Forest Ecology and Management 572 (2024) 122293

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Post-fire management and biocrust development interact in mid-term soil recovery after a wildfire

M. García-Carmona [a,b,*], A. Girona-García [b], Jan Jacob Keizer [c], Bruna R.F. Oliveira [d], Fuensanta García-Orenes [a], Jorge Mataix-Solera [a]

[a] GETECMA – Soil Science and Environmental Technologies Group, Department of Agrochemistry and Environment, University of Miguel Hernández de Elche, Alicante, Spain
[b] Biodiversity Research Institute (IMIB), CSIC-University of Oviedo-Principality of Asturias, Mieres, Spain
[c] GeoBioTec, Department of Environment and Planning, University of Aveiro, Aveiro, Portugal
[d] Centre for Environmental and Marine Studies (CESAM), Department of Environment and Planning, University of Aveiro, Aveiro, Portugal

ARTICLE INFO

Keywords:
Eucalyptus plantation
Logging
Moss biocrust
Mulching
Wildfire
Post-fire management

ABSTRACT

Understanding the role of biocrust-forming mosses in soil recovery after wildfires is necessary for assessing the resilience of managed ecosystems. The purpose of this study was to investigate the mid-term impacts of two contrasting post-fire management strategies on soil recovery in eucalypt plantations in north-central Portugal, where a high cover of biocrust-forming mosses developed post-fire, contributing to erosion control. Six years after a wildfire, we examined the legacy effects of salvage logging and two rates of mulch application using logging residues (a standard rate of 8.0 Mg ha^{-1} and a reduced rate of 2.6 Mg ha^{-1}) on soil properties, and explored the interaction between moss biocrusts and forest management practices on soils. Our findings reveal the resilience of soils to physical disturbance after logging operations, with no persistent negative effects on their physicochemical properties. Although forest residue mulches showed minimal influence on soils after six years, an interesting interaction with moss biocrusts was observed. In the absence of moss cover, direct contact of wood residues with soil at the standard mulch rate promoted higher nutrient content and biochemical activity, potentially attributed to accelerated decomposition processes. Regardless of the management applied, our study highlights the role of moss biocrusts in improving soil aggregation and biochemical processes in the mid-term. However, the severe water repellency observed in these soils may have impeded further biocrust expansion. Understanding the implications of forest management practices on soil recovery after wildfires is imperative for guiding strategies aimed at promoting ecosystem recovery and resilience in fire-prone managed forest ecosystems.

1. Introduction

Biological soil crusts, or biocrusts, represent complex communities of photoautotrophic organisms (e.g., cyanobacteria, algae, lichens, bryophytes) and heterotrophic organisms (e.g., bacteria, fungi, archaea) inhabiting the uppermost millimeters of the soil surface (Weber et al., 2022). In drylands, the ecological functions of biocrusts are well-established, including the stabilization of the soil surface, positive contribution to soil biodiversity, and enhancement of biochemical processes and soil fertility (Belnap et al., 2016). However, their influence in temperate biomes remains less explored, despite their potential to contribute to aboveground and belowground processes. In mesic environments, biocrust dominance is favored by disturbances that temporarily limit vascular plant productivity and litter ground cover, creating favorable opportunities for biocrust emergence (Corbin and Thiet, 2020; Gall et al., 2022b). Wildland fires exemplify disturbances that allow transitory dominance of biocrusts (Bowker et al., 2004; Grover et al., 2020); although their response may vary depending on disturbance history and factors such as fire severity (Palmer et al., 2020; Zaady et al., 2016). After a disturbance in temperate biomes, the presence of biocrust diminishes or is replaced over succession, unless stressful conditions for vascular plants persist, i.e., induced by subsequent disturbances such as soil compaction (e.g., by heavy machinery in post-fire management), enabling longer persistence of biocrusts in those

---

[*] Corresponding author at: Biodiversity Research Institute (IMIB), CSIC-University of Oviedo-Principality of Asturias, Mieres, Spain.
E-mail address: minerva.garcia@csic.es (M. García-Carmona).

https://doi.org/10.1016/j.foreco.2024.122293
Received 17 May 2024; Received in revised form 5 September 2024; Accepted 6 September 2024

environments (Corbin and Thiet, 2020; García-Carmona et al., 2023a).

Biocrust-forming mosses rapidly colonize bare soils following wildfires (De las Heras et al., 1994; Esposito et al., 1999), playing crucial roles in key soil processes as ecosystem engineers (Ferrenberg et al., 2017; Ladrón De Guevara and Maestre, 2022). Their function as soil stabilizers, facilitated by their fine rhizoids and protonema mats, promotes rapid particle cohesion and stabilizes exposed soils (Seppelt et al., 2016), contributing significantly to post-fire erosion mitigation (Gall et al., 2022a; Silva et al., 2019). In semi-arid Mediterranean forests, rapid biocrust soil stabilization following wildfires has been observed to enhance nutrient cycling and biochemical processes, and accelerate the recovery of microbial communities, although the effects on soils depend on the developmental stage of the biocrust (García-Carmona et al., 2022, 2020). Conversely, the role of biocrusts in facilitating water infiltration in soils is inconsistent, as factors such as pore clogging or the hydrophobicity of certain species can promote water runoff rather than infiltration (Kidron et al., 2022; Rodríguez-Caballero et al., 2013). Most studies have focused on dryland ecosystems, often overlooking research on biocrust under mesic conditions (Baumann et al., 2021; Corbin and Thiet, 2020; Gall et al., 2022b). Addressing this gap is relevant for understanding ecosystem resilience in managed fire-affected ecosystems, which is particularly urgent given the escalating fire activity linked to climate change in temperate latitudes (Bedia et al., 2015; Kolden et al., 2024).

Impacts of post-fire forest management on soils are complex and conditioned by multiple factors that are linked to previous wildfire effects (Leverkus et al., 2018; Wagenbrenner et al., 2015). While these impacts are frequently neglected in decision-making processes, they can significantly reduce the ecosystem's ability to recover (Pereira et al., 2018; Tomao et al., 2020). In the Mediterranean region, salvage logging stands out as a common post-fire forestry operation, especially in commercial plantations such as the eucalypt and pine stands in Portugal, where logging operations are conducted to recover timber economic values and facilitate future forestry plantations (Moreira et al., 2011). Ecological disturbances due to intensive salvage logging operations have been widely reported, with impacts highly dependent on site characteristics, soil erodibility, and logging methods and equipment (Fernández and Vega, 2016; García-Orenes et al., 2017). Negative consequences often include soil compaction due to heavy machinery, which, in turn, can modify hydrological responses (Malvar et al., 2017; Morgan et al., 2015; Slesak et al., 2015), delay vegetation recovery (Wagenbrenner et al., 2016), and have detrimental effects on nutrient cycling (Pereg et al., 2018), carbon fluxes (Hartmann et al., 2014; Serrano-Ortiz et al., 2011), and soil biodiversity (Thorn et al., 2018). Intensive salvage logging has also been found to negatively impact the cover of biocrust-forming mosses in diverse biomes, both at the short and medium term (Bradbury, 2006; García-Carmona et al., 2020; Pharo et al., 2013).

When the protective vegetation is lacking immediately after a wildfire, mulching is considered the most effective and cost-effective measure to mitigate post-fire erosion (Girona-García et al., 2023, 2021; Keizer et al., 2018; Robichaud et al., 2013). Wood residue-based mulches, with their strong resistance and longevity, are expected to positively influence soils at the long term, by improving microclimatic conditions and implying nutrient supply (Jonas et al., 2019; Lepinay et al., 2022). The effects of mulches on the soil biological response, however, remains relatively unexplored. A significant drawback of wood mulch may be its inhibitory effect on vegetation recovery (Bautista et al., 2009; Castro, 2021). The application of high doses of burnt wood mulch drastically suppressed biocrust development in semi-arid forests after one year, hence conflicting with soil recovery fostered by mosses (García-Carmona et al., 2023b). While protecting soil from erosion is a primarily goal in Mediterranean post-fire land management, a better understanding of biocrust ecology and its impact on soil properties recovery would be crucial to enhance soil protection through effective management guidelines.

In Portugal, wildfires annually affect approximately 124,000 ha per year (ICNF, 2023). In recent decades, land abandonment and the widespread introduction of fire-prone tree plantations have significantly contributed to increasing fire risk (Moreira et al., 2011; Shakesby, 2011; Valente et al., 2015). Given the intensification of wildfire regimes (Jones et al., 2019), understanding ecosystem resilience is essential for ensure the sustainable ecosystem management. With this purpose, we studied two nearby eucalypt plantations in north-central Portugal that were affected by a wildfire in 2015. The sites were subjected to salvage logging and forest-residues mulching as part of an experiment designed to quantify post-fire erosion (Malvar et al. 2017). At the latter site, additional experiments revealed the significant role of mosses in erosion during the first post-fire year (Silva et al., 2019). The objective of this study was to investigate, the legacies on soils of two contrasting types of post-fire management, salvage logging and forest residue mulching, six years after a wildfire in eucalypt plantations characterized by notable post-fire cover of biocrust-forming mosses. Specifically, we aimed to: (1) assess the medium-term legacies of post-fire management on soils, subjected to salvage logging and two contrasting rates of mulch application – a standard rate of 8.0 Mg ha^{-1} and a reduced rate of 2.6 Mg ha^{-1}; and (2) explore the relevance of biocrust-forming mosses for soil recovery under mesic conditions. We hypothesized that soil response after six years would differ under different management approaches, with salvage logging resulting in negative effects due to the potential physical disturbance, and mulching exhibiting increasingly positive effects as mulching rates increased due to its protective effect; and that the presence of biocrust would enhance soil recovery across a range of physicochemical, biological and biochemical soil properties. Evaluating these impacts would help to guide post-fire forest management practices, especially focused on promoting post-fire recovery and resilience in fire-prone managed forest ecosystems.

2. Material and methods

2.1. Study area and post-fire treatments

The research was conducted in two eucalypt plantations (*Eucalyptus globulus* Labill.) in Vale de Colmeias, located in the Miranda do Corvo municipality of north-central Portugal (40° 9.977′ N, 8° 19.506′ W). The climate of the study area is Mediterranean with an oceanic influence and can be classified as humid meso-thermal, with mild winters and dry and warm summers. Its mean annual temperature and precipitation are 12° and 851 mm. Eucalypt plantations is the predominant land cover of the study area. The soils of the study area were derived from pre-Ordovician schist of the Hesperic Massif (Pereira and FitzPatrick, 1995), and were classified in the field as an association of Epileptic and Cambic Umbrisols and Dystric Cambisols (IUSS Working Group, 2022). The field descriptions of soil profiles of several nearby eucalypt plantations furthermore revealed Ah horizons with a sandy loam to loamy field texture till a depth of 35–60 cm (Keizer et al., 2018; Prats et al., 2019).

The study area was affected by a wildfire that started on August 8th 2015, and ended on August 9th 2015, affecting a total area of 715 ha. The severity of the fire was predominantly moderate and high (EFFIS, 2015). Field observations of the consumption of tree canopies and litter layer as well as the color of the ash layer suggested a moderate fire severity at both study sites (Malvar et al., 2017; Silva et al., 2019). Both sites were furthermore similarly steep (27^{o} and 30 ^{o}), had a similar aspect (NNE), and were located at less than 500 m from the Ceira river.

Shortly after the wildfire, the two sites were subjected to two contrasting management operations, i.e. salvage logging and mulching with eucalypt logging residues. The salvage logging was conducted for operational purposes, while the mulching was done for demonstration purposes in the framework of the EU-FP7 project RECARE. As previously detailed in Malvar et al. (2017), three treatments were implemented immediately after the salvage logging, each instrumented with three erosion plots of 16 m^{2}. For the present study, the skid_low logging and control treatments were selected, in particular for being located on the same upper part of the slope (referred to "logging" hereafter instead of skid_low). The second site selected for the mulching experiment followed the same experimental setup with nine 16 m^2 plots, three replicates for each of the two mulching treatments and the control without mulch. The two mulching treatments corresponded to two contrasting application rates of 8.0 Mg ha^{-1} ("standard rate") and 2.6 Mg ha^{-1} ("reduced rate").

Previous research at the mulching site demonstrated the significant role of the high moss cover, up to 48% one year after the wildfire, in reducing post-fire soil erosion (Silva et al., 2019), and served as inspiration for the present study. At the logging site, despite ground cover was monitored during the first year after the fire in Malvar et al. (2017), the moss cover was not considered in the assessment. At the time of the field sampling for this study, six years after the wildfire, patches of moss biocrust were well observed at both study sites. Moss cover was visually estimated to be approximately 50% at the mulching site and 80% at the logging site.

Worth special reference was that the mean erosion rate at the logged site over the first post-fire year was markedly higher for the logging (skid_low) plots than the control plots, amounting to 7.7 and 5.1 Mg ha^{-1} respectively (Malvar et al., 2017). The first-post-fire-year erosion rates of the 16 m^2 plots at the mulched site were below 1 Mg ha^{-1} for all three treatments (unpublished data), in line with the range of values of 1.0–2.2 reported by Silva et al. (2019).

2.2. Experimental design and soil sampling

Soil sampling for this study was conducted on 13 July, 2021, almost six years after the wildfire. For each of the five treatments mentioned above (logging and its control, two rates of mulching and its control), ten mineral soil samples were collected at 0–2.5 cm depth. Each set of ten samples included five replicates from underneath moss biocrust soils and five from uncrusted soils, resulting in a total of 20 samples at the logged site and 30 samples at the mulched site. At each site, biocrust and uncrusted soil samples were randomly selected within the 16 m^2 plots. Biocrust soils were visually identified, and bare soil samples were collected from unvegetated interspaces with no apparent biocrust development. Figure A1 illustrates the visual aspects of both cover types.

From each soil sample, a subsample was stored at 4°C for measuring biological and biochemical parameters, while the remainder was air-dried at room temperature. From the dried samples, a part was sieved between 4 mm and 0.25 mm for the measurement of aggregate stability, whereas the remaining part was sieved at 2 mm for the physicochemical analyses.

2.3. Laboratory analyses of the soil samples

Soil organic carbon was determined by the Walkley-Black method (Nelson and Sommers, 1983), total nitrogen by the Kjeldahl method (Bremner and Mulvaney, 1982), and the available phosphorus by the Olsen method (Olsen, 1954).

To evaluate the impact on soil structure, we measured the aggregate stability and the total macroaggregate content in the 4–0.25 mm soil fraction, which represent the macroaggregate fraction, following the Roldán et al. (1994) procedure. This method quantifies the proportion of aggregates that remain stable after exposure to a simulated rainfall of known energy (279 J min^{-1} m^{-1}), which allows the calculation of macroaggregates formation within a sample. The Water Drop Penetration Time test (Wessel, 1988) was used to measure the persistence of water repellency in soils under controlled laboratory conditions (20°C, ~50% relative humidity) to ensure comparability between treatments given the potential microenvironment changes under field conditions and the steepness of the slopes. Values were classified as follows, according to Bisdom et al. (1993) and Doerr et al. (1998): wettable (<5 s), slightly water repellent (5 – <60 s), strongly water repellent (60 – <600 s), severely water repellent (600 – <3,600 s), and extremely water repellent (≥3,600 s).

Basal soil respiration was measured using an automated impedance-meter (BacTrac 4200 Microbiological Analyser, Sylab, Austria), based on changes in the impedance of a KOH solution (2%) after CO_2 emissions by soil microorganisms incubated at 30 °C. Microbial biomass carbon was estimated, also using an impedance-meter, as the substrate-induced respiration using glucose (3 mg per gram of soil) as carbon substrate, according to Anderson and Domsch (1978).

Urease and protease enzymatic activities were determined as described by Kandeler et al. (1999), quantifying the NH_4^+ released after the addition of urea or N-α-benzoyl-l-arginine amide substrates, respectively (Nannipieri et al., 1981). β-Glucosidase and acidic phosphatase activities were quantified by measuring the formation of p-nitrophenol after soil incubation with p-nitrophenyl-β-d-glucopyranoside (Tabatabai, 1983) and p-nitrophenyl phosphate (Naseby and Lynch, 1997; Tabatabai, 1983). Dehydrogenase activity was determined following the procedure described by Garcia et al. (1997), measuring the reaction product INTF (iodonitrotetrazolium formazan), which is formed by the reduction of the substrate INT (2-p-iodophenyl-3-p-nitrophenyl-5-phenyltetrazolium chloride).

2.4. Statistical analyses

The effects of post-fire forest management types and moss development on soil properties were tested statistically using the software package RStudio v. 4.0.5 (R Core Team, 2023). ANOVA models were selected for statistical testing after initial analysis revealed a reduced contribution in the variance component associated with individual experimental erosion plots. Two-way ANOVA were conducted at each site to test the treatment and biocrust effects on soil properties. Phosphorus content and soil water repellency were log transformed to meet the assumption of a normal distribution of errors, and values were back transformed to facilitate interpretation. To explore differences between management sites, treatments, and biocrust presence across the entire sample set, a perMANOVA analysis was conducted using the adonis2 function in vegan with 999 permutations. Then, the relationships among variables were explored with principal component analysis, using "FactoMineR" and "factoextra" packages (Kassambara and Mundt, 2017; Lê et al., 2008).

3. Results

3.1. Physical properties: soil water repellency and soil aggregation

Six years after the fire, soils revealed water repellency regardless of site and treatment (Fig. 1). At the logging site, the presence of mosses significantly influenced the hydrophobicity observed (p-value <0.001, Table A1). While uncrusted soils predominantly classified as extremely water repellent, soils under mosses exhibited mostly strong water repellency. Similarly, at the mulching site, reduced level of water repellency was related to the presence of mosses (p-value <0.05, Table A1), although the frequencies defined also varied with the mulch application rate. Most soils were strongly water repellent, with uncrusted soils under standard mulch rate tending to be more severely water repellent. Additionally, the latter soils did not show the "slightly water repellent" class, while control soils under mosses had the highest frequency of this class (Fig. 1).

Differences in soil aggregation were observed for both soil structural parameters measured, i.e. the total content of aggregates (or total macroaggregates) and the stability of soil aggregates (Fig. 2). The total aggregation of soils was notably and significantly influenced by the presence of mosses, resulting in higher aggregation values compared to uncrusted soils (see Table A1 in supplementary materials for more statistical details). In contrast, biocrust did not show statistical effect on aggregate stability. In general, lower values were observed in soils under

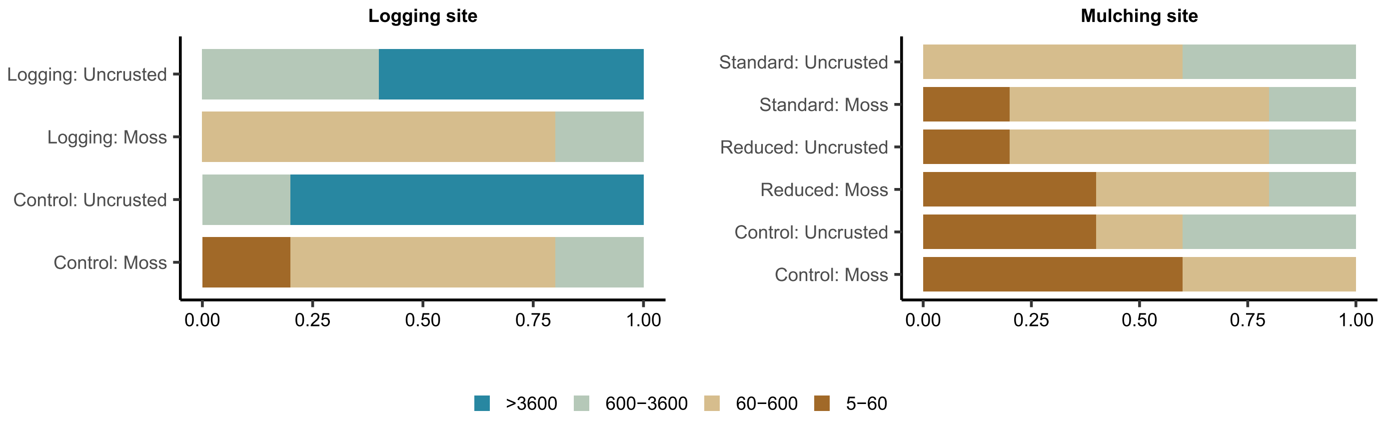

Fig. 1. Frequency of soil water repellency classes at the salvage logging and the mulch sites by treatment and biocrust presence (uncrusted and moss). Classes are identified as: wettable (<5 s), slightly water repellent (5–<60 s), strongly water repellent (60–<600 s), severely water repellent (600–<3,600 s), and extremely water repellent (>3,600 s).

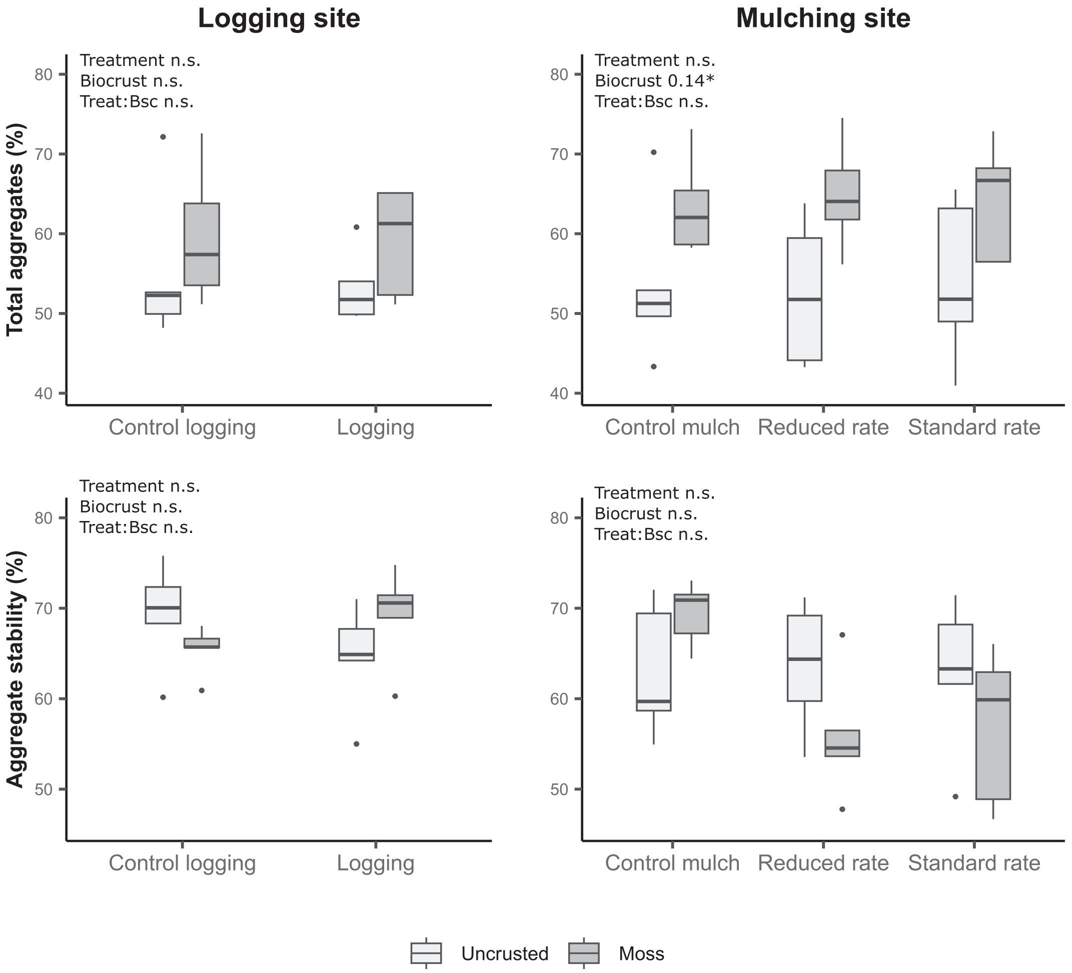

Fig. 2. Soil aggregation at the salvage logging and the mulching sites per treatment and biocrust presence (uncrusted and moss). Summary of statistical results for treatment and biocrust factors from two-way ANOVA are included. P-values indicate significant effect ('***' $p < 0.001$; '**' $p < 0.01$; '*' $p < 0.05$; 'ns' not significant).

mulch, while uncrusted soils remained relatively constant, showing similar values to those in logged soils (~ 65%).

3.2. Chemical properties: organic carbon, nitrogen, and phosphorus contents

At the logging site, organic carbon and total nitrogen contents were significantly lower under mosses compared to uncrusted soils (Fig. 3). However, biocrust did not significantly affect the available phosphorus content at the logging site, whereas the treatment did (p-value < 0.001), resulting in significantly higher values in the logged soils. By contrast, at the mulching site, neither biocrust nor treatment had a significant overall effect on organic carbon and nitrogen, while the phosphorus content revealed a significant interaction between the two factors. This interaction reflected a tendency for higher values for the uncrusted soils under the standard rate.

3.3. Biological and biochemical properties: microbial biomass, basal respiration, and enzyme activities

Microbial biomass did not show statistically significant differences based on treatment or biocrust presence at any site (Fig. 4). Overall, mulching site tended to show higher values compared to the logging site. At the mulching site, a trend to higher microbial biomass in soils under the standard rate of mulch compared to the reduced rate was observed, particularly in uncrusted soils compared to those under mosses. A similar pattern was observed for basal respiration. At the logging site, basal soil respiration significantly decreased due to the treatment, regardless of the presence of moss biocrusts.

All enzymes revealed differences between sites, and higher values were observed in the mulching site compared to the logging site (Table 2). Both dehydrogenase and urease enzymes showed a significant response to the biocrust presence, while only β-glucosidase showed a treatment effect in mulched soils (Table 2). Dehydrogenase activity significantly increased with the presence of mosses in both logging and mulching sites, regardless of the treatment applied. On the other hand, specific enzymatic activities related to nitrogen, carbon, and phosphorus cycles showed a tendency to higher activity under mosses in logged soils, although not statistically significant. In the mulching site, control soils without biocrust showed higher enzyme activities. Under the standard rate of mulch, soils under mosses registered lower values of activity compared to uncrusted soils.

3.4. Relationships between physical, chemical, and biological properties

Soils from logging and mulching sites were strongly and significantly different as indicated by the perMANOVA results (Table 3). These differences were also visually evident along the first axis of the principal component analysis (PCA), which explained 36.4% of the variability (Fig. 5).

When examining the distribution of samples per treatment, distinct patterns emerged (Fig. 5). At the logging site, small differences were observed between control and logged soils, with key soil properties explaining the differences such as water repellency, phosphorus content, and aggregate stability. In contrast, at the mulching site, treatment effects were more pronounced, in particular the standard mulching rate differed from the low rate and control soils, which exhibited similar behavior. All biological soil properties played a significant role in explaining the distribution of individuals. Phosphatase, β-glucosidase, and dehydrogenase activities showed similar scores, which contrasted with organic carbon and nitrogen contents along the Y-axis, clustering in the standard rate of mulch.

The presence of biocrust was a significant factor in the perMANOVA analysis (Table 3), with a significant interaction with site. This distinct clustering between uncrusted and moss samples was clearly observed along the X-axis at the logging site. Variables such as organic carbon, nitrogen, water repellency, and aggregate stability explained the distribution of uncrusted samples, while enzymatic activities, specifically β-glucosidase in control soils and dehydrogenase, phosphatase, and urease in logged soils, explained the clustering of moss samples. In contrast, at the mulching site, no clear pattern was discernible for the biocrust factor.

4. Discussion

Our findings confirm that contrasting post-fire forest management operations result in significant divergence in soil response, which holds profound implications for ecosystem recovery. The divergent trajectories between the two study sites could be partly attributed to the inherent heterogeneity of fire effects on soils (Keeley, 2009), as evidenced by differences between control soils. However, the adopted management strategy emerged as a critical determinant of soil properties after six years. While soils subjected to logging were expected to show strong negative legacies due to the potential physical disturbance caused by logging operations (Pereg et al., 2018; Thorn et al., 2018; Wagenbrenner et al., 2016), mulched soils were anticipated to improve biological response thanks to their protective effect (Bautista et al., 2009; García-Carmona et al., 2023b). However, mulched soils revealed a neutral response to mulch application with only small differences between the two - markedly different - mulching rates, while logged soils showed few indicators of degradation, thus revealing notable resilience to both fire and physical disturbances. Our findings aligned with those reporting minimal detrimental effects after logging under comparable soil and climate conditions in NW Spain (Fernández et al., 2021; Fernández and Vega, 2016). This suggests that soils under favorable climatic conditions that promote rapid vegetation recovery are potentially less vulnerable, even if soil fire severity and rainfall intensity after logging are critical factors (Fernández and Vega, 2016). Indeed, Malvar et al. (2017) reported for the logging site of this study that logging did not delay the short-term recovery of vegetation, despite an increase in soil compaction (14% increase in bulk density) and the increase in erosion (7.7 to 5.1 Mg ha^{-1} in control soils). In particular, the rapid establishment of biocrust-forming mosses played a significant role in reducing soil erosion in the short term (Silva et al., 2019), thus preventing soil structure degradation, promoting soil stabilization and accelerating biochemical processes over time, as it has been extensively reported for drylands (Belnap and Büdel, 2016; Ladrón De Guevara and Maestre, 2022).

At the logging site, soils that remained unvegetated (uncrusted) exhibited severe water repellency, a characteristic expressed regardless logging activities. Previous studies in *Eucalyptus globulus* plantations in Portugal indicate that those soils naturally develop water repellency (Doerr et al., 1996), and also exhibit it after wildfires (Ferreira et al., 2008; Keizer et al., 2008; Malvar et al., 2016). While fire can act as a trigger for soil hydrophobicity (Doerr et al., 2000), previous studies suggested that eucalyptus's litter inputs, rich in essential oils, are a natural driver of soil water repellency. However, high soil temperatures during fires can temporarily disrupt the hydrophobicity of naturally repellent soils (DeBano, 2000), creating wettable soil patches that serve as potential sinks for overland flows. This would facilitate the initial establishment of moss propagules transported by water and air, or already in the soil, enabling their colonization in naturally water-repellent soils. Once established, the subsequent expansion of biocrust-forming mosses would be facilitated by their alteration of surrounding surface conditions, both physically (by increasing moisture) and chemically (by changing the organic compounds) (Eldridge et al., 2020; Ferrenberg et al., 2018; Gao et al., 2020). Contrary to expectations, soils under mosses in the logging site had significantly lower organic matter content than in uncrusted soils. Therefore, the observed severe hydrophobicity in uncrusted soils may be related to a possible higher accumulation of hydrophobic organic compounds, potentially induced by the fire (Jiménez-Morillo et al., 2022) or eucalypt litter

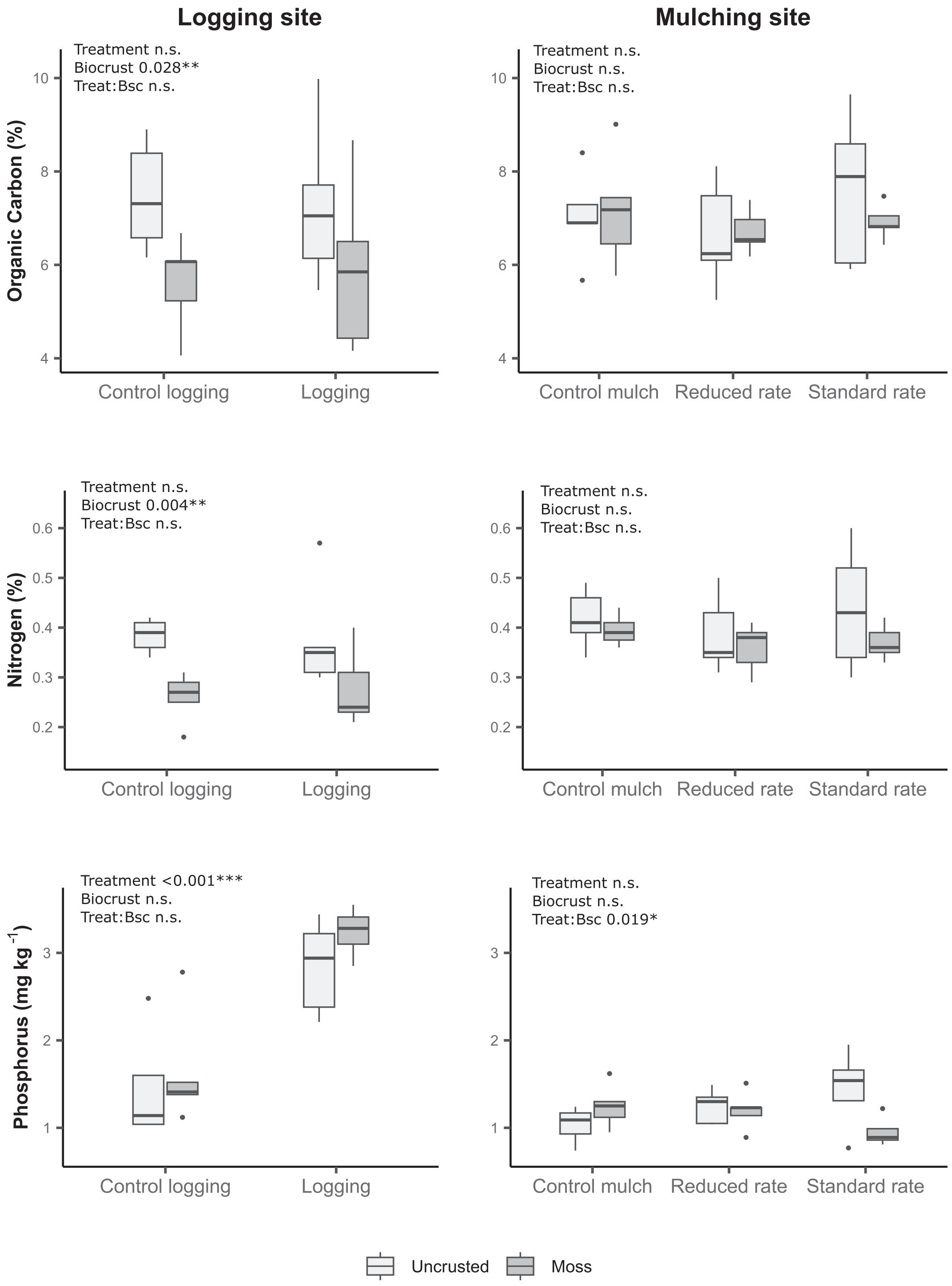

Fig. 3. Organic carbon, total nitrogen and available phosphorus contents in salvage logging and mulch sites for soils differentiated by treatments and biocrust presence (uncrusted and moss). Phosphorus values were log transformed for analyses, but back transformed in the table for clarity of interpretation. Summary of statistical results for treatment and biocrust factors from two-way ANOVA are presented. P-values indicate significant effect ('***' $p < 0.001$; '**' $p < 0.01$; '*' $p < 0.05$; 'ns' not significant).

deposition, hindering moss establishment in these patches.

A different scenario emerged for soils under mulch, where the decrease in water repellency is likely attributable to gradual changes in soil surface conditions over time. Water repellency fluctuates with soil moisture levels, as it naturally diminishes with increasing soil moisture (Doerr et al., 2000). This phenomenon explains the slightly reduced repellency observed at the highest mulch rate, where greater soil coverage would anticipate higher permanent soil moisture and consequently a decrease in soil hydrophobicity. This decrease is particularly notable for uncrusted soils under this rate, where residue materials are in direct contact with soils without a layer of moss between them.

One significant finding of our study is the consistently high level of total aggregation in soils under the moss biocrust, regardless of the forest management. The mid-term preservation and/or promotion of soil aggregation can be attributed to the well-known role of mosses in

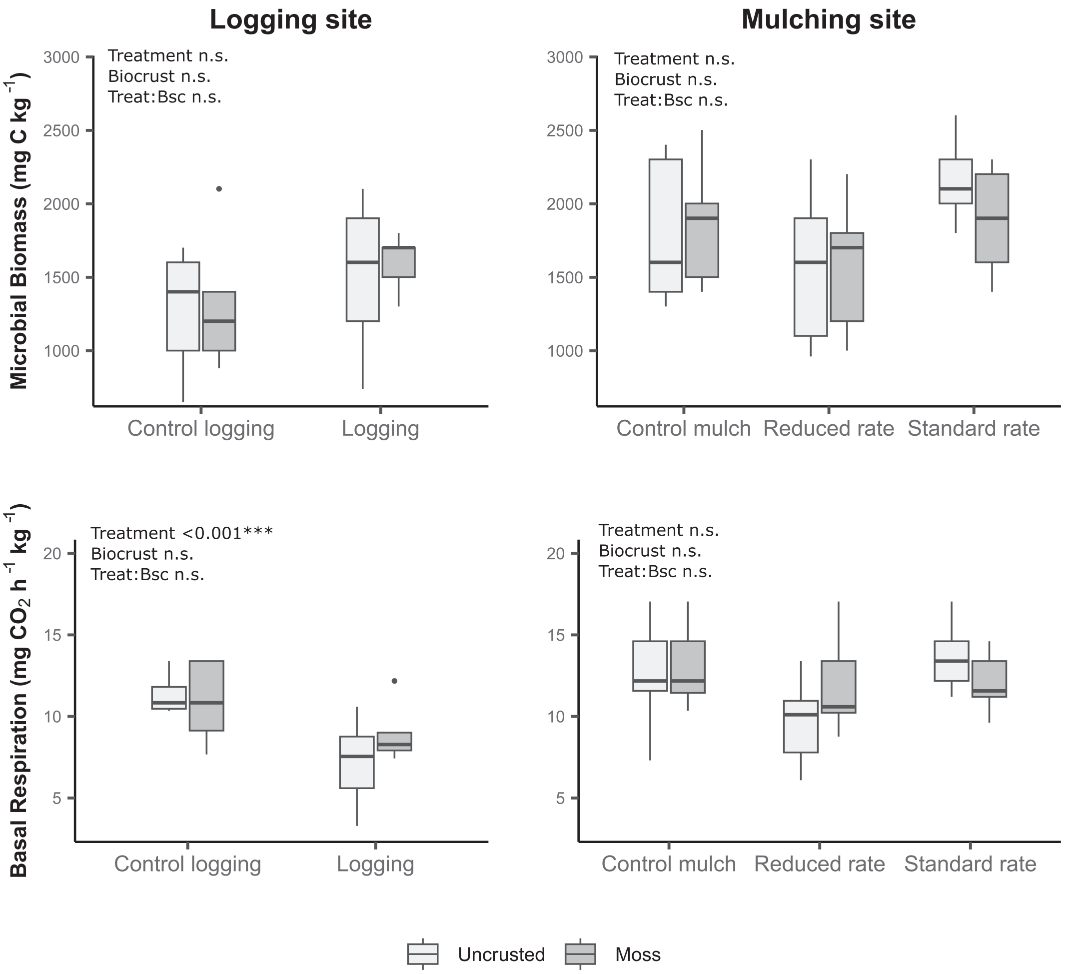

Fig. 4. Microbial biomass and basal respiration at the salvage logging and mulching sites per treatment and biocrust presence (uncrusted and moss). Summary of statistical results for treatment and biocrust factors from two-way ANOVA are presented. P-values indicate significant effect ('***' p <0.001; '**' p <0.01; '*' p <0.05; 'ns' not significant).

Table 2

Enzymatic activities in salvage logging and mulch sites for soils differentiated by treatments and biocrust presence (uncrusted and moss). Summary of statistical results for treatment and biocrust factors from two-way ANOVA are presented. P-values in bold indicate significant effect ('***' p <0.001; '**' p <0.01; '*' p <0.05; 'ns' not significant).

	Treatment	Biocrust	**Dehydrogenase** (µg INTF g^{-1})		**Protease** (µmol N-NH$_4^+$ g^{-1} h^{-1})		**Urease** (µmol N-NH$_4^+$ g^{-1} h^{-1})		**β-Glucosidase** (µmol PNP g^{-1} h^{-1})		**Phosphatase** (µmol PNP g^{-1} h^{-1})	
Logging site	Control	Uncrusted	4.12 ± 3.33		1.26 ± 0.78		0.61 ± 0.09		0.46 ± 0.48		2.07 ± 0.56	
		Moss	11.7 ± 3.65		0.91 ± 0.28		0.49 ± 0.12		1.00 ± 0.37		6.13 ± 2.94	
	Logging	Uncrusted	8.32 ± 3.65		0.89 ± 0.10		0.69 ± 0.31		0.46 ± 0.25		5.73 ± 4.32	
		Moss	13.0 ± 5.99		1.25 ± 0.34		0.77 ± 0.18		0.56 ± 0.26		6.65 ± 1.87	
			F-value	*P-value*	*F-value*	*P-value*	*F-value*	*P-value*	*F-value*	*P-value*	*F-value*	*P-value*
	Treatment		2.09	ns	0.01	ns	4.39	ns	1.82	ns	2.81	ns
	Biocrust		10.21	**0.005****	0.001	ns	0.07	ns	3.91	ns	3.98	ns
	Treatment: Biocrust		0.55	ns	3.05	ns	1.44	ns	2.12	ns	1.58	ns
Mulching site	Control	Uncrusted	18.8 ± 4.72		2.23 ± 1.33		1.45 ± 0.33		3.23 ± 1.61		19.4 ± 6.53	
		Moss	29.6 ± 10.7		1.72 ± 0.85		1.26 ± 0.26		3.29 ± 1.20		17.2 ± 5.63	
	Reduced rate	Uncrusted	22.8 ± 8.30		1.37 ± 0.56		1.31 ± 0.33		2.55 ± 0.96		13.1 ± 7.97	
		Moss	27.0 ± 9.25		1.43 ± 0.66		1.12 ± 0.18		2.61 ± 0.74		13.0 ± 3.67	
	Standard rate	Uncrusted	21.2 ± 15.6		2.01 ± 0.27		1.87 ± 0.77		2.41 ± 1.33		15.7 ± 4.33	
		Moss	32.8 ± 28.4		1.41 ± 0.61		0.95 ± 0.30		1.01 ± 0.30		12.6 ± 5.01	
			F-value	*P-value*	*F-value*	*P-value*	*F-value*	*P-value*	*F-value*	*P-value*	*F-value*	*P-value*
	Treatment		2.22	ns	0.85	ns	1.02	ns	4.89	**0.016***	2.38	ns
	Biocrust		5.42	**0.03***	0.57	ns	9.54	**0.005****	1.12	ns	0.74	ns
	Treatment: Biocrust		0.44	ns	1.03	ns	1.59	ns	1.43	ns	0.18	ns

Table 3

Summary of perMANOVA model results. Significant factors include “Site” (logging and mulching), “Treatments” (logging, control logging, mulch reduced rate, mulch standard rate, control mulching), “Biocrust” (moss and uncrusted), and the interaction between them. P-values in bold indicate significant effect (‘***’ $p < 0.001$; ‘**’ $p < 0.01$; ‘*’ $p < 0.05$; ‘ns’ not significant).

	df	Sums of Sqs	Mean Sqs	F-value	R^2	P-value
Site	1	1.107	1.107	20.78	0.217	**0.001*****
Treatments	3	0.149	0.049	0.93	0.029	0.456
Biocrust	1	0.814	0.814	15.27	0.159	**0.001*****
Site:Biocrust	1	0.859	0.859	16.11	0.168	**0.001*****
Treatment: Biocrust	3	0.039	0.013	0.24	0.008	0.962
Residuals	40	2.131	0.053		0.418	
Total	49	5.099			1	

enhancing soil stabilization after disturbances (Belnap and Büdel, 2016; Gao et al., 2020; García-Carmona et al., 2020). In contrast, the total aggregation and aggregate stability in uncrusted soils remained constant regardless of the treatment, which includes the potential physical disturbance of logging operations, such as soil compaction and destruction of stable aggregates (García-Orenes et al., 2017). While the higher variability in aggregate stability under mosses was not clearly related to the management practices (5% increase in logged soils and 7% decrease in mulched soils in moss soils compared to uncrusted soils), there was some evidence that potential increments in unprotected (uncrusted) and logged soils could be attributed to erosion processes. After a fire, erosion forces tend to selectively affect and displace weaker aggregates, leaving the more stable ones and therefore, apparently increasing the aggregate stability values in the short-midterm (Mataix-Solera et al., 2021). The low aggregate stability values highlight the vulnerability of the soils studied to erosion processes and emphasize the importance of both live covers (such as mosses) and inert covers (mulch) in promoting soil stabilization processes (Bautista et al., 2009; Vallejo et al., 2012).

As previously pointed out, the lower organic carbon observed in soils under mosses in logged sites do not seem to be a direct consequence of moss development, but potentially linked to carbon recalcitrance in uncrusted soils. While fast-growing mosses are able to mobilize nitrogen from soils during the colonization stage (Ladrón De Guevara and Maestre, 2022), moss-dominated biocrusts are expected over time to significantly increase nutrient content and carbon sequestration in soils. These observations have mostly been documented in drylands, where the contribution of mosses to soils is significant, particularly compared to other biocrust types, due to their larger litter inputs to soils (Eldridge et al., 2023; Tian et al., 2022; Weber et al., 2015). However, under mesic conditions, the presence of mosses did not lead to an increase in nitrogen and organic carbon content, as forest soils already have high levels of organic carbon and nitrogen making it difficult to discern differences due to moss litter inputs. On the other hand, the available phosphorus content did not respond to the biocrust presence but rather to the forest management, increasing after the logging operations. A possible explanation would be in line with the findings of García-Carmona et al. (2020), where this increase in phosphorus content could be attributed to the deposition of wind-borne soil particles originating from logging activities.

The application of mulch with forest residues did not significantly increase soil nutrient content after six years. Mulch application is expected to increase soil nutrient content over time due to their decomposition and improved soil microclimatic conditions, which stimulate microbial activity and biochemical processes (García-Carmona et al., 2023b; Jonas et al., 2019). However, given the inherent resistance to decomposition of woody materials (i.e., logging residues) with high lignin content and low nitrogen levels, increments of nutrients in soils are hardly expected in the first years post-application (Bonanomi et al., 2021; Kumaraswamy et al., 2014). Studies in Mediterranean regions

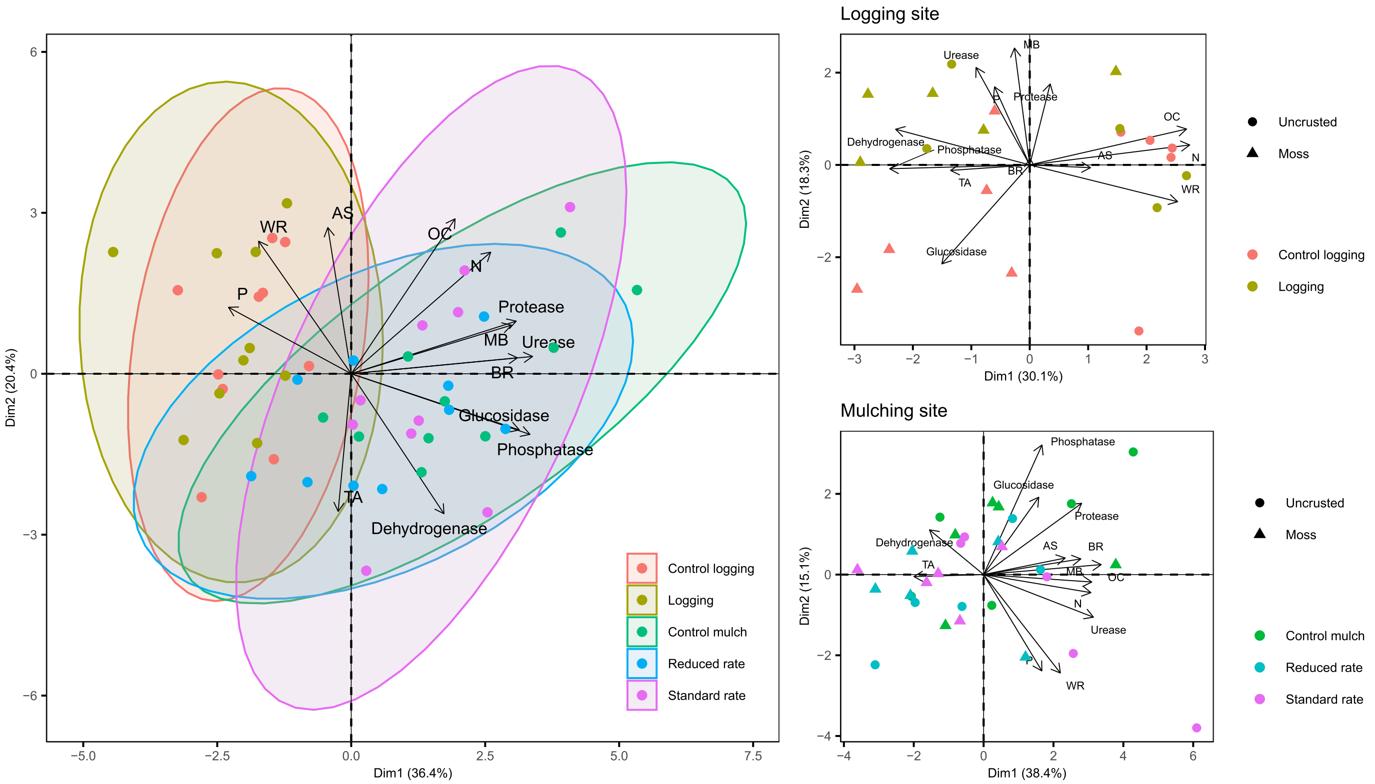

Fig. 5. Principal component analysis in salvage logging and mulch sites for soils differentiated by treatments at left, and at right separated by sites each one differentiated by treatments and biocrust (AS: aggregate stability; BR: basal respiration; MB: microbial biomass; OC: organic carbon; TA: total aggregates; WR: water repellency).

suggest that soil nutrient increments from dead wood materials occurs three to ten years after fire (Juan-Ovejero et al., 2021; Marañón-Jiménez and Castro, 2013). Therefore, the lack of a significant effect after six years may be due to specific wood properties that influence wood-decomposing communities and decay rates (Arnstadt et al., 2016; Kahl et al., 2017), as well as potential persistent effects of the wildfire on the soil microbial community composition. Nevertheless, a tendency towards higher nutrient and organic carbon was observed in soils under the standard rate of mulching compared to the reduced rate and control soils. This difference was only observed in uncrusted soils, suggesting that direct contact of wood residues with the soil accelerates their decomposition by providing wood decay fungi with access to moisture and essential nutrients required for their growth (Goodell et al., 2020). In contrast, mosses may act as a physical barrier slowing the nutrient incorporation from mulch residues to soils.

Consistent with the previously discussed findings on soil nutrients, the application of the standard rate of mulch correlated with a trend towards increased microbial biomass in uncrusted soils. This greater biomass was associated with higher microbial activity, not only in terms of basal respiration but also in specific enzymes such as β-glucosidase, protease, urease, and phosphatase. A high quantity of mulch not only reduced the soil and organic matter losses (unpublished data), but also stimulated biochemical processes by introducing organic materials and ameliorating the harsh surface conditions following a wildfire, thus improving microbial performance over time (Barreiro et al., 2016; Hu et al., 2023; Lucas-Borja et al., 2019). Nevertheless, the reduced rate of mulch did not result in improvements in nutrient cycling after six years, probably due to the lower material inputs or changes in soil microbial community diversity and functionality after the wildfire (Nelson et al., 2022). Previous research suggests that mulch application can alter the microbial community, favoring species with generalist degradation capabilities (Li et al., 2019; Yang et al., 2003). Compared to microbial communities under moss biocrust, those under forest residue mulch are reported to be transitorily less diverse in early post-fire stages (García-Carmona et al., 2023b), potentially impacting the decomposition of forest materials in the mid-term.

The microbial biomass in the salvage logging site was not markedly influenced by the presence of moss biocrusts. Values tended to be higher in logged soils, but this pattern did not translate to soil basal respiration, which instead tended to decrease. The lower soil basal respiration is probably a result of the physical degradation legacies of logging operations (i.e. compaction) (García-Orenes et al., 2013; Longepierre et al., 2021), which alters the microbial community composition and subsequently affects respiration rates (Hartmann et al., 2014; Hu et al., 2023; García-Carmona et al., 2021). The lower heterotrophic respiration in logged soils however did not correlate with dehydrogenase activity. Interestingly, dehydrogenase was consistently and positively associated with the presence of mosses at both the logging and mulching sites, regardless of the treatment applied. Therefore, six years after the wildfire, the presence of mosses notably impacted soil biochemistry as the biocrust microbiota increased the demand of soil nutrient resources increasing the enzyme activity. This effect extended to β-glucosidase and phosphatase activities, suggesting a greater stimulation of decomposition processes compared to uncrusted soils lacking a living cover. However, a contrasting pattern was observed for urease activity, with lower levels under mosses. This observation might suggest a temporary depletion of available nitrogen forms, although the total nitrogen content did not respond to moss presence. The lower values were mainly observed in mulched soils, particularly at the standard rate. This enzymatic response could be related to the higher complexity of compounds being degraded from the forest residues, compared to the rapid stimulation usually observed with straw mulches (Lucas-Borja et al., 2019). However, no correlation was observed for protease activity.

5. Conclusions

This case study provides valuable insights into the impacts of forest management practices on soil recovery following a wildfire in mesic conditions. We found that soils exhibit resilience to physical disturbance, with no lasting effects on their physicochemical properties. While forest residue mulches did not significantly affect soils after six years, an interesting interaction with moss biocrusts was observed; in the absence of moss cover, soil contact with mulch at a standard rate stimulated biochemical processes in soils. Our findings also highlight the role of moss biocrusts in midterm soil recovery. Biocrusts dominated by mosses played an interesting role in enhancing soil structure and promoting biochemical processes. However, the severe water repellency of these soils may hinder the spread of biocrusts. Further research into the dynamics of moss biocrust under mesic conditions is essential to better understand and support management practices that preserve ecosystem functionality. Considering that the impacts of wildfires on ecosystems and society are expected to increase due to global change, more information is urgently needed to develop effective management strategies.

CRediT authorship contribution statement

Bruna R.F. Oliveira: Writing – review & editing, Investigation. **Fuensanta García-Orenes:** Writing – review & editing, Supervision, Funding acquisition. **Jorge Mataix-Solera:** Writing – review & editing, Supervision, Funding acquisition. **Minerva García-Carmona:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Conceptualization. **Antonio Girona-García:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Jan Jacob Keizer:** Writing – review & editing, Investigation, Funding acquisition, Conceptualization.

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.

Ackowledgements

Antonio Girona-García is recipient of the Grant RYC2021-031262-I funded by MICIU/AEI/ 10.13039/501100011033 and by “European Union NextGenerationEU/PRTR”. 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 Minerva García-Carmona]. The authors acknowledge the CEBAS-CSIC for the enzymatic analyses.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122293.

References

Anderson, J.P.E., Domsch, K.H., 1978. A physiological method for the quantitative measurement of microbial biomass in soils. Soil Biol. Biochem. 10, 215–221. https://doi.org/10.1016/0038-0717(78)90099-8.

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. Ecol. Manag. 382, 129–142. https://doi.org/10.1016/J.FORECO.2016.10.004.

Barreiro, A., Bååth, E., Díaz-Raviña, M., 2016. Bacterial and fungal growth in burnt acid soils amended with different high C/N mulch materials. Soil Biol. Biochem. 97, 102–111. https://doi.org/10.1016/j.soilbio.2016.03.009.

Baumann, K., Eckhardt, K.-U., Acksel, A., Gros, P., Glaser, K., Gillespie, A.W., Karsten, U., Leinweber, P., 2021. Contribution of biological soil crusts to soil organic matter composition and stability in temperate forests. Soil Biol. Biochem. 160, 108315 https://doi.org/10.1016/j.soilbio.2021.108315.

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.

Bedia, J., Herrera, S., Manuel Gutiérrez, J., Benali, A., Brands, S., Mota, B., Moreno, J.M., 2015. Global patterns in the sensitivity of burned area to fire-weather: implications for climate change. Agric. Meteorol. 214, 369–379. https://doi.org/10.1016/j.agrformet.2015.09.002.

Belnap, J., Büdel, B., 2016. Biological Soil Crusts as Soil Stabilizers. In: Weber, B., Büdel, B., Belnap, J. (Eds.), Biological Soil Crusts: An Organizing Principle in Drylands. Springer, pp. 305–320. https://doi.org/10.1007/978-3-319-30214-0_16.

Belnap, J., Weber, B., Büdel, B., 2016. Biological soil crusts: an orgonizing principle in Drylands. In: Weber, B., Büdel, B., Belnap, J. (Eds.), Biological Soil Crusts: An Organizing Pricinple in Drylands. Springer, pp. 3–13. https://doi.org/10.1007/978-3-319-30214-0.

Bisdom, E.B.A., Dekker, L.W., Schoute, J.F.T., 1993. Water repellency of sieve fractions from sandy soils and relationships with organic material and soil structure. Geoderma 56, 105–118. https://doi.org/10.1016/0016-7061(93)90103-R.

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.

Bowker, M.A., Belnap, J., Rosentreter, R., Graham, B., 2004. Wildfire-resistant biological soil crusts and fire-induced loss of soil stability in Palouse prairies, USA. Appl. Soil Ecol. 26, 41–52. https://doi.org/10.1016/J.APSOIL.2003.10.005.

Bradbury, S.M., 2006. Response of the post-fire bryophyte community to salvage logging in boreal mixedwood forests of northeastern Alberta, Canada. . Ecol. Manag. 234, 313–322. https://doi.org/10.1016/j.foreco.2006.07.013.

Bremner, J.M., Mulvaney, C.S., 1982. Nitrogen total, in: 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.

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.

Corbin, J.D., Thiet, R.K., 2020. Temperate biocrusts: mesic counterparts to their better-known dryland cousins. Front. Ecol. Environ. 18, 456–464. https://doi.org/10.1002/FEE.2234.

De las Heras, J., Guerra Montes, J., Herranz, J.M., 1994. Stages of bryophytes succession after fire in Mediterranean forests (SE Spain). Int. J. Wildl. Fire 4, 33–34.

DeBano, L.F., 2000. Water repellency in soils: A historical overview, in: Journal of Hydrology. Elsevier Science B.V., pp. 4–32. https://doi.org/10.1016/S0022-1694(00)00180-3.

Doerr, S., Shakesby, R., Walsh, R.P., 1998. Spatial variability of soil hydrophobicity in fire-prone eucalyptus and pine forests, Portugal. Soil Sci. 164, 313–324.

Doerr, S.H., Shakesby, R.A., Walsh, R.P.D., 2000. Soil water repellency: its causes, characteristics and hydro-geomorphological significance. Earth Sci. Rev. 51, 33–65. https://doi.org/10.1016/S0012-8252(00)00011-8.

Doerr, S.H., Shakesby, R.A., Walsh, R.P.D., 1996. Soil hydrophobicity variations with depth and particle size fraction in burned and unburned Eucalyptus globulus and Pinus pinaster forest terrain in the hgueda Basin, Portugal. Catena 27, 25–47.

EFFIS, 2015. COPERNICUS - Emergency Management Service. ⟨http://effis.jrc.ec.europa⟩. eu/static/effis_current_situation/public/index.html [WWW Document].

Eldridge, D.J., Guirado, E., Reich, P.B., Berdugo, M., Samp, T., Blanco-Pastor, L., Tedersoo, L., Plaza, S., Ding, J., Sun, W., Mamet, S., Cui, H., He, J.-Z., Hu, H.-W., Sokoya, B., Abades, S., Alfaro, F., Bamigboye, A.R., Bastida, F., Ramp, L., Duramp, J., Gaitan, J.J., Guerra, C.A., Grebenc, T., Illamp, J.G., Liu, Y.-R., Makhalanyane, T.P., Mallen-Cooper, M., Molina-Montenegro, M.A., Moreno, L., Nahberger, T.U., Peamp, G.F., Picamp, S., Rey, A., Rodramp, A., Siebe, C., Teixido, A.L., Torres-Damp, C., Trivedi, P., Wang, Juntao, Wang, L., Wang, Jianyong, Yang, T., Zaady, E., Zhou, X., Zhou, X.-Q., Zhou, G., Liu, S., Delgado-Baquerizo, M., 2023. The global contribution of soil mosses to ecosystem services. Nat. Geosci. 16, 430–438. https://doi.org/10.1038/s41561-023-01170-x.

Eldridge, D.J., Reed, S., Travers, S.K., Bowker, M.A., Maestre, F.T., Ding, J., Havrilla, C., Rodriguez-Caballero, E., Barger, N., Weber, B., Antoninka, A., Belnap, J., Chaudhary, B., Faist, A., Ferrenberg, S., Huber-Sannwald, E., Malam Issa, O., Zhao, Y., 2020. The pervasive and multifaceted influence of biocrusts on water in the world's drylands. Glob. Chang. Biol. 26, 6003–6014. https://doi.org/10.1111/GCB.15232.

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.

Fernández, C., Fontúrbel, T., Vega, J.A., 2021. Cumulative effects of salvage logging and slash removal on erosion, soil functioning indicators and vegetation in a severely burned area in NW Spain. Geoderma 393, 115004. https://doi.org/10.1016/j.geoderma.2021.115004.

Fernández, C., Vega, J.A., 2016. Effects of mulching and post-fire salvage logging on soil erosion and vegetative regrowth in NW Spain. . Ecol. Manag. 375, 46–54. https://doi.org/10.1016/j.foreco.2016.05.024.

Ferreira, A.J.D., Coelho, C.O.A., Ritsema, C.J., Boulet, A.K., Keizer, J.J., 2008. Soil and water degradation processes in burned areas: Lessons learned from a nested approach. Catena 74, 273–285. https://doi.org/10.1016/j.catena.2008.05.007.

Ferrenberg, S., Faist, A.M., Howell, A., Reed, S.C., 2018. Biocrusts enhance soil fertility and Bromus tectorum growth, and interact with warming to influence germination. Plant Soil 429, 77–90. https://doi.org/10.1007/s11104-017-3525-1.

Ferrenberg, S., Tucker, C.L., Reed, S.C., 2017. Biological soil crusts: diminutive communities of potential global importance. Front. Ecol. Environ. 15, 160–167. https://doi.org/10.1002/FEE.1469.

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

Gall, C., Ohan, J., Glaser, K., Karsten, U., Schloter, M., Scholten, T., Schulz, S., Seitz, S., Kurth, J.K., 2022b. Biocrusts: Overlooked hotspots of managed soils in mesic environments. J. Plant Nutr. Soil Sci. https://doi.org/10.1002/JPLN.202200252.

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 Sediment. 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. Manag. 262, 110287 https://doi.org/10.1016/j.jenvman.2020.110287.

García-Carmona, M., García-Orenes, F., Arcenegui, V., Mataix-Solera, J., 2023a. The recovery of Mediterranean soils after post-fire management: The role of biocrusts and soil microbial communities. Span. J. Soil Sci. 13, 1–9. https://doi.org/10.3389/sjss.2023.11388.

García-Carmona, M., García-Orenes, F., Mataix-Solera, J., Roldán, A., Pereg, L., Caravaca, F., 2021. Salvage logging alters microbial community structure and functioning after a wildfire in a Mediterranean forest. Appl. Soil Ecol. 168, 104130 https://doi.org/10.1016/J.APSOIL.2021.104130.

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.

García-Carmona, M., Lepinay, C., Mataix-Solera, J., Baldrian, P., Arcenegui, V., Cajthaml, T., García-Orenes, F., 2023b. Post-fire wood mulch negatively affects the moss biocrust cover and its positive effects on microbial diversity in a semi-arid Mediterranean forest. Appl. Soil Ecol. 191 https://doi.org/10.1016/j.apsoil.2023.105026.

García-Orenes, F., Arcenegui, V., Chrenková, K., Mataix-Solera, J., Moltó, J., Jara-Navarro, A.B., Torres, M.P., 2017. Effects of salvage logging on soil properties and vegetation recovery in a fire-affected Mediterranean forest: a two year monitoring research. Sci. Total Environ. 586, 1057–1065. https://doi.org/10.1016/j.scitotenv.2017.02.090.

García-Orenes, F., Morugán-Coronado, A., Zornoza, R., Scow, K., 2013. Changes in soil microbial community structure influenced by agricultural management practices in a mediterranean agro-ecosystem. PLoS One 8, e80522. https://doi.org/10.1371/journal.pone.0080522.

García, C., Hernandez, T., Costa, F., 1997. Potential use of dehydrogenase activity as an index of microbial activity in degraded soils. Commun. Soil Sci. Plant Anal. 28, 123–134. https://doi.org/10.1080/00103629709369777.

Girona-García, A., Cretella, C., Fernández, C., Robichaud, P.R., Vieira, D.C.S., Keizer, J.J., 2023. How much does it cost to mitigate soil erosion after wildfires? J. Environ. Manag. 334, 117478 https://doi.org/10.1016/j.jenvman.2023.117478.

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.

Goodell, B., Winandy, J.E., Morrell, J.J., 2020. Fungal degradation of wood: emerging data, new insights and changing perceptions. Coatings 10, 1210. https://doi.org/10.3390/COATINGS10121210.

Grover, H.S., Bowker, M.A., Fulé, P.Z., 2020. Improved, scalable techniques to cultivate fire mosses for rehabilitation. Restor. Ecol. 28, S17–S24. https://doi.org/10.1111/rec.12982.

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, 226–244. https://doi.org/10.1038/ismej.2013.141.

Hu, M., Wang, J., Lu, L., Gui, H., Wan, S., 2023. Global recovery patterns of soil microbes after fire. Soil Biol. Biochem. 183, 109057 https://doi.org/10.1016/j.soilbio.2023.109057.

ICNF, 2023. 8º Relatório provisório de incêndios rurais.

IUSS Working Group, 2022. Base for Soil Resources. International soil classification system for naming soils and creating legends for soil maps., 4th ed. International Union of Soil Sciences (IUSS), Vienna, Austria.

Jiménez-Morillo, N.T., Almendros, G., Miller, A.Z., Hatcher, P.G., González-Pérez, J.A., 2022. Hydrophobicity of soils affected by fires: An assessment using molecular markers from ultra-high resolution mass spectrometry. https://doi.org/10.1016/j.scitotenv.2022.152957.

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. . Ecol. Managing. 453, 117567 https://doi.org/10.1016/J.FORECO.2019.117567.

Jones, M.W., Santín, C., van der Werf, G.R., Doerr, S.H., 2019. Global fire emissions buffered by the production of pyrogenic carbon. Nat. Geosci. 12, 742–747. https://doi.org/10.1038/s41561-019-0403-x.

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. . 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. . Ecol. Manag. 391, 86–95. https://doi.org/10.1016/J.FORECO.2017.02.012.

Kandeler, E., Stemmer, M., Klimanek, E.M., 1999. Response of soil microbial biomass, urease and xylanase within particle size fractions to long-term soil management. Soil Biol. Biochem. 31, 261–273. https://doi.org/10.1016/S0038-0717(98)00115-1.

Kassambara, A., Mundt, F., 2017. Factoextra: extract and visualize the results of multivariate data analyses. R. Packag. Version 1, 337–354.

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

Keizer, J.J., Doerr, S.H., Malvar, M.C., Prats, S.A., Ferreira, R.S.V., Oñate, M.G., Coelho, C.O.A., Ferreira, A.J.D., 2008. Temporal variation in topsoil water repellency in two recently burnt eucalypt stands in north-central Portugal. Catena 74, 192–204. https://doi.org/10.1016/j.catena.2008.01.004.

Keizer, J.J., Silva, F.C., Vieira, D.C.S., González-Pelayo, O., Campos, I., Vieira, A.M.D., Valente, S., Prats, S.A., 2018. The effectiveness of two contrasting mulch application rates to reduce post-fire erosion in a Portuguese eucalypt plantation. Catena 169, 21–30. https://doi.org/10.1016/j.catena.2018.05.029.

Kidron, G.J., Lichner, L., Fischer, T., Starinsky, A., Or, D., 2022. Mechanisms for biocrust-modulated runoff generation – A review. Earth-Sci. Rev. 231 https://doi.org/10.1016/J.EARSCIREV.2022.104100.

Kolden, C.A., Abatzoglou, J.T., Jones, M.W., Jain, P., 2024. Wildfires in 2023. Nat. Rev. Earth Environ. 5, 238–240. https://doi.org/10.1038/s43017-024-00544-y.

Kumaraswamy, S., Mendham, D.S., Grove, T.S., O'connell, A.M., Sankaran, K.V., Rance, S.J., 2014. Harvest residue effects on soil organic matter, nutrients and microbial biomass in eucalypt plantations in Kerala, India. . Ecol. Manag. 328, 140–149. https://doi.org/10.1016/j.foreco.2014.05.021.

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.

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

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.

Leverkus, A.B., Lindenmayer, D.B., Thorn, S., Gustafsson, L., 2018. Salvage logging in the world's forests: interactions between natural disturbance and logging need recognition. Glob. Ecol. Biogeogr. 27, 1140–1154. https://doi.org/10.1111/GEB.12772.

Li, W., Tian, X., Sheng, H., Ekawati, D., Zhou, Y., Zhang, R., 2019. Response of bacterial compositions to soil biochemical properties under mulching-intensive management in a Phyllostachys edulis forest. Appl. Soil Ecol. 150, 103436 https://doi.org/10.1016/j.apsoil.2019.103436.

Longepierre, M., Widmer, F., Keller, T., Weisskopf, P., Colombi, T., Six, J., Hartmann, M., 2021. Limited resilience of the soil microbiome to mechanical compaction within four growing seasons of agricultural management. ISME Commun. 1, 1–13. https://doi.org/10.1038/s43705-021-00046-8.

Lucas-Borja, M.E., Plaza-Álvarez, P.A., Ortega, R., Miralles, I., González-Romero, J., Sagra, J., Moya, D., Zema, D.A., De Las Heras, J., 2019. Short-term changes in soil functionality after wildfire and straw mulching in a Pinus halepensis M. forest. Ecol. Manag. 457, 117700 https://doi.org/10.1016/j.foreco.2019.117700.

Malvar, M.C., Prats, S.A., Nunes, J.P., Keizer, J.J., 2016. Soil water repellency severity and its spatio-temporal variation in burnt eucalypt plantations in North-Central Portugal. L. Degrad. Dev. 27, 1463–1478. https://doi.org/10.1002/LDR.2450.

Malvar, M.C., Silva, F.C., Prats, S.A., Vieira, D.C.S., Coelho, C.O.A., Keizer, J.J., 2017. Short-term effects of post-fire salvage logging on runoff and soil erosion. Ecol. Manag. 400, 555–567. https://doi.org/10.1016/j.foreco.2017.06.031.

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.

Mataix-Solera, J., Arellano, E.C., Jaña, J.E., Olivares, L., Guardiola, J., Arcenegui, V., García-Carmona, M., García-Franco, N., Valenzuela, P., 2021. Soil Vulnerability Indicators to Degradation by Wildfires in Torres del Paine National Park (Patagonia, Chile). Spanish J. Soil Sci. 11, 1. https://doi.org/10.3389/SJSS.2021.10008/BIBTEX.

Moreira, F., Arianoutsou, M., Corona, P., De las Heras, J. (Eds.), 2011. Post-Fire Management and Restoration of Southern European Forests. Springer Science and Business Media B.V.

Morgan, P., Moy, M., Droske, C.A., Lewis, S.A., Lentile, L.B., Robichaud, P.R., Hudak, A. T., Williams, C.J., 2015. Vegetation response to burn severity, native grass seeding, and salvage logging. Fire Ecol. 11 https://doi.org/10.4996/fireecology.1102031.

Nannipieri, P., Ceccanti, B., Cervelli, S., Matarese, E., 1981. Extraction of phosphatase, urease, proteases, organic carbon, and nitrogen from soil (NP-NP). Soil Sci. Soc. Am. J. 45. 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, 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.

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

Olsen, S.R., 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate (No. 939). US Dep. Agric.

Palmer, B., Hernandez, R., Lipson, D., 2020. The fate of biological soil crusts after fire: a meta-analysis. Glob. Ecol. Conserv. 24, e01380. https://doi.org/10.1016/j.gecco.2020.e01380.

Pereg, L., Mataix-Solera, J., McMillan, M., García-Orenes, F., 2018. The impact of post-fire salvage logging on microbial nitrogen cyclers in Mediterranean forest soil. Sci. Total Environ. 619–620, 1079–1087. https://doi.org/10.1016/j.scitotenv.2017.11.147.

Pereira, P., Francos, M., Brevik, E.C., Ubeda, X., Bogunovic, I., 2018. Post-fire soil management. Curr. Opin. Environ. Sci. Heal. 5, 26–32. https://doi.org/10.1016/j.coesh.2018.04.002.

Pereira, V., FitzPatrick, E.A., 1995. Cambisols and related soils in north-central Portugal: their genesis and classification. Geoderma 66, 185–212. https://doi.org/10.1016/0016-7061(94)00076-M.

Pharo, E.J., Meagher, D.A., Lindenmayer, D.B., 2013. Bryophyte persistence following major fire in eucalypt forest of southern Australia. Ecol. Manag. 296, 24–32. https://doi.org/10.1016/j.foreco.2013.01.018.

Prats, S.A., González-Pelayo, Ó., Silva, F.C., Bokhorst, K.J., Baartman, J.E., Keizer, J.J., 2019. Post-fire soil erosion mitigation at the scale of swales using forest logging residues at a reduced application rate. Earth Surf. Process. Landf. 44 (14), 2837–2848. https://doi.org/10.1002/esp.4711.

R. Core Team, 2023. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA URL. Boston, MA.

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.

Rodríguez-Caballero, E., Cantón, Y., Chamizo, S., Lázaro, R., Escudero, A., 2013. Soil Loss and Runoff in Semiarid Ecosystems: A Complex Interaction Between Biological Soil Crusts, Micro-topography, and Hydrological Drivers. Ecosystems 16, 529–546. https://doi.org/10.1007/S10021-012-9626-Z/FIGURES/7.

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.

Seppelt, R.D., Downing, A.J., Deane-Coe, K.K., Zhang, Y., Zhang, J., 2016. Bryophytes Within Biological Soil Crusts, in: Bettina, W., Büdel, B., Belnap, J. (Eds.), Biological Soil Crusts: An Organizing Principle in Drylands. Springer, Cham, pp. 101–120. https://doi.org/10.1007/978-3-319-30214-0_6.

Serrano-Ortiz, P., Marañón-Jiménez, S., Reverter, B.R., Sánchez-Cañete, E.P., Castro, J., Zamora, R., Kowalski, A.S., 2011. Post-fire salvage logging reduces carbon sequestration in Mediterranean coniferous forest. . Ecol. Manag. 262, 2287–2296. https://doi.org/10.1016/j.foreco.2011.08.023.

Shakesby, R.A., 2011. Post-wildfire soil erosion in the Mediterranean: review and future research directions. Earth-Sci. Rev. 105, 71–100. https://doi.org/10.1016/j.earscirev.2011.01.001.

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.

Slesak, R.A., Schoenholtz, S.H., Evans, D., 2015. Hillslope erosion two and three years after wildfire, skyline salvage logging, and site preparation in southern Oregon, USA. . Ecol. Manag. 342, 1–7. https://doi.org/10.1016/j.foreco.2015.01.007.

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.

Tian, C., Pang, J., Bu, C., Wu, S., Bai, H., Li, Y., Guo, Q., Siddique, K.H.M., 2022. The Microbiomes in Lichen and Moss Biocrust Contribute Differently to Carbon and Nitrogen Cycles in Arid Ecosystems. Microb. Ecol. 1, 1–12. https://doi.org/10.1007/S00248-022-02077-7/TABLES/1.

Tomao, A., Antonio Bonet, J., Castaño, C., de-Miguel, S., 2020. How does forest management affect fungal diversity and community composition? Current knowledge and future perspectives for the conservation of forest fungi. Ecol. Manag. 457, 117678 https://doi.org/10.1016/J.FORECO.2019.117678.

Valente, S., Coelho, C., Ribeiro, C., Liniger, H., Schwilch, G., Figueiredo, E., Bachmann, F., 2015. How much management is enough? Stakeholder views on forest management in fire-prone areas in central Portugal. . Policy Econ. 53, 1–11. https://doi.org/10.1016/j.forpol.2015.01.003.

Vallejo, V.R., Arianoutsou, M., Moreira, F., 2012. Fire Ecology and Post-Fire Restoration Approaches in Southern European Forest Types, in: Moreira, F., Arianoutsou, M., Corona, P., De las Heras, J. (Eds.), Post-Fire Management and Restoration of Southern European Forests. Managing Forest Ecosystems. Springer, Dordrecht, pp. 93–119. https://doi.org/10.1007/978-94-007-2208-8_5.

Wagenbrenner, J.W., MacDonald, L.H., Coats, R.N., Robichaud, P.R., Brown, R.E., 2015. Effects of post-fire salvage logging and a skid trail treatment on ground cover, soils, and sediment production in the interior western United States. Ecol. Manag. 335, 176–193. https://doi.org/10.1016/j.foreco.2014.09.016.

Wagenbrenner, J.W., Robichaud, P.R., Brown, R.E., 2016. Rill erosion in burned and salvage logged western montane forests: effects of logging equipment type, traffic level, and slash treatment. J. Hydrol. 541, 889–901. https://doi.org/10.1016/j.jhydrol.2016.07.049.

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.

Weber, B., Wu, D., Tamm, A., Ruckteschler, N., Rodríguez-Caballero, E., Steinkamp, J., Meusel, H., Elbert, W., Behrendt, T., Sörgel, M., Cheng, Y., Crutzen, P.J., Su, H., Pöschl, U., Wofsy, S.C., 2015. Biological soil crusts accelerate the nitrogen cycle through large NO and HONO emissions in drylands. Proc. Natl. Acad. Sci. U. S. A. 112, 15384–15389. https://doi.org/10.1073/PNAS.1515818112/SUPPL_FILE/PNAS.1515818112.SAPP.PDF.

Wessel, A.T., 1988. On using the effective contact angle and the water drop penetration time for classification of water repellency in dune soils. Earth Surf. Process. Landf. 13, 555–561. https://doi.org/10.1002/esp.3290130609.

Yang, Y.-J., Dungan, R.S., Ibekwe, A.Mark, Valenzuela-Solano, C., Crohn, D.M., David, ·, Crowley, E., 2003. Effect of organic mulches on soil bacterial communities one year after application. Biol. Fertil. Soils 38, 273–281. https://doi.org/10.1007/s00374-003-0639-9.

Zaady, E., Eldridge, D.J., Bowker, M.A., 2016. Effects of local-scale disturbance on biocrusts. In: Weber, B., Büdel, B., Belnap, J. (Eds.), Biological Soil Crusts: An Organizing Principle in Drylands. Springer, Cham, pp. 429–449. https://doi.org/10.1007/978-3-319-30214-0_21.