. Rep.* 13, 12577. doi:10.1038/s41598-023-39575-8
- Delavaux, C. S., Bever, J. D., Karppinen, E. M., and Bainard, L. D. (2020). Keeping it cool: soil sample cold pack storage and DNA shipment up to 1 month does not impact metabarcoding results. *Ecol. Evol.* 10, 4652–4664. doi:10.1002/ece3.6219
- Enright, D. J., Frangioso, K. M., Isobe, K., Rizzo, D. M., and Glassman, S. I. (2022). Mega-fire in redwood tanoak forest reduces bacterial and fungal richness and selects for pyrophilous taxa that are phylogenetically conserved. *Mol. Ecol.* 31, 2475–2493. doi:10.1111/mec.16399
- Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biol. Conserv.* 61, 1–10. doi:10.1016/0006-3207(92)91201-3
- Fernández-González, A. J., Martínez-Hidalgo, P., Cobo-Díaz, J. F., Villadas, P. J., Martínez-Molina, E., Toro, N., et al. (2017). The rhizosphere microbiome of burned holm-oak: potential role of the genus *Arthrobacter* in the recovery of burned soils. *Sci. Rep.* 7, 6008. doi:10.1038/s41598-017-06112-3
- Fernández-González, A. J., Lasa, A. V., Cobo-Díaz, J. F., Villadas, P. J., Pérez-Luque, A. J., García-Rodríguez, F. M., et al. (2023). Long-term persistence of three microbial wildfire biomarkers in forest soils. *Forests* 14, 1383. doi:10.3390/f14071383
- Fernández-González, A. J., Villadas, P. J., Díaz-Peña, F., Notario-del-Pino, J., Lizano-Bastardín, Á., Fernández-López, M., et al. (2024). Key microorganisms defining the microbial communities of an alpine legume-shrubland ecosystem on a volcanic island in natural and fire-affected soils. *Plant Soil* 498, 651–670. doi:10.1007/s11104-023-06465-x
- Forestry and Wildlife Committee Ministry of Ecology (2026). Geology and natural resources of the Republic of Kazakhstan. Available online at: <https://beta.gov.kz/memleket/entities/forest> (Accessed April 23, 2026).
- Fromin, N. (2025). Impacts of soil storage on microbial parameters. *SOIL* 11, 247–265. doi:10.5194/soil-11-247-2025
- Gladkov, G. V., Chebykina, E. Y., Evdokimova, E. V., Ivanova, E. A., Kimeklis, A. K., Zverev, A. O., et al. (2020). Restoration of soil microbiome in various soil horizons after crown and surface wildfires. *Ecol. Genet.* 18, 343–356. doi:10.17816/ecogen17641
- Grefing, L. L., Horn, J. L., Lange, J. G., Lindh, J. P., and Söner, P. A. N. (1803). *Kungl. Svenska Vetenskapsakademiens Handlingar*. Available online at: <https://www.biodiversitylibrary.org/item/180241> (Accessed April 01, 2026).
- Hamady, M., Walker, J. J., Harris, J. K., Gold, N. J., and Knight, R. (2008). Error-correcting barcoded primers for pyrosequencing hundreds of samples in multiplex. *Nat. Methods* 5, 235–237. doi:10.1038/nmeth.1184
- Kang, S.-M., Waqas, M., Hamayun, M., Asaf, S., Khan, A. L., Kim, A.-Y., et al. (2017). Gibberellins and indole-3-acetic acid producing rhizospheric bacterium *Leifsonia xyli* SE134 mitigates the adverse effects of copper-mediated stress on tomato. *J. Plant Interact.* 12, 373–380. doi:10.1080/17429145.2017.1370142
- Kaur, A., Scott, N. E., Herisse, M., Goddard-Borger, E. D., Pidot, S., and Williams, S. J. (2023). Identification of levoglucosan degradation pathways in bacteria and sequence similarity network analysis. *Arch. Microbiol.* 205, 155. doi:10.1007/s00203-023-03506-y
- Koblanova, S., Mukhtabayeva, S., Kakimzhanova, A., Orazov, A., Dyussebekova, D., and Abileva, G. (2024). Diversity of birch and alder forests in the Kostanay region of Kazakhstan. *Forests* 15, 1680. doi:10.3390/f15101680
- Köster, K., Aaltonen, H., Berninger, F., Heinonsalo, J., Köster, E., Ribeiro-Kumara, C., et al. (2021). Impacts of wildfire on soil microbiome in boreal environments. *Curr. Opin. Environ. Sci. Health* 22, 100258. doi:10.1016/j.coesh.2021.100258
- Kruskal, W. H., and Wallis, W. A. (1952). Use of ranks in one-criterion variance analysis. *J. Am. Stat. Assoc.* 47, 583–621. doi:10.2307/2280779
- Li, Y. P., You, L. X., Yang, X. J., Yu, Y. S., Zhang, H. T., Yang, B., et al. (2022). Extrapolymeric substances (EPS) in *Mucilaginibacter rubeus* P2 displayed efficient metal(loid) bio-adsorption and production was induced by copper and zinc. *Chemosphere* 291, 132712. doi:10.1016/j.chemosphere.2021.132712
- Li, X., Han, Y., Zhang, Y., Shao, Q., Dong, C., Li, J., et al. (2024). Effects of wildfire on soil microbial communities in karst forest ecosystems of southern Guizhou province, China. *Appl. Environ. Microbiol.* 90, e01245-24. doi:10.1128/aem.01245-24
- Lin, H., and Peddada, S. D. (2024). Multigroup analysis of compositions of microbiomes with covariate adjustments and repeated measures. *Nat. Methods* 21, 83–91. doi:10.1038/s41592-023-02092-7

- Ling, N., Wang, T., and Kuzyakov, Y. (2022). Rhizosphere bacteriome structure and functions. *Nat. Commun.* 13, 836. doi:10.1038/s41467-022-28448-9
- Lopez, A. M., Pacheco, J. L., and Fendorf, S. (2023). Metal toxin threat in wildland fires determined by geology and fire severity. *Nat. Commun.* 14, 8007. doi:10.1038/s41467-023-43101-9
- Loster, S., Dzwonko, Z., and Gawroński, S. (2011). *Early Post-fire Vegetation Regeneration in a Scots Pine Forest Site in Southern Poland*, 117–130.
- Macias, M., Irving, M. R., Bandow, K. M., Kim, K., Heredia, C., Hoskinson, C. A., et al. (2025). Effects of low wildfire burn severity due to pre-fire shrub thinning on the chaparral soil bacteriome in the Santa monica Mountains of Southern California. *Microbiol. Spectr.* 13, e00185–25. doi:10.1128/spectrum.00185-25
- Martin, M. (2011). Cutadapt removes adapter sequences from high-throughput sequencing reads. *EMBnet.J.* 17, 10–12. doi:10.14806/embnet.17.1.200
- Martino, C., Morton, J. T., Marotz, C. A., Thompson, L. R., Tripathi, A., Knight, R., et al. (2019). A novel sparse compositional technique reveals microbial perturbations. *mSystems* 4. doi:10.1128/msystems.00016-19
- Matus, G., Tóthmérész, B., and Papp, M. (2003). Restoration prospects of abandoned species-rich sandy grassland in Hungary. *Appl. Veg. Sci.* 6, 169–178. doi:10.1111/j.1654-109X.2003.tb00577.x
- Meyer, M., and Kircher, M. (2010). Illumina sequencing library preparation for highly multiplexed target capture and sequencing. *Cold Spring Harb. Protoc.* 2010, prot5448. doi:10.1101/pdb.prot5448
- Nelson, A. R., Narro, A. B., Rhoades, C. C., Fegh, T. S., Daly, R. A., Roth, H. K., et al. (2022). Wildfire-dependent changes in soil microbiome diversity and function. *Nat. Microbiol.* 7, 1419–1430. doi:10.1038/s41564-022-01203-y
- Niza Costa, M., Gil, T., Teixeira, R., Rodrigues dos Santos, A. S., Rebelo Romão, I., Sequero López, C., et al. (2023). Combined use of a bacterial consortium and early-colonizing plants as a treatment for soil recovery after fire: a model based on Los Guajares (Granada, Spain) wildfire. *Biology* 12, 1093. doi:10.3390/biology12081093
- Ozdemir, G., Ceyhan, N., Ozturk, T., Akirmak, F., and Cosar, T. (2004). Biosorption of chromium(VI), cadmium(II) and copper(II) by *pantoea* sp. TEM18. *Chem. Eng. J.* 102, 249–253. doi:10.1016/j.cej.2004.01.032
- Ozgeldinova, Z., Mukayev, Z., Zhanguzhina, A., Ulykpanova, M., and Aidarkhanova, G. (2025). Impact of forest fire on the heavy metal content in the soil cover of the Amankaragay pine forest, Kostanay region. *J. Ecol. Eng.* 26, 350–364. doi:10.12911/22998993/199472
- Pausas, J. G., and Keeley, J. E. (2014). Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytol.* 204, 55–65. doi:10.1111/nph.12921
- Pedregosa, F., Varoquaux, G., Gramfort, A., Michel, V., Thirion, B., Grisel, O., et al. (2011). Scikit-learn: machine learning in python. *J. Mach. Learn. Res.* 12, 2825–2830.
- Pérez-Valera, E., Verdú, M., Navarro-Cano, J. A., and Goberna, M. (2020). Soil microbiome drives the recovery of ecosystem functions after fire. *Soil Biol. Biochem.* 149, 107948. doi:10.1016/j.soilbio.2020.107948
- Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., et al. (2013). The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucleic Acids Res.* 41, D590–D596. doi:10.1093/nar/gks1219
- Rebele, F., and Lehmann, C. (2001). Biological Flora of central Europe: *calamagrostis epigejos* (L.) Roth. *Flora* 196, 325–344. doi:10.1016/S0367-2530(17)30069-5
- Robeson, M. S., O'Rourke, D. R., Kaehler, B. D., Ziemski, M., Dillon, M. R., Foster, J. T., et al. (2021). RESCRIPt: reproducible sequence taxonomy reference database management. *PLoS Comput. Biol.* 17, e1009581. doi:10.1371/journal.pcbi.1009581
- Rodríguez, J., González-Pérez, J. A., Turmero, A., Hernández, M., Ball, A. S., González-Vila, F. J., et al. (2018). Physico-chemical and microbial perturbations of Andalusian pine forest soils following a wildfire. *Sci. Total Environ.* 634, 650–660. doi:10.1016/j.scitotenv.2018.04.028
- Rognes, T., Flouri, T., Nichols, B., Quince, C., and Mahé, F. (2016). VSEARCH: a versatile open source tool for metagenomics. *PeerJ* 4, e2584. doi:10.7717/peerj.2584
- Shams, S., Kupdhoni, R., Khan, M. A. R., and Islam, M. N. (2023). *Chenopodium album*: a review of weed biology, status and the possibilities for biological control. *Turk. J. Weed Sci.* 26, 144–158.
- Shannon, C. E. (2001). A mathematical theory of communication. *Comput. Commun. Rev.* 5, 3–55. doi:10.1145/584091.584093
- Simanchuk, Y., and Sultangazina, G. (2023). Natural vegetation communities on the iron ore dumps in Northern Kazakhstan. *Biodiversitas J. Biol. Divers.* 24, 3414. doi:10.13057/biodiv/d240637
- Sultangazina, G. J., Kuprijanov, A. N., Kuanysbayev, S. B., Chashkov, V. N., Yskak, A., Nugmanov, A. B., et al. (2025). Forest conditions for the regeneration of *Pinus sylvestris* L. in burnt areas (island pine forests of Amankaragai and Kazanbasy, Kostanay region). *Bull. LN Gumilyov Eurasian Natl. Univ. Biosci. Ser.* 151, 111–128. doi:10.32523/2616-7034-2025-151-2-111-128
- Veselkin, D. V., Kupriyanov, A. N., Manakov, A., Betekhtina, A. A., and Prasad, M. N. V. (2015). "Mycorrhizal plants' accelerated revegetation on coal mine overburden in the dry steppes of Kazakhstan," in *Environmental Sustainability: Role of Green Technologies*. Editors P. Thangavel and G. Sridevi (New Delhi: Springer India), 265–280. doi:10.1007/978-81-322-2056-5_16
- Villadas, P. J., Díaz-Díaz, S., Rodríguez-Rodríguez, A., Del Arco-Aguilar, M., Fernández-González, A. J., Pérez-Yépez, J., et al. (2019). The soil microbiome of the laurel forest in garajonay national park (La gomera, Canary Islands): comparing unburned and burned habitats after a wildfire. *Forests* 10, 1051. doi:10.3390/f10121051
- Whitman, T., Woollet, J., Sikora, M., Johnson, D. B., and Whitman, E. (2022). Resilience in soil bacterial communities of the boreal forest from one to five years after wildfire across a severity gradient. *Soil Biol. Biochem.* 172, 108755. doi:10.1016/j.soilbio.2022.108755
- Xiong, X., Lian, J., Yu, X., Garcia-Perez, M., and Chen, S. (2016). Engineering levoglucosan metabolic pathway in *Rhodococcus jostii* RHA1 for lipid production. *J. Ind. Microbiol. Biotechnol.* 43, 1551–1560. doi:10.1007/s10295-016-1832-9
- Zhanbossinova, A., Mazhitova, Z., Saktaganova, Z., Atantayeva, B., Kulshanova, A., and Akhmetova, R. (2024). Forests in Kazakhstan: issues of conservation and environmental safety. *E3S Web Conf.* 524, 02010. doi:10.1051/e3sconf/202452402010
- Zhanguzhina, A., Ozgeldinova, Z., Mukayev, Z., Ulykpanova, M., and Zhanuzakova, P. (2025). Natural restoration of forests after a fire in the Amankaragay forest massif of the Kostanay region, Republic of Kazakhstan. *J. Bulg. Geogr. Soc.* 52, 93–114. doi:10.3897/jbgs.e144897
- Zhu, Y., Song, K., Cheng, G., Xu, H., Wang, X., Qi, C., et al. (2023). Changes in the bacterial communities in chromium-contaminated soils. *Front. Vet. Sci.* 9, 1066048. doi:10.3389/fvets.2022.1066048