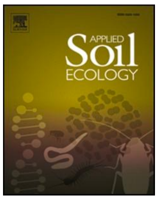
Applied Soil Ecology 191 (2023) 105026

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil



Post-fire wood mulch negatively affects the moss biocrust cover and its positive effects on microbial diversity in a semi-arid Mediterranean forest

Minerva García-Carmona [a,*], Clémentine Lepinay [b], Jorge Mataix-Solera [a], Petr Baldrian [b], Victoria Arcenegui [a], Tomáš Cajthaml [b], Fuensanta García-Orenes [a]

[a] GETECMA-Soil Science and Environmental Tecnologies Group, Department of Agrochemistry and Environment, Miguel Hernández University, Avenida de la Universidad s/n, 03202 Elche, Spain
[b] Institute of Microbiology of the Czech Academy of Sciences, Videnska 1083, 14220 Praha 4, Czech Republic

ARTICLE INFO

Keywords:
Biological soil crust
Deadwood
Microbial community
Moss
Post-fire management
Wildfire

ABSTRACT

Mulches are highly effective in mitigating the risk of erosion generated after wildfires in fire-prone ecosystems. Despite being a technique commonly used, it remains completely unexplored how mulches interact with the positive effects of the emergent moss biocrust on the recovery and resilience of soils and their microbial communities. For this purpose, the effects of wood-based mulch were assayed on the soil stability and moisture improvement, the nutrient inputs, and the response of microbial biomass, activity, composition, and diversity. Soils were studied after one year of wood mulch application at two rates representing possible scenarios, "Rate 1" (65 % of soil cover), and "Rate 2" (100 % of cover), and "Control" soils without mulch. The biocrust development had a positive impact on soil aggregate stability and moisture retention before mulch application. However, one year after the mulch application the biocrust cover was drastically inhibited, especially at the highest rate of mulch. Independently of the biocrust presence, soils at Rate 1 registered a tendency to higher nitrogen content, available phosphorous, basal respiration, and microbial biomass carbon, suggesting an incipient recovery of soil conditions and soil functionality. However, the microbial community composition became more homogeneous and less diverse under the mulch presence (regardless of the application rate), and the positive effect of moss biocrust emergence on the microbial diversity was diluted after one year. The fungal community was particularly sensitive to the wood mulch presence, increasing in richness in response to fresh wood incorporation to soils, in particular saprotrophs and yeasts. The fungal and bacterial compositional shifts after the mulch application reveal an incipient wood decomposition stage, but the transitory loss in beta diversity after the moss biocrust suppression warns about the necessity of including the microbial diversity information into post-fire management planning. Studying the effects of forest management on the above and belowground soil communities is essential to understanding the resistance and resilience of semi-arid forests to the increasing intensity and severity of wildfires.

1. Introduction

Fire has historically played a key role in shaping the structure and distribution of above and belowground communities in the Mediterranean ecosystems (McLauchlan et al., 2020; Pausas and Keeley, 2009). However, fire events are expected to become more frequent and severe in the near future as a result of land-use changes and climate-change induced scenarios (Moreira et al., 2020), threatening the ability of ecosystems to recover after extreme wildfires. Since soil microbial communities are involved in critical ecosystem services related to nutrient cycling and soil formation (Bardgett and Van Der Putten, 2014), understanding their recovery after wildfires is essential for the sustainable management of ecosystems in the context of increasing fire disturbances (Adkins et al., 2020; Pellegrini et al., 2018). High severity fires reduce soil microbial biomass, decrease microbiome diversity, and profoundly reshape the microbial community composition (Nelson et al., 2022; Pressler et al., 2019), a response that is indirectly modulated via changes in the biogeochemical soil properties and the post-fire vegetation recovery (Dove et al., 2020; Pérez-Valera et al., 2020). In particular, during the first years after high-intensity fires biocrust-

---

* Corresponding author at: Miguel Hernández University, Avenida de la Universidad s/n, 03202 Elche, Spain.
E-mail address: minerva.garciac@umh.es (M. García-Carmona).

https://doi.org/10.1016/j.apsoil.2023.105026
Received 10 October 2022; Received in revised form 19 June 2023; Accepted 22 June 2023

forming mosses dominate the colonization in semi-arid areas, revealing an interesting role as ecosystem engineers after the disturbance (Esposito et al., 1999; Ladrón De Guevara and Maestre, 2022; Weber et al., 2022), stabilizing the soil surface and accelerating the recovery of soil functions (García-Carmona et al., 2022; Muñoz-Rojas et al., 2021). Active restoration may be required if sites have suffered intense degradation; however, the combined effects of these operations with the passive effects of the emergent moss biocrust on soil microbial recovery remain unexplored.

Mulching is considered the most cost-effective treatment among the emergency stabilization actions to mitigate the risk of erosion after wildfires in fire-prone ecosystems (Girona-García et al., 2021). In particular, wood-based mulches are highly effective since comprise materials with great resistance to wind displacement and longevity due to their decay resistance (high lignin and low N content) (Jonas et al., 2019). However, relatively little is known about the potential implications of adding wood mulches for the recovery and resilience of above and belowground communities in fire-affected ecosystems. The major drawback of wood mulch is inhibiting vegetation recovery (Bautista et al., 2009; Castro, 2021), but the effect on biocrust development is particularly unclear. While most moss species are associated with humid and shaded sites, some of them take advantage of high light intensity, temperature, and soil nutrient status of open sites as in drylands (Ladrón De Guevara and Maestre, 2022). On the other hand, wood-based mulches could promote microbial activity and abundance throughout the softening of microclimatic conditions (e.g., increase soil moisture) or nutrient release, with subsequent shifts in the microbial community composition (Ammitzboll et al., 2022; Goodell et al., 2020). Indeed, after the strong perturbation that a wildfire represents to nutrient cycling, the burnt wood constitutes a nutrient stock that progressively fertilizes the soil, eventually supporting higher soil biodiversity (Juan-Ovejero et al., 2021; Thorn et al., 2018; Thorn et al., 2020; Tláskal et al., 2021). During the decay process, changes in composition and abundance of wood-inhabiting bacteria and fungi affect the diversity and composition of soil microbial communities (Baldrian et al., 2012; Urbanová et al., 2015), a process not examined in fire-affected soils after mulch application.

This study aims to evaluate whether the recovery and resilience of soil microbial communities are promoted after burnt wood mulch application in soils recently affected by a wildfire in a semi-arid Mediterranean forest, where an emergent moss biocrust pioneered soil colonization. In a previous work, it was shown ruderal mosses softened the impact of the wildfire on soils in the short term, allowing faster recovery of microbial communities toward the unburned soils (García-Carmona et al., 2022). The specific objectives of the study were (i) to determine the effects of wood mulch application in combination to moss biocrust on the soil physicochemical (aggregate stability, soil moisture, organic carbon, Kjeldahl nitrogen, available phosphorous), biological (soil basal respiration, microbial biomass, PLFAs), and biochemical (enzymatic activities) properties, (ii) to study the changes in diversity and composition of the microbial communities due to the mulch application, and elucidate the relevance of the interaction with the biocrust presence, and (iii) to identify which soil properties become dominant drivers of fungal and bacterial community compositional shifts. For this purpose, soils were studied after one year of wood mulch application at two rates representing different management scenarios (65 % and 100 % of soil cover). We hypothesized that the wood mulch applied at a moderate rate favours the activity, abundance, and diversity of soil microbial communities through nutrient introduction and the improvement of soil aggregation and moisture, while negatively interacting with biocrust development. Moreover, adverse consequences for the microbial abundance, activity, and diversity were expected under a total cover of mulch after the reduction in microenvironment heterogeneity. Understanding the soil microbiome response to the mulch application and the moss biocrust will provide valuable information for the success of post-fire management strategies toward accelerating the recovery and conservation of vulnerable semi-arid ecosystems affected by wildfires.

2. Materials and methods

2.1. Study site

The area of study was located in "Sierra de la Replana", a public land in Beneixama, Alicante (E Spain) that lacked previous management. Climate is characterized by a warm Mediterranean, dry-hot summers with 3–4 months of droughts, and wet-warm spring, autumn and winter. Annual mean temperature is 14.9 °C and annual mean precipitation 456 mm. Vegetation in the area is dominated by *Pinus halepensis* Mill. trees from afforestation of around 50 years old, together with *Quercus ilex* L. in lower abundance, 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 slopes are terraced and face south, with soils characterized by a shallow depth (30–40 cm) and clay loam texture (29 % clay, 49 % silt, 22 % sand) and classified as Typic Xerorthent (Soil Survey Staff, 2014).

A wildfire in July 2019 burned 862 ha with fire severity classified as moderate to high according to Keeley (2009): understory plants were charred or consumed, fine dead twigs on soil surface were consumed and logs charred, and soils were mainly covered by grey color ash. In early September 2019, salvage logging was carried out in the area, which consisted of a complete extraction of the burnt wood using heavy machinery. After strong precipitation events, soils were exposed to important erosion processes. Slopes facing south had evidence of the highest impact of soil degradation seven months after the wildfire, i.e., soil loss in surface, rills formation, and lower revegetation in comparison to slopes facing north. Biocrust-forming mosses dominated the vegetation colonization of the fire-affected soils, patchily distributed protecting soils from water erosion. The positive effects of the early appearance of ruderal mosses accelerating the recovery of soils and microbial communities were revealed in a previous study (García-Carmona et al., 2022).

2.2. Mulch treatments, experimental design and sampling

In February 2020, seven months after the wildfire and subsequent salvage logging, wood mulch, as soil protective intervention, was applied prior to the spring rainfalls in a representative degraded area of slopes facing south. Mulch composed of the chopped pine residues (*Pinus halepensis* Mill.) with wood chips around 5 cm wide and 0.5 cm thick was manually applied. Three treatments were evaluated, i.e., mulch application at two rates, a medium rate ("Rate 1") and a high rate ("Rate 2"), and non-application ("Control"). The rates were selected according to the percentage of soil covered by mulch, with Rate 1 covering 65 % of soil (11 Mg ha^{-1}), and Rate 2 reaching 100 % of soil covered (27 Mg ha^{-1}). The selection of rates simulates the mulch application rates that are possibly performed in the field, a minimum of 60 % of cover is suggested as being necessary to reduce post-fire erosion rates (reviewed in Robichaud et al., 2013), and a total soil cover simulating high accumulation of woodchips in extended areas.

Twelve experimental plots (2 m × 2 m) were randomly established along the same hillside at different altitudes. Three plots per treatment, nine in total, were established in the fire-affected area, and another three experimental plots used as reference in a nearby-unburned area located approximately 500 m and at least 100 m away from the fire edge. Two samplings were conducted, the first one right before the mulch application (February 2020), and the second, one year after the application (February 2021). The moss biocrust cover was 30 % on average at each experimental plot in the burned area. At each sampling, four soil samples were collected from the top 2.5 cm of soil, randomly extracted within each experimental plot (after the manual removal of wood mulch): two of them under the moss biocrust and the other two in soils without biological crust (uncrusted). In the unburned area, the presence of mosses was almost negligible (<5 %) and was not included in the experimental design considering the nature-based differences from the burned area (García-Carmona et al., 2022), thus two soil samples were collected per plot at 2.5 cm after the removal of organic debris. Due to logistical restrictions, 70 samples from the total 84 (3 treatments × 3 plots × 4 samples + 3 unburned plots × 2 samples, × 2 sampling years) were selected for the present study: 15 in uncrusted soils (5 per treatment), 15 under mosses (5 per treatment), and 5 from the unburned soils for each sampling.

The moss biocrust cover monitoring was performed at each experimental plot and each sampling (after the manual removal of mulch in the second sampling) using four random replicates of a 25 cm × 25 cm quadrat (divided into 100 cells).

2.3. Soil analysis

For each soil sample, one aliquot was sieved at 2 mm and frozen at −20 °C for DNA extraction and lipid fatty acid analysis, one aliquot was kept at 4 °C for biological (soil basal respiration and microbial biomass) and biochemical parameters (enzymatic activities), and the remainder was dried at room temperature. From the dry sample, one aliquot was sieved between 4 mm and 0.25 mm for the aggregate stability test, and the rest was sieved at 2 mm for the physicochemical analyses.

Aqueous extracts of 1:2.5 and 1:5 (w/v) were used to measure soil pH and electrical conductivity. Soil organic carbon was determined by the Walkley-Black method (Nelson and Sommers, 1983), the total nitrogen by the Kjeldahl method (Bremner and Mulvaney, 1982), and the available phosphorous by the Burriel-Hernando method for alkaline soils (Díez, 1982). For the aggregate stability, the proportion of aggregates that remained stable after an artificial rainfall was quantified (279 J min^{-1} m^{-1} of energy) (Roldán et al., 1994). Soil moisture was measured after drying field wet soils for 24 h at 105 °C.

The microbial biomass carbon was determined by the fumigation-extraction method (Vance et al., 1987), and soil basal respiration was estimated in an automated impedance-meter based on changes in the impedance of a KOH solution (2 %) after CO_2 emissions by soil microorganisms incubated at 30 °C for 24 h (BacTrac 4200 Microbiological Analyser, Sylab, Austria). Regarding the enzymatic activities, the urease activity measurement was based on the release of NH_4^+ from hydrolytic reactions where soil samples were exposed to the substrate urea (Nannipieri et al., 1981), and 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 and *p*-nitrophenyl phosphate disodium salt, respectively (Naseby and Lynch, 1997; Tabatabai, 1983).

The microbial community biomass was estimated by the phospholipid fatty acid analysis (PLFA) and neutral lipid fatty acid analysis (NLFA), extracted by chloroform-methanol-phosphate buffer mixture, and analysed by gas chromatography–mass spectrometry (450-GC, 240-MS ion trap detector, Varian, Walnut Creek, CA, USA) as described in Frouz et al. (2016). Fungal biomass was quantified based on 18:2ω6,9 content, and bacterial biomass as the sum of 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 biomass of arbuscular mycorrhiza was estimated using 16:1ω5 concentration in the NLFA fraction (Bååth, 2003).

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

The DNeasy PowerSoil Pro DNA isolation kit (Qiagen) was used to isolate the DNA, then quantified using the Qubit High Sensitivity dsDNA Assay (Thermo Fisher Scientific).

For the fungal community the ITS2 region was amplified using the primers ITS86F and ITS4 (Op De Beeck et al., 2014), and for the bacterial community the V4 region of the16S rDNA using the primers 515F-Y (Parada et al., 2016) and 806R (Apprill et al., 2015). PCRs were carried out 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. Libraries were purified using the Mag-Bind RXNPure Plus magnetic beads (Omega Biotek), and then 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 amplicon sequencing data was processed using the SEED 2 pipeline (Větrovský et al., 2018), in which paired-end reads are joined using fastq-join, reads are quality filtered, and short and long sequences are trimmed. 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), and the remaining sequences were clustered into operational taxonomic units (OTUs) using UPARSE implemented within USEARCH (Edgar, 2013) at a 97 % similarity level. After singletons removal, the most abundant sequence of each OTU was selected for cluster identification. The identification of bacterial and fungal sequences was performed using BLASTn against 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 merge into a single taxon, and when lower similarity, lower coverage, or both, the best available identification was used. 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).

The effect of the wood mulch application on the moss biocrust cover was tested with ANOVA test, after verifying the statistical parametric assumptions. For the study of soil properties, linear mixed models approach was adopted using the "nlme" package (Pinheiro et al., 2022). Fixed factors were "Time" (T0, experiment starting point, and T1, one year after the treatments), "Treatment" (Rate1, Rate2, and Control), "Mulch" (agglutination of both mulch application rates versus control), and "Crust" (uncrusted soils and moss biocrust soils). The experimental plots were included as random effect, and replicates within each plot were nested into plots to deal with the potential spatial correlation. Linear models, linear mixed models with plots as random effects, and mixed models with replicates nested into plots as random effects were evaluated, and the selection of the model was done according to the lowest AICc (second-order AIC) (see Appendix B for the summary of the statistical models). Unburned soils were excluded from these models but included when performed multiple comparisons (Tukey test, $p < 0.05$) for the combination of treatments and crust presence effects on soil properties at each sampling year. The relationship among all soil parameters was explored at T1 using principal component analysis (PCA) with the "FactoMineR" package (Lê et al., 2008).

For OTU tables, all samples were resampled to equal the smallest library size using the “phyloseq” package (McMurdie and Holmes, 2013). The effect of geographic distance among experimental plots along the slope on the microbial community was discarded after exploring possible distance-decay patterns (Morlon et al., 2008). From the rarefied matrices, OTU richness was calculated, and the effects of “Time”, “Treatment” and “Crust” explored (see Appendix B). To test the impact of “Time”, “Crust”, “Treatment” and “Mulch” in the microbial community structure in burned soils, permutational multivariate analysis (PERMANOVA) was carried out using 9999 permutations, and then visualized with non-metric multidimensional scaling (NMDS) ordination analysis based on Bray-Curtis distances of OTU relative abundances (including the unburned soils). Variation partitioning analyses were performed to explore the effects of factors and soil parameters on the microbial community variation. Then, the identification of the soil drivers was determined with redundance analyses (RDA). First, multicollinearity of variables was avoided with the calculation of the variance inflation factor (values > 10 were sequentially removed). Then, forward selection was performed to select the constraining variables. The compositional matrices were transformed using Hellinger transformation before the analysis.

Shifts of dominant fungal and bacterial taxa were explored after the treatment application and the crust presence at T1. Significant differences were tested using the relative abundances at different phylogenetic ranks (phylum to genus-level) with the non-parametric Kruskal-Wallis test, with p-values correction based on Benjamini–Hochberg false-discovery rate with 95 % confidence interval. The same analysis was performed for ecophysiological categories of the fungal community.

3. Results

3.1. Mulch effects on moss biocrust cover

The moss biocrust cover survey revealed remarkable differences in response to the rate of mulch application used (Fig. 1). With a starting point of 30 % of moss cover seven months post-fire, one year later the biocrust cover increased up to 82 % in soils without any treatment (control). In contrast, the development of mosses was negatively affected by the mulch application, with a 2-fold lower cover under Rate 1 (42 %), and 4-fold lower under Rate 2 (18 % of moss cover).

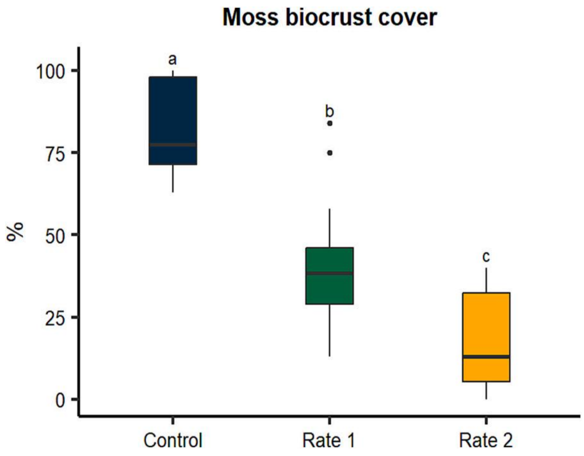


Fig. 1. Moss cover in soils after one year of mulch application. Different lowercase letters indicate significant differences among treatments (p-value <0.05, Tukey test).

3.2. Mulch effects on physicochemical, biological, and biochemical soil properties in crusted and uncrusted burned soils

The fire event significantly increased the P content in burned soils, whereas all biological and biochemical properties, except for basal respiration, were negatively impacted remaining low over time (Table 1). Microbial biomass carbon remained lower in Rate 2 than at control and Rate 1 soils, in which biomass significantly increased under moss biocrust. The higher aggregate stability in uncrusted soils at T0 was unnoticeable at T1 after the stability increase over time under mosses. Soil moisture was higher under moss biocrust at T0, but differences decreased at T1 due to a relatively higher increase in moisture in uncrusted soils than in biocrust soils. Regarding the PLFA and NLFA biomarkers, bacterial biomass increased over time while fungal biomass remained reduced after the wildfire, particularly in the case of arbuscular mycorrhiza (Table A1). Whereas the mulch application negatively impacted the fungi biomass, neither fungi nor bacteria responded to the moss biocrust.

The PCA (Fig. 2.) showed Rate 2 soils differed from Rate 1 soils, which shared more similarities with control soils. The slight increase in Rate 1 of organic carbon, N, and electrical conductivity grouped the variables close to the unburned soil, represented by the higher basal respiration and aggregate stability.

3.3. Richness and diversity of microbial communities

The evolution of fungal and bacterial richness differed over time (Fig. 3). Fungal richness experienced a significant increase during the year of the experiment, although values were still below the unburned soils 19 months after the fire. In contrast, bacterial richness remained constant over time, except under mosses in control soils which significantly decreased in T1.

Both fungi and bacteria communities expressed similar structure patterns. The time elapsed, the crust presence, and the mulch application (independently of the application rate) strongly shaped the fungal and bacterial communities (Table A2). The strong fire legacy on the microbial community was represented along the X-axis in the ordination plot, clearly separating the unburned and burned communities (Fig. 4). At the beginning of the experiment (T0), moss biocrust strongly influenced the microbial communities; however, those dissimilarities were not appreciable after one year of mulch application (Fig. A1). Communities treated with mulch expressed more similarity, independently of the crust presence, in contrast to control soils that showed more dispersion (Fig. 4).

3.4. Relationship the environmental variables under mulch and microbial communities

The variation partitioning revealed high stochasticity in the microbial assembly. However, most variation was attributable to soil properties (Table A3). For the fungal community, soil moisture strongly influenced communities under mosses, and variations in aggregate stability and nitrogen influenced control and Rate 1 soils, distributed oppositely to Rate 2 soils (Fig. 5). The bacterial community under mosses was statistically influenced by changes in the phosphorous, while variations in organic carbon and soil moisture influenced the community under both mulch treatments (Fig. 5).

Table 1
Physicochemical and biochemical soil properties after mulch application at two rates in soils with the presence of crust (moss biocrust) and without it (uncrusted soils). The data represent means and standard deviations at the beginning (T0) and end of the experiment (T1), and lowercase letters indicate significant differences among soils (post-hoc Tukey test, p-value <0.05). Significance for factors "Time" (T0 and T1), "Crust" (moss biocrust vs. uncrusted soils), "Treatment" (control and soils under mulch application at Rate1 and 2) are included, and the interaction between factors. n.s. not significant at p-value >0.05 (see Appendix B for the summary of the statistical models tested).

Treatment	Crust	Organic carbon (%)		Nitrogen (%)		Phosphorous (mg kg^{-1})		Aggregate stability (%)		Soil moisture (%)		Basal respiration (mg CO_2 kg^{-1})		Microbial biomass (mg CO_2 h^{-1} kg^{-1})		Glucosidase (μmol PNP g^{-1} h^{-1})		Phosphatase (μmol PNP g^{-1} h^{-1})		Urease (μmol N-NH^{4+} g^{-1} h^{-1})	
		T0	T1	T0	T1	T0	T1	T0	T1	T0	T1	T0	T1	T0	T1	T0	T1	T0	T1	T0	T1
Unburned		5.53 ± 1.64	5.50 ± 0.55	0.36 ± 0.11	0.38 ± 0.053	4.07 ± 1.25	4.07a ± 0.86	75.9 ± 12.5	83.0 ± 3	12.7 ± 5.7	16.3 ± 4.9	12.3b ± 3.4	15.4 ± 3.1	753b ± 179	614c ± 85	1.67 ± 0.22	2.14b ± 0.3	2.45b ± 0.53	2.39b ± 0.32	2.10b ± 1.07	1.82b ± 0.55
Control	Uncrusted	4 ± 1.22	5.01 ± 1.09	0.25 ± 0.07	0.33 ± 0.06	25.7 ± 22	29ab ± 25	77.7 ± 12	83.2 ± 10	11.8 ± 4.7	16 ± 3.8	8.2a ± 1.3	13 ± 1.8	220a ± 57	320ac ± 100	1.5 ± 0.28	1.05a ± 0.31	1.15a ± 0.3	1.07a ± 0.37	0.85a ± 0.44	0.45a ± 0.22
	Mosses	4.11 ± 0.59	4.19 ± 0.58	0.27 ± 0.02	0.29 ± 0.05	11.1 ± 2.8	40.7ab ± 29	76.1 ± 3.4	77.9 ± 3.5	19.5 ± 4.4	17.9 ± 5.1	7.8a ± 0.5	11.2 ± 1.4	244a ± 55	590bc ± 289	1.31 ± 0.20	1.04a ± 0.54	1.35a ± 0.35	0.92a ± 0.26	0.89a ± 0.28	0.38a ± 0.19
Mulch1	Uncrusted	4.61 ± 0.91	5.12 ± 1.6	0.27 ± 0.05	0.35 ± 0.11	28.4 ± 16	20ab ± 5.7	81.9 ± 3.2	79.7 ± 6.0	15.5 ± 3.4	18.7 ± 7	7.9a ± 1.4	13.5 ± 2.8	172a ± 68	257ab ± 195	1.13 ± 0.39	1.46ab ± 0.36	1.11a ± 0.42	1.11a ± 0.38	0.39a ± 0.18	0.84a ± 0.59
	Mosses	4.07 ± 0.69	4.89 ± 1.33	0.24 ± 0.04	0.32 ± 0.07	14.7 ± 4.6	27.2ab ± 19	64.2 ± 7.7	79.6 ± 6.1	17.5 ± 3.7	19 ± 2.7	7.9a ± 0.5	13 ± 3	277a ± 142	497ac ± 195	1.12 ± 0.13	1.34ab ± 0.70	1.49a ± 0.34	1.35a ± 0.77	0.87a ± 0.20	0.68a ± 0.43
Mulch2	Uncrusted	3.93 ± 1.67	4.46 ± 2.28	0.25 ± 0.09	0.29 ± 0.12	27.6 ± 24	52.4b ± 35	76.8 ± 9.7	77.4 ± 6.5	13.3 ± 3.6	16.3 ± 4.6	6.9a ± 1.4	12.8 ± 2.6	161a ± 19	203a ± 120	1.17 ± 0.50	1.17a ± 0.33	0.84a ± 0.24	0.92a ± 0.23	0.46a ± 0.39	0.51a ± 0.16
	Mosses	3.72 ± 1.28	3.96 ± 1.17	0.25 ± 0.08	0.25 ± 0.06	13.8 ± 5.5	37.9ab ± 29	67.1 ± 10	74.9 ± 5.2	19 ± 6.9	19 ± 6.1	7.2a ± 0.8	12.7 ± 3	366a ± 109	182a ± 117	1.2 ± 0.49	1.04a ± 0.43	1.15a ± 0.31	0.98a ± 0.21	1.01a ± 0.35	0.76a ± 0.39
Factors	Time	n.s.		0.014		0.012		0.013		n.s.		<0.001		0.006		n.s.		n.s.		n.s.	
	Crust	n.s.		n.s.		n.s.		0.002		0.006		n.s.		0.001		n.s.		n.s.		0.048	
	Treatment	n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.	
	Crust:Treat	n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.	
	Crust:Time	n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		n.s.	
	Treat:Time	n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		0.005		n.s.		n.s.		0.035	
	Crust: Treat:Time	n.s.		n.s.		n.s.		n.s.		n.s.		n.s.		0.022		n.s.		n.s.		n.s.	

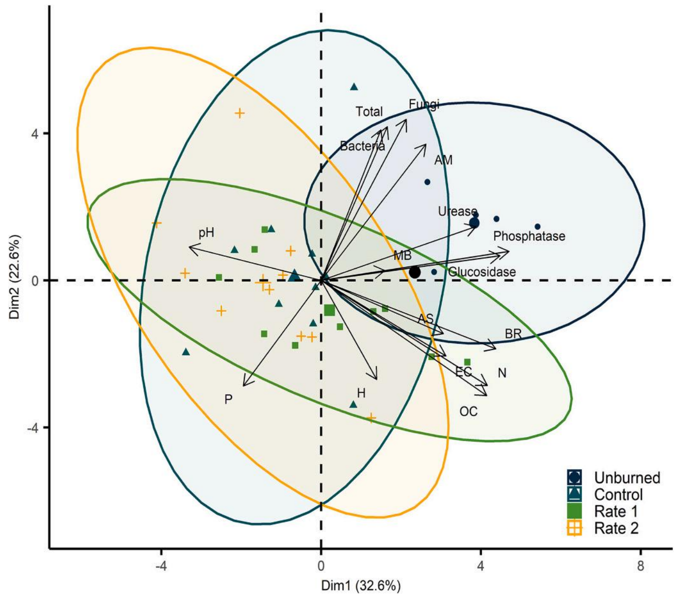


Fig. 2. Relationship among the physicochemical and biochemical soil properties after one year of mulch application for soils under treatment and unburned soils. Mean points for each treatment group are represented. (OC: organic carbon; N: Kjeldahl nitrogen; P: available phosphorous; H; soil moisture; MB: microbial biomass carbon; BR: basal respiration; AS: aggregate stability; EC: electrical conductivity; Bacteria: bacterial biomass; Fungi: fungal biomass; AM: arbuscular mycorrhiza biomass; Total: Total PLFA.)

3.5. Mulch effects on soil microbial communities

The study of the dominant taxa in the fungal community revealed the strong effects of the fire (Fig. 6). In particular, burned-control soils revealed the impact of moss biocrust presence in the community, whereas the composition of the dominant taxa under mulch were more homogeneous regardless the crust presence. Only some genera under moss in Rate 2 differed from the rest of treated soils.

The wildfire increased the relative abundance of Ascomycota while decreasing the Basidiomycota (Figs. A2, 6). With the mulch application, a significant increase was registered in Basidiomycota, Chytridiomycota phylum (genera *Rhizophlyctis*, *Spizellomyces*, and *Powellomyces*, especially under mosses), and Zygomycota due to the genus *Mortierella*. The increase in Ascomycota *Terfezia* (Pezizales) and *Sporormiella* (Pleosoporales) after the fire was reduced with the mulch, mainly in favour of genera *Paraphoma* (Pleosoporales) and the Basidiomycota *Naganishia* (Tremellales). Both *Naganishia* and *Paraphoma* were additionally promoted under moss biocrust. In addition, *Cryptococcus*, and to a lesser degree *Cyptococcus* (Tremellales) and several Sordariomycetes (*Clonostachys*, *Ophiocordyceps*, and *Humicola*), were positively influenced by mulch, while *Geminibasidium* and *Solicoccozyma* (Tremellomycete) were negatively affected.

Changes in the predicted fungal functional roles were registered after the wood mulch application. Ectomycorrhizal fungi tended to be lower under mulch, while significant increases in yeast were observed, especially under mosses in Rate 2 soils. The fire significantly reduced the lichenized fungi and parasites of lichen (Fig. 6).

The wildfire had the greatest impact on the soil bacterial community composition (Figs. A2, 6). In burned soils, after one year of wood mulch application very few bacterial genera responded to the treatments, and negligible effects were observed due to the crust presence (excluded in the figure). Proteobacteria were the most reactive to the wood mulch, with significant increases in Betaproteobacteria *Massilia*, *Comamonas* (Burkholderiales), and *Ramlibacter* (Burholdeeriales), and in Alphaproteobacteria *Devosia* (Rhizobiales), while *Sphingomonas* was significantly reduced. Some Actinobacteria reacted to the mulch, with significant an increase in *Arthrobacter* (Actinomycetales) and decreases in Solirubrobacteraes (*Conexibacter* and *Solirubobacter*).

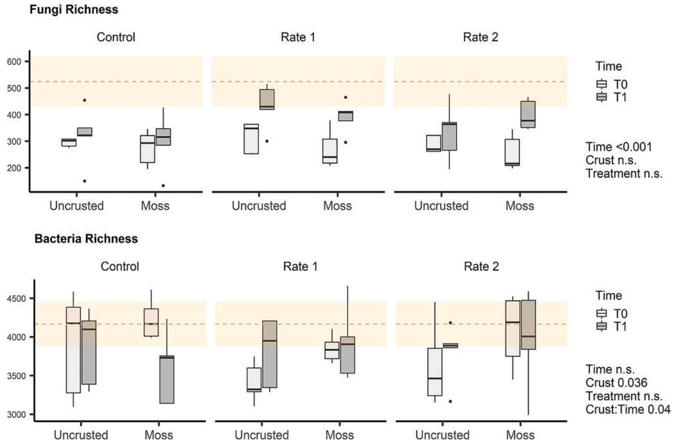


Fig. 3. Fungal and bacterial richness evolution over time (T0 and one year after, T1) to treatments application (controls and soils under mulch at Rate1 and 2), with and without the presence of crust (moss and uncrusted soils). The dashed line and shaded area represent the mean value and the confidence interval of unburned soils. The significance of factors ("Time", "Crust", and "Treatment") in the models are included, and interactions among factors when significant. n.s. = not significant.

4. Discussion

One year after the wood mulch application in recently fire-affected soils, the moss biocrust was drastically inhibited below the mulch cover, showing the strongest reduction under the thickest layer of mulch. This result is in accordance with other studies in which mulching controls vegetation recovery after fires (Bautista et al., 2009). Moreover, this response corroborates the idea that biocrust-forming mosses that emerge after fires present adaptive traits to high radiation and temperatures and a preference for open spaces characteristic of the early post-fire stages (Esposito et al., 1999; Ladrón De Guevara and Maestre, 2022).

The limited effect of mulch on the soil physicochemical properties after one year can be explained by the Mediterranean climate, where low precipitation combined with high temperatures and the low degradability of wood in early stages slow down the decomposition rate (Bonanomi et al., 2021; Goodell et al., 2020). The slight but significant change over time in N and P nutrients is in accordance with Marañón-Jiménez and Castro (2013), who reported in the first years after a wildfire in a Mediterranean forest a progressive N and P leaching from wood to soils. Additionally, the well-known effectiveness of moss biocrust in increasing soil moisture (Xiao et al., 2016) contributed to altering the biological and biochemical soil properties. In particular, the emergence of biocrust in combination with the initial wood decay promoted the microbial biomass carbon and the microbial activity (phosphatase and urease), initiating a positive cascading effect on soil nutrient cycling (Cheng et al., 2021; Kahl et al., 2017). Nonetheless, the microbial biomass carbon was adversely affected by the higher mulch

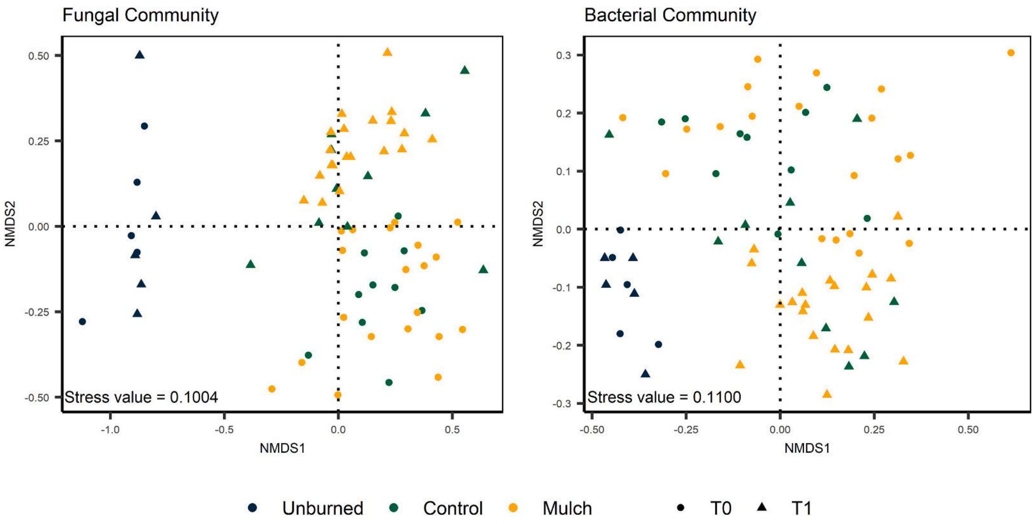


Fig. 4. Impact of mulch application over time in the composition of the microbial communities. Ordination plots represent two-dimensional non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarities at OTU level for fungal and bacterial communities, representing differences between "Time" (T0 and T1) and "Mulch" (unburned, controls and mulch soils) levels.

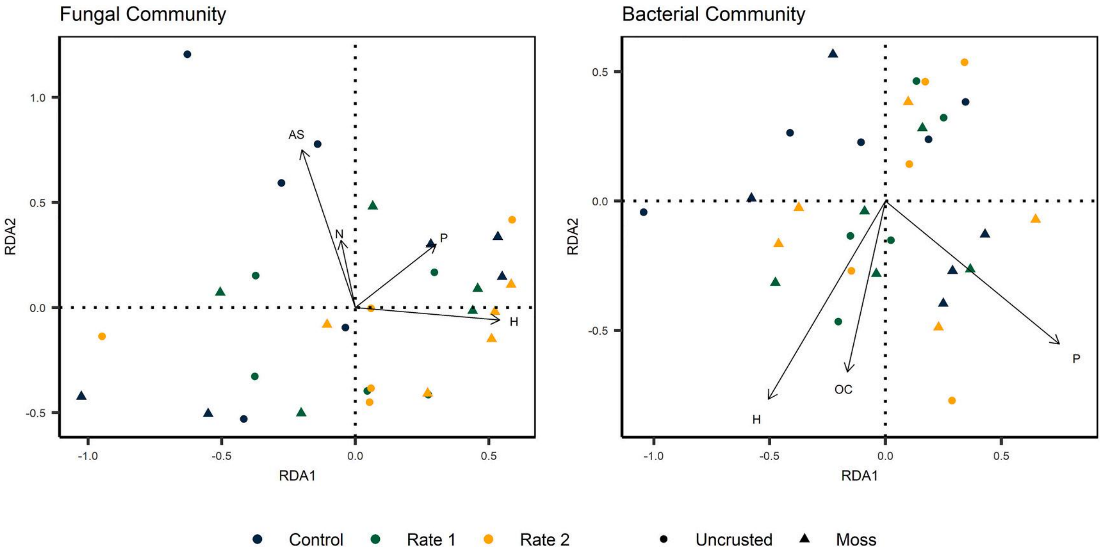


Fig. 5. Soil parameters related to the bacterial and fungal community composition at the end of the experiment. Plots represent redundancy analyses (RDA) at OTU level for fungal and bacterial communities, representing differences between "Treatment" (controls and soils under mulch application at Rate1 and 2) and "Crust" (uncrusted and moss soils) levels. The explanatory variables are expressed with arrows (AS: aggregate stability; H: soil moisture; OC: organic carbon; P: available phosphorous).

rate, presumably due to a transitory N microbial immobilization after the strong input of recalcitrant carbon low in N from the coniferous species (Kahl et al., 2017; Jonas et al., 2019). In contrast, adding mulch at a lower rate promoted an increase in organic carbon, N, microbial biomass, and respiration in soils, which suggests an acceleration of the recovery of soil conditions and its functionality toward the unburned soils.

The contrasting response between the fungal and bacterial biomass to the wildfire and subsequent wood mulch corroborates their different sensitivities to disturbances (Bastida et al., 2017; Muñoz-Rojas et al., 2016). Under natural wood decay conditions, a significant increase in fungal abundance is not expected until the late stages of wood decomposition (Baldrian et al., 2016). Thus, it is not surprising that fungal biomass remained low after being severely affected by a wildfire (Dooley and Treseder, 2012). However, fungal richness increased in response to the mulch application, especially at Rate 1. The explanation could be related to the higher microenvironment heterogeneity created, supporting more diversity, especially higher saprobes after the fresh wood incorporation as accounted at this rate (Arnstadt et al., 2016; Lepinay et al., 2021; Song et al., 2017). In contrast, the quick recovery in bacterial abundance after a wildfire is generally observed in response to high nutrient release during the fire (Pressler et al., 2019). In addition, diversity usually increases through improvement in soil stability over time (Garcia-Pichel et al., 2003); thus, the decrease in bacterial richness in moss biocrust without mulch was unexpected. The reason remains speculative but may be related to variations in the soil chemistry, i.e.,

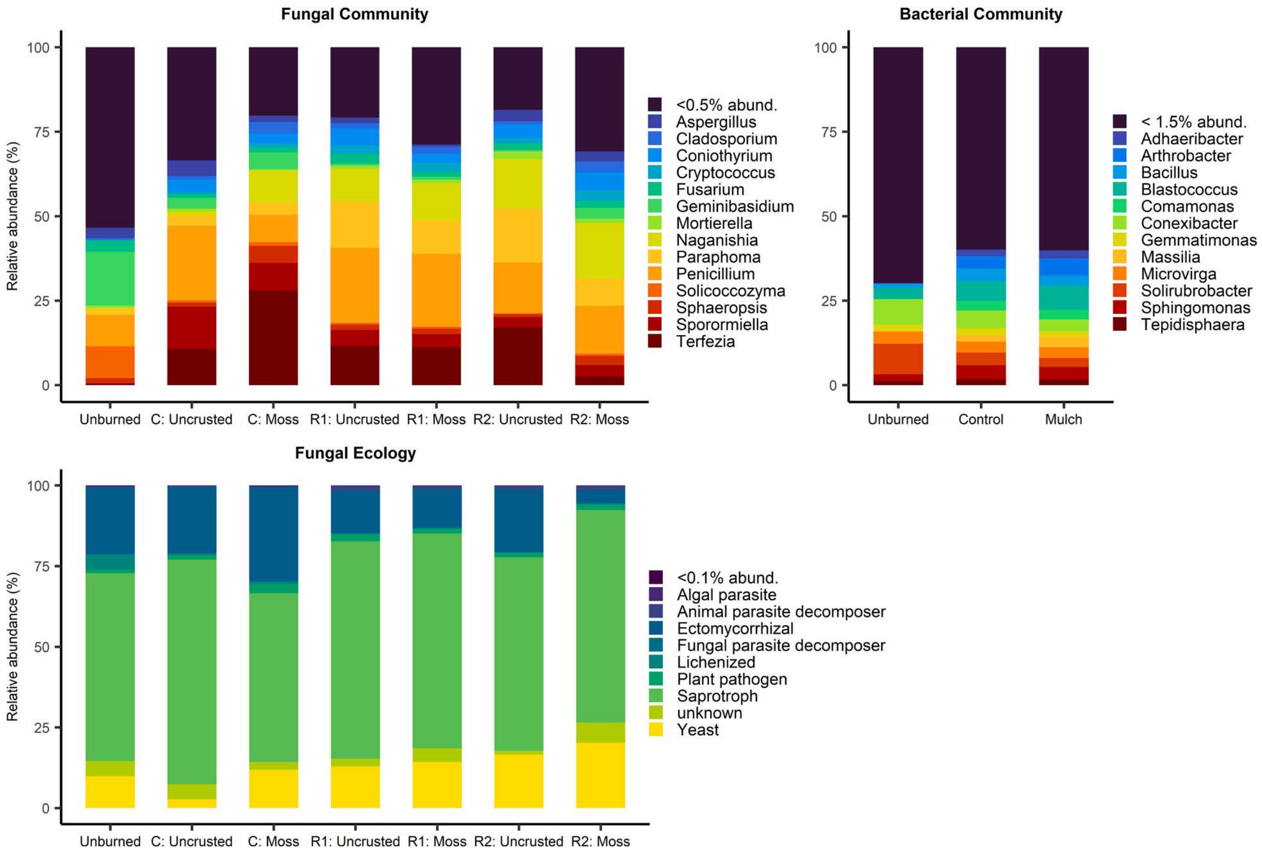


Fig. 6. Effects of mulch application and crust presence on the dominant fungal and bacterial genera and the dominant fungal ecological roles at the end of the experiment. Data represent the relative abundance for soils under “Treatment” (unburned soils, controls and soils under mulch application at Rate1 and 2), “Mulch” (unburned soils, controls and soils under mulch), and “Crust” presence (uncrusted and moss soils).

the transitory exhaustion of labile nutrients released after the fire invested in the microbial growth, corroborated by the increase in the microbial biomass carbon (Aanderud et al., 2019).

The alterations observed in the microbial community structure evidence the strong effects of fire and management practices on soil microbial assembly, sometimes with detrimental consequences for the functioning of forest ecosystems (Kohout et al., 2018; Pereg et al., 2018; Li et al., 2019). The fungal community was the most sensitive to the presence of wood, which is understandable due to its ability to colonize fresh wood and lead the degradation in the early stages (Lepinay et al., 2021). The high microbial diversity described seven months after the wildfire in moss biocrust soils was diluted after one year of mulch application. The loss in beta diversity (i.e., homogenization at landscape scale) is probably due to the colonization of fresh wood by opportunistic microbial taxa (Baldrian et al., 2016; Lladó et al., 2017). Deadwood from different tree species and debris sizes leads to diverse microbial assembly under natural conditions (Baldrian, 2017; Lepinay et al., 2022), but a homogeneous layer of wood mulch extensively applied to soils results in less heterogeneity of soil microbial communities, which could hamper the recovery of microbial diversity after a fire disturbance. Moreover, the manual application of mulch in this study allowed us to isolate the effect of the wood on soils without accounting for the additional disturbance of mechanical transit associated with its application, a factor known to largely contribute to soil microbial community alteration (Hartmann et al., 2014), which should be addressed in future studies.

The biocrust emergence slowly alters the underlying soils, filtering the fire-altered microbial communities (Ferrenberg et al., 2013; Li and Hu, 2021). The slight moisture increments in moss biocrust soils under the stressful semi-arid conditions strongly impacted the fungal community composition, together with the higher soil stability and enrichment in nutrients (Bao et al., 2019; Weber et al., 2016). The increase in available phosphorous after fires is of high relevance in nutrient-restrictive soils since this release facilitates plant community development (Certini, 2005; Fultz et al., 2016), and indirectly controlled both fungal and bacterial community assembly. Despite the microbial homogeneity induced by mulches, the slight differences in soils under the two application rates were transferred to the microbial community structure, a response fundamentally observed in fungi. In this regard, fungi were sensitive to the N content, suggesting a possible change in N availability and N microbial immobilization under the higher rate of wood mulch (Jonas et al., 2019; Laiho and Prescott, 2004).

The dominant fungal taxa responded to the mulch application and the biocrust presence. After the detriment in favour of Ascomycota in burned soils (Reazin et al., 2016; Smith et al., 2017), which generally dominate at the early stages of decomposition (Baldrian et al., 2016; Purahong et al., 2018), Basidiomycota, Chytridiomycota and Zygomycota (genus *Mortierella*) increased in mulch soils. The increase of these taxa is presumably due to the ability of degrade recalcitrant materials (Eichlerová et al., 2015; Smith et al., 2017), or the frequent association of the last one to decomposing fungal biomass (Baldrian et al., 2016; Brabcová et al., 2016).

Shifts in the fungal community composition were translated into fungal functional shifts in soils. The removal of vegetation after fire exposed soils (without mulch) to high solar radiation and low soil moisture, which may be the reason for the strong differences in the functional community between the uncrusted and moss biocrust soils (Hart et al., 2005; Xiao and Veste, 2017). Biocrust soils showed higher concentration of ectomycorrhiza, whose spore bank could be possibly protected by the rapid emergence of fire-responsive mosses and remain intact even after high severity fires (Glassman et al., 2016). Nevertheless, the substantial differences in genus dominance between uncrusted and biocrust soils were diluted under mulch. The highest response to mulch corresponds to the Basidiomycota yeasts (Tremellomycetes), in particular *Naganishia*, described as being able to utilize a wide spectrum of C sources materials (Mašínová et al., 2017). The initial degradation of wood mulch increased the abundance of yeasts and saprotrophs in soils. After fires, saprophytes, and pyrophilous fungi in special (Bruns et al., 2020; Reazin et al., 2016), can restore nutrients in soils and promote the conditions for plant succession to begin, stabilizing burned soils, reducing risks of soil erosion, and increasing soil humidity (Filialuna and Cripps, 2021). However, the phyrofilous fungi observed in the burned soils (*Pyronema*, *Pustularia*, and *Geopyxis*) were not stimulated under the mulch application, and the consequences for soils will be interesting to monitor in future works.

The dominant bacteria slightly responded to the wood mulch presence, and barely expressed differences to the soil crust. Changes observed at the OTU level in response to mulch and biocrust correspond to less abundant or rare taxa, which are described as reservoir of genetic and functional diversity (Chen et al., 2020; Lynch and Neufeld, 2015), and worth monitoring in detail in future efforts in order to identify threats to microbial diversity conservation. The wildfire imposed important shifts in the community; Firmicutes and Bacteroidetes increased to the detriment of Actinobacteria, as observed in many studies (García-Carmona et al., 2022; Nelson et al., 2022; Prendergast-Miller et al., 2017). Proteobacteria were almost the only phylum to slightly respond to wood mulch application led by Burkholderiales, specifically *Massilia*, *Comamonas*, and *Ramlibacter*, and Alphaproteobacteria Rhizobiales (*Devosia*). Burkholderiales bacteria are associated with wood due to their ability to break down phenolic compounds, including lignin (Lladó et al., 2017), and its association with wood-decaying fungi (Tláskal et al., 2017). Rhizobiales are responsive to cellulose (Eichlerová et al., 2015) and are commonly found at late stages of wood decomposition thanks to their N-fixation ability (Lladó et al., 2017).

Known the ability of mosses to effectively stabilize soil surfaces in fire-affected areas (Gall et al., 2022; Gao et al., 2020; Silva et al., 2019), 82 % of biocrust cover 19 months after the fire suggests that its development may be enough to counteract erosion processes. Therefore, additional mitigation techniques would be unnecessary, even more considering the long persistence of wood mulch on the forest floor disrupting the vegetation regrowth (Robichaud et al., 2020). In this case, the application of mulch for restoration purposes would conflict with the passive soil recovery performed by the moss biocrust, which has been demonstrated to accelerate the recovery of ecosystem functioning (García-Carmona et al., 2020, 2022). In this study, the moss biocrust that emerged after the wildfire in the semiarid area promoted higher soil microbial diversity compared to the managed soils.

5. Conclusions

After one year of wood mulch application following a wildfire in a semi-arid Mediterranean forest, mulch adversely affected the biocrust development interfering with the passive recovery of soils assisted by mosses. The moss biocrust had a positive impact on the aggregate stability, moisture retention, and the acceleration of biochemical processes in the fire-affected soils. Despite the low impact of mulch on physicochemical soil properties, an increase in N and P, the microbial biomass, and respiration was observed over time in mulch soils at Rate 1 (65 % of soil cover), a cover that partially simulates the natural heterogeneity of forest soil. However, after the mulch application, the beneficial effects of biocrust on microbial diversity were limited, as the microbial communities became transitorily highly stochastic and less diverse under mulch. These findings are limited to a local study, and the conclusions may depend on site-specific conditions or the impact of the previous fire event on soils. However, the results warn about the necessity of incorporating microbial diversity information in post-fire management planning. For that purpose, more research is needed in order to identify threats to microbial diversity and to support management practices that boost soil biodiversity and preserve ecosystem functioning.

Funding sources

This work was supported by funding by the “POSTFIRE_CARE” project of the Spanish Research Agency (AIE) and the European Union through European Funding for Regional Development (FEDER) [Ref.: CGL2016-75178-C2-1-R], and the Spanish Ministry of Economy and Competitiveness [grant FPI-MINECO BES-2017-081283 supporting M. G-C.].

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.

Data availability

Data will be made available on request.

Acknowledgements

The authors acknowledge AllGenetics & Biology SL (Spain) for DNA extraction and sequencing of soil samples. Special thanks are addressed to Beneixama council for the help, and Ana Isabel Sanchis Ayelo for her laboratory assistance. We sincerely thank the anonymous reviewers for their valuable comments and suggestions, which were pivotal in improving the quality and clarity of this article.

Appendices. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.apsoil.2023.105026.

References

Aanderud, Z.T., Bahr, J., Robinson, D.M., Belnap, J., Campbell, T.P., Gill, R.A., McMillian, B., St. Clair, S., 2019. The burning of biocrusts facilitates the emergence of a bare soil community of poorly-connected chemoheterotrophic bacteria with depressed dcosystem services. Front. Ecol. Evol. 7, 1–14. https://doi.org/10.3389/fevo.2019.00467.

Adkins, J., Docherty, K.M., Gutknecht, J.L.M., Miesel, J.R., 2020. How do soil microbial communities respond to fire in the intermediate term? Investigating direct and indirect effects associated with fire occurrence and burn severity. Sci. Total Environ. 745, 140957 https://doi.org/10.1016/j.scitotenv.2020.140957.

Ammitzboll, H., Jordan, G.J., Baker, S.C., Freeman, J., Bissett, A., 2022. Contrasting successional responses of soil bacteria and fungi to post-logging burn severity. For. Ecol. Manag. 508, 120059 https://doi.org/10.1016/J.FORECO.2022.120059.

Apprill, A., McNally, S., Parsons, R., 2015. Minor revision to V4 region SSU rRNA 806R gene primer greatly increases detection of SAR11 bacterioplankton. Aquat. Microb. Ecol. 75, 129–137. https://doi.org/10.3354/ame01753.

Arnstadt, T., Hoppe, B., Kahl, T., Kellner, H., Krüger, D., Bauhus, J., Hofrichter, M., 2016. Dynamics of fungal community composition, decomposition and resulting deadwood properties in logs of Fagus sylvatica, Picea abies and Pinus sylvestris. For. Ecol. Manag. 382, 129–142. https://doi.org/10.1016/J.FORECO.2016.10.004.

Bååth, E., 2003. The use of neutral lipid fatty acids to indicate the physiological conditions of soil fungi. Microb. Ecol. 45, 373–383.

Baldrian, P., 2017. Forest microbiome: diversity, complexity and dynamics. FEMS Microbiol. Rev. 41, 109–130. https://doi.org/10.1093/FEMSRE/FUW040.

Baldrian, P., Kolařík, M., Štursová, M., Kopecký, J., Valášková, V., Větrovský, T., Žifčáková, L., Šnajdr, J., Rídl, J., Vlček, Č., Voříšková, J., 2012. Active and total microbial communities in forest soil are largely different and highly stratified during decomposition. ISME J. 6, 248–258. https://doi.org/10.1038/ismej.2011.95.

Baldrian, P., Zrůstová, P., Tláskal, V., Davidová, A., Merhautová, V., Vrška, T., 2016. Fungi associated with decomposing deadwood in a natural beech-dominated forest. Fungal Ecol. 23, 109–122. https://doi.org/10.1016/J.FUNECO.2016.07.001.

Bao, T., Zhao, Y., Yang, X., Ren, W., Wang, S., 2019. Effects of disturbance on soil microbial abundance in biological soil crusts on the Loess Plateau, China. J. Arid Environ. 163, 59–67. https://doi.org/10.1016/j.jaridenv.2019.01.003.

Bardgett, R.D., Van Der Putten, W.H., 2014. Belowground biodiversity and ecosystem functioning. Nature 515, 505–511. https://doi.org/10.1038/nature13855.

Bastida, F., Torres, I.F., Andrés-Abellán, M., Baldrian, P., López-Mondéjar, R., Větrovský, T., Richnow, H.H., Starke, R., Ondoño, S., García, C., López-Serrano, F.R., Jehmlich, N., 2017. Differential sensitivity of total and active soil microbial communities to drought and forest management. Glob. Chang. Biol. 23, 4185–4203. https://doi.org/10.1111/gcb.13790.

Bautista, S., Robichaud, P.R., Bladé, C., 2009. Post-fire mulching. In: Cerda, A., Robichaud, P.R. (Eds.), Fire Effects on Soils and Restoration Strategies. CRC Press, pp. 369–388. https://doi.org/10.1201/9781439843338-17.

Bengtsson-Palme, J., Ryberg, M., Hartmann, M., Branco, S., Wang, Z., Godhe, A., De Wit, P., Sánchez-García, M., Ebersberger, I., de Sousa, F., Amend, A., Jumpponen, A., Unterseher, M., Kristiansson, E., Abarenkov, K., Bertrand, Y.J.K., Sanli, K., Eriksson, K.M., Vik, U., Veldre, V., Nilsson, R.H., 2013. Improved software detection and extraction of ITS1 and ITS2 from ribosomal ITS sequences of fungi and other eukaryotes for analysis of environmental sequencing data. Methods Ecol. Evol. 4, 914–919. https://doi.org/10.1111/2041-210X.12073.

Bonanomi, G., Zotti, M., Cesarano, G., Sarker, T.C., Saulino, L., Saracino, A., Idbella, M., Agrelli, D., D'Ascoli, R., Rita, A., Adamo, P., Allevato, E., 2021. Decomposition of woody debris in Mediterranean ecosystems: the role of wood chemical and anatomical traits. Plant Soil 460, 263–280. https://doi.org/10.1007/S11104-020-04799-4/FIGURES/4.

Brabcová, V., Nováková, M., Davidová, A., Baldrian, P., 2016. Dead fungal mycelium in forest soil represents a decomposition hotspot and a habitat for a specific microbial community. New Phytol. 210, 1369–1381. https://doi.org/10.1111/NPH.13849.

Bremner, J.M., Mulvaney, C.S., 1982. Nitrogen total. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), Methods of Soil Analysis, Part 2, Chemical and Microbiological Properties. American Society of Agronomy, Madison, pp. 595–624.

Bruns, T.D., Chung, J.A., Carver, A.A., Glassman, S.I., 2020. A simple pyrocosm for studying soil microbial response to fire reveals a rapid, massive response by Pyronema species. PLoS One 15. https://doi.org/10.1371/JOURNAL.PONE.0222691.

Castro, J., 2021. Post-fire restoration of Mediterranean pine forests. In: Ne'eman, G., Osem, Y. (Eds.), Pines and Their Mixed Forest Ecosystems in the Mediterranean Basin. Springer, Cham, pp. 537–565. https://doi.org/10.1007/978-3-030-63625-8_25.

Certini, G., 2005. Effects of fire on properties of forest soils: a review. Oecologia 143, 1–10. https://doi.org/10.1007/s00442-004-1788-8.

Chen, Q.L., Ding, J., Zhu, D., Hu, H.W., Delgado-Baquerizo, M., Ma, Y.B., He, J.Z., Zhu, Y. G., 2020. Rare microbial taxa as the major drivers of ecosystem multifunctionality in long-term fertilized soils. Soil Biol. Biochem. 141, 107686 https://doi.org/10.1016/j.soilbio.2019.107686.

Cheng, C., Gao, M., Zhang, Y., Long, M., Wu, Y., Li, X., 2021. Effects of disturbance to moss biocrusts on soil nutrients, enzyme activities, and microbial communities in degraded karst landscapes in southwest China. Soil Biol. Biochem. 152, 108065 https://doi.org/10.1016/J.SOILBIO.2020.108065.

Cole, J.R., Wang, Q., Fish, J.A., Chai, B., McGarrell, D.M., Sun, Y., Brown, C.T., Porras-Alfaro, A., Kuske, C.R., Tiedje, J.M., 2014. Ribosomal Database Project: data and tools for high throughput rRNA analysis. Nucleic Acids Res. 42, D633–D642. https://doi.org/10.1093/NAR/GKT1244.

Díez, J.A., 1982. Consideraciones sobre la utilización de la técnica extractiva de Burriel y Hernando para la evaluación del P asimilable en suelos. An. Edafol. Agrobiol. 41, 1345–1352.

Dooley, S.R., Treseder, K.K., 2012. The effect of fire on microbial biomass: a meta-analysis of field studies. Biogeochemistry 109, 49–61. https://doi.org/10.1007/s10533-011-9633-8.

Dove, N.C., Safford, H.D., Bohlman, G.N., Estes, B.L., Hart, S.C., 2020. High-severity wildfire leads to multi-decadal impacts on soil biogeochemistry in mixed-conifer forests. Ecol. Appl. 30, e02072 https://doi.org/10.1002/EAP.2072.

Edgar, R.C., 2010. Search and clustering orders of magnitude faster than BLAST. Bioinformatics 26, 2460–2461. https://doi.org/10.1093/bioinformatics/btq461.

Edgar, R.C., 2013. UPARSE: highly accurate OTU sequences from microbial amplicon reads. Nat. Methods 10, 996–998. https://doi.org/10.1038/nmeth.2604.

Eichlerová, I., Homolka, L., Žifčáková, L., Lisá, L., Dobiášová, P., Baldrian, P., 2015. Enzymatic systems involved in decomposition reflects the ecology and taxonomy of saprotrophic fungi. Fungal Ecol. 13, 10–22. https://doi.org/10.1016/J.FUNECO.2014.08.002.

Esposito, A., Mazzoleni, S., Strumia, S., 1999. Post-fire bryophyte dynamics in Mediterranean vegetation. J. Veg. Sci. 10, 261–268. https://doi.org/10.2307/3237147.

Ferrenberg, S., O'Neill, S.P., Knelman, J.E., Todd, B., Duggan, S., Bradley, D., Robinson, T., Schmidt, S.K., Townsend, A.R., Williams, M.W., Cleveland, C.C., Melbourne, B.A., Jiang, L., Nemergut, D.R., 2013. Changes in assembly processes in soil bacterial communities following a wildfire disturbance. ISME J. 7, 1102–1111. https://doi.org/10.1038/ismej.2013.11.

Filialuna, O., Cripps, C., 2021. Evidence that pyrophilous fungi aggregate soil after forest fire. For. Ecol. Manag. 498, 119579 https://doi.org/10.1016/J.FORECO.2021.119579.

Frouz, J., Toyota, A., Mudrák, O., Jílková, V., Filipová, A., Cajthaml, T., 2016. Effects of soil substrate quality, microbial diversity and community composition on the plant community during primary succession. Soil Biol. Biochem. 99, 75–84. https://doi.org/10.1016/J.SOILBIO.2016.04.024.

Fultz, L.M., Moore-Kucera, J., Dathe, J., Davinic, M., Perry, G., Wester, D., Schwilk, D.W., Rideout-Hanzak, S., 2016. Forest wildfire and grassland prescribed fire effects on soil biogeochemical processes and microbial communities: two case studies in the semi-arid Southwest. Appl. Soil Ecol. 99, 118–128. https://doi.org/10.1016/j.apsoil.2015.10.023.

Gall, C., Nebel, M., Quandt, D., Scholten, T., Seitz, S., 2022. Pioneer biocrust communities prevent soil erosion in temperate forests after disturbances. Biogeosciences 19, 3225–3245. https://doi.org/10.5194/BG-19-3225-2022.

Gao, L., Sun, H., Xu, M., Zhao, Y., 2020. Biocrusts resist runoff erosion through direct physical protection and indirect modification of soil properties. J. Soils Sediments 20, 133–142. https://doi.org/10.1007/S11368-019-02372-W/FIGURES/5.

García-Carmona, M., Arcenegui, V., García-Orenes, F., Mataix-Solera, J., 2020. The role of mosses in soil stability, fertility and microbiology six years after a post-fire salvage logging management. J. Environ. Manage. 262, 110287.

García-Carmona, M., Lepinay, C., García-Orenes, F., Baldrian, P., Arcenegui, V., Cajthaml, T., Mataix-Solera, J., 2022. Moss biocrust accelerates the recovery and resilience of soil microbial communities in fire-affected semi-arid Mediterranean soils. Sci. Total Environ. 846, 157467 https://doi.org/10.1016/J.SCITOTENV.2022.157467.

Garcia-Pichel, F., Johnson, S.L., Youngkin, D., Belnap, J., 2003. Small-scale vertical distribution of bacterial biomass and diversity in biological soil crusts from arid lands in the Colorado Plateau. Microb. Ecol. 46, 312–321. https://doi.org/10.1007/S00248-003-1004-0/FIGURES/6.

Girona-García, A., Vieira, D.C.S., Silva, J., Fernández, C., Robichaud, P.R., Keizer, J.J., 2021. Effectiveness of post-fire soil erosion mitigation treatments: a systematic review and meta-analysis. Earth Sci. Rev. 217, 103611 https://doi.org/10.1016/J.EARSCIREV.2021.103611.

Glassman, S.I., Levine, C.R., DiRocco, A.M., Battles, J.J., Bruns, T.D., 2016. Ectomycorrhizal fungal spore bank recovery after a severe forest fire: some like it hot. ISME J. 10, 1228–1239. https://doi.org/10.1038/ismej.2015.182.

Goodell, B., Winandy, J.E., Morrell, J.J., 2020. Fungal degradation of wood: emerging data, new insights and changing perceptions. Coatings 10, 1210.

Hart, S.C., DeLuca, T.H., Newman, G.S., MacKenzie, M.D., Boyle, S.I., 2005. Post-fire vegetative dynamics as drivers of microbial community structure and function in forest soils. For. Ecol. Manag. 220 (1–3), 166–184. https://doi.org/10.1016/j.foreco.2005.08.012.

Hartmann, M., Niklaus, P.A., Zimmermann, S., Schmutz, S., Kremer, J., Abarenkov, K., Lüscher, P., Widmer, F., Frey, B., 2014. Resistance and resilience of the forest soil microbiome to logging-associated compaction. ISME J. 8 (1), 226–244.

Jonas, J.L., Berryman, E., Wolk, B., Morgan, P., Robichaud, P.R., 2019. Post-fire wood mulch for reducing erosion potential increases tree seedlings with few impacts on understory plants and soil nitrogen. For. Ecol. Manag. 453, 117567 https://doi.org/10.1016/J.FORECO.2019.117567.

Juan-Ovejero, R., Molinas-González, C.R., Leverkus, A.B., Martín Peinado, F.J., Castro, J., 2021. Decadal effect of post-fire management treatments on soil carbon and nutrient concentrations in a burnt Mediterranean forest. For. Ecol. Manag. 498, 119570 https://doi.org/10.1016/J.FORECO.2021.119570.

Kahl, T., Arnstadt, T., Baber, K., Bässler, C., Bauhus, J., Borken, W., Buscot, F., Floren, A., Heibl, C., Hessenmöller, D., Hofrichter, M., Hoppe, B., Kellner, H., Krüger, D., Linsenmair, K.E., Matzner, E., Otto, P., Purahong, W., Seilwinder, C., Schulze, E.D., Wende, B., Weisser, W.W., Gossner, M.M., 2017. Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. For. Ecol. Manag. 391, 86–95. https://doi.org/10.1016/J.FORECO.2017.02.012.

Keeley, J.E., 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. Int. J. Wildland Fire 18, 116–126. https://doi.org/10.1071/WF07049.

Kohout, P., Charvátová, M., Štursová, M., Mašínová, T., Tomšovský, M., Baldrian, P., 2018. Clearcutting alters decomposition processes and initiates complex restructuring of fungal communities in soil and tree roots. ISME J. 123 (12), 692–703. https://doi.org/10.1038/s41396-017-0027-3.

Ladrón De Guevara, M., Maestre, F.T., 2022. Ecology and responses to climate change of biocrust-forming mosses in drylands. J. Exp. Bot. 73, 4380–4395. https://doi.org/10.1093/JXB/ERAC183.

Laiho, R., Prescott, C.E., 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. Artic. Can. J. For. Res. 34, 763–777. https://doi.org/10.1139/X03-241.

Lê, S., Josse, J., Rennes, A., Husson, F., 2008. FactoMineR: an r package for multivariate analysis. J. Stat. Softw. 25.

Lepinay, C., Jiráska, L., Tláskal, V., Brabcová, V., Vrška, T., Baldrian, P., 2021. Successional development of fungal communities associated with decomposing deadwood in a natural mixed temperate forest. J. Fungi 7, 412.

Lepinay, C., Tláskal, V., Vrška, T., Brabcová, V., Baldrian, P., 2022. Successional development of wood-inhabiting fungi associated with dominant tree species in a natural temperate floodplain forest. Fungal Ecol. 59, 101116 https://doi.org/10.1016/j.funeco.2021.101116.

Li, Y., Hu, C., 2021. Biogeographical patterns and mechanisms of microbial community assembly that underlie successional biocrusts across northern China. npj Biofilms Microbiomes 71 (7), 1–11. https://doi.org/10.1038/s41522-021-00188-6.

Li, W., Niu, S., Liu, X., Wang, J., 2019. Short-term response of the soil bacterial community to differing wildfire severity in Pinus tabulaeformis stands. Sci. Rep. 9, 1–10. https://doi.org/10.1038/s41598-019-38541-7.

Lladó, S., López-Mondéjar, R., Baldrian, P., 2017. Forest soil bacteria: diversity, involvement in ecosystem processes, and response to global change. Microbiol. Mol. Biol. Rev. 81, 1–27.

Lynch, M.D., Neufeld, J.D., 2015. Ecology and exploration of the rare biosphere. Nat. Rev. Microbiol. 13 (4), 217–229.

Marañón-Jiménez, S., Castro, J., 2013. Effect of decomposing post-fire coarse woody debris on soil fertility and nutrient availability in a Mediterranean ecosystem. Biogeochemistry 112, 519–535. https://doi.org/10.1007/S10533-012-9744-X.

Mašínová, T., Bahnmann, B.D., Větrovský, T., Tomšovský, M., Merunková, K., Baldrian, P., 2017. Drivers of yeast community composition in the litter and soil of a temperate forest. FEMS Microbiol. Ecol. 93, 223. https://doi.org/10.1093/FEMSEC/FIW223.

McLauchlan, K.K., Higuera, P.E., Miesel, J., Rogers, B.M., Schweitzer, J., Shuman, J.K., Tepley, A.J., Varner, J.M., Veblen, T.T., Adalsteinsson, S.A., Balch, J.K., Baker, P., Batllori, E., Bigio, E., Brando, P., Cattau, M., Chipman, M.L., Coen, J., Crandall, R., Daniels, L., Enright, N., Gross, W.S., Harvey, B.J., Hatten, J.A., Hermann, S., Hewitt, R.E., Kobziar, L.N., Landesmann, J.B., Loranty, M.M., Maezumi, S.Y., Mearns, L., Moritz, M., Myers, J.A., Pausas, J.G., Pellegrini, A.F.A., Platt, W.J., Roozeboom, J., Safford, H., Santos, F., Scheller, R.M., Sherriff, R.L., Smith, K.G., Smith, M.D., Watts, A.C., 2020. Fire as a fundamental ecological process: research advances and frontiers. J. Ecol. 108, 2047–2069. https://doi.org/10.1111/1365-2745.13403.

McMurdie, Holmes, 2013. phyloseq: an R package for reproducible interactive analysis and graphics of microbiome census data. PLoS One 8 (4), e61217.

Moreira, F., Ascoli, D., Safford, H., Adams, M.A., Moreno, J.M., Pereira, J.M., Catry, F.X., Armesto, J., Bond, W., González, M.E., Curt, T., 2020. Wildfire management in Mediterranean-type regions: paradigm change needed. Environ. Res. Lett. 15, 011001 https://doi.org/10.1088/1748-9326/ab541e.

Morlon, H., Chuyong, G., Condit, R., Hubbell, S., Kenfack, D., Thomas, D., Valencia, R., Green, J.L., 2008. A general framework for the distance–decay of similarity in ecological communities. Ecol. Lett. 11 (9), 904–917.

Muñoz-Rojas, M., Erickson, T.E., Martini, D., Dixon, K.W., Merritt, D.J., 2016. Soil physicochemical and microbiological indicators of short, medium and long term post-fire recovery in semi-arid ecosystems. Ecol. Indic. 63, 14–22. https://doi.org/10.1016/j.ecolind.2015.11.038.

Muñoz-Rojas, M., Machado de Lima, N., Chamizo, S., Bowker, M.A., 2021. Restoring post-fire ecosystems with biocrusts: living, photosynthetic soil surfaces. Curr. Opin. Environ. Sci. Health, 100273. https://doi.org/10.1016/j.coesh.2021.100273.

Nannipieri, P., Ceccanti, B., Cervelli, S., Matarese, E., 1981. Extraction of phosphatase, urease, proteases, organic carbon, and nitrogen from soil. Soil Sci. Soc. Am. J. 45, NP-NP. https://doi.org/10.2136/sssaj1981.03615995004500020048x.

Naseby, D.C., Lynch, J.M., 1997. Rhizosphere soil enzymes as indicators of perturbations caused by enzyme substrate addition and inoculation of a genetically modified strain of Pseudomonas fluorescens on wheat seed. Soil Biol. Biochem. 29, 1353–1362. https://doi.org/10.1016/S0038-0717(97)00061-8.

Nelson, D., Sommers, L., 1983. Total carbon, organic carbon, and organic matter. In: AL (Ed.), Methods of Soil Analysis, Part 2. Chemical and Biological Methods, p. 816.

Nelson, A.R., Narrowe, A.B., Rhoades, C.C., Fegel, T.S., Daly, R.A., Roth, H.K., Chu, R.K., Amundson, K.K., Young, R.B., Steindorff, A.S., Mondo, S.J., Grigoriev, I.V., Salamov, A., Borch, T., Wilkins, M.J., 2022. Wildfire-dependent changes in soil microbiome diversity and function. Nat. Microbiol. 7, 1419–1430. https://doi.org/10.1038/s41564-022-01203-y.

Nilsson, R.H., Larsson, K.H., Taylor, A.F.S., Bengtsson-Palme, J., Jeppesen, T.S., Schigel, D., Kennedy, P., Picard, K., Glöckner, F.O., Tedersoo, L., Saar, I., Kõljalg, U., Abarenkov, K., 2019. The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. Nucleic Acids Res. 47, D259–D264. https://doi.org/10.1093/NAR/GKY1022.

Op De Beeck, M., Lievens, B., Busschaert, P., Declerck, S., Vangronsveld, J., Colpaert, J. V., 2014. Comparison and validation of some ITS primer pairs useful for fungal metabarcoding studies. PLoS One 9, e97629. https://doi.org/10.1371/JOURNAL.PONE.0097629.

Parada, A.E., Needham, D.M., Fuhrman, J.A., 2016. Every base matters: assessing small subunit rRNA primers for marine microbiomes with mock communities, time series and global field samples. Environ. Microbiol. 18, 1403–1414. https://doi.org/10.1111/1462-2920.13023.

Pausas, J.G., Keeley, J.E., 2009. A burning story: the role of fire in the history of life. Bioscience 59, 593–601. https://doi.org/10.1525/bio.2009.59.7.10.

Pellegrini, A.F.A., Ahlström, A., Hobbie, S.E., Reich, P.B., Nieradzik, L.P., Staver, A.C., Scharenbroch, B.C., Jumpponen, A., Anderegg, W.R.L., Randerson, J.T., Jackson, R. B., 2018. Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. Nature 553, 194–198. https://doi.org/10.1038/nature24668.

Pereg, L., Morugán-Coronado, A., McMillan, M., García-Orenes, F., 2018. Restoration of nitrogen cycling community in grapevine soil by a decade of organic fertilization. Soil Tillage Res. 179, 11–19. https://doi.org/10.1016/j.still.2018.01.007.

Pérez-Valera, E., Verdú, M., Navarro-Cano, J.A., Goberna, M., 2020. Soil microbiome drives the recovery of ecosystem functions after fire. Soil Biol. Biochem. 149 https://doi.org/10.1016/j.soilbio.2020.107948.

Pinheiro, J., Bates, D., R Core Team, 2022. nlme: linear and nonlinear mixed effects models. R package version 3.1-161. https://CRAN.R-project.org/package=nlme.

Põlme, S., Abarenkov, K., Henrik Nilsson, R., Lindahl, B.D., Clemmensen, K.E., Kauserud, H., Nguyen, N., Kjøller, R., Bates, S.T., Baldrian, P., Frøslev, T.G., Adojaan, K., Vizzini, A., Suija, A., Pfister, D., Baral, H.O., Järv, H., Madrid, H., Nordén, J., Liu, J.K., Pawlowska, J., Põldmaa, K., Pärtel, K., Runnel, K., Hansen, K., Larsson, K.H., Hyde, K.D., Sandoval-Denis, M., Smith, M.E., Toome-Heller, M., Wijayawardene, N.N., Menolli, N., Reynolds, N.K., Drenkhan, R., Maharachchikumbura, S.S.N., Gibertoni, T.B., Læssøe, T., Davis, W., Tokarev, Y., Corrales, A., Soares, A.M., Agan, A., Machado, A.R., Argüelles-Moyao, A., Detheridge, A., de Meiras-Ottoni, A., Verbeken, A., Dutta, A.K., Cui, B.K., Pradeep, C. K., Marín, C., Stanton, D., Gohar, D., Wanasinghe, D.N., Otsing, E., Aslani, F., Griffith, G.W., Lumbsch, T.H., Grossart, H.P., Masigol, H., Timling, I., Hiiesalu, I., Oja, J., Kupagme, J.Y., Geml, J., Alvarez-Manjarrez, J., Ilves, K., Loit, K., Adamson, K., Nara, K., Küngas, K., Rojas-Jimenez, K., Bitenieks, K., Irinyi, L., Nagy, L.L., Soonvald, L., Zhou, L.W., Wagner, L., Aime, M.C., Öpik, M., Mujica, M.I., Metsoja, M., Ryberg, M., Vasar, M., Murata, M., Nelsen, M.P., Cleary, M., Samarakoon, M.C., Doilom, M., Bahram, M., Hagh-Doust, N., Dulya, O., Johnston, P., Kohout, P., Chen, Q., Tian, Q., Nandi, R., Amiri, R., Perera, R.H., dos Santos Chikowski, R., Mendes-Alvarenga, R.L., Garibay-Orijel, R., Gielen, R., Phookamsak, R., Jayawardena, R.S., Rahimlou, S., Karunarathna, S.C., Tibpromma, S., Brown, S.P., Sepp, S.K., Mundra, S., Luo, Z.H., Bose, T., Vahter, T., Netherway, T., Yang, T., May, T., Varga, T., Li, W., Coimbra, V.R.M., de Oliveira, V. R.T., de Lima, V.X., Mikryukov, V.S., Lu, Y., Matsuda, Y., Miyamoto, Y., Kõljalg, U., Tedersoo, L., 2020. FungalTraits: a user-friendly traits database of fungi and fungus-like stramenopiles. Fungal Divers. 105, 1–16. https://doi.org/10.1007/S13225-020-00466-2/FIGURES/3.

Prendergast-Miller, M.T., de Menezes, A.B., Macdonald, L.M., Toscas, P., Bissett, A., Baker, G., Farrell, M., Richardson, A.E., Wark, T., Thrall, P.H., 2017. Wildfire impact: natural experiment reveals differential short-term changes in soil microbial communities. Soil Biol. Biochem. 109, 1–13. https://doi.org/10.1016/j.soilbio.2017.01.027.

Pressler, Y., Moore, J.C., Cotrufo, M.F., 2019. Belowground community responses to fire: meta-analysis reveals contrasting responses of soil microorganisms and mesofauna. Oikos 128, 309–327. https://doi.org/10.1111/oik.05738.

Purahong, W., Wubet, T., Krüger, D., Buscot, F., 2018. Molecular evidence strongly supports deadwood-inhabiting fungi exhibiting unexpected tree species preferences in temperate forests. ISME J. 12, 289–295. https://doi.org/10.1038/ismej.2017.177.

Reazin, C., Morris, S., Smith, J.E., Cowan, A.D., Jumpponen, A., 2016. Fires of differing intensities rapidly select distinct soil fungal communities in a Northwest US ponderosa pine forest ecosystem. For. Ecol. Manag. 377, 118–127. https://doi.org/10.1016/J.FORECO.2016.07.002.

Robichaud, P.R., Lewis, S.A., Wagenbrenner, J.W., Ashmun, L.E., Brown, R.E., 2013. Post-fire mulching for runoff and erosion mitigation: part I: effectiveness at reducing hillslope erosion rates. Catena 105, 75–92. https://doi.org/10.1016/J.CATENA.2012.11.015.

Robichaud, P.R., Lewis, S.A., Wagenbrenner, J.W., Brown, R.E., Pierson, F.B., 2020. Quantifying long-term post-fire sediment delivery and erosion mitigation effectiveness. Earth Surf. Process. Landf. 45, 771–782. https://doi.org/10.1002/ESP.4755.

Roldán, A., García-Orenes, F., Lax, A., 1994. An incubation experiment to determine factors involving aggregation changes in an arid soil receiving urban refuse. Soil Biol. Biochem. 26, 1699–1707. https://doi.org/10.1016/0038-0717(94)90323-9.

RStudio Team, 2021. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. URL. http://www.rstudio.com/.

Silva, F.C., Vieira, D.C.S., van der Spek, E., Keizer, J.J., 2019. Effect of moss crusts on mitigation of post-fire soil erosion. Ecol. Eng. 128, 9–17. https://doi.org/10.1016/j.ecoleng.2018.12.024.

Smith, J.E., Kluber, L.A., Jennings, T.N., McKay, D., Brenner, G., Sulzman, E.W., 2017. Does the presence of large down wood at the time of a forest fire impact soil recovery? For. Ecol. Manag. 391, 52–62. https://doi.org/10.1016/j.foreco.2017.02.013.

Soil Survey Staff, 2014. Keys to Soil Taxonomy, 12th ed. USDA-Natural Resources Conservation Service, Washington, DC.

Song, Z., Kennedy, P.G., Liew, F.J., Schilling, J.S., 2017. Fungal endophytes as priority colonizers initiating wood decomposition. Funct. Ecol. 31, 407–418. https://doi.org/10.1111/1365-2435.12735.

Stella, T., Covino, S., Burianová, E., Filipová, A., Křesinová, Z., Voříšková, J., Větrovský, T., Baldrian, P., Cajthaml, T., 2015. Chemical and microbiological characterization of an aged PCB-contaminated soil. Sci. Total Environ. 533, 177–186. https://doi.org/10.1016/J.SCITOTENV.2015.06.019.

Tabatabai, M.A., 1983. Soil enzymes. In: Methods of Soil Analysis: Part 2 Chemical and Microbiological Properties, pp. 903–947.

Thorn, S., Bässler, C., Brandl, R., Burton, P.J., Cahall, R., Campbell, J.L., Castro, J., Choi, C.Y., Cobb, T., Donato, D.C., Durska, E., Fontaine, J.B., Gauthier, S., Hebert, C., Hothorn, T., Hutto, R.L., Lee, E.J., Leverkus, A.B., Lindenmayer, D.B., Obrist, M.K., Rost, J., Seibold, S., Seidl, R., Thom, D., Waldron, K., Wermelinger, B., Winter, M.B., Zmihorski, M., Müller, J., 2018. Impacts of salvage logging on biodiversity: a meta-analysis. J. Appl. Ecol. 55, 279–289. https://doi.org/10.1111/1365-2664.12945.

Thorn, S., Chao, A., Georgiev, K.B., Müller, J., Bässler, C., Campbell, J.L., Castro, J., Chen, Y.H., Choi, C.Y., Cobb, T.P., Donato, D.C., Durska, E., Macdonald, E., Feldhaar, H., Fontaine, J.B., Fornwalt, P.J., Hernández, R.M.H., Hutto, R.L., Koivula, M., Lee, E.J., Lindenmayer, D., Mikusiński, G., Obrist, M.K., Perlík, M., Rost, J., Waldron, K., Wermelinger, B., Weiß, I., Żmihorski, M., Leverkus, A.B., 2020. Estimating retention benchmarks for salvage logging to protect biodiversity. Nat. Commun. 11, 1–8. https://doi.org/10.1038/s41467-020-18612-4.

Tláskal, V., Zrůstová, P., Vrška, T., Baldrian, P., 2017. Bacteria associated with decomposing dead wood in a natural temperate forest. FEMS Microbiol. Ecol. 93, 157. https://doi.org/10.1093/FEMSEC/FIX157.

Tláskal, V., BrabcovÁ, V., Větrovský, T., Jomura, M., López-Mondéjar, R., Oliveira Monteiro, L.M., Saraiva, J.P., Human, Z.R., Cajthaml, T., Nunes da Rocha, U., Baldrian, P., 2021. Complementary roles of wood-inhabiting fungi and bacteria facilitate deadwood decomposition. mSystems 6. https://doi.org/10.1128/MSYSTEMS.01078-20/SUPPL_FILE/REVIEWER-COMMENTS.PDF.

Urbanová, M., Šnajdr, J., Baldrian, P., 2015. Composition of fungal and bacterial communities in forest litter and soil is largely determined by dominant trees. Soil Biol. Biochem. 84, 53–64. https://doi.org/10.1016/J.SOILBIO.2015.02.011.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biol. Biochem. 19, 703–707. https://doi.org/10.1016/0038-0717(87)90052-6.

Větrovský, T., Baldrian, P., Morais, D., 2018. SEED 2: a user-friendly platform for amplicon high-throughput sequencing data analyses. Bioinformatics 34, 2292–2294. https://doi.org/10.1093/bioinformatics/bty071.

Weber, B., Bowker, M., Zhang, Y., Belnap, J., 2016. Natural recovery of biological soil crusts after disturbance. In: Weber, B., Büdel, B., Belnap, J. (Eds.), Biological Soil Crusts: An Organizing Principle in Drylands. Springer, Cham, pp. 479–498. https://doi.org/10.1007/978-3-319-30214-0_23.

Weber, B., Belnap, J., Büdel, B., Antoninka, A.J., Barger, N.N., Chaudhary, V.B., Darrouzet-Nardi, A., Eldridge, D.J., Faist, A.M., Ferrenberg, S., Havrilla, C.A., Huber-Sannwald, E., Malam Issa, O., Maestre, F.T., Reed, S.C., Rodriguez-Caballero, E., Tucker, C., Young, K.E., Zhang, Y., Zhao, Y., Zhou, X., Bowker, M.A., 2022. What is a biocrust? A refined, contemporary definition for a broadening research community. Biol. Rev. 97, 1768–1785. https://doi.org/10.1111/BRV.12862.

Xiao, B., Veste, M., 2017. Moss-dominated biocrusts increase soil microbial abundance and community diversity and improve soil fertility in semi-arid climates on the Loess Plateau of China. Appl. Soil Ecol. 117, 165–177. https://doi.org/10.1016/j.apsoil.2017.05.005.

Xiao, B., Hu, K., Ren, T., Li, B., 2016. Moss-dominated biological soil crusts significantly influence soil moisture and temperature regimes in semiarid ecosystems. Geoderma 263, 35–46. https://doi.org/10.1016/J.GEODERMA.2015.09.012.