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Moss biocrust accelerates the recovery and resilience of soil microbial communities in fire-affected semi-arid Mediterranean soils

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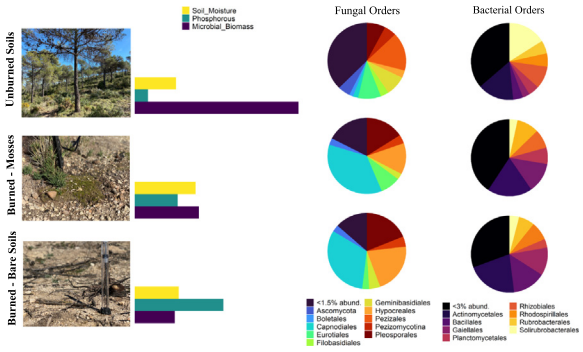
HIGHLIGHTS

- Mosses allow faster recovery of soil properties and microbial communities.
- Moss biocrust allows higher bacterial diversity in fire-affected soils.
- Bacteria and fungi composition are positively affected by the presence of mosses.

GRAPHICAL ABSTRACT



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ABSTRACT

After wildfires in Mediterranean ecosystems, ruderal mosses are pioneer species, stabilizing the soil surface previous to the establishment of vascular vegetation. However, little is known about the implication of pioneer moss biocrusts for the recovery and resilience of soils in early post-fire stages in semi-arid areas. Therefore, we studied the effects of the burgeoning biocrust on soil physicochemical and biochemical properties and the diversity and composition of microbial communities after a moderate-to-high wildfire severity. Seven months after the wildfire, the biocrust softened the strong impact of the fire in soils, affecting the diversity and composition of bacteria and fungi community compared to the uncrusted soils exposed to unfavourable environmental stress. Soil moisture, phosphorous, and enzyme activities representing the altered biogeochemical cycles after the fire, were the main explanatory variables for biocrust microbial community composition under the semi-arid conditions. High bacterial diversity was found in soils under mosses, while long-lasting legacies are expected in the fungal community, which showed greater sensitivity to the fire. The composition of bacterial and fungal communities at several taxonomical levels was profoundly altered by the presence of the moss biocrust, showing a rapid successional transition toward the unburned soil community. Pioneer moss biocrust play an important role improving the resilience of soil microbial communities. In the context of increasing fire intensity, studying the moss biocrust effects on the recovery of soils microbiome is essential to understanding the resistance and resilience of Mediterranean forests to wildfires.

1. Introduction

Wildfires, one of the most important disturbances shaping soil biochemistry, vegetation and microbial communities in Mediterranean ecosystems (McLauchlan et al., 2020), are currently increasing in intensity favoured

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by warmer and drier conditions driven by decades of land-use change and fire suppression policies (Moreira et al., 2020). Understanding how ecosystems regenerate after a fire is essential for the development of measures to improve post-fire ecosystem recovery, of special importance in semi-arid areas, the most sensitive to climate change-induced scenarios (IPCC, 2013). After wildfires, the fast colonization of ruderal mosses preceding vascular vegetation establishment effectively stabilizes the soil surface and counteracts erosion in early post-fire stages (Silva et al., 2019). Ruderal mosses pioneer colonization by responding to fire with wide dispersal of diaspores and rapid protonemal and gamethophye growth, facilitated by their ability to develop on unstable substrates like charred surfaces and ashes (Esposito et al., 1999; Smith et al., 2014). Although biocrust recovery rates tend to be slow (Root et al., 2017), under favourable climatic and stable soil conditions mosses initiate the biocrust succession development, often been observed after fire disturbances (Weber et al., 2016; Weber et al., 2022). Moreover, forests affected by high-intensity fires in Mediterranean ecosystems are largely dominated by ruderal moss biocrusts during the first 2–3 years (De las Heras et al., 1994; Esposito et al., 1999; Stinca et al., 2020), revealing the high resilience to the post-fire environment of mosses (Reed et al., 2016; Condon and Pyke, 2018). Despite the relevance in the vegetation succession dynamics, it is rather unknown if the pioneer moss biocrust play a key role in the resilience of post-fire disturbed ecosystems.

Biocrusts are complex assemblages of cyanobacteria, lichen, and/or bryophyte that support a huge diversity of microorganisms (Warren et al., 2019), which provide key ecosystem functions such as stabilization of soil surface, increase soil fertility, control of local hydrological dynamics, facilitate plant germination and establishment, and promote microbial abundance (Belnap and Lange, 2013). Considering their functional roles in ecosystems, the pioneer moss biocrust may accelerate the recovery of the ecosystem functioning in the early stages after the fire disturbance, through the mitigation of the detrimental consequences of fires in soils. Nevertheless, growing biocrust to rehabilitate fire-affected soils has been recently studied as a promising stabilizing technique, either inoculating cyanobacteria (Muñoz-Rojas et al., 2021) or cultivating mosses (Grover et al., 2020). Apart from soil stabilization, the repercussion for soil microbial biodiversity is far to be understood and still needs to be elucidated. Understanding the soil biochemistry and microbiome response to the early biocrust emergence is required to provide valuable information to apply in management strategies toward accelerating recovery in semi-arid ecosystems prone to degradation.

Fire dramatically alters the aboveground and belowground soil communities. Extremely high temperatures usually decline microbial biomass and profoundly reshape the microbial communities, whose resilience to fire is indirectly modulated via alterations in biogeochemical soil properties, microclimate, and vegetation presence (Pressler et al., 2019; Whitman et al., 2019; Pérez-Valera et al., 2020). Moreover, soil microorganisms differ in their sensitivity to fire; fungal communities usually report drastic decline with long-lasting legacies, whereas bacteria express faster recovery rates after wildfires (Adkins et al., 2020; Ammitzboll et al., 2022). Biocrust emergence on recently burned soils in semi-arid areas may act as an intermediary that softens the harsh conditions providing soil stability, shade, moisture, and enriching the underlying mineral soil with organic matter and nutrients (Bao et al., 2019; García-Carmona et al., 2020). Therefore, microbial communities living in soils under the influence of the pioneer ruderal mosses might be benefited from its early presence, recovering faster in biomass and diversity after the disturbance, ultimately accelerating the ecosystem productivity and functionality restoration (Maestre et al., 2012).

Knowing their relevance in the post-fire vegetation succession dynamics in Mediterranean ecosystems, we speculated that pioneer moss biocrust plays an important role in the recovery and resilience of soils and microbial communities in recently fire-affected soils. To test the hypothesis, physicochemical and biochemical soil properties and the microbial communities were studied in moss biocrust soils and soils without mosses seven months after a wildfire and intensive logging operations, compared to unaffected soils. It was tested whether (1) the altered by the fire physicochemical and biochemical soil properties recover faster under the moss biocrust, (2) the moss biocrust supports higher microbial diversity and abundance compared to the uncrusted bare soils exposed to unfavourable environmental stress (3) the structure of the microbial communities responds to the biocrust presence and the physicochemical and biochemical soil properties, and, (4) dominant bacterial and fungal taxa, and the ecological roles of fungal community, are resilient to fire disturbance thanks to the moss biocrust.

2. Materials and methods

2.1. Site description

The study area is located in “Sierra de la Replana” in Beneixama, Alicante, Spain (38°44′15″ N, 0°44′56″ W, 940 m). The area has a warm Mediterranean climate, 3–4 months of summer droughts, dry-hot summer, and wet-warm spring, autumn and winter. The average temperature is 14.9 °C and the average annual precipitation is 456 mm. The vegetation is mainly composed of50 years old *Pinus halepensis* Mill. trees from afforestation, and *Quercus ilex* L., and typical Mediterranean shrubs species such as *Quercus coccifera* L., *Rosmarinus officinalis* L., *Juniperus phoenicea* L., *Juniperus oxycedrus* L., *Ulex parviflorus* Pourr., *Erica multiflora* L., *Stipa tenacissima* L., and *Stipa offneri* Breistr. The steep slopes are terraced facing south, where soil was classified as a Typic Xerorthent (Soil Survey Staff, 2014) with low depth and clay loam texture (29 % clay, 49 % silt, 22 % sand).

A wildfire in July 2019 burned a total of 862 ha. Fire severity was classified as moderate to high according to Keeley (2009), understory plants were charred or consumed, fine dead twigs on soil surface were consumed and log charred, and soils were covered by grey colour ash. In early September, salvage logging operations were carried out in the area, consisting of a complete extraction of the burned wood using heavy machinery. After that, soils were exposed to erosion processes, triggered by events of strong precipitations (40 mm in an hour in October 2019). Seven months after the wildfire, slopes facing south showed evidences of surface runoff and soil erosion, and harsher conditions for plant regrowing. Ruderal mosses forming an emergent biocrust colonized the fire-affected soils, creating spatial heterogeneity through a mosaic of moss patches surrounded by bare soils.

2.2. Experimental design, biocrust monitoring, and soil sampling

Sampling was conducted in February 2020, seven months after the fire event. In order to facilitate the monitoring of the moss biocrust cover, experimental plots (2 m × 2 m) were placed in the study area. Plots were randomly established along the same hillside to minimize environmental factors, nine sampling plots in the fire-affected area, and another three sampling plots in a nearby-unburned area used as control at a distance of approximately 500 m. The unburned plots were at least 100 m away from any fire edge. Since the salvage logging effects on soils cannot be evaluated separately from the wildfire effects, the fire disturbance discussed in the manuscript includes the additional effects of burnt wood extraction.

A biocrust monitoring study was performed before the soil sampling using four random replicates of a 25 cm × 25 cm quadrat (divided into 100 cells) at each experimental plot, revealing an average of 30 ± 14 % of soils covered by ruderal mosses. In the unburned area (50-year afforestation), the presence of mosses was almost negligible (<5 %), possibly due to bryophytes communities are displaced in later successional stages in Mediterranean vegetation dynamics (De las Heras et al., 1994; Esposito et al., 1999), in addition to the high density of pine needles covering soils reducing the sunlight in soil surface that hinder the moss development. Therefore, we did not consider the presence of mosses in the unburned area for the experimental design due to the high differences of the conditions with the burned area.

Soil samples were collected from the top 2.5 cm of the soil surface. Within each experimental plot in the burned area, four soil samples were collected, two of them consisting of soils under the moss-biocrust and the other two in bare soils. At the unburned area, two soil samples were collected per plot at 2.5 cm after the removal of organic debris. From the total number of samples representative of the area, for operative purposes in the present study we randomly selected 15 samples representing bare soils, 15 samples under mosses, and 5 samples from the unburned soils ($n = 35$).

For each soil sample, one part was sieved at 2 mm and frozen at −20 °C for DNA extraction and lipid fatty acid analyses, another part was kept at 4 °C to measure biological and biochemical parameters, and the remainder was dried at room temperature. From the dry sample, one part was sieved between 4 mm and 0.25 mm for the aggregate stability test, and the remaining was sieved at 2 mm for the physicochemical analyses.

2.3. Laboratory analyses

Soil pH and electrical conductivity were measured in a 1:2.5 and a 1:5 (w/v) aqueous extract, respectively. Soil organic carbon was determined by the potassium dichromate oxidation by the Walkley-Black method (Nelson and Sommers, 1983); total nitrogen was analysed by the Kjeldahl method (Bremner and Mulvaney, 1982); and available phosphorus was extracted and measured by the Burriel-Hernando method (Díez, 1982). The aggregate stability was measured as the proportion of aggregates that remain stable after the soil sample (sieved between 4 and 0.25 mm) is subjected to an artificial rainfall of known energy (279 J min^{-1} m^{-1}) (Roldán et al., 1994). Soil moisture was determined by gravimetry from field wet soils after drying for 24 h at 105 °C.

The soil microbial biomass carbon was determined by the fumigation- extraction method (Vance et al., 1987). Soil basal respiration was measured in an automated impedance-meter (BacTrac 4200 Microbiological Analyser, Sylab, Austria), based on the changes in the impedance of a KOH solution (2 %) due to the CO_2 emissions by soil microorganisms incubated at 30 °C for 24 h. The estimation of urease activity was based on the release of NH^{4+} from hydrolytic reactions where soil samples were exposed to the substrate urea (Nannipieri et al., 1981). β-Glucosidase and alkaline phosphomonoesterase activities were quantified colorimetrically as the p-nitrophenol produced during the incubation of soil with the substrates *p*-nitrophenyl-β-D-glucopyranoside (Tabatabai, 1983) and *p*-nitrophenyl phosphate disodium salt, respectively (Naseby and Lynch, 1997).

To estimate the biomass of the microbial community, phospholipid fatty acid analysis (PLFA) and neutral lipid fatty acid analysis (NLFA) were used. Lipids were extracted with a chloroform–methanol–phosphate buffer mixture (1:2:0.8), and then fractionated using solid-phase extraction cartridges (LiChrolut Si 60, Merck), eluted in three fractions containing neutral lipids, glycolipids and phospholipids with 2 mL of chloroform, 6 mL of acetone and 2 mL of methanol, respectively. The first fraction and the third fractions were subjected to mild alkaline methanolysis. The free methyl esters of NLFA and PLFAs were analysed by gas chromatography–mass spectrometry (450-GC, 240-MS ion trap detector, Varian, Walnut Creek, CA, USA), the instrument and program settings described in Frouz et al. (2016). Methylated fatty acids were identified according to their mass spectra and by using a mixture of chemical standards from Sigma–Aldrich (Prague, Czech Republic) and Matreya LLC (Pleasant Gap, PA, USA). Fungal biomass was quantified based on the 18:2ω6,9 content, and bacterial biomass was quantified as the sum of the contents of the fatty acids i14:0, i15:0, a15:0, 16:1ω7t, 16:1ω9, 16:1ω7, 10Me-16:0, i17:0, a17:0, cy17:0, 17:0, 10Me-17:0, 10Me-18:0, and cy19:0 (Stella et al., 2015). The content of arbuscular mycorrhiza biomass was estimated using 16:1ω5 concentration in the NLFA fraction (Bååth, 2003). The total PLFA was calculated as the sum of all the fatty acids.

2.4. DNA extraction and sequencing analysis of bacterial and fungal communities

DNA was isolated using the DNeasy PowerSoil Pro DNA isolation kit (Qiagen), strictly following the manufacturer's instructions. DNA was resuspended in a final volume of 100 μL and quantified using the Qubit High Sensitivity dsDNA Assay (Thermo Fisher Scientific).

For library preparation, a fragment of the ITS2 region of fungal rRNA was amplified using the primers ITS86F and ITS4 (De Beeck et al., 2014), and the V4 region of bacterial 16S rRNA was amplified using the primers 515F-Y (Parada et al., 2016) and 806R (Apprill et al., 2015). Illumina sequencing primers were attached to these primers at their 5′ ends. PCRs were carried out in a final volume of 12.5 μL, containing 1.25 μL of template DNA, 0.5 μM of the primers, 6.25 μL of Supreme NZYTaq 2× Green Master Mix (NZYTech), and ultrapure water up to 12.5 μL. The reaction mixture was incubated as follows: an initial denaturation step at 95 °C for 5 min, followed by 35 cycles of 95 °C for 30 s, 49 °C for 30 s, 72 °C for 45 s, and a final extension step at 72 °C for 7 min. A negative control that contained no DNA was included in every PCR round to check for contamination during library preparation. The libraries were run on 2 % agarose gels stained with GreenSafe (NZYTech), and imaged under UV light to verify the library size. The oligonucleotide indices which are required for multiplexing different libraries in the same sequencing pool were attached in a second PCR round with identical conditions but only 5 cycles and 60 °C as the annealing temperature. Libraries were purified using the Mag-Bind RXNPure Plus magnetic beads (Omega Biotek), following the instructions provided by the manufacturer. Then, libraries were pooled in equimolar amounts according to the quantification data provided by the Qubit dsDNA HS Assay (Thermo Fisher Scientific). The pool was sequenced in a fraction of a NovaSeq PE250 lane (Illumina). The sequence data have been deposited into the National Centre for Biotechnology Information database under the accession number PRJNA857296.

The amplicon sequencing data were processed using the SEED 2 pipeline (Větrovský et al., 2018). Briefly, paired-end reads were joined using fastq-join (Aronesty, 2013), reads were quality filtered based on a quality score of 30, short and long sequences were trimmed (sequences with <40 bases were removed for ITS, <200 and >350 bases for 16S). The ITS2 region was extracted using the ITSx software before processing (Bengtsson-Palme et al., 2013). Chimeric sequences were detected and deleted using Usearch 8.1.1861 (Edgar, 2010). Sequences were clustered into operational taxonomic units (OTUs) using UPARSE implemented within USEARCH (Edgar, 2013) at a 97 % similarity level. After singleton removal, 2896 OTUs for ITS and 23,914 OTUs for 16S were kept for further analyses. The most abundant sequence of each OTU was selected to represent it and perform cluster identification. The identification of bacterial and fungal sequences was performed using BLASTn at the Ribosomal Database Project (Cole et al., 2014) and UNITE (Nilsson et al., 2019), respectively. Sequences identified as non-bacterial or non-fungal were discarded. Identification at genus-level was performed at ≥97 % similarity and ≥95 % coverage to merged into a single taxon, and when lower similarity, lower coverage or both, the genus-level identification, or the best available identification, was used. Based on the published literature, fungal genera were used to assign putative ecophysiological categories using the FungalTraits (Põlme et al., 2020).

2.5. Statistical analysis

All the analyses were performed using RStudio v. 4.0.5 (RStudio Team, 2021). In order to study the recovery of soil properties and PLFAs and NLFA content in the presence of the moss biocrust in burned soils, linear mixed models were fitted including the distribution of samples along the experimental plots as random effects, using the "lmer" function from "lme4" package. The relationship of the microbial biomass (PLFA and NLFA) with the physicochemical and biochemical parameters in soils under mosses and bare soils was explored using principal component analysis (PCA) with the "FactoMineR" package (Lê et al., 2008).

Diversity parameters were estimated from OTU tables in which all samples were resampled to equal the smallest library size to reduce the effect of variation in sequencing depth using the "rarefy_even_depth" function in "phyloseq" package. Previous to further statistical analysis, exploring distance-decay patterns, we discarded the possible effects of the geographic distance among experimental plots along the slope on the microbial community structure (Morlon et al., 2008). For that, we determined the level of similarity in the microbial communities, examining the correlations between the OTU abundance matrix (i.e., Bray-Curstis dissimilarities of OTU relative abundance) and the spatial distance matrix (i. e., cartesian coordinates). From the rarefied matrices, we calculated OTU richness (function "specnumber") and α-diversity indices for both bacteria and fungi to identify whether moss biocrust support higher diversity indices for bacterial and fungal diversity. Non-metric multidimensional scaling (NMDS) ordination analysis based on Bray-Curtis distances of OTU relative abundances was performed for recognize variations in the structure of the bacterial and fungal communities, using the "metaMDS" function from the "vegan" package. The effect of the biocrust presence on the microbial community structure was statistically tested by permutational multivariate analysis (PERMANOVA) with the "adonis2" function using 9999 permutations comparing the communities in biocrust and bare soils.

To understand which factors among the fire-affected soil physicochemical and biochemical properties are related with bacterial and fungal community composition in burned soils, soils under mosses and bare soils, canonical correspondence analyses (CCA) were performed with "cca" function. In order to avoid multicollinearity, variance inflation factor was calculated and variables with values >10 were removed sequentially. The remaining variables were subjected to a forward selection procedure to select the subset of constraining variables that better explain the communities' variation in the CCA final model with "ordistep" function. The significance of the CCA final models was tested by Monte-Carlo permutational test (999 permutations). The compositional matrices were transformed using Hellinger transformation before the statistical analysis.

With the aim of identifying shifts in the dominance of bacterial and fungal taxa in response to the moss biocrust presence and to the fire event, the microbial community composition was analysed for significant differences systematically at different taxonomic ranks using relative abundances with non-parametric "kruskal" function with *p*-values correction based on Benjamini–Hochberg false-discovery rate with 95 % confidence interval. It was also performed for the ecological categories in fungi community to detect the recovery state of the fungal functionality after the fire event and the emergence of the moss biocrust. The identification of indicator taxa of bacteria and fungi (at genus and OTUs level) representative of the conditions in each soil studied (moss biocrust soils, bare soils, and unburned soils), was provided with the Indicator Value (IndVal), a predictive value for each "specie" (biological taxa) as indicators of each soil (De Caceres et al., 2013), after the "multipatt" function at the "indicspecies" package.

3. Results

3.1. Fire and biocrust effects on soil properties, and the relationship with the microbial biomass

Seven months after the wildfire and the subsequent forest management, fire legacies were visible on most soil properties (Table 1). The severity of the fire was reflected in the significant reduction of organic carbon and nitrogen content and the strong impact on the biological and biochemical properties measured, with significantly lower values reported for basal respiration, microbial biomass, and enzyme activities in fire-affected soils.

The moss biocrust influenced the underlying burned soils (Table 1). Soils under mosses registered a significant decrease (more than two-fold) in available phosphorous content compared to the bare soils, presumably consumed by mosses after being highly released by the fire event. Significantly higher soil moisture was observed in soils under mosses. In addition, the microbial biomass carbon was a sensitive parameter to the moss biocrust presence, showing significantly higher values in soils under mosses compared to bare soils, 296 mg C kg^{-1} and 184 mg C kg^{-1}, respectively, both values markedly lower compared to the biomass carbon in the unburned soils (753 mg C kg^{-1}).

The total PLFAs, significantly reduced in the fire-affected soils in all cases (Fig. 1), did not significantly respond to the moss biocrust, although a trend to higher biomass was found for bacterial and total biomass in soils under mosses (Fig. 1). In comparison with bare soils, moss biocrust soils concentrated higher bacteria biomass and thus higher extracellular enzyme activities associated (Supplementary data, Fig. A1). With lesser effect, soils under moss biocrust also concentrated higher fungi biomass, correlated to the higher moisture in those soils. Contrary, the arbuscular mycorrhizal biomass was highly correlated to the slight increase in organic carbon and nitrogen content and basal respiration found in bare soils (Fig. A1).

3.2. Microbial community diversity and composition, and their relationship with soil variables

Alpha diversity values for soil bacterial community were higher under the moss biocrust (Fig. A2), reaching the same levels as in unburned soils, while bare soils were identified to have significantly lower bacterial richness (i.e., number of phylotypes) and diversity indices (Shannon and Chao1). In contrast, the fire strongly impacted the fungal community, significantly decreasing values for richness and diversity indices, without registering any effect due to the moss biocrust (Fig. A2).

Regarding the structure of the microbial communities, both bacterial and fungal communities were drastically altered by the fire, and then reshaped after the biocrust emergence. Fig. 2 shows bacterial communities in unburned soils and burned soils to cluster separately, and moss communities and bare soil in burned soils to cluster separately as well. The effect of a biocrust in burned soils was confirmed by the PERMANOVA analysis,

Table 1
Mean ± standard deviation of soil physical-chemical and biochemical properties of burned soils, with mosses and without mosses bare soils, and unburned soils. Lowercase letters indicate statistical differences at $p < 0.05$ (post-hoc Tukey test).

	Bare soil	Mosses	Unburned
pH (H_2O. 1:2.5)	8.45 ± 0.11a	8.41 ± 0.13ab	8.28 ± 0.06b
Electrical conductivity (μS/cm)	180 ± 26b	217 ± 36a	208 ± 47ab
Organic carbon content (%)	4.18 ± 1.25ab	3.97 ± 0.86b	5.53 ± 1.64a
Total nitrogen (%)	0.26 ± 0.07b	0.25 ± 0.05b	0.36 ± 0.11a
Available phosphorus (mg kg^{-1})	27.22 ± 19.60a	13.21 ± 4.44b	4.07 ± 1.25b
Aggregate stability (%)	78.82 ± 8.59a	69.14 ± 8.78b	75.87 ± 12.5ab
Soil moisture (%)	13.53 ± 3.97b	18.67 ± 4.86a	12.74 ± 5.69b
Basal soil respiration (μg C-CO_2 h^{-1} g^{-1} soil)	7.64 ± 1.36b	7.63 ± 0.678b	12.3 ± 3.36a
Microbial biomass carbon (mg C kg^{-1} soil)	184 ± 55c	296 ± 113b	753 ± 179a
β-Glucosidase (μmol PNP g^{-1} h^{-1})	1.27 ± 0.41ab	1.21 ± 0.30b	1.67 ± 0.22a
Urease (μmol N-NH_4^+ g^{-1} h^{-1})	0.57 ± 0.39b	0.92 ± 0.27b	2.1 ± 1.07a
Alkaline phosphatase (μmol PNP g^{-1} h^{-1})	1.03 ± 0.33b	1.33 ± 0.34b	2.45 ± 0.528a

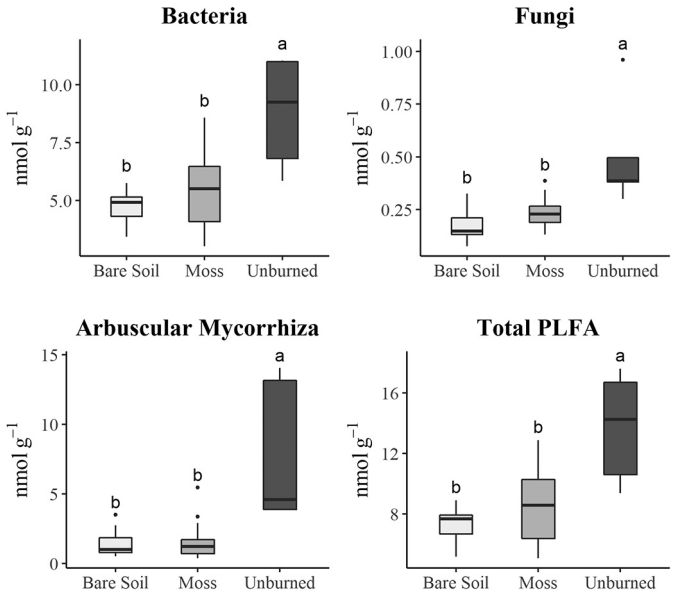

Fig. 1. Box-plot of bacterial, fungal, arbuscular mycorrhiza biomass and total PLFAs, measured in of burned soils, with mosses and without mosses bare soils, and unburned soils. Lowercase letters indicate statistical differences at $p < 0.05$ (post-hoc Tukey test).

which showed bacterial communities under mosses statistically differ from those in bare soils ($F = 3.273$, p-value < 0.001). The effect of burning on fungal community structure was even more marked than for bacteria, separating the unburned and burned communities along the X-axis (Fig. 2). Communities of fungi under mosses clustered separately along the Y-axis from those in bare soils, a difference that was confirmed after the PERMANOVA analysis ($F = 2.343$, p-value < 0.001).

The environmental and soil properties related to the community composition of bacteria and fungi were similar in both cases (Fig. 3). The significant constraining variables for the bacterial communities were the enzymatic activities (β-glucosidase, phosphatase and urease), soil moisture (H), and available phosphorous, although explaining only 22.75 % of the total inertia in the CCA model. The composition of bacterial communities under mosses showed strong association with the enzymatic activities and soil moisture, while communities in bare soils associated with the high content of phosphorous in soils (Fig. 3).

The fungal community structure was related to the variables glucosidase activity, soil moisture (H) and available phosphorous, all of them selected for the final CCA model after forward selection and explaining the 13.07 % of the total inertia. As for the bacteria, the available phosphorous in bare soils markedly associated with fungal community composition, while glucosidase and soil moisture associated with fungal communities under mosses (Fig. 3).

3.3. Bacterial community composition

The study of the bacterial community showed a drastic shift in burned soils. However, the biocrust buffered the effect of fire on the bacterial community, for which the relative abundances of most of the dominant phyla showed values intermediate between the values for unburned soils and those for bare soils. The dominant phylum, Actinobacteria, significantly decreased after burning, shifting the dominance to Proteobacteria in bare soils (see Supplementary data, Fig. A3). Fire promoted Firmicutes and Bacteroidetes, in this case with lower values in soils under mosses than in bare soils. Similarly, higher abundances compared to bare soils were found under mosses for phylum Planctomycetes and Chloroflexi, which decreased with burning.

At the genus level, around 50 % of sequences belong to genera with mean relative abundance <1 %, especially found in unburned soils. The most abundant genera in soils revealed important changes after the fire event and the moss biocrust presence (Fig. 4). *Arthrobacter* (Micrococcaceae), was the dominant genus in biocrust soils and bare soils, and experienced a high increase after burning. Similarly, genera increased after the fire were *Bacillus* (Firmicutes), *Blastococcus* (Actinomycetales), *Massilia* (Burkholderiales), *Sphingomonas* (Alphaproteobacteria), *Paenisporosarcina* (Firmicutes), and *Comamonas* (Burkholderiales), expressing significantly lower values in soils under mosses *Massilia*, *Shingomonas* and *Comamonas*. On the other hand, several genera were significantly reduced by the fire, e. g. *Solirubrobacter* and *Conexibacter* (Solirubrobacterales), both with the highest abundance in the unburned soils, but showing intermediate values under mosses.

A high number of responsive OTUs were found for bare soils (441), mosses (318), and unburned soils (2152) (Supplementary data, Tables A1 and A2), the majority corresponding to taxa with low abundance in soils. At the genus level, *Arthrobacter* highlighted as the most abundant indicator

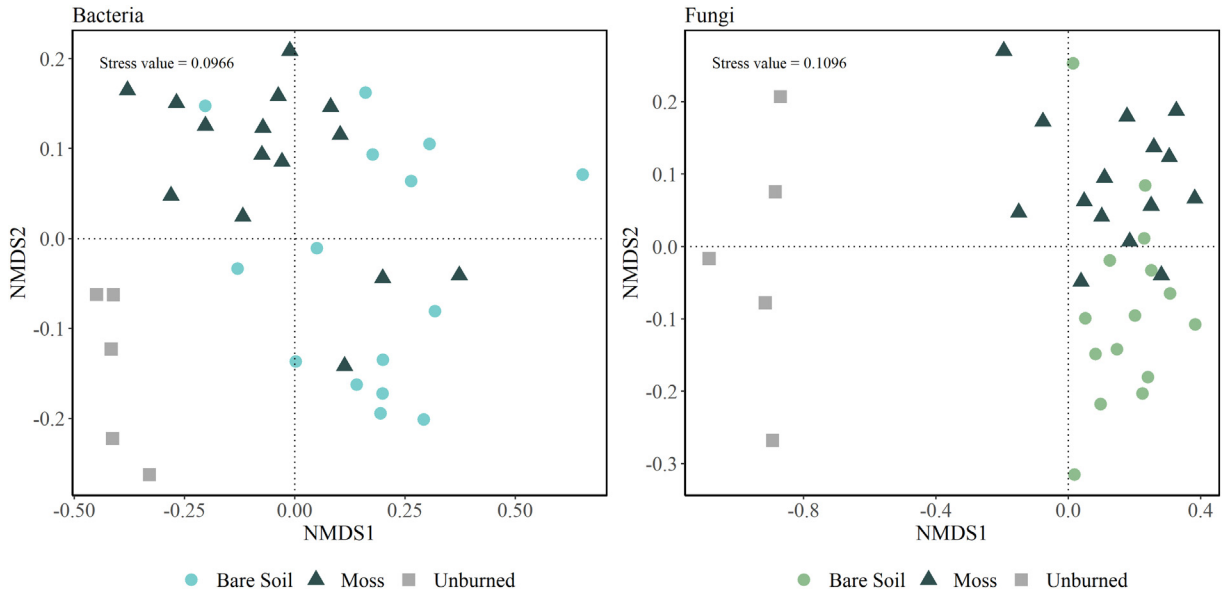

Fig. 2. Two-dimensional non-metric multidimensional scaling (NMDS) ordination based on Bray-Curties dissimilarities at OTU level for bacterial and fungal communities.

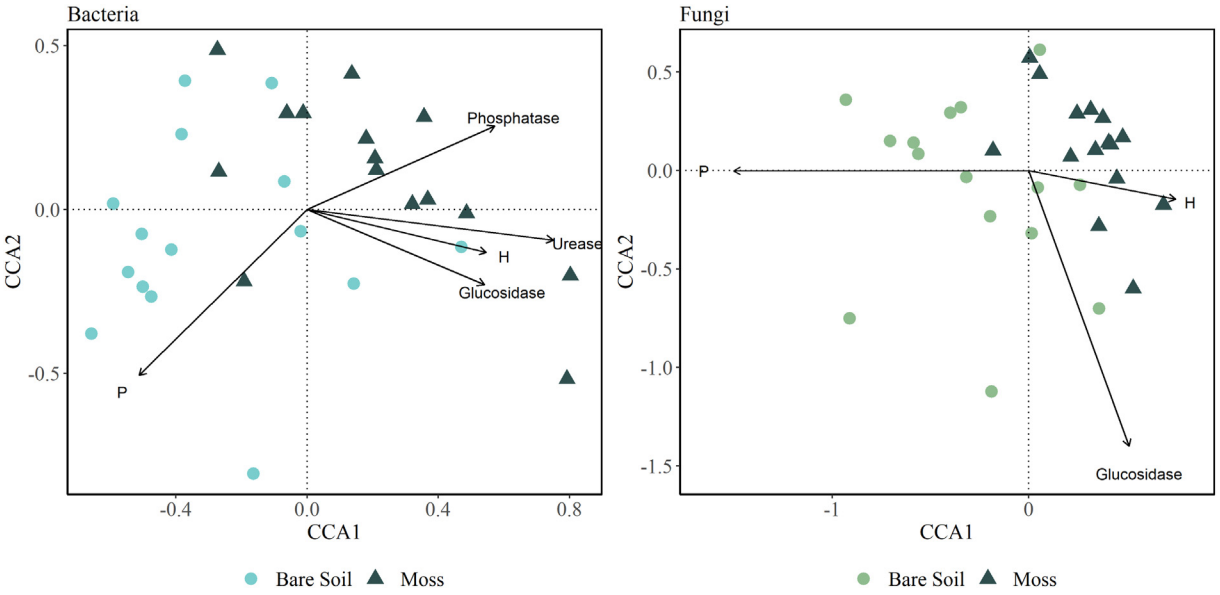

Fig. 3. Canonical correspondence analysis (CCA) at OTU level for bacterial and fungal communities of burned bare soils and moss biocrust. The explanatory variables are expressed with arrows (H: soil moisture; P: available phosphorous).

for soils under mosses (8 % versus 3.2 % in bare soils and 0.12 % in unburned soils), whereas indicator genera at bare soils reported were *Blastococcus*, *Bacillus*, *Massilia*, *Comamonas*, *Shingomonas*, *Paenisporosarcina*, *Adhaeribacter*, and others.

3.4. Fungal community composition

The fire disturbance strongly changed the composition of the dominant groups of the fungal community; additionally, the moss biocrust influenced some fungal taxa that expressed intermediate abundances between the unburned soils and bare soils (Fig. A3, Fig. 4). An increment in the dominance of Ascomycota after fire was revealed (60–70 %) in detriment of the Basidiomycota (from 34.1 % in unburned soils to 23.6 % in bare soils values in soils under mosses in between). In fire-affected soils, a significant increment in phyla Chytridiomycota was found (genera *Phlyctochytrium* and *Spizellomyces*), and a significant decrease in Glomeromycota with values almost negligible in bare soils. The increase in Ascomycota in burned soils was highly represented by the dominant *Penicillum*, followed by the increase in *Naganishia* (Basidiomycota) and *Sporormiella* (order Pleosoporales), among others. Contrary, genera that were negatively

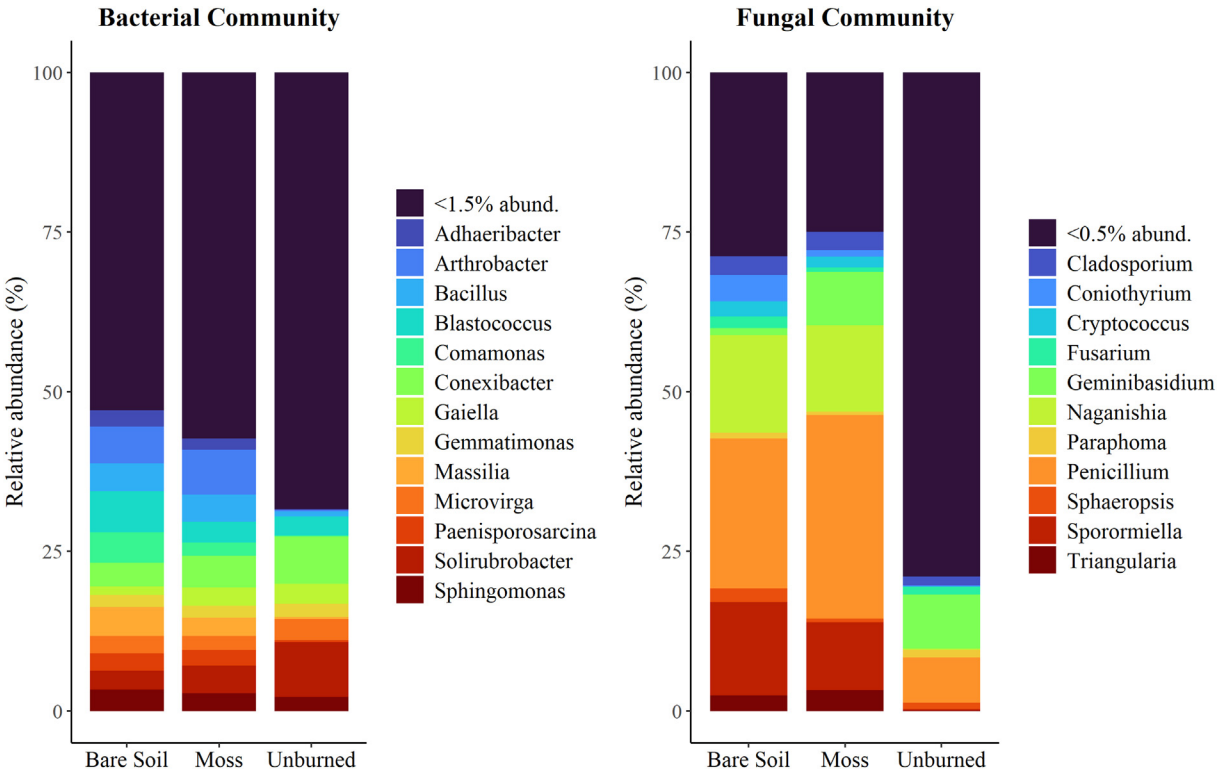

Fig. 4. Relative abundances of the dominant bacterial and fungal genera of burned soils, with mosses and without mosses bare soils, and unburned soils.

affected by fire were represented by the common yeast *Solicoccozyma* or *Paraphoma* (Pleosoporales). Fungal genera in moss biocrust that showed the same abundance than in unburned soils were *Geminibasidium* (Basidiomycota) and *Rhizopogon* (Boletales). Contrary, soils under mosses registered a significant decrease (2-fold) of *Fusarium* (Hypocreales).

The indicator species analysis, performed at both genus and OTUs level (Tables A3, A4), highlighted the saprotroph *Coniothyrium* as the major indicator of bare soils, followed by *Pyronema*, *Filobasidium*, and *Papilotrema*, with fungal parasite decomposer function, or the yeasts *Naganishia* and a *Saitoella*. For soils under mosses, the most representative and abundant indicator was the saprotroph *Penicillium*, followed by the other saprotrophs as *Clonostachys* or *Geminibasidium*.

The study of the fungal functional roles showed how the wildfire altered the main functions associated with fungal communities (Fig. 5). A significant decrease in ectomycorrhizal (36.6 % in unburned while around 2.6 % in burned soils) in favour of significant increases in saprotrophs was detected in the fire-affected soils (unburned with 41.8 %, bare soils and mosses around 74 %). In addition, a significant increase was detected in yeast (from 3.8 % to 16.5 % in mosses and 18.5 % in bare soils). Different abundances were found between bare soils and mosses in fungal parasite decomposers, being higher in bare soils.

4. Discussion

Seven months after the fire disturbance, the reduction of organic carbon and nitrogen content and the unfavourable response of the biological properties, with the microbial activity and biomass severely affected, reflected the legacies of a medium to high severity fire. The posterior emergence of the moss biocrust in the affected soils, creating a mosaic of heterogeneous soil microenvironments, greatly influenced the physicochemical soil properties and, consequently, the microbial composition and activity. Knowing that biocrusts help to stabilize the soil surface (Silva et al., 2019; Cania et al., 2020), together with the fact that mosses as primary producers with significant contributions to nutrient cycling (Cheng et al., 2021; Xu et al., 2022), an increment in soil fertility compared to their neighbouring bare soils was expected. However, contrary to expected, bare soils registered the highest aggregate stability, which is presumably related to a selection of the most stables aggregates after the erosion processes occurred post-fire in those soils (Mataix-Solera et al., 2021). In addition, soils

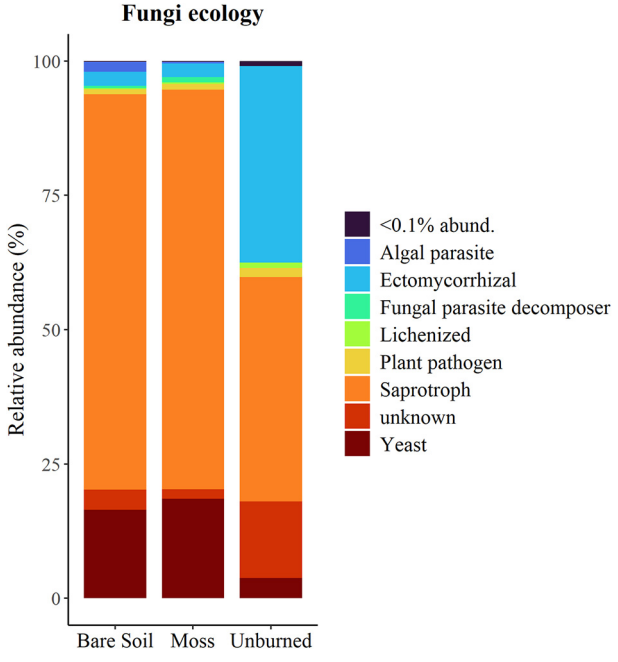

Fig. 5. Relative abundances of the dominant fungal ecological roles of burned soils, with mosses and without mosses bare soils, and unburned soils.

beneath moss biocrust registered a slight lower OC content, either due to the exhaustion of labile forms released after the wildfire by the burgeoning microbial community, or the preference of mosses to establish where lower recalcitrant organic matter concentrates after the fire (González-Pérez et al., 2004). The strong impact observed in the soil properties is commonly found after high severity fires, nutrients cycling is profoundly altered and the microbial activity immediately reduced, which is expected to takes time to recover to pre-fire levels under semi-arid conditions (Pérez-Valera et al., 2020).

Shifts in the microbial community composition in moss biocrust soils positively favour the extracellular enzymatic activities, suggesting a relative indirect contribution of moss biocrust to the nutrient cycling through microbial activities (Xu et al., 2022), an influence in soil expected to be greater at the early successional stages of the biocrust than in the later (Ferrenberg et al., 2022). The improvement in soil moisture thanks to the moss biocrust enhancing the water sorption capacity on soil surface (Li et al., 2021), would in turn promote the microbial activity and biochemical processes in the fire-affected soils under semi-arid conditions (D'Ascoli et al., 2005; Baldrian et al., 2010). Therefore, the post-fire harsh conditions on the soil surface (e.g., desiccation, high temperature, and solar radiation), were counteracted by the biocrust emergence providing favourable microhabitats that promoted the microbial growth, most probably benefiting from the pulse of easily mineralizable compounds after the fire (Goberna et al., 2012; Xiao et al., 2019). While the higher microbial biomass carbon found under the moss biocrust compared to bare soils supports the idea of microbial growth thanks to the biocrust, the PLFA content as indirect measure of total biomass (bacteria and fungi) did not significantly differ between moss biocrust soils and bare soils. However, the expected increase in soil stability and softening of severe conditions over time are expected to boost bacteria and fungi abundance and diversity in soils under biocrust (Garcia-Pichel et al., 2003; Maier et al., 2016). Nevertheless, the forest management, removing all the burned wood, possibly hindered the spreading of moss cover as reported in a previous work (García-Carmona et al., 2020), thus creating less opportunities for microbial establishment affecting at larger scales.

Despite the drastic decrease in the microbial abundance, only seven months after the fire, bacterial community in moss biocrust reached diversity values comparable to the unburned soils. Under favourable conditions bacteria reproduce rapidly; hence, increases in Chao1 and Shannon indices may indicate an increment in rare species simultaneously to frequent species, suggesting higher community complexity as described by Miralles et al. (2020) under later successional biocrust. On the contrary, fungi diversity, known as more sensitive than bacteria to disturbances (Bastida et al., 2017), remained low in burned soils regardless the biocrust presence. Biocrusts are considered as hotspots of fungal and bacterial diversity, but it highly depends on their successional stage (Maier et al., 2016; Liu et al., 2017). Immediately after fires, stochastic processes strongly structure the microbial community, but subsequent evolution of soil properties acts as an intense filter on the biocrust microbial composition (Ferrenberg et al., 2013; Li and Hu, 2021). Soil properties related to the for microbial community shifts described in the study (i.e., soil moisture and phosphorous) are common restrictive soil properties for microbial development after fires, as well as important factors for biocrust microbial assembly in semi-arid conditions (Ghiloufi et al., 2019; Warren et al., 2019). The structure of the bacterial community was highly determined by the soil nutrient status, observed in how the enzymatic activities responded to the community structure. The urease and glucosidase enzymes correlated well with the nitrogen and OC content, while the phosphatase and available phosphorous showed an opposite pattern, the enzyme probably inhibited after the high release of available P after fire (López-Poma and Bautista, 2014; Turner and Wright, 2014). On the other hand, the enzyme glucosidase was related with the fungal community, enzyme that is involved in the degradation of complex carbon substrates (Rousk and Bååth, 2011).

The dominance of the major phyla of bacteria and fungi shifted after the wildfire, recolonization being pioneered by microorganisms with sporeformers or fast-growth strategies and with adaptations to the high nutrients

release (Goberna et al., 2012). That was reflected in the relative abundance increment of Firmicutes, Bacteroidetes, and Ascomycota, all positively influenced by fire disturbances (Prendergast-Miller et al., 2017; Pérez-Izquierdo et al., 2020). Generally, copiotrophic taxa dominate in early post-fire environments, replaced later by more oligotrophic taxa to consume the remaining less labile substrates (Fierer et al., 2012). Despite the strong effects of burning and forest management, microbial communities under moss biocrust registered intermediate composition between the bare soils and unburned soils for the dominant phyla, suggesting a rapid successional transition to a more complex and oligotrophic environment, expected to occur in later successional stages with changes in nutrient availability (Ortiz-Álvarez et al., 2018; Zhou et al., 2020). However, the high available P content in bare soils did not suppose the promotion of taxa with traits for P consumption as other studies have reported under P fertilization (Leff et al., 2015), just decreases in oligotrophic taxa as Acidobacteria and Planctomycetes. In addition, the extraction of burned wood is a disturbance that induces alterations in soil moisture and C cycling, driving changes in microbial communities (Serrano-Ortiz et al., 2011; García-Carmona et al., 2021), particularly in fungal communities, highly sensitive to logging management expressing long-term legacies (Ammitzboll et al., 2022).

The fire-associated Firmicutes, Bacteroidetes and Betaproteobacteria were favoured in the severely burned soils (Prendergast-Miller et al., 2017; Rodríguez et al., 2018). *Arthrobacter* (Micrococcaceae), the major indicator found for moss biocrust soils, is known to play an important role in the nitrogen cycle and plant growth in Mediterranean burned forests (Cobo-Díaz et al., 2015; Fernández-González et al., 2017), while *Blastococcus*, the indicator of bare soils, is commonly described as pioneers in extreme environments (Xing et al., 2020; Miralles et al., 2020). Whereas Proteobacteria dominate in bare soils, Actinobacteria dominate in moss biocrust soils, suggesting key roles in initial crust development (Belnap and Lange, 2013). Copiotrophic Proteobacteria presumably increased with the release after fire of labile carbon (Goldfarb et al., 2011), then decreasing in abundance once consumed by the higher bacterial biomass growth under moss biocrust soils. Lower abundance in moss biocrust was detected for *Massilia* and *Comamonas* (Burkholderiales), usually found in burned soils due to their ability to degrade labile and recalcitrant carbon compounds (Puentes-Téllez and Salles, 2020; Stinca et al., 2020) and in biocrust in drylands (Moquin et al., 2012; Li and Hu, 2021), and Sphingomonadaceae, especially associated with bryophyte crusts (Cutler et al., 2017; Maier et al., 2018). Bacillales family (mainly *Bacillus*), increased after fire and indicator, is described as desiccation-tolerant copiotrophs with the ability to degrade hydrocarbons accumulated after fires (Ferrenberg et al., 2013), and families of Bacteroidetes Cytophagaceae (genus *Adhaeribacter*) and Sphingobacteriacea were already described as indicators of Mediterranean burned soils (Stinca et al., 2020; García-Carmona et al., 2021) and moss biocrust in drylands (Moquin et al., 2012).

Seven months after the fire, shifts in the fungal composition at the phylum level revealed the common detriment after fires in Basidiomycota in favour of Ascomycota (Smith et al., 2017; Ammitzboll et al., 2022), the decrease in Glomeromycota, as obligate symbionts forming arbuscular mycorrhiza (Treseder et al., 2004), and the increase in Chytridiomycota. This phylum has been often associated with mosses thanks to their capacity to retain soil moisture (Letcher and Powell, 2002; Davey et al., 2012). Ascomycota indicators in burned soils were the common saprobe *Penicillium* (Whitman et al., 2019), and the pyrophilous fungi *Pustularia* and *Pyronema* (Reazin et al., 2016; Pulido-Chavez et al., 2021), responsible for aggregating soil particles after fires and enhancing moisture retention (Filialuna and Cripps, 2021), also found in moss crusts (Raudabaugh et al., 2020). Moss biocrust was dominated by the Ascomycota phyla, the majority saprotrophs as frequently reported (Maier et al., 2016; Liu et al., 2017; Xiao and Veste, 2017). Among the indicators in moss biocrust soils highlighted the yeast Naganishia, common in dry soils resistant to UV radiation (Solon et al., 2018), and the fire-adapted saprobe *Geminibasidium*, known to initiate post-fire succession (Reazin et al., 2016; Pulido-Chavez et al., 2021).

Despite the compositional differences in the fungal community found between bare soil and mosses, both resulted functionally similar at community level. Wildfire leads to indirect long-term effects in fungi via host mortality and shifts in plant dominance (Fox et al., 2022), especially ectomycorrhiza fungi, although in fire adapted ecosystems the spore bank can remain intact even after high severity fires (Glassman et al., 2016). Through changes in the composition and recalcitrance of the soil organic matter, the decomposition ability of microbial communities is affected determining the community composition (Treseder et al., 2004; Ling et al., 2021). Since fungi are primary decomposers, monitoring the changes in fungal communities associated to moss biocrust is of particular relevance to understanding the functioning of burned Mediterranean forest, and predict the nutrient cycling changes in a context of increasing severity fires.

5. Conclusions

Seven months after the wildfire, the burgeoning biocrust softened the impact of the fire disturbance in soils and in the bacterial and fungal communities at several taxonomical levels. Moss biocrust soils harboured higher bacteria diversity, and the relative abundances of most of the dominant taxa showed intermediate values between the values for unburned soils and bare soils. Biocrust growing in patches along the landscape contributes to biological diversity and accelerates the ecosystem recovery in the vulnerable semi-arid areas, which is particularly important in the case of soil fungi, given their slow recovery and important functional roles in soils. Our results emphasize the necessity of minimizing the disturbances to moss biocrust during their spreading right after fire disturbance, to secure the potential recovery of soils thanks to more complex and developed microbial communities. In addition, more research on the dynamics of microbial communities associated with moss biocrust will be essential for other common forest management practices in the Mediterranean forest.

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CRediT authorship contribution statement

Minerva García-Carmona: Conceptualization, Formal analysis, Writing - original draft, Writing - review & editing. **Clémentine Lepinay**: Formal analysis, Writing - review & editing. **Fuensanta García-Orenes**: Writing - review & editing, Supervision, Funding acquisition. **Petr Baldrian**: Supervision, Writing - review & editing. **Victoria Arcenegui**: Investigation. **Tomáš Cajthaml**: Investigation. **Jorge Mataix-Solera**: Writing - review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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