



Key microorganisms defining the microbial communities of an alpine legume-shrubland ecosystem on a volcanic island in natural and fire-affected soils

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Abstract

Background Teide National Park (Canary Islands) is an alpine volcanic ecosystem with shrub vegetation in which legume *Spartocytisus supranubius* is the most characteristic key species for nitrogen input to the ecosystem.

Aims and methods Bacterial and fungal communities in bulk and rhizosphere soils were analysed through high-throughput sequencing in undisturbed

and wildfire-impacted areas to identify key microorganisms in burned and unburned soils.

Results Microbial communities in undisturbed areas exhibited comparable diversity in bulk and rhizosphere soils, but differed in structure and composition. An unusual abundance of non-photosynthetic Chloroflexi from the oligotrophic class Ktedonobacteria dominated the bulk soils, surpassing Proteobacteria, Acidobacteria and Actinobacteria. The *rhizosphere effect* resulted in a microbiome with a more balanced abundance of these four phyla and enriched in potentially plant growth-promoting microorganisms. The impact of a wildfire on the shrub vegetation resulted in a microbial community, especially the fungal community, reduced in diversity and changed in structure and composition, with many of the most characteristic rhizosphere genera becoming vanished, while others took advantage of the postfire conditions and became predominant.

Conclusion The microbial communities of Teide National Park in fire-affected soils, particularly in the rhizosphere environment of the legume shrubland are significantly altered two years after a wildfire, remaining far from unburned scenarios, suggesting a slow recovery in alpine ecosystem with dry volcanic soils. *Pseudarthrobacter* (Actinobacteria) and *Coprinellus* (Basidiomycota), the two most fire-favoured genera, are good indicators of fire severity and are proposed as bioindicators to monitor the recovery of the soil ecosystem.

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Introduction

Microorganisms play many different roles in soils, ranging from their participation in the development of a well-structured soil to a variety of essential functional activities that drive soil fertility, plant diversity and productivity (Bardgett and van der Putten 2014; Schnitzer et al. 2011). Soil serves as the seed bank from which plants select their rhizosphere-specific microbiome (Ling et al. 2022; Vandenkoornhuyse et al. 2015). By expanding host gene functions like a second genome, the rhizosphere microbiome helps plants cope with adverse environmental conditions (Li et al. 2021; Ling et al. 2022).

High altitude ecosystems contain a considerably large microbial diversity regardless of the low temperatures and other naturally occurring harsh environmental conditions (Adamczyk et al. 2019; Costello et al. 2009; Díaz et al. 2022). It is not possible to reach consensus on a specific microbiome of high-altitude soils. Nevertheless, several studies in recent years point to the predominance of certain phyla in these habitats, albeit with varying degrees of abundance (Adamczyk et al. 2019; Schmidt et al. 2018; Tebo et al. 2015; Yabe et al. 2017). Most studies on microbiota in alpine environment have been conducted in continental ecosystems. The present study characterized the microbial communities in soils of Teide National Park (NP) a high-mountain ecosystem on a volcanic oceanic island (Tenerife, Canary Islands). The characteristic vegetation of this alpine ecosystem is a shrubland (thriving between 2000 and 3100 m above the sea level (a.s.l.), in which *Spartocytisus supranubius* (the ‘Teide broom’) is the dominant species, giving this vegetation its name (*summit broom*). In these nitrogen (N)-poor soils, this legume provides the main N input to these soils through symbiosis with N-fixing rhizobia (Pulido-Suárez et al. 2021a). In the current scenario of global warming, increased frequency of heat waves and drought is already having a clearly negative effect on the high mountain ecosystem of Tenerife, with less palatable species (*Pteroccephalus lasiospermus*) being favoured in expansion, while *S. supranubius* is negatively

affected, being currently declining at an accelerated rate (Cubas et al. 2022).

Fires pose other significant threat. In May 15th 2019, a wildfire devastated about 40 ha of the broom scrubland within Teide NP. Fires have very serious consequences on the Canary Islands, a small territory with a high percentage of endemic species. Compared to other insular ecosystem such as the pine forest, fires are rather sporadic in the usually colder Teide summit shrubland and normally affect small areas (Dorta-Almenar et al. 2015; Notario del Pino et al. 2007). Increased temperatures and decreased precipitation with longer drought periods (almost half of the year) in the Park have been reported to be related to global warming (Olano et al. 2017; Martín-Esquivel et al. 2020). This fact, together with increasing episodes of African weather with hot dry winds, enhance the risk of fires in the high mountain of the island. The alteration of soil microbiome is another notable consequence of fires (Certini et al. 2021). In fact, soil microbial communities are initially and directly impacted by the high temperatures during the fire, decreasing their survival with fire intensity (Holden et al. 2016). Nevertheless, the effect of temperatures on microorganisms also depends on the occurring microbial taxa, as long as some of them are more sensitive to heat than others, for instance, symbiotic fungi being more sensitive than many bacteria (Holden et al. 2016; Dove and Hart 2017). In addition, soil microbiomes decline in diversity and changes in community composition may last for months to years after the fire occurrence (Whitman et al. 2019), among which the prevalence of copiotrophic taxa shows a direct correlation with fire severity. Moreover, soil pH and total inorganic N are some of the most frequently altered physicochemical parameters of burned soils (Certini 2005) and have the greatest effect on maintaining intermediate to long-term microbial dysbiosis (Adkins et al. 2022; Fernández-González et al. 2023). Pyrophilous microbes exhibit distinct traits in post-fire environments. Microbial successional dynamics in these habitats are characterized by emergence of thermotolerant species at the short term, with subsequent enrichment in alkalophilous and fast growers and, in longer term, a predominance of competitive microorganisms capable to exploit efficiently the available resources more (Pulido-Chavez et al. 2023). Furthermore, pyrophilous show a remarkable affinity for N mineralization and pyrogenic carbon (mainly

aromatic compounds), playing a crucial role in nutrient cycling in these ecosystems (Nelson et al. 2022). Therefore, this post-fire ecosystem provides a unique niche for these specialized microbes to thrive. In addition, it has been shown that certain phyla like *Actinobacteria* display enhanced xerotolerance in response to drought conditions (Hinojosa et al. 2016), which gives them the ability to withstand post-fire arid conditions. Soil analyses in another previous wildfire in a broom shrubland close to Teide NP showed correlation between ash input from the combustion of plant material and important changes in the chemical properties of the surface soil layer (Notario del Pino et al. 2007, Dorta Almenar et al., 2015), but the effect on soil communities had never been studied.

Rhizosphere microbiomes are determined by soil physicochemical properties, environmental conditions and the host plant itself. It is widely accepted that, due to the ‘*rhizosphere effect*’, soil microbial diversity is generally lower in the plant vicinity and the rhizosphere is enriched in specific taxa (Ling et al. 2022). *S. supranubius* is a perennial shrubby legume whose adult individuals typically grow on average to reach 2–3 m in height and more than 5–10 m in diameter. It forms areas of dense scrub interspersed with patches of scarce or null vegetation. We hypothesise that, owing to the challenging environmental conditions of bulk soils, species richness and diversity will be lower compared to rhizosphere, which are sheltered by the permanent shrubland cover, where a higher organic C content due to the accumulation of plant debris beneath the large canopy of adult brooms can be expected together with a higher N content due to the symbiotic biological N fixation by rhizobia (Pulido-Suárez et al. 2021a). In terms of microbial community composition, the bulk-soil microbiome is expected to be rich in oligotrophic taxa, whereas the rhizosphere microbiome will recruit more copiotroph and beneficial plant-growth promoting microorganisms. We also postulate that the shrubland, due to the large size of adult *S. supranubius* plants and their high caloric content, caused drastic damage to the rhizosphere microbiome for which we anticipate a recovery that will take several years, aggravated by the rising frequency of droughts. Specific objectives are: (i) What microorganisms define the microbial communities in unburned and burned soils within the Teide alpine ecosystem and how are they modified in areas under legume shrub vegetation? (ii) How does

the microbiome of the high mountain volcanic soils in Teide NP compare to other similar ecosystems? Future climate change scenarios predict increased temperatures and reduced precipitations in the high mountain ecosystem of Teide NP (Olano et al. 2017; Martín-Esquivel et al. 2020; Cubas et al. 2022). Identifying the soil microbial community associated with this fragile island habitat can help monitor the ecosystem’s response to progressively adverse conditions by tracking changes in key microorganisms of the soil microbiome.

Materials and methods

Study area

This study was carried out in the alpine ecosystem of Tenerife (Canary Islands, Fig. 1A). It extends from 2000 to 3718 m a.s.l. at the top of Teide stratovolcano and is mostly within the protected area of the Teide National Park (NP) (Fig. 1B). From a bioclimatic point of view, the territory has a mediterranean climate type, which extends within the supra-mediterranean dry or humid at the lowest altitudes, to oromediterranean dry to arid, at the highest elevations (del Arco-Aguilar and Rodríguez, 2018). Solar exposure is intense and rainfall low (200–500 mm. yr⁻¹) with extremely dry summers. Temperatures show wide annual and daily variations with an annual average temperature ranging from 3.5–11 °C, irregular snowfall in autumn or winter, and frosts may last up to six months at 3500 m a.s.l. (del Arco-Aguilar and Rodríguez-Delgado 2018). The most characteristic vegetation is a shrubland where three species predominate, *Erysimum scoparium*, *Pteroccephalus lasiospermus* and the perennial shrubby legume *Spartocytisus supranubius* (Christ ex G. Kunkel).

Experimental design and sampling

Particularly, this study was conducted close to a height known as La Fortaleza, in the north-eastern of Teide NP (2040 m a.s.l.; 28°18′40.05″ N, 16°36′9.40″ W). Two legume shrubland areas were studied, inside and outside the northern portion of the 2019 fire perimeter (Fig. 1C), being about 150 m apart. Both areas were initially similar in terms of vegetation (adult *S. supranubius*) and soils (that can

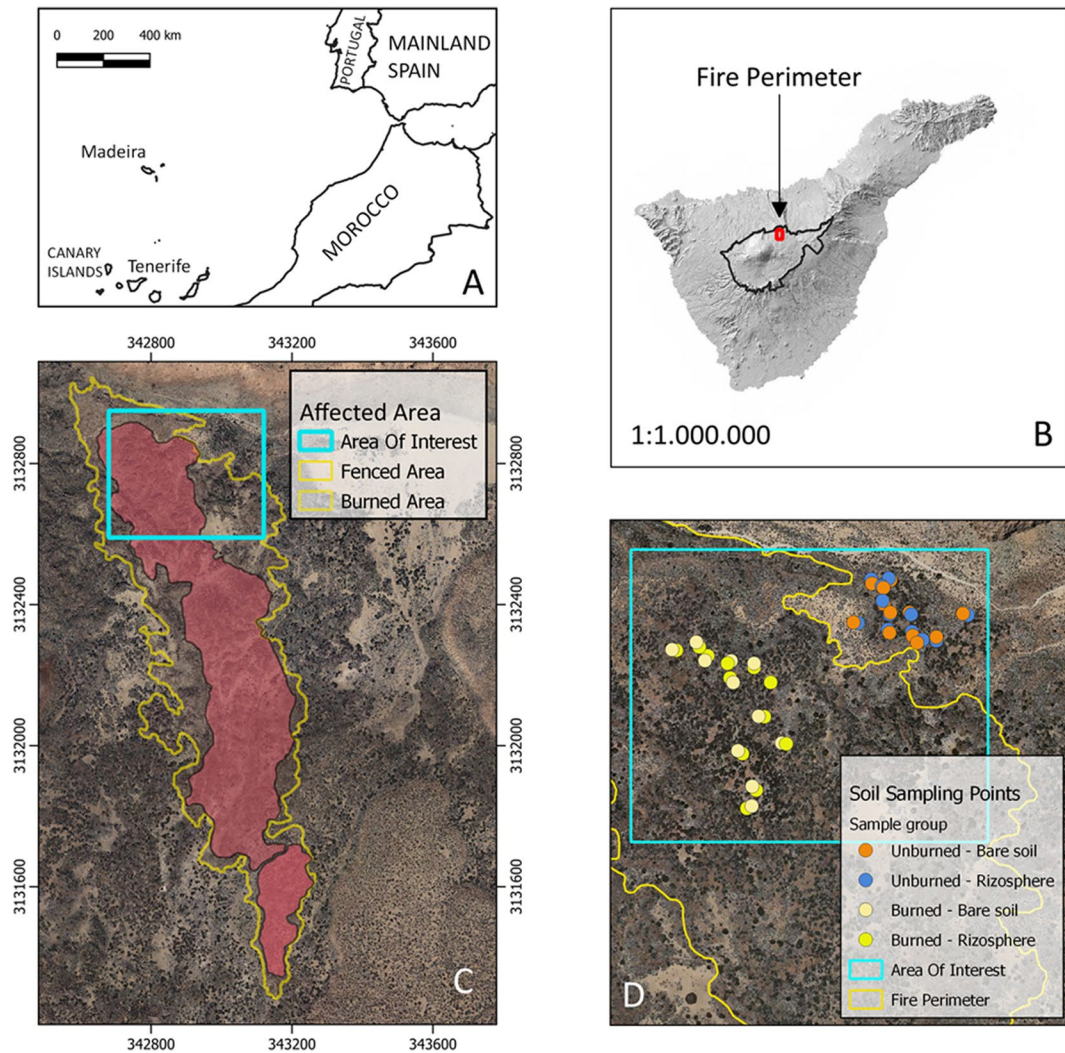


Fig. 1 Map showing the location of the Canary Islands relative to the African continent and mainland Spain (A); perimeter of Teide National Park in Tenerife (B); sampling area (blue

square) within the fire perimeter (C) and the sampling points within the burned shrubland and the adjacent unburned shrubland (D)

be classified as Andic Leptosols, WRB 2022). Four different types of sampling points were considered to collect soil samples: 1) Rhizosphere of *S. supranubius* in the unburned shrubland (uR); 2) Rhizosphere of *S. supranubius* in the burned shrubland (bR); 3) Bulk soils within the unburned shrubland (uB), and 4) Bulk soils within the burned shrubland (bB). Both unburned and burned soil samples were collected the same day, June 1st, 2021 (i.e., two years after the wildfire). Permission for sampling was obtained from Sustainability Area, Environment, Water and Safety, Teide NP, Cabildo de Tenerife (island council).

The experimental authorized area for collecting burned soil samples was roughly one third of the total perimeter burned area (Fig. 1D), which was fenced off by the Park authorities to keep herbivores (mouflons and rabbits) out. A similar, nearby, unburned broom shrubland was selected as a control. After selecting *S. supranubius* adults of about 2 m in height (burned brooms kept upright trunks, see Fig. S2), soil rhizosphere samples were randomly gathered in the unburned (uR) and burned (bR) areas. As *S. supranubius* is a threatened species (uprooting is not allowed) rhizosphere sampling avoided damage

to the roots. For uR samples, soils adhered to roots was collected from accessible fine secondary roots at 0–10 cm from main root in the top 0–10 cm depth. The bR soil samples from burned brooms (without surface roots) included the 0–10 cm soils around the main root at the same 0–10 cm depth. For bulk soils, uB and bB, targeted sampling was taken in adjacent areas, 3–7 m away from the previously randomly selected broom plants. Bulk soils, without broom plants, are bare most of the year with the possibility of other plants growing seasonally. Twelve-point samples were collected for each of the four scenarios, each one resulting from 2 combined sub-samples. All soil samples were taken at the upper 0–10 cm of soils, after removal of soil debris (stones, plant litter). Soil samples for physicochemical analysis were stored in plastic bags at room temperature. Soil samples for sequence analysis were stored in ice-filled containers and taken to the laboratory to be refrigerated immediately after collection. DNA was extracted within 24 hours.

Physicochemical characteristics of soils

Soil samples were air-dried and passed through a 2 mm sieve prior to analysis. Physicochemical analyses were performed following Standard Methods (Soil Survey Staff 1996). Assessed parameters were: particle size (sand, silt and clay) by hydrometer; pH and electrical conductivity (EC) in 1:5 soil to water extract; soluble cations (Ca^{2+} , Mg^{2+} , Na^+ , K^+ and NH_4^+) and anions (Cl^- , SO_4^{2-} , NO_3^-) in 1:5 soil to water extract by ion chromatography; exchangeable cations by equilibrium extraction using 1 M ammonium acetate (pH 7.0) and subsequent determination by atomic absorption/emission spectrometry; soil organic carbon (SOC) and total nitrogen content (N) by dried combustion and measurement of resulting gases with a LECO CN828 equipment; and available phosphorus (P) by the Olsen method. Significant differences in properties between soils were evaluated by one-way ANOVA and post-hoc Tukey HSD. Non-parametric Kruskal-Wallis test with Nemenyi post-hoc was applied when parameters did not conform to a normal distribution (Shapiro-Wilk normality test) and homogeneity of variance (Bartlett test). Statistical methods were performed using Rstudio software version 4.1.2 (R Core Team-2022) and level of significance for all tests was set to $p \leq 0.05$.

Plant vegetation index and fire severity

The Soil Adjusted Vegetation Index (SAVI) (Huete 1988) was used as a proxy to estimate plant coverage in the study area, as other attempts to measure the fraction of vegetation cover (namely FVC from Sentinel-2B imagery processed with the ESA SNAP software package) proved to be unsuccessful. The differential Normalized Burn Ratio (dNBR) was calculated from two Sentinel-2 images with a spatial resolution equal to 20 m, taken on 6th May 2019 and 31st May 2019, so as to obtain a quantitative measurement of fire severity in the area (Fig. 1C).

Soil DNA extraction and sequencing of bacterial and fungal DNA

Total bacterial and fungal genomic DNA were extracted from soils using the DNeasy PowerSoil Kit (QIAGEN) following the manufacturer's recommendations. Extracted genomic DNA was quantified in Qubit 3.0 fluorometer (Life Technologies, NY) and sequenced with Illumina MiSeq platform at the genomics service of Instituto de Parasitología y Biomedicina López Neyra (CSIC; Granada, Spain). For sequencing bacterial DNA, a 16S *rRNA* gene library was constructed amplifying the hypervariable regions V3-V4 using the primer pair Pro341F (5'-CCTACG GGNBGCASCAG-3') and Pro805R (5'-GACTAC NVGGGTATCTAATCC-3') as described (Takahashi et al. 2014). For fungal DNA sequencing, a library was constructed amplifying the ITS2 region using the primer pair ITS4 (5'-TCCTCCGCTTATTGATAT GC-3') (White et al. 1990) and fITS7 (5'-GTGART CATCGAATCTTTG-3') (Ihrmark et al. 2012). The paired-end 2×300-bp (PE 300) strategy was used for both libraries.

Sequencing and ecological data analysis

From raw reads to ecological and statistical data analyses, our homemade publicly available workflow (https://nuriamw.github.io/micro4all/tutorial/package_workflow.html) was followed (Wentzien et al. 2023). In brief, this tutorial makes use of some of the most common tools for processing data from metabarcoding studies (16S *rRNA* gene and ITS regions) by means of R packages. DADA2 (Callahan et al. 2016) pipeline (<https://benjjneb.github.io/dada2/tutorial>)

ial.html) is followed for reads quality trimming and Amplicons Sequence Variants (ASVs) identification and taxonomical classification. Furthermore, primers sequences were removed with CutAdapt (<https://cutadapt.readthedocs.io/en/stable/>) in both, bacterial and fungal libraries. For 16S rRNA gene sequences, trimming was performed with Figaro (<https://github.com/Zymo-Research/figaro#figaro>). Due to the large variability in the size of the ITS2 region, the fungal ITS sequences were not size-trimmed. Taxonomy was assigned with Ribosomal Data Base Project (RDP-II) training set v.18 database and UNITE v.8.2 dynamic database for Bacteria and Fungi, respectively. ASVs accounting for less than 0.005% of total high-quality sequences were considered sequencing artefacts and removed (Bokulich et al. 2013). Mitochondrial, chloroplast and unclassified prokaryote and eukaryote sequences were also removed. Rarefaction curves were calculated with the *rarecurve* function of *vegan* package (Oksanen et al. 2020). Bioinformatics analysis of the high-throughput sequencing data was performed with $n = 10$ samples per scenario, after eliminating the two samples with the highest variability in the beta diversity analysis, considered as outliers. This study maintains the phyla names previous to the publication by Oren and Garrity (2021).

Diversity and structure of the microbial communities

Rarefied libraries (*rarefy_even_depth* function) were used to calculate alpha diversity (*estimate_richness* function) by means of *phyloseq* package (McMurdie and Holmes 2013) and compared with one-way ANOVA and Tukey HSD, while the remaining analyses were carried out with non-rarefied data. For Beta diversity PERMANOVA and BETADISPER (*adonis* and *betadisper* functions from *vegan* package with 9999 permutations) were performed in normalized data using the “trimmed means of M” (TMM) method with the *BioConductor* package *edgeR*. The effect of soil physicochemical properties on the microbiota distribution was analysed with *capscale*. Function *ordistep* was used for model construction, *envfit* to address the statistical significance of the environmental factors selected by adjusting the *P* values with Bonferroni’s method (these 3 functions belong to *vegan* R package; Oksanen et al. 2020). To plot sample distribution in the multivariate space, 2D PCoA (Principal coordinates analysis) and CAP (Canonical

Analysis of Principal coordinates) using weighted Unifrac and Bray-Curtis dissimilarities were run for bacterial and fungal datasets, respectively.

Relative abundance statistical comparison

Comparison in relative abundance of taxa was carried out at phylum, genus and ASV levels with Analysis of Compositions of Microbiomes with Bias Correction (ANCOM-BC) (Lin and Peddada 2020), ANCOMBC package in R. Taxa present in less than 10% of samples were excluded. *P* values of comparisons were FDR corrected by Holm’s method, included in the function.

Microbial ecological network

Bacterial and fungal co-occurrence networks were built through the Molecular Ecological Network Analysis Pipeline (MENAP) website (<http://ieg4.rccc.ou.edu/mena/main.cgi>) with default parameters, except for similarity matrix correlation coefficient (Spearman’s Rho using: $r_s = \rho_{r_{gx}, r_{gy}} = \frac{\text{cov}(r_{gx}, r_{gy})}{\sigma_{r_{gx}} \sigma_{r_{gy}}}$). A network was analysed for each scenario ($n = 10$), unburned/burned bulk soil (uB, bB) and unburned/burned rhizosphere (uR, bR), and extracted global topological properties for Student *t* test comparisons between treatments (unburned and burned) of each compartment (bulk soil and rhizosphere) separately. Furthermore, keystone ASVs for each network were highlighted according to their *Z_i* (within-module connectivity) and *P_i* (among-module connectivity) values. Finally, the four networks were drawn with Cytoscape v.3.9.1 (Shannon et al. 2003).

Results

Context and considerations

Shrubland vegetation at the unburned study site is dominated by adult *S. supranubius* individuals about 20–40 years old (Fig. S1), as was the case in nearby shrubland prior to the May 2019 wildfire (Fig. S2). Despite the fact that the burned area (about 40 ha) may seem small, it well represents the impact of a wildfire on the soil and the microbiome of the summit vegetation, as it occurred on a small island where

Teide NP occupies a large part of it (Fig. 1B) with great ecological value. According to the SAVI values (from images taken nine days before the fire), the mean plant coverage in the study site was approximately 50%, which can be regarded as representative of a typical Teide broom shrubland. A visual examination of fire-induced damages in broom plants showed that most of them had burned to death (Fig. S2), therefore pointing to high severity. These observations disagree with fire severity as expressed by the dNBR index (Fig. S3), that never exceeds 0.40, thus suggesting moderate severity (Key and Benson 2006). Such apparent inconsistency between field surveys and satellite data can certainly be attributed to the coarse resolution of the freely available images, as just a few burned broom plants may exist within 20 m × 20 m the area represented by a given pixel.

Larger alteration of physicochemical characteristics in rhizosphere

All sites had sandy loam textures with clay plus silt contents representing around 30% of soil particles, with no changes observed between burned and unburned soils (Table 1). Soil organic carbon (or

total C, as no carbonates can occur at the pH values we have measured) and N contents were significantly higher in the rhizosphere soil unaffected by fire than in bulk soil. Several soil properties in burned soils showed detectable effects two years after the fire. Thus, electrical conductivities were significantly higher in burned soils (both rhizosphere and bare), by a factor of 2–3 with regard to unburned samples. Consequently, and as expectable, several basic cations (namely soluble Na^+ and Mg^{2+} and exchangeable Na^+ and Ca^{2+}) were significantly higher in bB with regard to uB. However, the greatest impact of fire was detected in rhizosphere soils, affecting soil pH values, exchangeable and soluble cations (save for soluble Na^+) and inorganic N forms (NH_4^+ and NO_3^-), that were significantly increased in bR compared to uR. Globally, results show a larger alteration of chemical properties in rhizosphere soil, which points to a higher fire severity in those zones.

Sequence quality

Total number of raw reads were 2,651,211 for 16S rDNA bacterial samples and 3,290,353 for fungal ITS, which after trimming resulted in 1,234,478 and

Table 1 Soil physicochemical properties in four different scenarios

Soil properties	uB	bB	uR	bR
pH _{1:5}	6.0 ± 0.2 a	5.9 ± 0.6 a	6.1 ± 0.2 a	6.8 ± 0.6 b
EC _{1:5} $\mu\text{S cm}^{-1}$	77.4 ± 40.0 a	234.4 ± 115.0 b	114.8 ± 39.5 a	333.9 ± 115.9 c
SOC g kg ⁻¹	46.6 ± 10.3 a	55.9 ± 17.7 ab	71.6 ± 20.0 b	86.4 ± 55.0 b
N g kg ⁻¹	4.0 ± 0.8 a	5.4 ± 2.0 ab	6.2 ± 1.4 b	7.7 ± 4.1 b
P mg kg ⁻¹	11.0 ± 4.2 a	11.8 ± 7.4 a	14.0 ± 6.7 a	12.7 ± 3.9 a
Sol. Ca^{2+} mg L ⁻¹	5.9 ± 5.0 a	14.5 ± 6.5ab	5.9 ± 3.1 a	14.8 ± 13.3 b
Sol. Mg^{2+} mg L ⁻¹	1.0 ± 0.5 a	3.5 ± 1.7 bc	1.7 ± 1.0 ab	4.9 ± 3.8 c
Sol. K^+ mg L ⁻¹	2.7 ± 1.2 a	13.1 ± 4.6 a	10.5 ± 5.9 a	43.7 ± 21.2 b
Sol. Na^+ mg L ⁻¹	3.7 ± 1.1 a	11.1 ± 7.3 b	4.9 ± 1.6 a	7.7 ± 3.9 ab
Sol. NH_4^+ mg L ⁻¹	0.2 ± 0.3 a	1.6 ± 2.9 ab	0.2 ± 0.3 a	3.1 ± 3.4 b
Cl^- mg L ⁻¹	6.7 ± 0.8 a	7.5 ± 1.5 a	7.4 ± 1.6 a	8.0 ± 2.6 a
SO_4^{2-} mg L ⁻¹	4.8 ± 2.5 a	4.7 ± 2.3 a	2.9 ± 0.2 a	4.0 ± 1.9 a
NO_3^- mg L ⁻¹	21.2 ± 15.5 a	103.3 ± 71.1 b	38.7 ± 17.8 a	103.7 ± 64.1 b
Exch. Ca^{2+} cmol _c kg ⁻¹	1.3 ± 0.8 a	2.2 ± 1.1 b	3.9 ± 1.8 ab	6.2 ± 2.8 c
Exch. Mg^{2+} cmol _c kg ⁻¹	0.2 ± 0.1 a	0.6 ± 0.6 a	0.9 ± 0.6 a	2.5 ± 1.5 b
Exch. K^+ cmol _c kg ⁻¹	0.3 ± 0.1 a	0.8 ± 0.5 a	0.8 ± 0.4 a	2.3 ± 1.1 b
Exch. Na^+ cmol _c kg ⁻¹	0.2 ± 0.0 a	0.7 ± 0.2 b	0.3 ± 0.1 a	0.6 ± 0.1 b
Sand g kg ⁻¹	657.8 ± 45.8 a	711.1 ± 78.5 a	607.6 ± 50.2 a	684.5 ± 48.7 a
Silt g kg ⁻¹	232.3 ± 38.6 a	214.4 ± 72.6 a	287.6 ± 51.3 a	223.4 ± 36.0 a
Clay g kg ⁻¹	109.8 ± 9.1 a	74.5 ± 9.7 a	104.8 ± 9.6 a	92.1 ± 1.35 a

Mean ± standard deviation; n = 10; different letters indicate significant differences among sites ($p < 0.05$)

pH_{1:5}, pH in 1:5 soil-water extract; EC_{1:5}, electrical conductivity in 1:5 soil-water extract; SOC, soil organic carbon; N, total nitrogen; P, available phosphorus; Sol. (soluble) Ca^{2+} ; Sol. Mg^{2+} ; Sol. Na^+ ; Sol. K^+ ; Sol. NH_4^+ ; Exch. (exchangeable) Ca; Exch. Mg^{2+} ; Exch. K; Exch. Na. uB, unburned bulk soil; bB, burned bulk soil; uR, unburned rhizospheric soil; bR, burned rhizospheric soil

1,945,737 high-quality sequences, for bacteria and fungi respectively and a total of 3091 bacterial and 795 fungal ASVs. The rarefaction curves tended towards the asymptote (Fig. S4), guaranteeing that the number of sequences obtained was representative of the bacterial and fungal communities in these four soils.

Rhizosphere and fire drive the bacterial and fungal communities' assembly

In terms of α -diversity in unburned scenarios, no rhizosphere effect was observed in the microbial communities. Thus, in both bacteria and fungi, the species richness (observed ASVs), diversity and evenness indices showed very similar values in bulk soils (Fig. 2). In contrast, an effect of fire on the diversity indices was observed, higher in presence of permanent vegetation. This effect was not the same for bacteria and fungi. In the bacterial community, a decrease in evenness due to the fire was observed,

but only in the rhizosphere samples (Fig. 2A). On the other hand, within the fungal community, fire had a greater impact, resulting in a decline in all diversity indices. This effect was observed in both the bulk soil and, notably, in the rhizosphere (Fig. 2B).

Both the *rhizosphere effect* and the fire impact shaped the microbial communities (Fig. 3, Fig. S5, Table S1). In the case of the bacterial community, the presence or absence of the legume was the most important factor, followed by far by the fire effect (Table S1). Furthermore, a statistically significant interaction between the two factors was observed, i.e. the effect of fire was not the same in the bulk soil, where uB and bB samples are not well separated and the p value marginally significant, while in the rhizosphere a clear and marked difference was observed between samples from two scenarios. In the case of the fungal community, both factors had a very similar contribution and there was also interaction between them (Table S1). Therefore, in this case, a greater impact of fire on bulk soils was observed. In short,

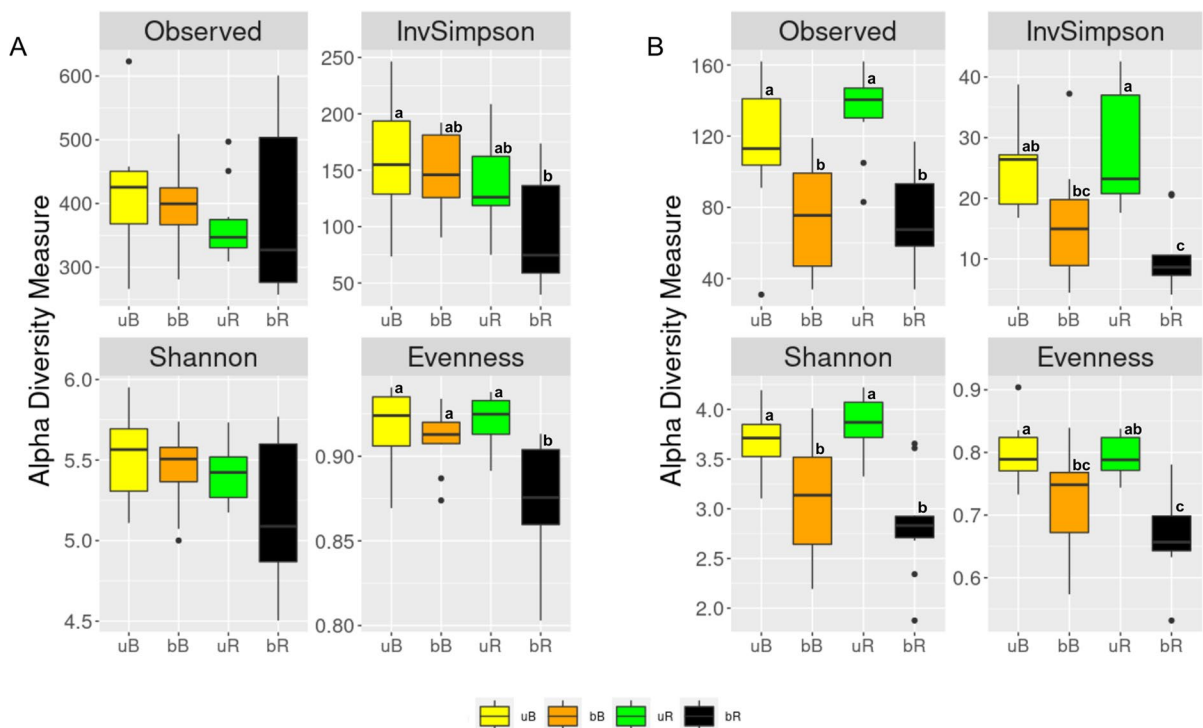


Fig. 2 Microbial diversity. Alpha diversity indices of Bacterial (A) and Fungal (B) communities of bulk and rhizosphere soils in unburned and burned areas of Teide NP. Statistically significant differences (p value <0.05 with the Tukey test) are indi-

cated with letters. uB: unburned Bulk soil, bB: burned Bulk soil, uR: unburned Rhizosphere soil, bR: burned Rhizosphere soil

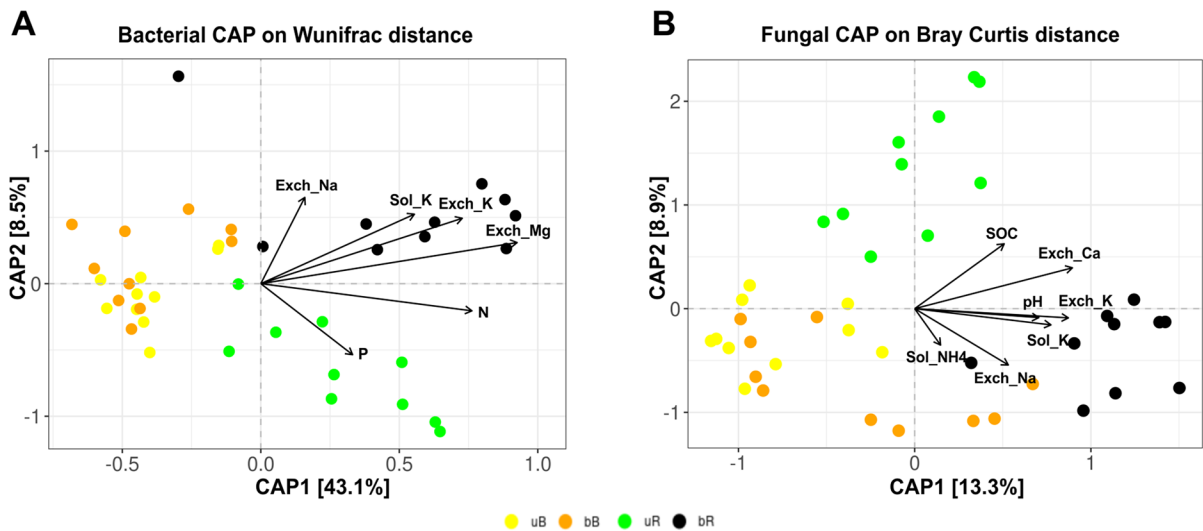


Fig. 3 Canonical Analysis of Principal coordinates (CAP) of bacterial (A) per treatment of Weighted Unifrac distances and fungal (B) communities per treatment of Bray-Curtis dissimilarities, both with all the independent physicochemical parameters. EC: electrical conductivity; SOC: soil organic carbon;

N: total nitrogen content; P: available phosphorus content; Sol. (soluble) Ca^{2+} , Sol. Mg^{2+} ; Sol. K^{+} ; Exch. (exchangeable) Ca^{2+} , Exch. Mg, Exch. K, Exch. Na. uB, unburned bulk soil; bB, burned bulk soil; uR, unburned rhizospheric soil; bR, burned rhizospheric soil

it was found that the fire effect was greater, on both taxonomic groups (Bacteria and Fungi), in the rhizosphere than bulk soils. On the other hand, the rhizosphere effect was also observed in both groups, but much more marked in the bacterial community. The ordination of the bacterial communities in relation to the soil properties showed that the uR communities were linked to a large content of assimilable P and N (Fig. 3A), which may reflect the importance of symbiotic microorganisms (mycorrhiza and N-fixing rhizobia) associated with the roots of broom plants. However, the bacterial community in the bR was positively correlated with high levels of some cations (K^{+} and Mg^{2+}), which is consistent with the release of ions after the combustion of organic materials. On the other hand, fungal communities (Fig. 3B) in uB soils responded to low levels of soil organic carbon (SOC) and cations, attributable to the absence of shrub cover that limits organic inputs to the soil surface. In the burned locations, fungal communities were positively correlated with exchangeable Na^{+} and soluble NH_4^{+} (both increase after combustion). Furthermore, in the bR this community was positively correlated with high levels of cations (in this case K^{+} and Ca^{2+}), and to a lesser extent, the pH. Overall, the soil samples that could be better discriminated were firstly those

from bulk soil versus rhizosphere and secondly, in the latter, a greater differentiation between burned and unburned areas was observed, probably indicating a greater fire severity in soils under the shrub legume vegetation.

The distinctive taxonomic microbial profile of the studied ecosystem

Focusing on unburned scenarios, it was observed that bacterial communities in bulk soils (uB) are dominated by phylum Chloroflexi (Fig. 4A), which represents 27% relative abundance, surpassing the three most abundant phyla in most of the soils, Proteobacteria, Actinobacteria and Acidobacteria (which ranged between 14 and 18%). These four phyla with Firmicutes (6.24%) accounted for 80% of the bacterial community's relative abundance. The rhizosphere (uR) is made up of the same phyla, but with markedly different relative abundances (Table S2): Chloroflexi are halved (11.49%), while Bacteroidetes, a minor phylum in uB, increase significantly (6.35%) surpassing Firmicutes (which drop to half). The Chloroflexi identified in Teide soils belong to the non-photosynthetic lineage of class Ktedonobacteria with a single genus, *Ktedonobacter* having 12% of the relative

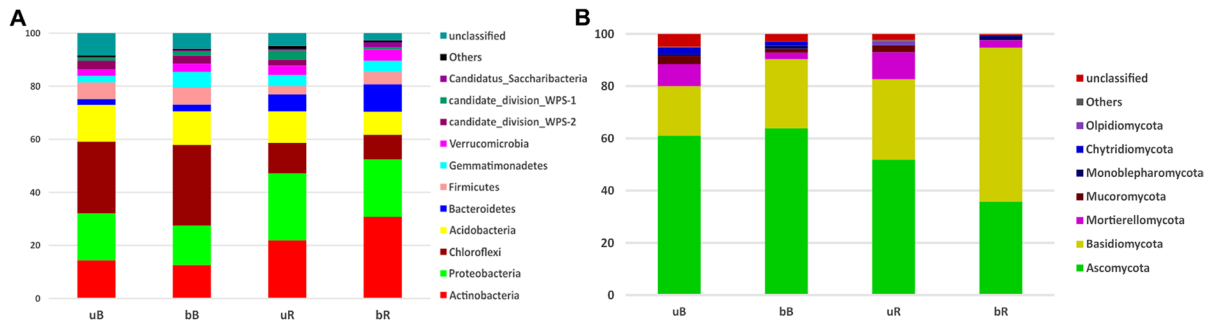


Fig. 4 Microbial community composition at phylum level. Bacterial (A) and fungal (B) community composition at the phylum level. Phyla with relative abundance below 1% were

included as *Others*. Unclassified phyla accounted for 8.36%. uB: unburned Bulk soil, bB: burned Bulk soil, uR: unburned Rhizosphere soil, bR: burned Rhizosphere soil

abundance of uB bacterial community (Fig. 5A). This genus decreased to 4.9% (Table S3) in the uR, sharing predominance with *Crossiella* (4.5%, Actinobacteria), *Gp3* (4.1%, Acidobacteria) and *Bradyrhizobium* (3.3%, Alphaproteobacteria) (Fig. 5A, Table S3, Fig. S5). When comparing the uB and uR microbiomes, *Ktedonobacter*, alongside *Thermosporothrix* (another Chloroflexi) and *Gp1* (Acidobacteria) are three main genera that significantly decrease in rhizosphere (Fig. 5A, Table S3). Bacteroidetes *Mucilaginibacter* and *Flavitalea* and Actinobacteria *Kribbella* stand out as the most representative genera that showed differences between the two scenarios in the opposite direction (Table S3).

The fungal community (Fig. 4B) is predominantly composed of the phyla Ascomycota (61.04% in uB

and 51.90% in uR, respectively) and Basidiomycota (19% uB and 30.8% uR) followed by Mortierellomycota (8.3% in uB and 10.3% in uR). None of these three main phyla differed statistically in abundance between uB and uR soils (Table S4). Differentially abundant were minor phyla as Chytridiomycota, more abundant in uB soils and conversely Olpidiomyces and Glomeromycota more abundant in the rhizosphere. Surprisingly, neither of the two most abundant genera *Mortierella* and *Solicoccozyma* (Fig. 5B) belong to the most abundant phylum Ascomycota, and both are similarly abundant in the uB and uR fungal community. Statistically specific to the rhizosphere were several other more moderately abundant genera, such as the Ascomycota *Pseudogymnoascus* (the most abundant Ascomycota), *Pleiochaeta* and

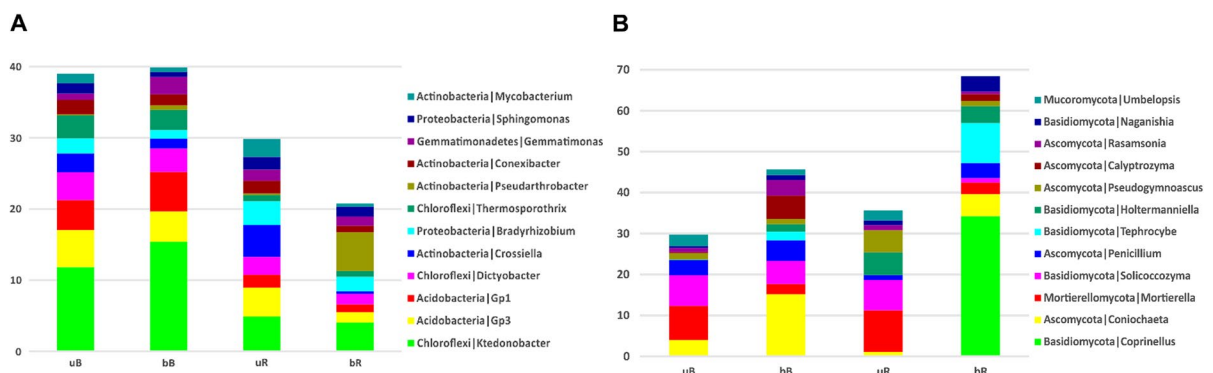


Fig. 5 Microbial community composition at the genus level. Bacterial (A) and fungal (B) genera community composition. Only the 12 most abundant genera are represented. uB: unburned Bulk soil, bB: burned Bulk soil, uR: unburned Rhizosphere soil, bR: burned Rhizosphere soil. Unclassified

genera, not represented in the figure, accounted for a relative abundance of 41.96% (uB) and 37.76% (uR) for the bacterial community and 33.25% (uB) and 28.30% (uR) for the fungal community

Cladophialophora, and the Basidiomycota *Holtermanniella* and *Trechispora* (Table S5).

Bacterial and fungal response to fire in the rhizosphere shrubland

In bulk soils, the effect of fire on the bacterial community was scarcely noticed two years after the fire. Only the decrease in phylum Proteobacteria was significant ($P=0.043$) (Table S2), but none of the genera with relative abundance $\geq 1\%$ changed significantly (Fig. 5A, Table S3). A distinct scenario was observed in the rhizosphere, where two years following the fire, the microbiome composition remains significantly transformed. At phylum level bacterial composition only show statistically significant decreases in less abundant phyla (Fig. 4A and Table S2). However, the impact of the fire on the most distinctive rhizospheric genera was clear at the genus level (Fig. 5A and Table S3). *Mycobacterium* and *Crossiella*, two prevalent Actinobacteria in the undisturbed rhizosphere, virtually disappeared from the burned rhizosphere and *Mucilaginibacter*, an important polysaccharides degrader genus of the Bacteroidetes decreased by a half. By contrast, there was a significant rise in various bacteria following the fire (Fig. 5A and Table S3), with Actinobacteria displaying a noteworthy predominance particularly in genera *Pseudarthrobacter* (5.4%) and *Kribbella* (3.27%) (Fig. 5A, Table S3). Within other phyla, increases in *Pedobacter* (1.89%) (Bacteroidetes) and *Massilia* (1.61%) (Betaproteobacteria) were also significant (Fig. S6). The more dramatic impact of fire on the fungal community was observed even at the highest taxonomic level of the phylum: Ascomycota, Mortierellomycota, Mucoromycota, Glomeromycota and Olpidiomy-cota decreased significantly while Basidiomycota, Chytridiomycota and Monoblepharomycota increased in parallel (Fig. 4B and Table S4). Many abundant genera in the unburned rhizosphere (*Mortierella*, the Basidiomycota *Solicoccozyma* and *Trechispora* and the Ascomycota *Pseudogymnoascus*, *Pleiochaeta*, *Cladophialophora*, *Hormonema* and *Venturia*) underwent steep declines or vanished after the fire (Fig. 5B and Table S5). Meanwhile the burned rhizosphere displays a completely altered microbiome dominated by an impressive explosion in the Basidiomycota genus *Coprinellus* (Fig. S5, Table S5). This genus with 34.25% of relative abundance of the fungal

community is dominated by 2 main AVS (27.74%. Noteworthy is the abundance in *Tephrocyebe*, not detected in uR, only one ASV reached 9.43% relative abundance in bR (Fig. S5, Table S5).

What ecological networks reveal about the rhizosphere effect and the fire impact

The co-occurrence networks also demonstrated bulk soil microbial communities distinct from the rhizosphere. In addition, a clear distinction was made between burned and unburned soils.

In the unburned bulk soil community, four module hubs (*Aquihabitans*, *Alphaproteobacteria* ASV, *Fusidium* and *Conexibacter*) and four connectors (*Conexibacter*, *Ktedonobacter*, *Puia* and *Firmicutes* ASV) were detected. Furthermore, no keystone was shared between both networks, the bulk soil network being more abundant and diverse (Table S6). The comparison of rhizosphere (uR) versus bulk soil (uB) co-occurrence networks (Fig. 6), showed unexpectedly that in the presence of plant roots there is a decrease in network complexity (avgK) and both global (number of nodes and links) and intramodular connectivity (CS). At the same time, there was an increase in geodesic distance (GD), which correlates with a weaker interaction between ASVs and higher compartmentalization (higher avgCC and Modularity) in the rhizosphere. With regard to the effects of fire, we found a similar level of complexity when comparing bulk soils in unburned (uB) and burned (bB) areas (avgK, see Table S6), although the modules were reduced in size and less connected with each other in samples affected by fire (greater importance of modularity (avgCC) and weaker connections (GD)). However, neither were any differences noted in modularity or intra-modular connectivity (CS). Interestingly, the absence of keystone ASVs was notable in the fire-affected community (Fig. 6). In the rhizosphere, a greater number of network properties were altered in burned (bR) compared to unburned rhizospheres (uR). Fire simplified and weakened network complexity (avgK, Table S2) and intramodular connectivity (CS), but strengthened connectivity (GD) and modularity, although most modules was significantly reduced in size (Fig. 6). No connectors were found in either bR or uR microbial communities. Only hubs were active in the main module of each network (*Acidobacteria Gp1* and Proteobacteria

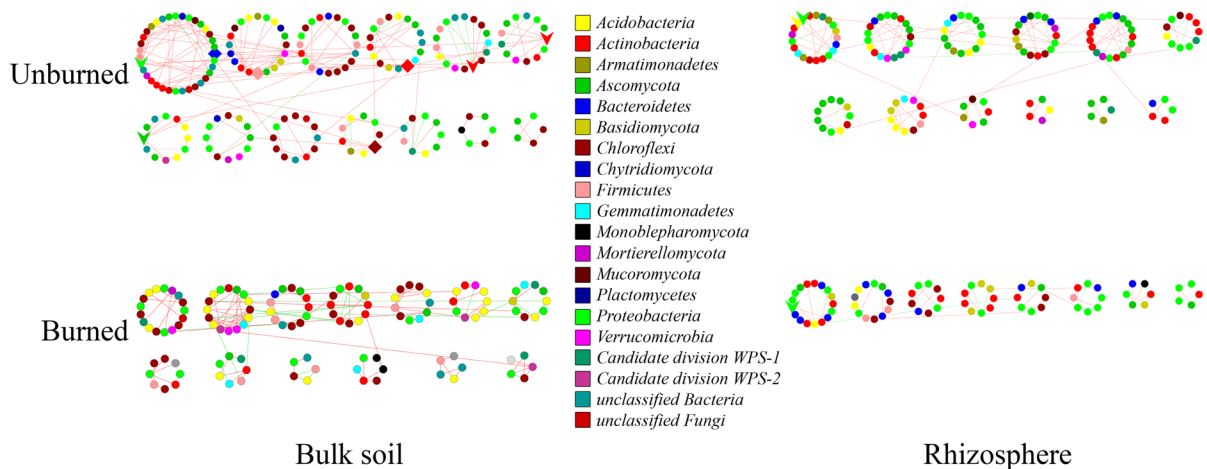


Fig. 6 Microbial ecological co-occurrence networks. Each coloured dot is a node and corresponds to a different ASV. Nodes were coloured based on their taxonomical annotation at phylum level. Diamonds = connectors; Arrowheads = module hubs

Comamonadaceae ASV in uR, and *Sphingomonas* in bR). Moreover, in both bB soil and the bR, the percentage of positive connections increased due to fire (see PEP in Table S6).

Discussion

Key microorganisms of soil microbial communities in an alpine legume shrub ecosystem

Teide NP stands apart from many other alpine ecosystems because it is warmer, drier and has poorly evolved volcanic soils. This alpine ecosystem on an oceanic island is also unique in terms of endemic species and its characteristic shrub vegetation is highly threatened by global warming (Cubas et al. 2022). In this study we have characterised the soil bacterial and fungal communities of this peculiar ecosystem.

Plants determine their rhizosphere microbiome to a large extent, as well as microbial communities correlate positively with plant diversity (Adamczyk et al. 2019; Li et al. 2021). Overall, plants exert a selective effect on the bulk soil microbiota, leading to a reduction in diversity in the rhizosphere. However, certain types of vegetation have an opposing effect, showing higher diversity in the rhizosphere than in bulk soils (Ling et al. (2022)). Due to the harsher environmental conditions found in bulk soils of the Teide ecosystem in contrast to soils covered by the legume shrubland

vegetation, we hypothesized a reduced richness and diversity in bulk soils. On its part, co-occurrence networks showed bulk soil networks more abundant and diverse than the rhizosphere, following the tendency to decrease diversity in the rhizosphere. Therefore, these results did not confirm our hypothesis that the harsher environmental conditions of more exposed bulk soils would reduce species richness and diversity compared to the rhizosphere. However, our results based on beta diversity, ecological networks and taxonomic profiling showed that broom-plants are a key factor influencing the microbial community, in agreement with other studies (Sáenz de Miera et al. 2020; Zalman et al. 2023). Analyses of the taxonomic composition of microbial communities demonstrate the rhizosphere effect. The most remarkable feature of the bulk soils in Teide is the enormous and unusual relative abundance of *Chloroflexi* (27%), well above the values found in most other alpine ecosystems, where they are among the five most abundant phyla, but without exceeding 14% (Adamczyk et al. 2019; Costello et al. 2009; Frey et al. 2016). In particular, class *Ktedonobacteria* represented the almost total abundance of this phylum in our study, and its dominance in bulk soils agrees with other studies (Weber and King 2010). These non-photosynthetic *Chloroflexi* have a filamentous actinomycete-like morphology and are typically oligotrophs (Cavaletti et al. 2006; Yabe et al. 2010). Although they are widespread bacteria in terrestrial systems (Yabe et al. 2017), the evidence

accumulated over time suggests that they are a prevalent group in extreme environments (Adamczyk et al. 2019; Costello et al. 2009; Schmidt et al. 2018). What was unexpected in the alpine soils of Teide is that Chloroflexi surpassed other most commonly abundant phyla as Proteobacteria. This dominance, atypical for most alpine ecosystems, is increasingly common in alpine soils of volcanic origin (Hernández et al. 2020; Schmidt et al. 2018; Tebo et al. 2015). Ktedonobacteria thriving environments are mostly acidic (Lynch et al. 2012; Tebo et al. 2015) and raising soil pH can negatively affect them (Adamczyk et al. 2019; Kim et al. 2015). Despite similar pHs in undisturbed soils of Teide, Ktedonobacteria were twice as abundant in uB soils. A significant increase in pH in bR soils after the fire did not significantly modify their abundance. This suggests that pH is not a significant factor for the Teide Ktedonobacteria which could belong to species unaffected by pH, and their higher abundance in bulk soils could be more linked to its oligotrophic lifestyle. Consequently, its abundance in the rhizosphere may be reduced by higher levels of SOC and N, due to plant matter accumulation under the canopy and biological N fixation by symbiotic rhizobia (Pulido-Suárez et al. 2021a). Conversely, the rhizosphere would favour more copiotrophic fast-growing groups (Ling et al. 2022). A key role for Ktedonobacteria in the Teide soils is supported by the fact that *Ktedonobacter* is the most abundant bacterial genus and one of the 4 connectors in the ecological networks of the bulk soils. Isolation and in vitro culture are needed to disentangle the functional roles of this group in our ecosystems. From previous studies in volcanic soils, it has been proposed an essential role of Ktedonobacteria as CO-oxidizers (Hernández et al. 2020; Tebo et al. 2015), as well as a potential role for sulphur (S) in the metabolism of Ktedonobacteria come from the finding of S as the most informative soil parameter in the bacterial community assembly (Díaz et al. 2022). On the other hand, spore resistance is a good adaptation to cope with long dry periods and direct exposure to the sun in areas without vegetation cover. Spore production by Ktedonobacteria (Cavaletti et al. 2006; Yabe et al. 2010) could also be other reason for their abundance in bulk soils and not to be affected by fire in our study.

After *Ktedonobacter*, it is noteworthy that the predominance of *Crossiella* and *Bradyrhizobium* in the rhizosphere is primarily attributed to a single ASV for

each (Fig. S5), suggesting a functional contribution of specific genotypes to the ecosystem. *Crossiella* sequences are frequently detected in various environments including the rhizosphere of multiple plants (Martin-Pozas et al. 2023), indicating the widespread presence of this filamentous Actinomycetes. Nevertheless, due to its challenging culture, only two species have been currently described. In vitro and in silico analyses reveals the potential of *Crosiella* as a biocontrol agent and a promising source of active compounds (Martin-Pozas et al. 2023). Nonetheless, further research is needed to elucidate its role in plant interaction. On its part, *Bradyrhizobium* was the most abundant Proteobacteria (Table S4). We have previously shown that inoculation with specific strains of this genus plays a crucial role in providing N to the Teide ecosystem through its N-fixing symbiosis with *S. supranubius* (Pulido-Suárez et al. 2021b) and that a genotype (closely relate to species *B. canariense*) dominated the root nodules of *S. supranubius* (Pulido-Suárez et al. 2021a), a result that correlates with the dominance of an ASV in the bradyrhizobia sequences. The rhizosphere effect was even more pronounced in the fungal community, where differential abundance between bulk soil and rhizosphere genera was higher than for bacteria. Interestingly, many of these fungal genera of Teide-broom rhizosphere are also widespread in other cold ecosystems, many are rhizosphere colonisers and some plant growth promoting fungi (PGPF) (Zhao et al. 2021; Liu et al. 2022; Sarabia et al. 2018; Vanegas-León et al. 2019). *Mortierella* and *Solicoccozyma* are the two most abundant fungal genera in Teide soils (uB and uR), suggesting their importance in alpine ecosystems. *Mortierella*, a common saprotrophic fungus, has emerged as a plant-root coloniser with tremendous potential for promoting plant growth through the uptake of P and Fe, phytohormone production and biocontrol agent (Ozimek and Hanaka 2021; Zhang et al. 2011). As a proficient phosphate solubilizer, *Mortierella* has shown the ability to synergistically promote plant growth in combination with arbuscular mycorrhizal fungi (AMF) (Zhang et al. 2011). In this regard, the low relative abundance of AMF in the rhizosphere microbiome of Teide-brooms could be compensated by *Mortierella*. Yeast *Solicoccozyma* is another proven PGPF that directly promotes plant growth and facilitates adaptation to stress (Sarabia et al. 2018; Carvajal et al. 2023). On its part, the

colonisation of plant roots by *Trechispora* mycelium suggests an ectomycorrhizal association and potential as PGPF (Vanegas-León et al. 2019). *Pseudogymnoascus*, another genus prevalent in the broom rhizosphere, is a cellulolytic fungus (Xia et al. 2021) with not PGPF potential yet described. Other abundant fungi in the broom-rhizosphere, such as *Pleiochaeta*, *Cladophialophora* and *Holtermanniella*, have been associated with plant root rot or human clinical concern, but a role for environmental strains remains undetermined. We anticipate that a high proportion of fungi colonizing the rhizosphere of Teide-brooms exhibit plant growth-promoting activity. The confirmation of this hypothesis needs in vitro isolation and subsequent characterization.

Microbial communities in burned shrubland soils

The impact of a wildfire can vary depending on the vegetation type. Due to the large input of highly combustible tinder, fires in shrubland ecosystems are generally more severe than those in forests (González de Vega et al. 2016; Sáenz de Miera et al. 2020). Moreover, the effects of increasingly frequent and severe wildfires are exacerbated under drought conditions (Fernández-García et al. 2019), affecting the resilience of Mediterranean ecosystems to fire (Hinojosa et al. 2016). Teide's alpine ecosystem has a Mediterranean climate. Rising temperatures and prolonged droughts in recent years are adversely affecting it. (Olano et al. 2017). The effects of wildfires on the microbiota of these soils have not been previously investigated. In this study examined its impact on the soil physicochemical properties and bacterial and fungal communities and showed that the effects persist in the ecosystem after two years. Previous studies on wildfires in the Teide shrubland were limited to determine short-term (i.e., within the first year) changes on soils physicochemical properties (Notario del Pino et al. 2007; Dorta-Almenar et al. 2015). These studies detected in particular large changes in inorganic N forms. Burned soils had elevated levels of NH_4^+ which remained constant within the year, and NO_3^- had a linear increase throughout the 12 months by a factor of 15 in comparison to unburned soils (Notario del Pino et al. 2007). This is in line with our findings of higher contents in N-inorganic even 2 years after the fire (Table 1). Elevated NH_4^+ levels can arise directly from organic

matter combustion (Zalman et al. 2023). Therefore, the higher NH_4^+ contents in the burned rhizosphere would support higher fire severity associated to the vegetation. In addition, the high caloric content of the legume shrubland vegetation was an important factor in determining the severity of the wildfire on the rhizosphere microbiome. The cover of broom plants within the study area was typical of a mature shrubland (Fig. S3A). The 2019 fire caused the death of broom plants, no resprouting was observed in the following two years, which evidence a high fire severity in the rhizosphere. However, the analysis of the remote sensing images suggests moderate severity in the burned area (Fig. S3). This apparent discrepancy could be explained by the low resolution of the free available images, in which each square of 20×20 m to include adult broom vegetated soil as well as bare soils, resulting in a moderate index on average. Several studies have shown that fire severity is heavily influenced by vegetation cover (Wang et al. 2016; Panico et al. 2020; Santorufo et al. 2021). Certain types of vegetation result in different effects on soil microorganisms following a wildfire. For example, fires in shrubland vegetation may be more severe than those in forests due to the abundance of highly combustible tinder (González de Vega et al. 2016; Sáenz de Miera et al. 2020). The milder impact of fire on unvegetated bulk soils can be attributed to the fact that these soils were only exposed to heat radiation from the adjacent burning plant material, resulting in lower intensity and less impact on soil microbiota. In contrast, the severe affection of the broom rhizosphere microbiome agrees with other studies showing a strong relationship between fire severity and the type of vegetation (Wang et al. 2016; Panico et al. 2020; Santorufo et al. 2021).

The impact of fire on the microbial community diversity was revealed by a noteworthy reduction in species richness (ASV) and all diversity indices (Fig. 2). The lower evenness index in the burned rhizosphere community indicates loss of homogeneity and species dominance, which was corroborated in the taxonomic analysis by the dominance of particular ASVs. Noteworthy examples include *Pseudathrobacter*, *Coprinellus*, and *Tephrocye*, wherein one or two ASVs account for the entirety of each genus's relative abundance (Fig. S7). Furthermore, there was variation in both the structure (Fig. 3) and composition (Figs. 4 and 5) of the microbial communities. Compared to

bulk soils, co-occurrence networks exhibited reduced complexity in the rhizosphere microbial community. This same trend (Fan et al. 2018), as well as the opposite (Wang et al. 2022), has been reported previously. Reduced network complexity in the rhizosphere has been associated with disturbed communities that cannot optimally benefit their host plant as do more complex networks in the unburned plant rhizospheres (Fernández-González et al. 2020; Jiemeng et al. 2018). According to our hypothesis, we expected less complex networks in bulk soils. However, the results indicated the opposite. It could be speculated that the harsher environmental conditions require the bulk soil microbial communities to form more complex and interconnected networks to thrive in adverse conditions.

With regard to how fire affected the bacterial community composition, Actinobacteria in general stood out with many of the most abundant and rhizosphere-specific genera changing greatly in their relative abundance. Genus *Crossiella* decreased by more than 90%, while *Kribella*, *Actinoallomurus* and *Pseudarthrobacter* were fire favoured genera. *Arthrobacter* is a common genus favoured after fire (Fernández-González et al. 2017), but in our study *Pseudarthrobacter* (a recently created genus from the so-called “*Arthrobacter oxydans* group”, Busse 2016) stood out with a more than 20-fold increase. Actinobacteria were therefore good bacterial fire-biomarkers. Previous studies have shown contradictory response of Actinobacteria to fire. Indeed, they have been described to increase (Fernández-González et al. 2017; Sáenz de Miera et al. 2020; Nelson et al. 2022), decrease (Villadas et al. 2019) or not to be affected (Isobe et al. 2009; Xiang et al. 2014) by fire. We observed in the rhizosphere a post-fire increase in the Actinobacteria that at the phylum was statistically non-significant, but demonstrate a strong genus dependent response of Actinobacteria, which underlines the importance of the taxonomic level of analysis in the interpretation of fire response. Among other phyla, several studies found that *Pedobacter* (Bacteroidetes), *Massilia* (Betaproteobacteria) and *Paenibacillus* (Firmicutes) correlate positively with severe fires, and, together with *Arthrobacter* (Actinobacteria), are the four bacterial genera most commonly proposed as the best post-fire indicators (Fernández-González et al. 2017; Fernández-González et al. 2023; Pérez-Valera et al. 2017; Sáenz de Miera et al.

2020; Villadas et al. 2019; Whitman et al. 2022). Increases in *Pedobacter*, *Massilia* and *Arthrobacter* were also statistically significant in our bR soils, although not the dominant genera, and *Paenibacillus*, normally a good fire indicator, was unnoticed (0.01%) in bR soils. Indeed, our study revealed an unexpected result for phylum Firmicutes, as their increase in burned soils was negligible, despite the fact that sporulated Firmicutes typically increase after fire (Xiang et al. 2014; Pérez-Valera et al. 2017; Sáenz de Miera et al. 2020; Villadas et al. 2019).

The consumption of plants negatively affects soil microbial communities, especially the most sensitive groups in the surface layers, such as decomposer and plant symbiotic fungi (Holden et al. 2016; Dove and Hart 2017). In fact, the post-fire effect was more drastic on the rhizosphere fungal community, consistent with some other reports showing slower recovery of the fungi (Ammitzboll et al. 2022; Dove and Hart 2017; Liu et al. 2022). Indeed, in bR soils 2 years after the fire, the species richness is half than the initial one, all diversity indices are lower, the community structure clearly different and its composition strongly modified. Basidiomycota became dominant, while the trend for Ascomycota is in the opposite direction. At the genus level, the most abundant and representative genera of the rhizosphere have been almost extinguished and substituted by common pyrophilous (Ammitzboll et al. 2022; Day et al. 2020; Whitman et al. 2019). Our results coincide with the successional changes of fungal taxa showed in severely burned soils (Ammitzboll et al. 2022), which describe a first post-fire year with abundance in Ascomycota followed by a later dominated of other more competitive Basidiomycota pyrophilous, such as *Tephrocye* and *Coprinellus* (9.76% and 34.25% relative abundance in our burned soils). *Coprinellus* is indeed an obligate pyrophile (Hughes et al. 2020). The virtual absence of *Coprinellus* in unburned soils of Teide confirms that the conditions created in the rhizosphere of the burned broom-plants were conducive to its enormous posterior abundance. Indeed, the significant rise in Basidiomycota (Fig. 4B) can be virtually attributed to *Coprinellus*, with a noteworthy contribution from *Tephrocye*. A single ASV (9.43%) accounting for the total abundance of genus *Tephrocye* and 2 ASVs (27.74%) for *Coprinellus* (Fig. S6) are two good examples of species dominance in bR soils. Overall, fungal communities were better

predictors than bacteria in differentiating the four characterised scenarios, the burned soils bB and bR as well as the undisturbed soils uB and uR.

From a practical and positive perspective, despite the transformation of microbial communities in post-fire rhizosphere soils and the expected negative effects due to the reduction of many symbiotic and potentially plant growth-promoting microorganisms, certain pyrophilic microorganisms may be key to ecosystem recovery and to some extent replace lost functions that the usual rhizosphere microbiome would perform in undisturbed soils. For instance, a potential role for *Pedobacter* in burned soils has never been proposed, and it may merely be an opportunist bacterium that benefits from conditions in burned soils. However, *Massilia* may contribute to plants fitness during the initial establishment of seedlings that appear in burned soils, as it is a common colonizer in the rhizosphere of many early-stage plants (Ofek et al. 2012). Attention should be also paid to *Kribella* which is able to live as endophytes of legume root nodules (Trujillo et al. 2006), a plant environment that have been proved to be a rich source for plant growth-promoting Actinobacteria. In this context, one of the most promising genera is *Pseudarthobacter*, the most abundant bacterium in the burned soils of Teide. It is a genus for which several strains exhibiting potential as plant growth-promoting have been described (Ham et al. 2022; Issifu et al. 2022). No evidence of a benefit to plants has been reported from most pyrophilous fungi. Noteworthy is that the most abundant fungal pyrophilous in our soils, *Coprinelus*, has been recently related to plant promotion (Maldonado et al. 2020). Hence, the high predominance of these two microorganisms in our burned soils suggests an opportunistic adaptation but is also highly suggestive that they may be a key player in the recovery of the Teide ecosystem.

Conclusions

The most characteristic feature of the soil microbial community in the Teide alpine ecosystem (Tenerife, Canary Islands) is the abundance of the non-photosynthetic Chloroflexi, outnumbering more common groups such as Proteobacteria, Acidobacteria and Actinobacteria. This feature, rather unusual in most alpine ecosystems, is emerging as a distinctive

signature of high-altitude microbial communities in oligotrophic volcanic soils. Further research is needed to elucidate the functional role of Chloroflexi in the soil ecosystem. Our study shows that the characteristic legume shrubland vegetation in Teide NP shapes a unique rhizosphere microbiome with presence of many potential plant growth-promoting microorganisms which were vanished after a wildfire. The microbiomes of the rhizosphere and bulk soils exhibited comparable diversity. However, co-occurrence networks revealed less complex microbial communities in the rhizosphere than in bulk soil. This could be attributed to the more stable conditions in the plant surroundings. In contrast, microbial communities in bare soil may need to establish more complex and interconnected networks to survive harsher environmental conditions.

The large differences that remain two years after a wildfire suggest a slow recovery of the soil microbial communities in dry volcanic soils, which must influence soil dynamics and ultimately vegetation growth. Defining functional role of the rhizosphere microbiome is essential for designing new strategies to address ecosystem recovery. Our results characterizing the soil microbiome may help to develop more effective strategies for rehabilitating fire-damaged ecosystems. The presence of vegetation is an important feedback in the dynamics of soil recovery after a fire. In the coming years, a major effort should be made to cultivate the key bacterial and fungal genera of the microbiome and assess their potential as plant growth promoters to incorporate their use as inoculants in reforestation strategies for alpine vegetation. Fungi, in particular, were the best predictors of the different scenarios in terms of microbial diversity and composition, and so, they could be the best biomarkers to ecosystem monitoring.

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Data availability The datasets generated and analysed in the present study are publicly available in the NCBI Sequence Read Archive (SRA) under the BioProject number PRJNA914530.

Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose

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